DISSERTATION

CHELICERAL MORPHOLOGY OF SOLIFUGAE (ARACHNIDA): PRIMARY HOMOLOGY, TERMINOLOGY, AND CHARACTER SURVEY

Submitted by

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In partial fulfillment of the requirements

For the Degree Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 2015

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ABSTRACT

CHELICERAL MORPHOLOGY OF SOLIFUGAE (ARACHNIDA): PRIMARY HOMOLOGY, TERMINOLOGY, AND CHARACTER SURVEY

Arachnids of the order Solifugae (solifuges, false spiders, sunspiders, camelspiders, Walzenspinne, windspiders) possess the largest jaws for body size in the Chelicerata. The chelicerae provide the most important character systems for solifuge systematics, including dentition and the male flagellum, both used extensively in species delimitation and diagnosis. However, the terminology used for cheliceral characters is unstandardized and often contradictory, in part because it fails to represent homologous structures among taxa. Misinterpretation of character homology may introduce errors in phylogenetic analyses concerning relationships within Solifugae and among the orders of Chelicerata. This contribution presents the first comprehensive analysis of cheliceral morphology across the order Solifugae, the aims of which were to provide a broad survey of cheliceral characters for solifuge systematics, to identify and reinterpret structures based on primary homology, revise the terminology to be consistent with homology hypotheses, and provide a guide to synonyms of terminology and character interpretations in the literature. Chelicerae were studied in 188 exemplar species (17 % of the total), representing all twelve solifuge families, 17 of the 19 subfamilies, 64 genera (46 % of the total), and the full range of variation in cheliceral morphology across the order. In total, 157 species representing 49 genera and 17 subfamilies are illustrated. Hypotheses of character transformation, particularly concerning the male flagellum, and a standardized terminology, are presented. The functional morphology of the chelicerae is discussed and the role of sexually dimorphic modifications to the male chelicerae in mating behavior emphasized. The revised terminology, based on hypotheses of primary homology, will facilitate solifuge revisionary systematics and provide a stronger basis for reconstructing phylogenetic relationships within the order and evaluating its position within Chelicerata.

Keywords: Chelicerata, chaetotaxy, dentition, functional morphology, male flagellum, stridulatory apparatus, comparative morphology, homology, terminology

ACKNOWLEDGEMENTS

Thanks to my committee members (Paula Cushing, Boris Kondratieff, Melinda Laituri, Lorenzo Prendini, and Robert Wharton) for advice and input; Lorenzo Prendini (AMNH), Charles Griswoldt, (CAS), Paula Cushing (DMNS), Ariel Chipman (HUJI), Lars Lundqvist (ZMLU), Gonzalo Giribet (MCZ), Christine Rollard (MNHN), Rudy Jocqué (MRAC), Ansie Dippenaar-Schoeman (ARC-PPRI), Peter Jaeger (SMF), Efrat Gavish-Regev (HUJI; TAU), and Martin Krüger (TM) for loans or access to materials in the collections of their institutions; Lorenzo Prendini (AMNH) and Paula Cushing (DMNS) for workspace at their institutions; and friends and colleagues for assistance with foreign texts, especially in Russian (Vladimir Ovtcharenko) and German (Martin Krüger). Images were kindly provided by Sanjay Das (Pl. 1F), Sergio Henriques (Pls. 24C, 33E, F, 34A, B, 60G, H, 61J, 65E), Melek Erdek (Pls. 85C, D, 139A, B), Chris Grinter and Paula Cushing (most eremobatid images), Lorenzo Prendini (Pl. 1A, D) and Thomas Noergaard (Fig. 24F), and images for verifying characters by Ariel Chipman (*Ceratobiton*) and Peter Jaeger (*Siloanea*). During the years 2007–2012, my work was largely supported by National Science Foundation grants DBI-0640245 to Paula Cushing and DEB 0640219 to Lorenzo Prendini, with additional financial support from an AMNH Collections Study Grant (2009), two grants from the Theodore Roosevelt Memorial Fund of the AMNH (2010, 2012), and an Ernst Mayr Travel Grant in Animal Systematics from the MCZ (2011). I am very grateful to Eric Warrant, Thomas Noergaard and Ola Gustafsson of the Vision Study Group (Lund University) for funding to visit their institution to use SEM facilities, and their memorable hospitality during my stay in Lund. The work was greatly assisted by the Catalogue of the Smaller Arachnid Orders of the World by Mark Harvey. I thank Ricardo Botero-Trujillo for valuable suggestions incorporated herein. I am deeply indebted to Steve Thurston, AMNH graphic artist, for preparing plates, revising images, sending me tutorials on Photoshop, and always walking the extra mile. I thank EduVentures, the National Museum of Namibia, and the Gondwana Collection for logistic support in the lab and the field, and Jack Brookhart, Alexander Gromov, Kristie Reddick, Warren Savory and Robert Wharton for assistance with identifications. Colleagues and friends assisted in numerous ways: Heide Beinhauer, Jack Brookhart, Pete and Kyran Cadmus, Melek Erdek, Nadine Faschina, Telane Greyling, Tauno Iipinge, Hermine Inana, John Irish, Corris Kaapehi, Anja Klann, Benson Muramba, Thomas Noergaard, André and Jeanita Schoeman, Jessie Shade, Annie Wallin and, especially, Holger Vollbrecht, together with too many others to mention. I thank my sister, Annemarie Loots, who was always willing to help without reservation across continents, Hennie Loots for assistance with formatting the text of this contribution, my family for support, my parents for help in too many ways to mention and for facilitating this path for me and, especially, my husband Chris Bird, who made innumerable sacrifices, and was supportive and extraordinary throughout.

DEDICATION

To my parents, Hennie and Olivia Steyn, and to Chris.

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INTRODUCTION

The Solifugae (Pl. 1) is a relatively poorly known order of arachnids (Harvey, 2002b), also known as solifuges, solifugids, solpugids, and various other vernacular names describing either the order, or specific families for genera within it, e.g., baardskeerders, camelspiders, false spiders, haarskeerders, jaag- or jagspinnekoppe, jerrymanders, red romans, roman spiders, sunspiders (or sun scorpions), Walzenspinnen, windspiders (or wind scorpions). This mesodiverse order currently comprises 12 extant families, 139 genera, and 1103 species (Harvey, 2003a; Prendini, 2011; see Appendix 1). Although the phylogenetic placement of Solifugae within Chelicerata remains unresolved (e.g., Alberti and Peretti, 2002; Dabert et al., 2010; Pepato et al., 2010; Sharma et al. 2014), morphological and molecular analyses have repeatedly confirmed its monophyly (e.g., Hayashi et al., 1992; Wheeler and Hayashi, 1998; Giribet et al., 2002; Shultz, 2007; Giribet and Edgecombe, 2012).

The most comprehensive treatment of Solifugae to date was the work of Roewer (1932–1934), who summarized most of the available literature, and added many new observations and interpretations of solifuge morphology. Nearly eight decades on, Roewer (1932–1934) remains the primary citation for solifuge morphology. For example, Shultz (2007) cites Roewer (1934) sixteen times as a source of information for coding solifuge characters for his study on chelicerate phylogeny, fourteen as the sole citation.

Roewer (1932, 1933, 1934, 1941, 1942, 1952a,b,c, 1954a,b,c,d, 1957, 1960, 1961) laid the foundation of the modern classification of Solifugae, but was extensively criticized for emphasizing characters, especially leg “spination” and cheliceral dentition that are “variable” (Birula, 1936b; Panouse 1950, 1961a,b; Muma, 1951, 1976; Lawrence, 1955, 1976; Turk, 1960; Simonetta and Delle Cave, 1968; Wharton, 1981; Gromov, 2000, 2003a; Harvey, 2002b, 2003), even on individual specimens (e.g., Panouse, 1961a,b). However, there remains little evaluation and quantification of both intra- and interspecific variation in Solifugae. Roewer’s (1934) classification, described as “confusing” and “chaotic” (Vachon, 1950: 107; Turk, 1960), was refined by Muma (1976), who placed greater emphasis on male secondary sexual characters, particularly the cheliceral flagellum, cheliceral dentition, and associated structures, but remains devoid of phylogenetic content (Harvey, 2002b, 2003). No subordinal or suprafamilial groupings exist. Several families and many genera are unlikely to be monophyletic. Subfamilial groupings have been criticized as superficial (e.g., Lawrence, 1953; Muma, 1976; Wharton, 1981). Except for one work on the New World *scaber* group of *Eremobates* Banks, 1900 (Brookhart and Cushing, 2004), no phylogenetic analyses have been published on solifuges and comprehensive revisionary syntheses are lacking for most families and genera.

The absence of a phylogenetic framework for Solifugae may, in large part, be attributed to the absence of a unified synthesis of homologous characters across the order. Related to this is the absence of standardized terminology. Characters proposed by Roewer (1934) were adopted by some solifuge workers, but not others, often without clear definitions, resulting in an inconsistent assortment of terms and interpretations across the solifuge literature. Attempts to homologize structures across Solifugae and base terminology thereon, are non-existent, with few exceptions, e.g., some non-cheliceral terminologies based on homology assessments between Solifugae and other chelicerate orders (Dunlop, 2000, 2002; Dunlop et al., 2012). Harvey's (2002b: 366) statement that "[m]uch work must be undertaken to even begin to sort out the confusion" in Solifugae taxonomy is equally applicable to solifuge morphology, which requires precise, standardized terms, based on hypotheses of homology, to facilitate communication.

Early on, Dufour (1861: 344) stressed the importance of comparing structures before promoting terms in solifuge morphology. Indeed, efforts to base standardized terminology on hypotheses of homology are common in biology, but with various levels of acceptance depending on the extent to which the term/s to be replaced are established in the literature. For example, Snodgrass (1948) proposed new terminology for the mouthparts of Acari, based on careful investigations of mouthpart homology across arachnids (including terms recently promoted for the Solifugae rostrum; see Dunlop, 2000), which was largely ignored by acarologists, because a relatively standardized terminology was already in place. Given the inconsistency in solifuge morphological terminology, and the renewed interest in solifuge research (e.g., Ballesteros and Francke, 2007; Catenazzi et al., 2009; Klann, 2009; Carvalho et al., 2010; Erdek, 2010; Reddick et al., 2010; Bayram et al., 2011; Cushing and Castro, 2012; Dunlop et al., 2012; González Reyes and Corronca, 2013; Karataş and Uçak, 2013; Cushing et al., 2014; Botero-Trujillo, 2014; Iuri et al., 2014, Wharton and Reddick, 2014), it is an opportune time to unify and redefine solifuge morphological terminology in light of modern concepts of character homology, advances in technology, and the availability of new material.

The present contribution is concerned with characters of the **chelicerae** of

Solifugae, which bear the greatest concentration and arguably the most important characters for solifuge systematics, from species delimitation to phylogenetic reconstruction (Kraepelin, 1908a; Hewitt, 1919b; Cloudsley-Thompson, 1984: 195). The aims of the project were to (i) survey external cheliceral characters across a broad selection of exemplar species, representing the taxonomic and morphological diversity of the order; (ii) evaluate variation in characters or character systems within and among solifuge taxa to determine their utility for systematics; (iii) propose hypotheses of primary homology across the order; (iv) present a precise, standardized and unambiguous terminology, reflecting the hypothesized homology of structures; (v) provide a guide to terminological synonyms and character interpretations in the literature; (vi) identify potential synapomorphies for taxa (with an emphasis on the family level but extending to the genus level); and (vii) discuss the functional morphology of the chelicerae.

Importance of Chelicerae in Solifugae

The chelicerae are the first pair of appendages on the prosoma of Chelicerata (Giribet and Edgecombe, 2012). Their homology with “head” structures in other arthropod taxa has long been debated. The chelicerae of solifuges were variously interpreted as structures without any counterpart in insects (Savigny, 1809: 176), as homologous to the antennae (Latreille, 1829) or mandibles (e.g., Blanchard, 1847: 233) of insects, or to the first (Viallanes, 1892) or second (Latreille, 1829) antennae of crustaceans. Snodgrass (1965) homologized the solifuge chelicera with the second antennae of Crustacea, and with the putatively lost intercalary segment of insects. Latreille (1829: 207) was the first to homologize the chelicerae with mandibulate antennae, and introduced the terms *chelicerae* (Gr. *chele*, claw; *keras*, horn) or *antenne-pinces*. This view came full circle with recent evolutionary developmental studies, which confirmed the homology of chelicerae, mandibulate antennae, and the first antenna (antennules) of crustaceans (e.g., Giribet and Edgecombe, 2012), initially supported by deutocerebral innervation and the absence of Hox gene expression in the cheliceral/antennal segment, and later by similarities in the expression of genes that pattern the proximodistal axis of these appendages (e.g., Sharma et al., 2012).

Solifuges are easily distinguished from other arachnids by their massive two-segmented, chelate chelicerae (Fig. 1), usually bearing a flagellum in the adult male. Solifuge chelicerae are the largest per body size within Chelicerata (Roewer, 1934: 52), rivaled only by those of basal pseudoscorpions in the superfamilies Chthonioidea and Neobisioidea (Chamberlin, 1931; Shultz, 1990). The chelicerae perform a greater diversity of functions in Solifugae than in any other chelicerate order. Solifuges use the chelicerae for prey capture and feeding (Muma, 1966c; Wharton, 1987; Cloudsley-Thompson, 1977a), fighting with conspecifics (Muma, 1967), defense, burrowing (Muma, 1966a; Cloudsley-Thompson, 1977a) and mating (Heymons, 1902; Cloudsley-Thompson, 1961, 1967a,b; Amitai et al., 1962; Junqua, 1962; Muma, 1966b; Wharton, 1987; Punzo, 1998b; Peretti and Willemart, 2007; Hrušková-Martišová et al., 2008a, 2010a). Whereas in adult females, the primary function of the chelicerae remains feeding, the chelicerae of adult males, which are often markedly dimorphic, serve a crucial secondary function, namely reproduction. The exact role of the chelicerae during mating remains poorly understood, however. The chelicerae are thought to subdue a struggling female (e.g., holding her hind leg), to induce or play a part in inducing a state of temporary paralysis, to prepare the female for mating, and/or to transfer the sperm to the female gonopore (Heymons, 1902; Cloudsley-Thompson, 1961, 1967a,b; Amitai et al., 1962; Junqua, 1962; Muma, 1966b; Wharton, 1987; Punzo, 1998b; Peretti and Willemart, 2007; Hrušková-Martišová et al., 2008a, 2010a).

Among many arthropods, the sole purpose of adult males to reproduce often results in their being short-lived and incapable of feeding. This switch in primary function is usually accompanied, on one hand, by reduction or absence of structures associated with feeding and, on the other, by modification of structures for sperm transfer and other aspects related to mating. This is true for many arachnids. Examples where one pair of prosomatic appendages is modified to function as an intromittent organ include the pedipalps in Araneae and the third pair of legs in Ricinulei. Solifugae is the only arachnid order in which the chelicerae are modified for mating, often as an intromittent organ, and thus the only chelicerate that carries a large percentage of secondary sexual characters on the chelicerae (Kraepelin, 1908a; Hewitt, 1919b; Roewer, 1932–1934). In addition to reduced dentition, other sexually dimorphic cheliceral modifications include size and shape, shape of the fingers (mainly the dorsal or fixed finger), especially the apices thereof, **chaetotaxy**, processes and carinae, and the presence of a male flagellum or flagellar complex.

Although little is known about the functional morphology of solifuge chelicerae, the richness in characters associated with these structures highlights their importance in many aspects of solifuge behavior, especially mating (Tables 1–4). Unsurprisingly, cheliceral characters are of fundamental importance for solifuge systematics, from species to family level. The primary character systems of the chelicerae include dentition, male **flagellar complex** and chaetotaxy. Dentition and the male flagellum are covered in detail in the present contribution. Other character systems discussed more briefly include the shape of cheliceral **manus** and fingers, chaetotaxy, the **stridulatory apparatus** and the integument (flanges, carinae, granulation and canals, sensory structures, etc.).

ON HOMOLOGY AND TERMINOLOGY

The concept of homology is fundamental to comparative biology (Bock, 1973; Assis, 2014). Statements of homology provide the foundation for the explanatory and predictive power of phylogenetic hypotheses and the classifications derived from them (Patterson, 1982; De Pinna, 1991; Brower and Schawaroch, 1996; Rutishauser and Moline, 2005; Schuh & Brower, 2009). Patterson (1982, 1988) proposed three tests of homology, i.e. similarity (in form and topographical correspondence, i.e. position), conjunction and congruence. According to Patterson (1988: 605), similarity validates a character as worthy of testing, conjunction reveals what is not homologous, and congruence tests for synapomorphy. De Pinna (1991) clarified the discovery of homology as a two-step process, whereby primary homology refers to statements based on structural and positional similarity, proposed *a priori* to the construction of a character matrix, and secondary homology refers to primary homology that is corroborated by a test of congruence with other characters (during phylogenetic analysis). Primary homology assessment was further subdivided into two steps by Brower and Schawaroch (1996: 266), according to whom topographic identity is the discovery of characters (“comparable features among taxa”) and contributes to the columns in a character matrix, whereas character state identity hypothesizes homology within these characters (coding of character states), a step that involves scoring characters identified by topographic identity. Patterson’s (1982) approach to homology assessment, which Brower and Schawaroch (1996: 266) summarized as “conjectural homology assessment prior to cladistic analysis” (homology as similarity) and “corroborated homology assessments after cladistic analysis” (homology as synapomorphy), has been widely accepted by the systematics community. Primary homology is recognized as an integral part of character analysis prior to phylogenetic analysis (e.g., Delfino et al., 2010; Maidment and Porro, 2010; Vogt et al., 2010; Candela and Rasia, 2012) and, indeed, as “the prime determinant of the outcome of cladistic analysis” (e.g., Hawkins et al., 1997: 278). Hypotheses of primary homology represent potential synapomorphies to be coded into a character matrix and tested for secondary homology. Those which pass the test of congruence with other characters in a phylogenetic analysis become the synapomorphies upon which taxonomic classifications are based.

Even when primary homology determination is not part of tree building, detailed character analysis remains essential (e.g., Ramirez, 2007: 15) and some have argued that character analysis and description should precede primary homology assessment (Vogt et al., 2010: 303). Morphological data are most appropriately used for phylogeny reconstruction when hypotheses of homology are unambiguous (Scotland et al., 2003) but this is not straightforward, as “morphological character analysis requires considerable effort, involving many methodological decisions and implicit assumptions at every step of the process” (Wiens, 2001: 689).

Accurate terminology is integral to the primary homology assessment of morphological characters, providing the vocabulary for defining characters recognized by similarity in structure and position. More generally, the translation of observations into descriptive statements “is crucial for the outcome of all subsequent scientific reasoning and the entire scientific argumentation” because it conceptualizes sensual input (Vogt et al., 2010: 303).

Delimitation and description of morphological characters may precede or accompany their assessment for primary homology. However, whereas statements of homology remain hypotheses subject to change, terminology is fixed. Therefore, the terms (vocabulary) applied to characters should reflect similarity, not hypotheses of putative homology (Vogt et al., 2010).

Formulating a terminology is not trivial. The comparative approach, among the most important in biological research, requires data to be comparable and communicable (Edgecombe, 2008; Fusco, 2008; Bonato et al., 2010; Richter et al., 2010; Scholtz, 2010). Identified as “the core problem of morphological data” (Vogt et al., 2010: 309), unstandardized terminology among authors, studies and scientific communities, i.e. the “linguistic problem of morphology,” reduces the communication and comparison of data, resulting in incomplete descriptions, and the introduction of errors into character matrices, analyses and classifications. Addressing this problem is a long and laborious process (Vogt et al., 2010: 308):

> "Tracing back the different applications of a specific term by different authors and in different periods of time … is usually time-consuming as one has to translate every single paper into one's own terms and definitions. In some cases, due to lack of a comprehensible documentation and lack of voucher specimens, this translation is impossible. As long as such effort is not recorded and made publicly accessible, it has to be conducted by every morphologist anew, which significantly slows scientific progress."

Such a scenario could not be more true for Solifugae, in which few characters are unambiguously defined, terminology is used inconsistently and without explanation, and region-specific usage (different terminology used by workers in the U.S.A., Latin America and Africa, for example) is commonplace. Terms were seldom defined in the historical literature, leaving much open to individual interpretation. An example of terms applied differently in the historical literature is the use of "flagellum" to refer to the ventral of the two flagellar structures in the karschiid *Eusimonia* Kraepelin, 1899 by, e.g., Hirst (1908: 247), Birula (1913: 321) and Kraepelin (1901: 140) versus the dorsal of the two structures by, e.g., Kraepelin (1908a: 222) and Roewer (1934: 299). Such different applications of terms not only hinders navigation through historical literature, but may lead to erroneous descriptions and character coding. Contradictory usage of terminology is not restricted to older literature. More recent examples regarding dentition are discussed in the relevant section.

MATERIALS AND METHODS

LITERATURE SURVEY

During the course of the study presented here, nearly 700 publications, representing over 50% of the literature on solifuge morphology, systematics and behavior from Linneaus to the present, were consulted to collate and synthesize existing terminology and hypotheses of homology. This literature included the seminal papers on the order (e.g., Koch, 1842; Simon, 1879, Dufour, 1861; Bernard, 1896; Kraepelin, 1899, 1901; Sørensen, 1914; Roewer, 1934), as well as major regional works (e.g., Putnam, 1883; Purcell, 1899; Banks, 1900; Birula, 1913, 1938; Hewitt, 1919b; Lawrence, 1955; Muma, 1951, 1970a; Wharton, 1981; Maury, 1984). Although every effort was made to cover existing literature as comprehensively as possible, some important works could not be treated as extensively, notably Birula (1938) on the Solifugae of the USSR, published in Russian.

Given the importance of the context in which terms were used, page numbers are provided for in-text citations or obscure usages. Published figures and plates, often essential to understand the morphological character interpretations of previous authors, are referenced as thoroughly as possible. These are listed throughout as “fig.” and “pl.”; those newly appearing in the present contribution as “Fig.” and “Pl.”. Following others (e.g., Lawrence, 1965b; Muma 1976; Shultz, 2007), Roewer’s (1932–1934) monograph, published in five parts over three years (Issues 1–5) is cited using only the 1934 date, followed by a page number, where applicable, to facilitate reference to the year of print.

TAXON SAMPLING

Exemplar species (Prendini, 2001) were chosen to represent the breadth of taxonomic and morphological diversity in Solifugae, to the extent possible, given the availability of high quality, intact material. Consequently, some enigmatic genera such as *Toreus* Purcell, 1903 (Ceromidae Roewer, 1933) and *Syndaesia* Maury, 1980 (Daesiidae Kraepelin, 1899) were omitted, and the central Asian Gylippidae Roewer, 1933, as well as some subfamilies and genera within the diverse Daesiidae, were less well sampled. Despite the paucity of well-preserved material for many solifuge taxa, the sample included monotypic genera of uncertain placement, such as the daesiids, *Ammotrechelis* Roewer, 1934 and *Ceratobiton* Delle Cave and Simonetta, 1971, Dinorhaxinae Roewer, 1933, and Namibesiinae Wharton, 1981, and an adequate representation of enigmatic higher level taxa such as Ceromidae, Hexisopodidae Pocock, 1897, Melanoblossiidae Roewer, 1933, and Lipophaginae Wharton, 1981(southern African Gylippidae), each including representatives of several genera. Sampling was slightly skewed towards southern African taxa, which comprise approximately 29% of the global genera and 16% of the global species, as well as families Eremobatidae Kraepelin, 1899 and Solpugidae Leach, 1815, which are part of larger studies and were more readily available. In total, 510 specimens, representing all twelve solifuge families and 17 of the 19 subfamilies, 64 genera (46 % of the total) and 188 species (17 % of the total) were examined (Appendix 1), of which 157 species representing 49 genera, and all 17 subfamilies which were examined, were illustrated (Figs. 1–26; Pls. 1–159), 45 species represented by both sexes. The generic representation is in all likelihood artificially depressed, given the problems with the generic classification of several families, e.g., Rhagodidae Pocock, 1897, which Lawrence (1956: 120) euphemistically described as “a fantastic proliferation of genera.”

MATERIAL EXAMINED

Material examined is deposited in the following collections: American Museum of Natural History, New York, U.S.A. (AMNH); California Academy of Sciences, San Francisco, CA, U.S.A. (CAS); Denver Museum of Nature and Science, CO, U.S.A. (DMNS); Hebrew University of Jerusalem, Israel (HUJI), Kirikkale University, Turkey (KU); Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A. (MCZ); Muséum National d’Histoire Naturelle, Paris, France (MNHN); Musée Royal de l’Afrique Central, Tervuren, Belgium (MRAC); National Collection of Arachnida, Plant Protection Research Institute, Pretoria, South Africa (NCA); National Museum of Namibia, Windhoek, Namibia (NMNW); Senckenberg Museum, Frankfurt, Germany (SMF), including the Roewer collection (R); Tel Aviv University, Zoology Museum, Israel (TAU); Transvaal Museum, Pretoria, South Africa (TM); Zoological Museum, Lund University, Sweden (ZMLU), Zoologisches Museum der Universität Hamburg, Germany (ZMUH).

SPECIES IDENTIFICATION

An attempt was made to identify the material examined to species as accurately as possible but, given the inadequacy of keys and the general absence of modern revisions, misidentifications at the species level cannot be ruled out. Species identification is particularly difficult for females. Females lack a cheliceral flagellum, and their chelicerae and associated characters are conserved and mostly uniform among species, and in some cases among genera and families. Roewer (1934) provided keys to females, but these proved unreliable (Lawrence, 1955: 153) and several authors (e.g., Hewitt, 1919b, Turk; 1960) cautioned against identifying females. Interspecific variation in female opercular shape permits identification of females in three taxa only: Eremobatidae (e.g., Muma, 1951), Gylippinae (Birula, 1913) and Karschiidae (e.g., Gromov, 2003a). Some juveniles remain impossible to identify to species, and sometimes even to family, unless collected as part of larger series. With few exceptions, species identification therefore depends on adult males (e.g., Lawrence, 1963), and primarily on the cheliceral characters thereof. In the present study, females were usually identified by reference to series that included adult males. Conclusions were based on large series wherever possible, but for many taxa these were unavailable, or of inadequate quality.

DISSECTIONS AND SPECIMEN PREPARATION

Specimens rather than illustrations were used to formulate and apply hypotheses of homology. Line drawings seldom portray subtle differences in size and sclerotization, whereas photographic images may not accurately represent relative sizes, depending on the angle and extent of illumination. Manipulation of chelicerae was usually required to assess the relative overlap of dentition, which cannot be inferred from illustrations. Illustrations in the literature were, however, of value in estimating character diversity.

When permitted by curators, a chelicera was removed for examination, because manipulating free chelicerae was found to result in less damage to fragile, taxonomically important characters such as setae. The dextral chelicera was usually removed, except when damaged, by carefully cutting through the cheliceropeltidial articular membrane, ligaments and muscle tissues at its base with a pair of ophthalmic scissors, thereby freeing the condyle from its socket in the cheliceropeltidial articulation, while taking care not to cut through the chitinous layer or damage the rostrum. Removing cheliceral **setae** to expose the teeth and detail of the dorsal finger, and to indicate the origins of setae is common practice among New World workers, and useful especially in Eremobatidae, but should be discouraged when few specimens are available because of the damage to characters of potential importance in solifuge systematics. No setae were removed during the present study but, where found to have been previously removed, setal origins were indicated in figures.

Chelicerae preserved with the fingers closed were opened to expose all teeth. When permitted by the curator, closed fingers were relaxed using a method recommended by Muma (1985). The chelicera was placed in a small, open vial containing approximately 20% ethanol and heated in a microwave oven, or with a hair drier, for ca. 1–2 minutes, depending on size of chelicera. This treatment usually loosened the tissue sufficiently to facilitate opening the fingers without risk of damage. The pattern of closure and overlap of the fixed and movable finger dentition was also examined. As the manner in which teeth are situated, relative to one another, when the **cheliceral fingers** are closed is not always apparent when fingers are open, the cheliceral fingers of some specimens were forceably closed using minuten pins placed in silicon sealant set to harden. The chelicera was carefully wedged between the pins, starting from a position in which the chelicera forms an angle with the surface, and then turning it to a position in which it was parallel to the surface. The fingers closed as they were gently “forced” between the closely inserted pins.

Teeth were used as landmarks to evaluate positional homology among flagella, rather than absolute position on the chelicera. The position of the point of attachment of the flagellum, relative to a particular tooth, was determined by drawing a line parallel to the cutting edge of the fixed finger and a second line, perpendicular to the first and passing through the point of attachment.

MICROSCOPY AND IMAGING

Specimens were examined using a Nikon SMZ 1500 stereoscope (AMNH) and an Olympus CKX41 compound scope (Colorado State University, Fort Collins, U.S.A). Most cheliceral images were taken with a Nikon D300 camera mounted on a Microptics

ML-1000 digital-imaging system at the AMNH. The focal planes of single image stacks were combined with CombineZM software (Hadley, 2012). A typical stack comprised 10–15 images, although the number ranged from three to 40. Most images of Eremobatidae (Pls. 65, 67, 68, 70, 72, 76, 79, 82) and a few species belonging to other families were taken with a Canon 5d (Passport II, Visionary Digital system) and combined using Zerene Stacker (Littlefield, 2013) at the DMNS. Some images of Daesiidae (Pls. 142, 143, 144) and Solpugidae (Pls. 102E–H, 109A–F, H, 124E, F) were taken with a Leica EZ40 digital stereoscope. Line drawings were prepared by tracing digital images on a WACOM (Intuos4) tablet, while simultaneously checking the specimen imaged under a stereoscope for accuracy, especially if dentition was partially obscured by setae in the image. Adobe Photoshop CS6 was used for editing images and drawings. Scanning electron microscopy (SEM) was used to image morphological structures which could not be clearly illustrated with other techniques. Specimens were critical-point dried and sputter coated with gold-palladium (40/60) prior to SEM with a JEOL 5600 at Lund University, Sweden, a Hitachi S4700 FE-SEM, at the AMNH, or a JEOL-JSM 6500F at Colorado State University.

PRIMARY HOMOLOGY ASSESSMENT

A major aim of the present contribution was to survey the variation among cheliceral characters and character systems of Solifugae and develop hypotheses of primary homology. Primary homology was assessed using the criteria of Remane (1952) and Patterson (1982, 1988). Remane's (1952) three criteria are position (similarity in topology, including similarity in relation or connectivity), structure (similarity in form), and continuum (linkage of intermediate forms). Patterson's (1982, 1988) three tests of homology include two of relevance to primary homology assessment, i.e. similarity (in form and topographical correspondence) and conjunction (two structures observed on the same individual organism cannot be homologous). Topographical (positional) similarity is often the most powerful criterion (Rutishauser and Moline, 2005). There may be conflict among the criteria, e.g., similarity in position but difference in structure (Ramirez, 2007). Such conflict was encountered in the male cheliceral dentition and flagellar character systems, due to a diversity of structures and differences in cheliceral shape. These conflicts were resolved by applying additional, character-specific criteria to discriminate among alternative hypotheses of similarity (in dentition; Appendix 3) or position (male flagellum). Where competing hypotheses remained, the most plausible advanced, with alternatives mentioned to permit testing in future analyses (e.g., indicator hypotheses concept; Rieppel, 2005; Ramirez, 2007).

TERMINOLOGY AND CONVENTIONS

Another aim of the present contribution was to develop an accurate, concise and unambiguous (Gordh and Headrick, 2001) terminology for characters hypothesized to be homologous based on similar structure and position. In developing terminology, current and traditional usages were considered to facilitate stability, and many of the terms applied here are not new to the solifuge literature, e.g., fond (Putnam, 1883; Fichter, 1940; 1941; Muma, 1970b) and distal tooth (Millet and Vachon, 1949). Some guidance was obtained from terminology applied to other arachnid taxa, e.g., paturon, from the spider literature (Ramirez, 2014). However, information content (especially descriptive accuracy), comparability among characters within a character system (e.g., among different series of setae on the prolateral surface of the chelicera), and consistency were given primacy over legacy usage. Standardized abbreviations were developed to render some positional terminology more concise.

As the aim was for accurate and intuitive terminology, reasons for the choice of terms are not elaborated, except in the case of pro- and retrolateral as descriptors for the opposing lateral surfaces of the chelicerae. These terms for cheliceral orientation, which have not previously been used to describe solifuge morphology, form the basis of many other terms newly proposed here.

There is no consensus in the solifuge literature regarding the terminology for cheliceral orientation, despite its importance for understanding position. The terms inner and outer and variants, internal, external, interior, exterior, adaxial, are common (e.g., Dufour, 1861; Purcell, 1899; Hewitt, 1919b; Lawrence, 1931, 1955; Mello-Leitão, 1938; Panouse 1960a,b; Levi and Shulov, 1964; Simonetta and Delle Cave, 1968; Wharton, 1981; Maury, 1984; Armas, 1994; Klann & Alberti, 2010). Other authors used medial or median and lateral (Roewer, 1934; Kraus, 1956; Turk, 1960; Wharton, 1981; Reddick et al., 2010). Hewitt (1919b: 24) used mesial (also used by Brookhart, 1965) interchangeably with inner. Muma (1951) introduced mesal (inner) and ectal (outer), terminology subsequently followed, with few exceptions (e.g., Gromov, 1993), by workers in the New World, especially in the U.S.A. (e.g., Brookhart and Cushing, 2004, 2008; Catenazzi et al., 2009; Carvalho et al., 2010).

Unfortunately, none of the abovementioned terms are accurate descriptors of orientation as per their definitions. Mesal is defined as “descriptive of structure that is positioned on or in the median plane of the body” (Gordh and Headrick, 2001: 569) and is therefore appropriate for describing the position of the rostrum, but not the surface of the chelicera adjacent to the midline. Mesial is defined as “descriptive of something near an imaginary line dividing the body into left and right halves; the median plane of the body” (Gordh and Headrick, 2001: 570). Although more accurate than mesal in referring to the surface of the chelicera adjacent to the midline, mesial cannot be applied to the other serially homologous appendages (pedipalps and legs) and offers no antonym for the opposite surface of the chelicera. Ectal, defined as “directed outward or toward the outer surface of the … body” (Gordh and Headrick, 2001: 303), has mistakenly been used as the antonym of mesial. However, this term and its antonym, ental, along with their synonyms, outer, external, exterior, and inner, internal and interior, more appropriately describe the position of structures inside versus outside the integument, rather than the opposing surfaces of the chelicera (see Acosta et al., 2008). Lateral is defined as “descriptive of structure or movement relating to the side” (Gordh and Headrick, 2001: 512). As such, its use in referring to the surface of the chelicera adjacent to the midline or to its opposite surface is correct in the same way that “lateral” refers to the side of the body. However, the term fails to distinguish between the two surfaces of the chelicerae or to account for the fact that the chelicerae are serial homologs of the pedipalps and legs, to which consistent terminology should be applied.

A consensus in terminology among different orders of arachnids is obviously desirable. Inner and outer are the predominant descriptors of cheliceral orientation, e.g., in Amblypygi (Shear, 1970) and Araneae (Schütt, 2000; Henning et al., 2002), although other terms include mesial in Scorpiones (Alexander, 1958), anterior and posterior (e.g., Platnick, 2000), prolateral (Bosselaers and Jocqué, 2002), frontal (Bosselaers and Jocqué, 2002) and pro- and retromarginal (as terminology to specific margins; Gillespie, 1994; Bosselaers and Jocqué, 2002; Ramirez, 2014) in Araneae, and ventral and lateral in Opiliones (Snegovaya, 1999). Terms of orientation that attempt to reflect the homology of the cheliceral surfaces are complicated by the fact that the chelicerae have undergone considerable rotation, at least in some segments, among the different orders. For instance, the chelicerae of scorpions are set at such an angle that the surface adjacent to the midline in effect faces mesoventrally. The orientation is similar in opilionids, such that the surface adjacent to the midline and its opposite surface are more commonly referred to as ventral and lateral, respectively. The orthognathous and labidognathous orientations of the chelicerae of spiders (Kraus and Kraus, 1993; Zonstein, 2004) lead to a complicated terminology including anterior and posterior, mesal and ectal, and the prefixes “pro” and “retro” to refer to different positions on the chelicera (e.g., Ramirez, 2014).

Pro- and retrolateral are commonly used in spider (e.g. Platnick, 2000; Ramirez, 2014) and, more recently, scorpion literature (e.g., Acosta et al., 2008; González-Santillán and Prendini, 2013) pertaining to the pedipalps and legs, the lateral surfaces of which face forward (pro-) or backward (retro-). The chelicerae, pedipalps and walking legs are accepted as serial homologs in chelicerates (Boxshall, 2013). Therefore, the terms pro- and retrolateral are appropriate to describe the homologous surfaces of all these appendages, despite the fact that the chelicerae do not project laterally like the pedipalps and legs.

The terms prolateral and retrolateral, considered more intuitive and accurate in accounting for position and serial homology, are applied throughout the present contribution to describe the surfaces of the chelicera respectively facing towards and away from the midline of the body. Subdivision and fusion of these terms with others referring to topological position creates precise positional descriptors for structures situated on different surfaces, for example prodorsal, proventral, retrodorsal, retroventral, etc.

A glossary of terms (Appendix 2), each with a descriptive statement and a list of historical synonyms and interpretations, is provided for reference. Terms in the glossary are indicated in bold when first mentioned in the text. The glossary provides more than a dictionary of terms, however; it supplements character discussions in the text, as each term in the glossary is referred to in the annotated illustrations of voucher specimens. Interpreted illustrations accompanying character descriptions provide empirical substantiation for descriptive statements and increase the transparency of data (Vogt et al., 2010).

Other terms and phrases used throughout include “distally directed”, “proximally directed” and “sclerotization.” “Distally directed” and “proximally directed” refer to position with respect to the chelicera, i.e., directed anteriorly or posteriorly with respect to the body, respectively. “Sclerotization” refers to the base color intensity of the cuticle, assumed to be a function of the thickness of the cuticle, and not to the density of pigmentation.

A comparative approach is followed throughout the present contribution. All discussions and examples pertain to male characters, unless stated otherwise. In order to assist with orientation, the illustrations were standardized such that the distal side of the chelicera faces left in prolateral view and right in retrolateral view, with few exceptions.

Discussions of functional morphology require understanding current knowledge of reproductive behavior. Muma (1966b) identified three phases in mating behavior (attack, contact, and release) but overlap in behaviors and assumptions of function fail to accommodate observations of mating in non-eremobatid taxa. Male reproductive behavior is here divided into three main phases (somatic contact phase, genital contact phase, and release phase), each with further subdivisions (Table 2).

CHELICERAE

CHELICERAL TERMINOLOGY

The first cheliceral segment, referred to here as the **paturon** in accordance with spider literature (e.g., Ramirez, 2014), consists of the manus (broad basal section of the chelicera), and terminates in an outgrowth, the **fixed (dorsal) finger** (Fig. 1). The manus contains the cheliceral muscles, which extends somewhat into the fixed finger along with the trachea (Klann, 2009; Van der Meijden, et al., 2012). Sørensen (1914: 161) mentioned adipose tissue inside the fingers in engorged specimens. The **movable (ventral) finger** is the second cheliceral segment. Although various terminologies have been applied to cheliceral finger in solifuge literature, the term fingers is preferred here (Table 5). Each finger bears dentition (teeth) along its cutting edge, i.e. the median and fondal series of teeth on the fixed finger and the **median series** of teeth on the movable finger. A slight broadening at the base of the fixed finger between the two diverging rows of **fondal teeth** is termed the **fond** (Simon, 1879a: 126, 1880: 402; Putnam, 1883:257; Fichter, 1941; Muma, 1951). The fond is not synonymous with the **fondal notch**, present in many eremobatid males (see below). The distal part of each finger is termed the **mucron** (Maury, 1970), redefined here as the part of finger distal to the distal tooth on the fixed finger (FD), and distal to the medial tooth on the movable finger (MM), as measured from the notch of the tooth directly distal to FD or MM to the terminal tooth (FT and MT; tip of finger). The mucra are usually toothless. Although the position of FD and MM can often be approximated, when absent, by comparison with related taxa, this is not always possible, and the proximal margin of the mucron is therefore often neither identifiable, nor deducible.

The movable finger articulates ventrally with the fixed finger (Figs. 1, 2, Pl. 2) via a circular opening (Roewer, 1934: fig. 48), referred to here as the **interdigital foramen**, at the base of the fixed finger. The foramen is flanked distally by the fond, and demarcated by the basal fondal margin, bearing small to reduced **basifondal (BF) teeth** in some taxa. An **interdigital articular membrane (iam)** connects the fixed and movable fingers, and permits articulation (Van der Meijden et al., 2012). The part of the membrane visible in the fondal area is referred to here as the **fondal interdigital articular membrane (fiam)** and the part connecting the movable finger ventrally with the manus a **ventral interdigital articular membrane (viam)**. The viam is flanked on each side by a fortified asetose area, probably serving as muscle or ligament attachment points, at the base of the movable finger (ventral digital plagula, vdp), and on the manus (ventral manus plagula, vmp). The vmp terminates at each end in a distinct, rounded and strongly sclerotized, external articulation sclerite (Muma, 1985), referred to respectively as the pro- and retrolateral **interdigital condyli** (pic and ric), articulating into the **pro- and retrolateral interdigital sockets** of the movable finger. These condyli together form a ventral bicondylar hinge through which the movable finger articulates with the fixed finger. The bicondylar hinge restricts movement of the fingers to the dorsoventral plane, allowing the teeth to overlap in a scissor-like manner (Kraepelin, 1901) and transforming the chelicerae into the powerful offensive and defensive appendages they are (Roewer, 1934: 54). The two interdigital condyli determine the rotation axis of the fingers (Van der Meijden et al., 2012). The movable finger closes prolateral to the fixed finger. However, the movable finger of some chelicerae closed retrolateral to the fixed finger (Pl. 94C) as an artifact of forced closure to examine dental overlap in the present study.

The chelicera articulates basally with the propeltidium (Figs. 1A, 3, Pl. 3). The opening through which the chelicera connects internally with the rest of the prosoma is referred to here as the **cheliceropeltidial foramen**. At the external margins of the chelicera, the exoskeleton is markedly bent inwards to form a broad collar-like **basal cheliceral apodeme** which surrounds the foramen. The basal apodeme projects retrolaterally to form a sclerotized protuberance, the **cheliceropeltidial condyle** (cpc), which articulates with the propeltidium of the prosoma to form an anterolateral cheliceropeltidial articulation (chelicerocarapacal articulation *sensu* Shultz, 1990) situated within the **anterolateral propeltidial lobe** of the prosoma (Fig. 1A, Pl. 3A, B; Roewer, 1934: 32). The articulation site is often visible on the external surface of the propeltidial lobe as a pale area, the **external cheliceropeltidial condylar attachment (ecpca)**. A **cheliceropeltidial articular membrane (cpam)** connects the chelicera to the prosoma. This membrane is fixed to the chelicera along the margin separating the external chelicera from the basal apodeme, thus forming a membranous collar around the basal apodeme and foramen. Sections of this membrane are prominent and clearly visible anterior to the propeltidial lobe, and ventral to the propeltidium and ocular tubercle in intact specimens (Fig. 1A).

SIZE AND SHAPE

MEASUREMENTS: Solifuge chelicera are often markedly sexually dimorphic. Although the absolute size and shape of the chelicera, and its relative dimensions (e.g., aspect ratios and relative finger lengths) are sexually dimorphic (Fig. 4), this is often difficult to quantify. When measurements are presented in the solifuge literature, these usually are dimensions of length and height (depth) of the chelicera, although width (breadth) is occasionally included (e.g., Maury, 1980a). With few exceptions (e.g. Maury, 1980), the terms “width” (e.g., Muma, 1951; Brookhart and Muma, 1981; Vázquez and Gaviño-Rojas, 2000; Peretti and Willemart, 2007; Catenazzi et al., 2009) and “breadth” (Cloudsley-Thompson, 1961) are traditionally used to describe the vertical axis of the chelicera in the solifuge literature. In the present contribution, following Botero-Trujillo (2014) and in accordance with common usage in other groups (e.g., scorpion pedipalp chela, Vignoli and Prendini, 2009; Lourenço et al., 2012; crustacean cheliped propodus, Gregati and Negreiros-Fransozo, 2007) this is substituted with “height,” whereas width (breadth) is reserved for the horizontal axis measured in dorsal view (Fig. 5).

RATIOS: Various indices exist to quantify cheliceral shape (Fig. 5). The “jaw-index” of Cloudsley-Thompson (1961: 149) calculates the aspect ratio of the chelicera (length/height), which Cloudsley-Thompson (1961) reported as larger in males than females, a general trend across the Solifugae, based on data from others (e.g., Panouse, 1960b; Punzo, 1998b; Peretti and Willemart, 2007). This ratio, referred to here as the **CL/CH** ratio (Fig. 5D), is synonymous with the L/W (length/width) ratio of Brookhart and Muma (1981) and the CL/CW index of Vázquez & Gaviño-Rojas (2000).

Higher CL/CH and **CL/CW** ratios do not indicate a larger chelicera, but a less voluminous (robust) chelicera (Fig. 4). The **CL/CW** ratio (length/width) (Fig. 5E), newly proposed in the present contribution, similarly measures the relative volume of the chelicera. The CL/CH (traditionally referred to as CL/CW) and newly defined CL/CW ratios thus quantify sexual dimorphism in cheliceral dimensions (gracile, narrower, in males and robust in females), rather which sex has the larger chelicera relative to body size. Note that the CL ("cheliceral line") of Punzo (1998a: 228, fig. 7–13A) should not be confused with CL for cheliceral length (in the present work).

According to Punzo (1998a), the **A/CP** ratio (Brookhart and Muma, 1981) is a more precise comparative measure of cheliceral size between sexes than the "jaw-index", or CL/CH ratio. However, the A/CP index (Fig. 5F) was never intended to compare cheliceral sizes as it quantifies the ratio of appendages (A = sum of the lengths of pedipalp, leg I, and leg IV) to body length (CP = sum of the lengths of chelicera and propeltidium), not the ratio of cheliceral length to part of body length. Long-legged species present a higher A/CP value than short-legged species. The A/CP ratio is, therefore, inadequate for comparing relative cheliceral sizes between sexes because cheliceral length is included within the "body length" measurement and "body length" is compared to the length of non-cheliceral appendages, which are typically longer in males than females. A/CP values are thus expected to be higher for males. In addition, the A/CP ratio can be used to distinguish between long-legged and short-legged species. Brookhart and Muma (1981: 286) found the A/CP ratio to be a reliable species indicator for both sexes. Muma (1951) initially included the opisthosoma in the calculation of total body length, but it was subsequently omitted (Brookhart and Muma, 1981, 1987; Muma and Brookhart, 1988) due to the capacity of the opisthosoma to greatly extend when gravid or engorged.

Two-dimensional measurements (cheliceral length, height and width) provide indications of variation within the sexes, and absolute differences between the sexes (e.g., smaller cheliceral length in males found by Punzo, 1998b), but fail to account for sexual dimorphism in body size. An apparent generally smaller (measured in absolute size) male chelicera may be an artifact of differences in body size. Peretti and Willemart (2007: 32, 33, table 1) reported larger chelicerae in males, but this is based on an erroneous interpretation of their aspect ratio values; a higher aspect ratio in males does not indicate larger chelicerae in males, but a *relatively higher* aspect ratio chelicerae in females due to the larger denominator in the latter. Van der Meijden et al. (2012: 3412) mentioned that rhagodid males are smaller than females but that their chelicerae are “much larger” than those of females, whereas male Galeodidae Sundevall, 1833 “generally do not have enlarged chelicera” but failed to quantify these statements. Geometric morphometric analyses would provide a better indication of the relative proportions of male and female chelicerae across the order.

Several eremobatid-specific ratios (Fig. 5H) have been proposed (Brookhart and Muma, 1981, 1987; Muma and Brookhart, 1988; Punzo, 1998a: 228, figs. 7–13A; Brookhart and Cushing, 2002, 2004: 285, fig. 2), including the **FNL/FNH** ratio (fondal notch length/fondal notch height), **FNH/FFH** ratio (fondal notch height/fixed finger height), and **CH/FFH** ratio (cheliceral height/fixed finger height) ratios. The latter was introduced by Brookhart and Cushing (2002: 84; their CW/FFW and CW/WFF) to provide measurements for “species in which the fondal notch was absent or obscure,” such as *Hemerotrecha cornuta* Brookhart and Cushing, 2002 (Pl. 79I, J). This ratio is a useful indicator for species which exhibit a sudden narrowing of the fixed finger, as was the case for the species examined by these authors. Catenazzi et al. (2009: 151), citing Brookhart and Cushing (2002), suggested that width (or "height" as per terminology in the present manuscript) should be measured at the "base of the finger" in species without a fondal notch, but did not provide actual measurements and, as far as can be determined, the CH/FFH ratio has only been calculated in species which exhibit abrupt narrowing of the fixed finger. There is no reason why the CH/FFH ratio should not be applicable to conserved cheliceral shapes, provided the point of measurement (landmark) is specified and used consistently among taxa. Given that the modified eremobatid fixed finger narrows into a **stylet-like** structure directly proximal to the proximal tooth (FP), this point is the most appropriate landmark for FFH measurements in chelicerae with conserved shapes (Fig. 5I).

Other measurements used on solifuge chelicerae include (i) the length of the space occupied by the teeth on the movable finger, measured from the apex of the proximal tooth (MP) to the apex of the medial tooth (MM) (Muma, 1951: 122), and (ii) the length of the **retrodorsal process (RDP)** on the fixed finger relative to the length of the fixed finger in male specimens of the *palpisetulosus* group of *Eremobates* (Muma and Brookhart, 1988; who also described the relative placements of the retrodorsal process).

LANDMARKS: The shape of the chelicera and the manner of its attachment to the propeltidium hinder the identification of unambiguous landmarks for recording measurements, often resulting in subjectivity. Height and width of the cheliceral manus or finger are measured as the distance between the furthest points (Fig. 5A, B), and length of the fondal notch as the maximum distance within the fond (Fig. 5H). Cheliceral shape determines the highest point of the chelicera. For example, Muma (1951) measured height across the manus in Eremobatidae and across the base of the movable finger in Ammotrechidae Roewer, 1934. The line of measurement for cheliceral length is also ambiguous. Pocock (1895: 78, footnote) measured the retrolateral side from the "point of articulation to the apex of the immovable **fang**." Purcell (1899: 407) also measured "apex to hinge." A similar measurement was applied to Eremobatidae by Muma (1951) and Brookhart and Cushing (2004: 285, fig. 2). Muma (1951: 40) clarified that this was conducted "in such a manner that the line of measurement was always within the chelicera" and when "the fixed finger was bent or curved, stadia permitting the longest line of measurement were utilized." It is unclear how this was achieved. A caveat of using the basal articulation as a landmark is that the chelicera has to be removed from the prosoma with the cheliceropeltidial condyle intact (Fig. 5A), or the articulation point must be approximated, e.g., from the external cheliceropeltidial condylar attachment (ecpca). Fortunately, the latter is usually visible on the anterolateral propeltidial lobes (Fig. 1A, Pl. 3A, B). Three alternatives would be to measure retrolaterally in a direct line from the fingertip to the anterior margin of the cheliceropeltidial lobe (Fig. 5B, line i.); retrolaterally in a line parallel to the cheliceral axis from the fingertip to the anterior margin of the cheliceropeltidial lobe (Fig. 5B, line ii.); or dorsally from the fingertip to the anterior margin of the propeltidium (Fig. 5C). The third metric was found to be easiest in intact specimens, but not in specimens from which the chelicera was removed. The former (Fig. 5B, line i) is recommended in the current contribution because of its utility in both attached and removed chelicerae. As the axix of measurement used may yield different measurements, consistency of landmarks in length measurements between studies is imperative for repeatability and comparison. For the same reason these should be stated in measurements of height and width.

Statements concerning the relative lengths of the fixed and movable fingers are often made (e.g., Hrušková-Martišová, et al., 2010a, Wharton, 1981: 40), but remain subjective because the landmark defining the start of the fixed finger is arbitrarily defined. The interdigital condyli, which represent the start of the fixed finger, are here proposed as an unambiguous landmark for measuring the length of the fixed and movable fingers (condyle-to-fingertip line; Fig. 5G). This landmark also accounts for the rotation axis which affects how the fingertips close relative to one another.

SHAPE: Most modifications in shape concern the fixed (dorsal) cheliceral finger which, in some species, is elaborately to bizarrely modified in adult males (Fig. 6, Pl. 137). The fixed finger is usually unmodified in adult females and immatures although, in some Ammotrechidae and Mummuciidae, the fixed finger is more modified dorsally in females than in males due to a more pronounced angular dorsal margin, or dorsal crest ("dorsal hump" of Iuri et al. 2014: 21; Muma, 1951: 124, 126, figs. 289–262, 272, 273; Botero-Tujiro, 2014: 325, figs. 11, 17). Modifications of the movable (ventral) finger tend to be less pronounced but may involve slight differences in dentition or shape towards the apex (mucron) including, e.g., varying degrees of concavity, or a sudden narrowing at the apex to form a **ventral notch (VN)** (Fig. 7B; Muma and Brookhart, 1988). The mucron of the fixed finger is usually more slender in males, and may be more markedly hooked, bent or angular (e.g., *Karschia* Walter, 1889, males in Pl. 50) or less strongly curved (e.g., Galeodidae, males in Pl. 62). Interfamilial trends are evident in cheliceral shape, e.g., a narrow chelicera is common in Ammotrechidae (Pl. 146), a robust chelicera in Dinorhaxinae (Pl. 56B), Hexisopodidae (Pl. 129) and Rhagodidae (Pl. 56C–H), and a narrow chelicera, often with long fingers, in Melanoblossiinae (Pl. 154). Another recurrent pattern is the 'eremobatid shape', which comprises a prominent, vertical fond (see below) and a fixed finger shaped like a stylet for most of its length, with or without a fondal notch separating the finger from the fond (Fig. 7A, B). A similar shape is evident, albeit often to a lesser degree, in other solifuge families, including Daesiidae, e.g., *Biton* (*B.*) *subulatus* (Purcell, 1899) (Kraepelin 1901: 93, fig. 62, as *Daesia subulata*), Gylippinae (Pl. 85B), Karschiidae (Pl. 50A), Lipophaginae (Pl. 87H), and Ceromidae (Pl. 91H).

Several taxa exhibit distinct gaps (notches, or diastemas) between teeth (Fig. 7). The fondal notch (FN) is situated proximal to the median series FP (Fig. 7A, B). It is usually toothless, although **denticles** are present in some eremobatid species (Pl. 2B). A diastema within the median series, referred to here as the **medial notch (MN)**, is a toothless areas between the fixed finger medial (FM) tooth and the fixed finger submedial (FSM) tooth, the latter always situated close to, or on the distal edge of the **fixed finger proximal (FP) tooth** in the presence of a diastema (Fig. 7C, D). A medial notch is most prominent in Solpugidae, and is a diagnostic character for *Solpugema* Roewer, 1933 (Roewer, 1934: 420). Similarly positioned, but less pronounced toothless spaces occur in other Solpugidae, e.g., in *Solpugista hastata* (Kraepelin, 1899), some Ammotrechidae (Fig. 7D), and apparently Karschiidae (Roewer, 1934: 143, fig. 141C).

Because the fondal notch is situated proximal to the median series, whereas the medial notch is situated within the median series, these toothless areas are not considered homologous (Fig. 7). The medial notch and dentition associated with it is further discussed under Dentition, Solpugidae.

FUNCTIONAL MORPHOLOGY

MATING BEHAVIOR: The size and shape of the chelicerae is often associated with reproduction (e.g., Hrušková-Martišová et al., 2010a; Van der Meijden et al., 2012). For example, Van der Meijden et al. (2012) speculated that a reproductive function (e.g., male-male antagonism) might explain the apparently larger chelicerae reported for male Rhagodidae (although how this was measured was not mentioned). Others (e.g., Hrušková-Martišová et al., 2010a) have suggested that cheliceral shape may be adapted for direct involvement during copulation.

The fixed finger of males is the part of the chelicera most involved in mating. The male flagellum originates on the fixed finger and the finger itself may be modified in general size and shape, as well as in the shape of the mucron. Modifications of the movable finger are relatively rare and include a concave mucron, more pronounced in males of some taxa, e.g., *Namibesia pallida* Lawrence, 1962 (Pls. 132A, 133A) and *Trichotoma michaelseni* (Kraepelin, 1914)(Pls. 87A–D, 88A). The functional significance of modifications to the fixed and movable fingers are mostly unknown, but some possibilities can be suggested based on a few species in which mating has been reported.

The relative length of the cheliceral fingers, and specifically a shorter fixed (dorsal) finger, in males may be of functional significance when the movable finger holds, or kneads, the outside of the female's body in the area of the genital operculum while the fixed finger remains inserted in the female's gonopore (Table 2). However, no such correlation appears to exist for the two species in which this behavior was reported (Hrušková-Martišová et al., 2010a; Peretti and Willemart, 2007). A marked difference in the length of the fingers is evident in *Gluvia dorsalis* (Latreille, 1817) (Pl. 132I, J) but not in *Oltacola chacoensis* Roewer, 1934. Furthermore, the relative length of the fingers is difficult to quantify, emphasizing the need for standardized measurements based on unambiguous landmarks, and accounting for the axis of rotation.

The shape of the fixed finger is probably important for its insertion into the female reproductive tract. The fixed finger was observed to be inserted into the female reproductive tract in representatives of Ammotrechidae (Peretti and Willemart, 2007), Daesiidae (Hrušková-Martišová et al., 2010a), Eremobatidae (Muma, 1966b) and Galeodidae (Hrušková-Martišová et al., 2008a, 2010a) (Table 2), but how deep the fingers are inserted (e.g., most of the finger or only the mucron) is unclear due to differing interpretations regarding the proximal limit of the fixed finger. The narrow, tapering shape of the fixed finger, combined with the presence of a fondal notch, may facilitate a "deep" insertion in Eremobatidae, the only family for which the depth of insertion was explicitly mentioned (Muma, 1966b). The tapering finger of male eremobatids may also be an adaptation to enter and pass through the narrowing oviducts of eremobatid females (Table 4).

The shape and intersection of the apices of the male cheliceral fingers have been suggested to be sexual dimorphic, functioning more effectively as “pincers” during mating (Peretti and Willemart, 2007). Intersection of the finger apices is not restricted to males (e.g., Pl. 62D), however, and is probably widespread in solifuges, even in species with a stylet-shaped fixed finger. e.g., *Lipophaga trispinosa* Purcell, 1903 (Pl. 85H), for which pinching or gripping may appear challenging. Examples of recorded behaviors which may be relevant to mucron shape include clasping the female during initial contact, presumably to subdue or manipulate her (Peretti and Willemart, 2007), gripping the female genital operculum in preparation for insemination (Peretti and Willemart, 2007; Hrušková-Martišová et al., 2010a), dragging the female up a vertical surface for insemination (Cloudsley-Thompson, 1961), or closing the genital opening post-insemination (Heymons, 1902; Amitai et al., 1962). None of these behaviors was reported in Eremobatidae (Muma, 1966b; Punzo, 1998b), all of which possess a very straight, apically pointed cheliceral fixed finger in the adult male. As observations suggest that sperm is deposited in the form of a viscous sperm droplet, regardless of the type of packaging (Table 3), mucron morphology is assumed to play a role in picking up (Amitai et al., 1962; Wharton, 1987; Hrušková-Martišová et al., 2010, 2008a) or catching (Cloudsley-Thompson, 1961) and subsequently holding and inserting the sperm droplet into the female (Wharton, 1987). In all Eremobatidae observed to date, sperm transfer was direct and the chelicera never handled the sperm droplet (Muma, 1966b). This behavior correlates with the straight, stylet-like mucron of the fixed finger of eremobatids, a morphology that would appear to be suboptimal for such a task.

It is here suggested that modifications in the shape of the chelicerae, especially the fixed finger, are adaptations for pre- and post copulatory probing of the female genital area, rather than insemination. The fact that the chelicera is not used to pick up sperm in Eremobatidae may have freed the fingers for other purposes in this family. This hypothesis is supported by the observation that some of the most markedly sexually dimorphic species occur in Eremobatidae, the family with direct insemination. Unfortunately, the paucity of data concerning both morphology and mating behavior restricts further understanding of this matter. However, it is noteworthy that the "typical"' eremobatid chelicera (e.g., Pl. 65H) with a toothless, stylet-like fixed finger, is observed in other, diverse families, suggesting the possibility of convergence due to similar mating strategies (e.g., Pl. 85A). Another example of possibly convergent cheliceral morphology is the similarity in mucron shape in the ammotrechid, *Nothopuga cuyana* Maury, 1976 (Pl. 146H), and the karschiid, *Karschia* (Pl. 50B, F). A comparison and possible correlation among mating behavior, female genital anatomy and similar male cheliceral morphology (e.g., similarities in cheliceral shapes in many species of *Biton* Karsch, 1880, Pl. 143) may improve understanding of the functional morphology of the male chelicera, both among distantly related taxa and closely related species.

OTHER BEHAVIOR: Sexual dimorphism in shape is not necessarily linked only to mating behavior. Hrušková-Martišová et al. (2010a: 94) described the chelicerae of two species observed by them as being "straighter" and more elongated in males than females, and inferred that this difference in shape might confer a benefit during insemination, in particular during the "contact phase." Although supported by observations of insertion of the entire chelicera into the female reproductive tract during mating (Amitai et al., 1962), few reports of mating described insertion of an entire chelicera, although the male chelicera is generally more gracile across the order.

Deconstructing sexual dimorphism in shape (Fig. 4) suggests that the “straight” appearance of the male chelicera is mostly caused by its straight fixed finger and narrower manus, whereas the robust female chelicera is mostly caused by its curved fixed finger and wider and deeper manus. The fixed finger of the male is commonly inserted into the female genital tract. As the manus contains the muscles which provide the bite force of the fingers necessary, e.g., to break the hard exoskeleton of prey, a more voluminous manus is expected to accommodate larger muscles in females with their voracious appetites. Conversely, in addition to the reduced feeding reported in males (Junqua, 1962; Wharton, 1987), differences in prey preference have also been reported. For example, Hrušková-Martišová et al. (2010b) found that males of *Gluvia dorsalis* did not feed on sclerotized beetles in the laboratory, unlike conspecific females, which readily did so. It may therefore be concluded that the sexual difference in cheliceral manus volume is more likely the consequence of selection for improved predation ability, leading to a larger manus, in females, rather than selection for a smaller manus in males to assist in mating.

The mechanical “bite force” of galeodid and rhagodid species was measured by Van der Meijden et al. (2012), who found the aspect ratio of the chelicera to be negatively correlated with bite force, being higher in Rhagodidae, with low cheliceral aspect ratio, than in Galeodidae, with high cheliceral aspect ratio. Van der Meijden et al. (2012: 3417) also suggested that a low aspect ratio may be an adaptation to “reduce the risk of structural failure” of the chelicera when subjected to force, as might be experienced by fossorial solifuges, e.g., Rhagodidae and Hexisopodidae, during burrowing. This suggestion is supported by evidence that fossorial rhagodids possess a greater bite force at the tips of the chelicerae than surface-living galeodids (Van der Meijden et al., 2012). However, a greater force strength was found over the movable finger proximal tooth (MP), i.e. the “main tooth” of Van der Meijden et al. (2012), in Galeodidae. These authors thus suggested that galeodids might be less effective burrowers than rhagodids, but with a greater ability to crush sclerotized beetles than rhagodids. It may therefore be possible to associate the shape of the chelicera of different solifuge families to their dietary preferences, but no other study to date has investigated the components of cheliceral morphology necessary to handle prey. A large body of research on the chela (claw) of the crustacean cheliped may offer parallel insights into the functions of solifuge chelicerae. For example, in Crustacea, robust chelae possess a higher pinch force, at the cost of a slower closure. Such chelae typically possess larger, more blunt-edged molars (teeth) whereas slender chelae with long, narrow fingers are typically weaker but faster, and possess smaller, sharper and more numerous molars (Taylor, 1999). Extending these observations to Solifugae, the slender, **multidentate** chelicerae of the small Melanoblossiinae (Pl. 154), for example, might be an adaptation for speed over force in dealing with small, fast running prey.

INTEGUMENT

ASETOSE AREAS: The chelicerae of solifuges are covered in setae except in specific areas devoid thereof, and referred to here as **asetose areas** (Fig. 1B, C, Pl. 4). Large areas of the distal parts of the cheliceral fingers, extending along the fixed finger, and always including the teeth and cutting edges, are asetose, as are the smooth and shiny **stridulatory plate**, bearing the **stridulatory ridges** (see Stridulatory Apparatus), the interdigital condyli and **ventral manus plagula (vmp)** at the ventrodistal end of the manus, and the similar **ventral digital plagula (vdp)** at the base of the movable finger which connects the sockets ventrally (Pls. 2C, 6A). Asetose areas are usually well defined and heavily sclerotized (Pl. 4). In Hexisopodidae, the heavily sclerotized asetose area on the fixed finger is usually lobate dorsally, and referred to as a **callus** (Fig. 6A, Pls. 127C, 128D, E); Wharton, 1981). The callus often possesses blunt spine-like processes, or tubercles.

Setae and structures derived from setae (e.g., the male flagellum) never originate within asetose areas and, if situated near the margins thereof, the sclerotized area usually curves around the base of the structure (Pl. 4A–C). Apparent exceptions include the gylippine flagellum which appears to originate on the asetose area of the fixed finger (Pl. 4D) and the setae occurring in the fondal notch of many Eremobatidae (Pl. 4F). However, the flagellum of Gylippinae is hypothesized to originate in the setose area, the basal part being fused with and impossible to distinguish from the sclerotized section of the fixed finger, much like the shaft of the flagellum of Solpugidae, which is fused to part of the fixed finger (see section on Male Flagellum and Flagellar Complex). Closer examination of the setae apparently situated within the fondal notch of Eremobatidae (*rlf* in Pl. 4F) reveals that the asetose area is still present, but somewhat displaced prolaterally, and reduced to a narrow strip which sometimes contains denticles (Pl. 4E). Unlike setae, taxon-specific hornlike cheliceral processes and macrostructures (flanges, carinae and toothlike projections), especially common in Solpugidae, are restricted to the asetose areas of the fingers (e.g., Pl. 20G; also see “Taxon survey” under

Flagellum).

CANALS AND GRANULATION: Prominent narrow canals, extending approximately perpendicular to the axis of the finger and apparently traversing the width of the endocuticle to the surface, are usually visible through the cuticle of the asetose areas of solifuge fingers (Pl. 5A; Bernard, 1896; Hewitt, 1919b: 12; Roewer 1934: 118). The function of these **cuticular canals** is unknown. Hewitt (1919b) speculated that they may be sensory. So-called **granulations** (e.g., Lawrence, 1972: 99), situated on the asetose areas of the cheliceral fingers (Fig. 1B, Pl. 5B, C), are most prominent on the retrolateral surface of the movable finger, but may also be present on the prolateral surface, on both surfaces arranged in a longitudinal row along a low longitudinal carina of the finger. A similar row of granules occurs on the fixed finger of some species. Less distinct granules, the functions of which are unknown, are often distributed randomly towards the apices of the fingers. Some of the canals visible through the cuticle terminate in these granules. Although the canals were reported to open externally through pores (e.g., Hewitt, 1919b), no external openings were observed in the present study (Fig. 8). Bernard (1896: 232) suggested that the granules are setal pores ("pores of vanished hairs"), a hypothesis supported by the observation of "pores" (granules) which continue to transverse the finger distal to the apicalmost prolateral movable finger setae. Further support for this hypothesis is evident on the retrolateral surface, where a cluster of setae, referred to here as the **retrolateral proximal cluster (*rlpc*) of setae**, is situated at the base of the row of granules (Pls. 18, 19). Narrow canals, connecting to setae, are also visible on other parts of the chelicera, notably the retrolateral surface of the fixed finger. Females and juveniles possess similar granulation and, in some cases, even more prominent and/or extensive granulation than males, especially on the fixed finger (compare sexes in e.g., Pls. 67B, D, J, L, 104B, D, 124B, D, 126B, G, 132B, D, 136F, H).

SENSE ORGANS: Hansen (1893: 178, pl. 3, fig. 6) identified two lyriform organs situated ventrally on the chelicera, near the interdigital articulation, one on the movable finger, slightly distal to the point of articulation, and the second on the first cheliceral segment, slightly proximal to the point of articulation (Pl. 6A). Hansen (1893) described these depressions as consisting of a small number of canals flattening towards the surface to open to the outside via narrow fissures, each with a small central dilation. In the few taxa available for study, Hansen (1893) observed a slight change in the position of this organ on the manus, noting in particular its more prolateral position in *Galeodes* Olivier, 1791. Close to these structures, and reported here for the first time, is a series of less defined round to oval depressions situated proventrally on the stridulatory area, and referred to here as the **medioventral organ** (Pl. 6; also distinctly visible as an irregular depressed area on the ventral margin of the stridulatory plate in Carvalho et al., 2010: 26, fig. 19). Although more distinct in some taxa than others, this organ appears to be present in both sexes of all species. The depressions comprising the medioventral organ are all situated on or near the ventral margin of the stridulatory plate which is less clearly demarcated than its dorsal and distal margins. Closer inspection reveals the margin in many species to be largely irregular due to the presence of a few setae, which may be associated with the medioventral organ (see Pl. 6B–D), situated dorsal to the ventral margin of the stridulatory plate.

A concentration of sense organs occurs on the ventral surface of the chelicera in the area where the fingers articulate. The pedipalpal coxal gland is situated on the dorsal surface of the pedipalp coxa directly ventral to the chelicera. The coxal glands present a distinct outer morphology comprising an anterodorsally (slightly laterally) directed papilla referred to by Buxton (1913: 253; *Mündungsapparat* of Alberti, 1979) as the nozzle. Associated with the nozzle, referred to here as the coxal gland nozzle (cgn), are coxal gland setae (*cgs*) and coxal gland nozzle setae (*cgns*), respectively situated anterior to and on the nozzle itself (Pl. 7). The coxal gland opening is situated on the dorsal side of the nozzle at its base (Alberti, 1979). The placement and form of the nozzle appears to serve as a conduit for channeling gland secretions towards the chelicera (Pl. 7), as noted by Buxton (1913). Some taxonomic variation was observed in nozzle morphology and the number and directionality of the *cgs* and *cgns* setae associated with it. Regardless of such differences, however, the structure retained the anterodorsally directed orientation of the nozzle and coxal gland setae in all taxa examined. The morphology and position of the coxal gland optimizes contact with the ventral chelicera. The palpal coxal gland is not discussed further in the present contribution because it is not part of the chelicera. A possible association with the sensory organs of the chelicera should be further investigated, however.

STRIDULATORY APPARATUS

TERMINOLOGY: Audible stridulation in solifuges, by rubbing the chelicera together, was reported by P.S. Pallas in the 18th century (Bernard, 1896). A smooth, well defined area of ridges, situated on the prolateral surface of the cheliceral manus (Fig. 1, Pls. 8–

10) was first documented by Dufour (1861: 393). Hansen (1893: 184) ascribed a stridulatory function to the “sharp keels” and “naked, shiny, square plane,” and named it the stridulatory apparatus. Kraepelin (1899) used the term stridulatory ridges for the first time, and the surface on which these ridges are placed was later referred to as the stridulatory area (e.g., Hewitt, 1931) or stridulatory plate (Turk, 1960). Turk (1960) was the first to associate the modified setae distal to the stridulatory plate with the stridulatory apparatus, and referred to these as **stridulatory setae** (Fig. 9; Pls. 10, 11). Hrušková-Martišová et al. (2008b) suggested that a stridulatory apparatus consists of two identical files, one on each chelicera.

MORPHOLOGY: The structure of the stridulatory apparatus varies among solifuge taxa. The stridulatory plate at the base of the manus is present in all Solifugae. The approximately parallel stridulatory ridges commonly found on the stridulatory plate do not cover the entire surface, but are concentrated dorsodistally. The extent to which the plate is covered by ridges, and their number and development, differ among taxa (Figs. 23A, 24D, 26A, Pls. 8, 9). Hansen (1893) was the first to compare the stridulatory ridges among families. The first SEM images of stridulatory ridges (an ammotrechid, a galeodid, and a rhagodid) were provided by Cloudsley-Thompson and Constantinou (1984), who summarized the family-level differences reported earlier by Hansen (1893). Based on the observations of Hansen (1893) and Cloudsley-Thompson and Constantinou (1984), SEM images provided by later workers (Hrušková-Martišová et al., 2008b; Carvalho et al., 2010; Erdek, 2010; Bayram et al., 2011; González Reyes and Corronca, 2013; Botero-Trujillo, 2014; Iuri et al., 2014), and material examined in the present study, the following family-level differences were identified.

Stridulatory ridges appear to be absent in Karschiidae (Pl. 8A–C; Hansen, 1893). Short, well developed ridges are arranged in a strip at the distal border of the stridulatory plate in Rhagodidae (Pl. 10; Hansen 1983; Cloudsley-Thompson and Constantinou, 1984: 367, fig. 2). Vestigial ridges with short distal corrugations occur in Galeodidae (Hansen 1893; Cloudsley-Thompson and Constantinou, 1984: 366, fig. 1; Hrušková-Martišová et al., 2008b: 444, fig. 1). The ridges are well developed but relatively short and of similar length in Lipophaginae (Fig. 23A) but very vague in Gylippinae (Pl. 8D, E). Stridulatory ridges are also barely visible in Ceromidae (Pl. 8F). Well developed, parallel ridges cover the dorsodistal surface of the stridulatory plate in Solpugidae (Fig. 24A, D, Pl. 9A, B). A reticulation of fine ridges at the distal border of the stridulatory plate is all that is present in Hexisopodidae (Kraepelin, 1901: 8; Hewitt, 1931; but see Purcell, 1899: 383). Well developed, parallel ridges, the dorsal ridges of which are especially long, also occur in Ammotrechidae (Cloudsley-Thompson and Constantinou, 1984: 368, fig. 3; Iuri et al., 2014: 28, fig. 23), Mummuciidae Roewer, 1934 (Carvalho et al., 2010: 25, 26, figs. 13, 19; González Reyes and Corronca, 2013: 541, figs. 4, 5; Botero-Trujillo, 2014:325, figs. 10, 12), and Daesiidae (Pl. 9C–F; Erdek, 2010: xlii, lxx, figs. 3.16, 3.48; Bayram et al., 2011: 125, figs. 3A6, B6). A few well developed ridges occur in Melanoblossiinae (Fig. 26A). Ridges in Dinorhaxinae are less robust, but remain well differentiated, restricted to the dorsal half of the stridulatory plate, more or less arranged in parallel. Kraepelin’s (1899) key distinguished between Daesiinae (current Daesiidae) and Dataminae (currently Eremobatidae) partly on the basis of the stridulatory ridges being well defined in daesiids, and reduced or restricted to short ridges at the distal margin of the plate in eremobatids. Irregular areas in the ridges were noted in some Solpugidae, in apparently distantly related species (Pls. 97A, 123A). Irregularities in *Biton* (*B.*) *zederbaueri* (Werner, 1905) (Daesiidae) were imaged by Erdek (2010: xlii, figs. 3.16, 3.48) and Bayram et al. 2011: 126, fig. 6 A11). Erdek found the irregularities did not occur in all specimens, and suggested these may have been caused by rubbing of the chelicerae together (M. Erdek, personal commun.).

Stridulatory setae belong to the **promedial (*pm*) setal field**, the field of setae between the stridulatory plate and the distal transverse series (Pl. 10; see section on Chaetotaxy). These setae vary from unmodified to highly modified. Distinctly modified, regularly spaced stridulatory setae occur in Eremobatidae (Fig. 9E, Pl. 11E), Rhagodidae (Fig. 9D, Pls. 10, 11F) and Galeodidae (Fig. 9A–C, Pl. 11G–I). All distinctly modified stridulatory setae possess a swollen base, inserted or bent in a manner to be distally directed, sometimes markedly so (e.g., Birula, 1925; Cloudsley-Thompson and Constantinou, 1984: 367, fig. 2c), and a thin, filamentous and hair-like (acuminate) tip (Fig. 9). The swollen base is a cuticular elevation of the socket in Eremobatidae, whereas the base of the seta itself is swollen in other families. The acuminate tip was found to "bear small forking branches" in *Galeodes granti* Pocock, 1903 (Cloudsley-Thompson and Constantinou, 1984: 366). Turk (1960) identified three main forms of stridulatory setae in Galeodidae, within which further variations were observed. Type I (*arabs*-type) setae possess a swollen, rod-like base, which abruptly and asymmetrically transitions into a very long, very fine, filamentous hair (Fig. 9A, Pl. 11I; Birula, 1925: 191, fig. 3a; Turk, 1960: 112, fig. 1; Cloudsley-Thompson and Constantinou, 1984: 366, fig. 1b–d). Type II (*araneoides*-type) setae possess a swollen, gradually tapering base, the tip of which transitions asymmetrically into a long filamentous hair (Fig. 9B, Pl. 11G, H; Birula, 1925: 191, fig. 3b; Turk, 1960: 114, fig. 2; Cloudsley-Thompson and Constantinou, 1984: 367, fig. 2b–c). Type III (*medusae*-type) setae possess a laterally compressed base that gradually broadens until it abruptly narrows to a long filamentious hair offset asymmetrically from the flat base, from which the filamentous hair arises gradually and asymmetrically (Turk, 1960: 115, fig. 4, reproduced here in Fig. 9C). The setae of rhagodids resemble galeodid type II setae (Fig. 9D, Pl. 11F). The extent of movement of setae depends on the nature and extent of their swollen bases, as well as the angle of insertion (Cloudsley-Thompson and Constantinou, 1984). Birula (1925) was the first to call attention to the value of stridulatory setae in galeodid taxonomy. A detailed survey of the stridulatory setae and evaluation of their taxonomic significance is needed.

FUNCTION AND MECHANISM: Sound production is commonly reported for larger species of Solifugae (Hutton, 1843; Pocock, 1898, 1900a) but may be inaudible to the human ear or absent in smaller species (e.g., Punzo, 1998c). Hansen (1893) was the first to test the stridulatory function (sound production by friction) of the apparatus. By rubbing the chelicerae of a large specimen against one another, a sound reportedly audible up to three meters was manually reproduced. Beyond these early investigations, the precise mechanism(s) of sound production remain little understood (Hrušková-Martišová et al., 2008b). Different forms of stridulatory setae may affect the type and amplification of sound produced. Hypotheses for sound generation were proposed by Dumortier (1964) and Cloudsley-Thompson and Constantinou (1984). These hypotheses involve sound production by scraping the stridulatory bristles over the stridulatory ridges of the opposite chelicera (Dumontier, 1964; Cloudsley-Thompson and Constantinou, 1984, for Rhagodidae), rubbing of the enlarged, relatively ridged bases together, and amplification thereof through vibrations of the long, filamentous hair (Cloudsley-Thompson and Constantinou, 1984, for Galeodidae), or rubbing well developed ridges on opposing chelicerae together (Cloudsley-Thompson and Constantinou, 1984, for Ammotrechidae). Hrušková-Martišová et al. (2008b: 440) suggested that intrageneric similarity in stridulatory apparatus morphology may produce genus-specific sounds, and suggested it might reduce intraspecific "cannibalistic tendencies." Another hypothesis proposed by these authors is that solifuges might imitate those "accoustically aposematic organism[s]" with which they share a habitat such as vipers (Hrušková-Martišová et al., 2008b: 447).

Hrušková-Martišová et al. (2008b) observed relative stability in the number and morphology of ridges among life stages, with length of ridges and thickness of stridulatory setae increasing isometrically with body size in *Galeodes caspius subfuscus* Birula, 1937. These observations, in turn, correlated with similarities in the sounds produced at different life stages. Hrušková-Martišová et al. (2008b) concluded that the primary role of stridulation is defense, rather than intraspecific (i.e., intersexual) communication, a conclusion in accord with previous authors (Hutton, 1843; Pocock, 1898; Cloudsley-Thompson and Constantinou, 1984). Stridulatory ridges appear to be more developed in nocturnal than diurnal taxa (Hewitt, 1919b) but this requires further investigation. Unlike the stridulatory apparatuses of spiders and scorpions, which are quite varied in structure and position, solifuges possess only a single kind of stridulatory apparatus (Bernard, 1896; Dumortier 1964).

Stridulation itself might not be the only, or even the primary function of this structure in solifuges. Pocock (1897) and Hewitt (1919b) speculated that the ridges might serve a masticatory rather than a stridulatory function, at least in some species. The ridges are often slightly less developed (cf. males in Pl. 9A, C with females in Pl. 9B, D; Birula, 1913: 330; Hewitt, 1934) or absent (Hewitt, 1919b) in males compared to conspecific females. The grinding of food between the stridulatory ridges is included in the concept of the **cheliceral mill**, which refers to the combination of movements made by the chelicerae and cheliceral fingers during feeding (Lawrence, 1949a; Muma, 1966c). Prey is crushed into pulp in a combined scissor-and-saw movement, the former due to the nature of the articulation between the two fingers, and the latter an alternative forwards and backwards movement of the chelicerae (Bernard, 1897; Turner, 1916). Also associated with the chelicera is the rostrum (Pl. 92A), which filters food through plates of anastomosed setae, and contains the mouth and pharynx. The rostrum is situated between the chelicerae in such a manner that the mouth at its tip is optimally positioned to receive liquid food and perhaps also masticated food particles (Muma, 1966c), flowing from the ridges. If the stridulatory apparatus plays a role in feeding, e.g., in grinding solid food and directing liquid food towards the mouth, it would be more developed in females given that males, at least in some species, rarely feed (Junqua, 1962; Wharton, 1987). In conclusion, it is likely that the stridulatory apparatus possesses a dual feeding (masticatory) and stridulatory function. The latter may even have evolved subsequent to the former, or vice versa.

CHAETOTAXY

One of the most striking features of Solifugae is their extensive chaetotaxy (Lamoral, 1973) and the chelicerae are no exception. The only areas devoid of setae are the asetose areas described above (Fig. 1B, C, Pl. 4). A full survey of cheliceral setation is beyond the scope of this work, but basic patterns in cheliceral setal arrangements are discussed as no work on chelicerae is complete without setation, and because a discussion on the flagellum is impossible without an understanding of cheliceral chaetotaxy. In the present contribution, setae stands for **macrosetae**, taken as large, dark, sclerotized setae that can be spiniform (rigid) or setiform (flexible), as opposed to **microsetae** which refer to small, pale, unsclerotized setae. Spiniform macrosetae were traditionally referred to as "spines." However, these structures are usually hollow, socketed processes, a typical setal morphology (Gorb, 2001), as opposed to **spines** which are multicellular processes fixed immovably to the body surface. True spines are rare in solifuges (Lamoral, 1973) and, on the chelicera, are restricted to the horn- and toothlike cheliceral processes observed in species of *Eusimonia* (Karschiidae) (Pls. 30D, 31B) and some Daesiidae, although the teeth strictly speaking also fit the definition of spines. Lamoral (1973) thus suggested use of spine-like instead of "spine" for spiniform setae. In the present manuscript the more precise term, spiniform macrosetae (or spiniform setae) is preferred. **Bifid setae** (Fig. 10A) are common on the body and appendages of solifuges but, on the chelicera, are restricted to the setae placed with the retrolateral setae, where they can be of various lengths and thicknesses. "Typical" **plumose setae** (Fig. 10B) are restricted to the prolateral surface of the chelicera (proventral distal setae, *pvd*; movable finger prodorsal setae, *mpd*; **movable finger fondal setae, *mff***), and the lateral lips of the rostrum (lateral lip flagella, Pl. 92A), areas closely associated with feeding. The dorsalmost of the retrolateral proximal cluster (*rlpc*) of setae is weakly plumose in some species. Depending on the species, setal plumosity varies from symmetric to asymmetric, sparse to dense, and covering the distal third to four fifths of the seta (e.g., Birula, 1913: 325, fig. 3a) or the entire length of the seta (e.g., Lawrence, 1968: 75, figs. 7b,e for *Trichotoma brunnea* Lawrence, 1968). Plumose setae are absent in male Hexisopodidae. Even fondal setae and the lateral lip flagella of the rostrum are, at most, striated in hexisopodids. The plumose setae of male Rhagodidae tend to be restricted to a few setae close to the interdigital articulation.

PATURON PROLATERAL SURFACE: Setae on the prolateral surfaces of the chelicerae (**prolateral setae**) of both sexes are arranged in a distinct pattern (Carvalho et al., 2010: 36, fig 19), comprising longitudinal series (rows) and fields of setae named in accordance with position and setal morphology (Pls. 12–14). This pattern is distinct in most, but not all taxa. Hexisopodidae represent the best example of the absence of such a pattern. Hexisopodid males possess a largely homogeneous covering of setiform prolateral setae, except for slightly more stiff, robust proventral distal setae (*pvd*) (Hewitt, 1931) and a small field of short spiniform setae (**prodorsal cluster of spiniform setae, *pdcs***) prodistally on the fixed finger next to the callus in some *Chelypus* Purcell, 1902 species (Pls. 32C, 33E, 130D). The cheliceral setae of Rhagodidae and Dinorhaxinae are also relatively uniform, but less so than those of Hexisopodidae. Birula (1913: 331, fig. 9) provided the most complete categorization of prolateral cheliceral setae, but covered only the most prominent setal groups. Based on placement and basic morphology, six groups of prolateral setae are here identified on the paturon (Pls. 12–14): the proventral distal (*pvd*) setae ("gefiederte Wangenborstenreihe" of Birula, 1913), **proventral subdistal (*pvsd*) setae**, **prodorsal distal (*pdd*) setae**, **prodorsal proximal (*pdp*) setae** ("Langsreihe" of Birula, 1913), promedial (*pm*) setal field ("Querreihe von Borsten" of Birula, 1913; "Mittelfeld der Innerseite der Mandibeln" of Birula, 1929*a*), and **proventral (*pv*) setae**. These are discussed below based on "typical," unmodified patterns. Distinct modifications of individual setae in males are mentioned, but a more detailed discussion is presented in the section Male Flagellum and Flagellar Complex.

The proventral distal setae (*pvd*) comprises one to three regular to slightly irregular rows of straight to curved setae along the ventral prolateral margin of the fixed finger, from its base to the asetose area at its apex (Hewitt, 1919b; Birula, 1913). These setae are plumose although, in some families, the plumosity is presumed to be secondarily lost or greatly reduced in all (e.g., male Hexisopodidae, Pl. 129A, C, E, F) or most setae (e.g., male Rhagodidae, Pl. 56C, E). The *pvd* setae are often more plumose and densely spaced proximally in the *pvd* row near the interdigital articulation, especially in females, and often also in males. The opposite is true for some males; the more distal *pvd* setae are increasingly longer, and particularly distinct in some male Eremobatidae (Pl. 38A, B, D), *Ceroma* Karsch, 1885 (Pl. 32A) and *Karschia* (Pls. 30A, 31A). The proventral subdistal setae (*pvsd*) comprises acuminate setae, which are never plumose. Basal *pvsd* setae are straight, rigid and arranged in a short, regularly spaced comb-like row (Hewitt, 1919b), referred to here as the setal comb (or **proventral**

subdistal setal comb). The *pvd* and *pvsd* setae are thus arranged in two approximately parallel series of setae. The prodorsal distal setae (*pdd*) comprises a row of approximately six to eight setae arranged in a single, often well spaced row directly ventral to the asetose area of the fixed finger (e.g., Pls. 12A, 13). The apical *pdd* and *pvd* setae, especially the setae along the pdd margin (pddm) of the asetose area, are hypothesized to be involved primarily in the development of the flagellum and flagellar complex. The apicalmost seta on the finger of females and immatures is typically plumose and, based on its position, clearly identifiable as the apicalmost seta in the *pvd* series. Directly dorsal and slightly proximal to this seta is an elongated, non-plumose and slightly recurved seta identifiable as the apicalmost seta in the *pdd* series (Pls. 12A, 47A). These setae or their homologs are hypothesized to give rise to the male flagella and are here termed the **ventral flagellar seta (*vfs*)** and the **dorsal flagellar seta (*dfs*)**, respectively (see section on Male Flagellum and Flagellar Complex). The **flagellar complex subspiniform or spiniform (*fcs*) setae** of Ceromidae (Pls. 32 B, 33C), Galeodidae (Pls. 4C, 30G, H, 31 E, F), Gylippinae (Pls. 32H, 33I) and Karschiidae (Pls. 30A–D, 31A, B) might also have originated from *pdd* setae, whereas the setiform flagellar complex of Eremobatidae (Pls. 37–39), Lipophaginae (Pl. 36A–F) and Melanoblossiinae (Pl. 36G–I) exhibit configurations that developed from setae identified to belong to either or both of the *pvd* and *pdd* rows.

The prodorsoproximal setae (*pdp*) are situated in a row that extends longitudinally along the prodorsal surface of the chelicera, dorsal to the stridulatory plate (Pls. 8, 9, 12A). This row comprises two to approximately ten, relatively regularly spaced setae, sometimes with elevated sockets (Pl. 8D). The *pdp* setae are always acuminate, but differ in their extent of differentiation among taxa, from weakly differentiated from the surrounding setae in *Dinorhax rostrumpsittaci* (Simon, 1877) and Solpugidae, through pronounced and robust in Eremobatidae (Pls. 12A, 72), Gylippinae (Pls. 8D, 85A, C, E) and some Karschiidae (Pls. 50, 51), to exceptionally well developed in Rhagodidae (Pl. 10), and long and slender in Ceromidae (Fig. 11A, B, Pl. 91). The *pdp* setae are markedly prodistally directed, creating a lattice-like pattern with their homologs on the opposite chelicera in dorsal view (Fig. 11B, D). Weaker setae may be interspersed among the *pdp* setae. A second, weaker row of setae diverging from the prominent *pdp* setae, structurally most similar to the *pdp* (e.g., Pl. 76E), or to the *pdp* and *pm* setae (Pl. 10), may also be present, and are here referred to as *secondary pdp* setae. Birula (1913: 331) reported the *pdp* setae to be more strongly developed in male than female Gylippinae, but this was not confirmed in the present study.

The promedial setal field (*pm*) refers to a field of setae between the setal comb and the stridulatory area comprising stridulatory setae, or homologs thereof (Fig. 9, Pls. 10, 11), interspersed with weaker, apparently unmodified setae (see section on Stridulatory Apparatus). A dense cluster of short, fine, setiform setae lining the proximodorsal margin of the stridulatory plate are also clearly visible in dorsal view (Fig. 11D). Based on structure and position, these setae show greatest structural similarity with the finer setae in the *pm* setal field and are here termed the **promedial proximal cluster of setae**, or *pmpc* (Pls. 12A, 14B).

The proventral setae (*pv*) comprises a narrow, longitudinal field of setae between the ventral margin of the stridulatory plate and the ventral margin of the chelicera (Pls. 12, 14A).

MOVABLE FINGER PROLATERAL SURFACE: The prolateral setae of the movable finger are situated on a narrow strip that recesses into the asetose area of the finger (Figs. 12, 13, Pls. 12A, 13A, C, 15). As with the prolateral paturon setae, the **movable finger prolateral setae** may also be divided into different longitudinal series (rows). These setal series are named in accordance with their position (dorsal, medial or ventral), predominant projection at origin (dorsally, ventrally or distally projecting), and setal morphology (plumose or acuminate) (Fig. 13), although the ease with which series can be distinguished from one another varies among taxa (Pl. 15). The dorsal setae of the movable finger, here termed the **movable finger prodorsal (*mpd*) setae**, are often plumose and directed dorsally to slightly dorsodistally. The putative apicalmost *mpd* seta projects distally at its origin, is straight and resembles the apicalmost seta of the fixed finger *pdd* series (the dorsal flagellar seta, *dfs*) by being distinctly longer than the other movable finger prolateral setae (Fig. 13A, B, arrow). This seta was never observed to be plumose in the present study. The ventral setae, referred to here as **movable finger proventral (*mpv*) setae**, are ventrodistally directed at the point of origin, and may be straight, gently or markedly curved distally, but never plumose. More distally located setae in the *mpv* series present a more pronounced curvature. Between the *mpd* row lining the dorsal margin of the setose area and the *mpv*, lining this area ventrally, a narrow field of setae, referred to here as **movable finger promedial (*mpm*) setae**, is observed. Although these setae may curve dorsally, they typically project distally, or ventrodistally at the origin.

The prolateral setae on the movable finger of males generally do not exhibit the same level of modification on the fixed finger. However, in some taxa, the *mpv* setae of males become more robust and thickened towards the apex of the movable finger (Fig. 13, Pls. 110A, 111A, 118A, C, G), as on the fixed finger, where the setae become increasingly modified towards the apex (Pl. 27). Prolateral setae on the movable finger do not appear to have been used in solifuge systematics at any level, but this character system merits further exploration, as various patterns are evident. Examples include the thin, filiform, dorsally-curved tips of the distal setae of *Bdellophaga angulata* Wharton, 1981 (Pl. 87G); the two robust, ventrodistally directed subdistal *mpv* setae of male *Trichotoma michaelseni* (Pl. 87C); and the straight, ventrally directed *mpv* setae, curved only near the tips of all Galeodidae examined (Pl. 62A, E, G, I).

MOVABLE FINGER FONDAL SETAE: In addition to the setae on the pro- and retrolateral surfaces of the chelicera, a short series of plumose setae is present within the fond, where the fixed and movable fingers articulate (Pls. 2B, 12A, 13A). These setae, described here for the first time, were observed in all taxa examined and are here referred to as the movable finger fondal setae (*mff*). Fondal setae arise on the proximal margin of the movable finger, with more setae situated towards the prolateral compared to the retrolateral side. Fondal setae vary in number, plumosity, and robustness, and may therefore be of systematic importance.

PATURON DORSAL AND RETROLATERAL SURFACES: Setae on the retrolateral surface of the paturon are distinct from those on the prolateral surface, although division between series (rows) and fields of setae is less obvious (Fig. 14, Pls. 12B, 16). Dorsal setae, even those originating slightly on the prolateral surface of the chelicera (Pl. 17), show greatest structural similarity with setae situated on the retrolateral surface, with which they are therefore grouped here. A great diversity in form has been documented among these setae (Roewer, 1934: 120, fig. 101e) but understanding of their morphology or function is far from complete. Although relatively homogeneous in females, **retrolateral setae** are typically more diverse and robust in males (e.g., Roewer, 1934: 122; Lawrence, 1961: 156, fig. 1b; Martins et al., 2004; Peretti and Willemart, 2007; Hrušková-Martišová et al. 2010a), especially along the dorsodistal surface of the chelicera (cf. males in Pl. 16A, C with females in Pl. 16B, D). Based on similarities in shape, robustness, and directionality, the retrolateral setae may be divided into the **retrolateral manus (*rlm*) setae**, and the **retrolateral finger (*rlf*) setae**.

The *rlm* setae are relatively uniform in females, whereas these comprise different types of setae, usually including robust, spiniform setae (Kraepelin, 1908a) directed more or less perpendicular to the cheliceral surface, in males. The *rlm* setae become increasingly robust and sclerotized from proximoventral to dorsodistal. Distinct differentiation of single *rlm* setae is observed only in male Gylippinae in the form of the retrolateral manus spiniform seta (*rlms*), a very robust seta, the *Mandibulardorn* of Birula (1913) which was considered part of the male flagellar complex (Pls. 85B, 86B). Another pattern often observed in males is when the dorsal setae, particularly those situated slightly prolaterally, are arranged in a row along the prodorsal edge of the chelicera, curving proximoventrally near the proximal border of the chelicera (Pl. 17).

The *rlf* setae are more homogeneous and characteristic in shape, position and directionality in both sexes and all life stages of Solifugae than the *rlm* setae, and comprise several long, thin, distally directed setae, typically extending beyond the tips of the fingers (Fig. 14, Pl. 16). As with setae on the prolateral surface of the fingers, the *rlf* setae are arranged in three or four series (rows) along the margins of the asetose areas, with setae regularly spaced within them. Setae in the row closest to the teeth, i.e. along the asetose area of the cutting surface, are more closely spaced, shorter and less robust than those situated more proximally. One or two dorsal *rlf* setae are distinctly differentiated in male *Blossia* Simon, 1880 (Daesiidae), with or without spicules (Fig. 14, Pls. 144, 145, arrows; Lawrence, 1972, 116, fig. 6b, c), and commonly referred to as "principal setae." Lawrence (1963) cited the presence of "principal setae" as a diagnostic character by means of which *Blossia* may be distinguished from *Biton*. Lawrence's (1963) character may be redescribed as different states of the *rlf* setae, i.e. *Blossia* possesses one to three modified (more robust, often spiculate) dorsal *rlf* setae whereas the *rlf* setae in *Biton* are unmodified. These setae were also described in other taxa, e.g., as two distinctly elongated setae in Galeodidae (Pl. 16A, arrows; Lawrence, 1954: 118), but their homology with the modified *rlf* setae of *Blossia* was previously unrecognized. Modified, dorsally located *rlf* setae are here termed **principal retrolateral finger (*principal rlf*) setae** (see Appendix 2 for other historical uses of principal setae), with varying levels of modification among different taxa.

MOVABLE FINGER RETROLATERAL SURFACE: The retrolateral proximal cluster of setae (*rlpc*) is a clump of setae, first identified by Muma (1985) and termed the ECCS, situated proximal to the asetose area at the base of the movable finger (Fig. 15, Pls. 18, 19). An *rlpc* is typically comprised of a dorsal weakly plumose to striated seta, and a ventral longitudinal cluster of acuminate setae, but with various apparently taxon-specific modifications. Few studies have illustrated the *rlpc* (Brookhart and Muma, 1987; Muma 1987, 1989; Vázquez 1990; Vázquez and Gavico-Rojas, 2000). Brookhart and Cushing (2004) mentioned investigating its potential taxonomic utility, but considered the *rlpc* setae of no value for the taxonomy of the *scaber* group of *Eremobates*. The present study identified some family level variation in setal morphology and position relative to the proximal end of the movable finger granulation, and marked interfamilial variation in the shape of the setose area on which the *rlpc* setae are situated (Pls. 18, 19). Examples of the shape of the setose area range from being divided into two areas, a medial triangular area in addition to a narrow proximoventral area (Rhagodidae, Galeodidae, Eremobatidae; Pl. 18A–F), to fusion of the medial and proximoventral areas to form a continuous setose region proximally on the movable finger, either retaining indications of the medial asetose division (e.g., Ceromidae, Daesiidae, Gylippinae, Solpugidae; Pls. 18G, H, K, L, 19A, B, E, F) or without an indication of medial area (e.g., Ammotrechidae, Mummuciidae, Namibesiinae, Lipophaginae; Pls. 18I, J, 19C, D, I–L). Muma (1985) identified up to four types of setae in the Eremobatidae *rlpc* but suggested that a survey may identify more. The significance of the *rlpc* for solifuge systematics merits detailed examination and will probably provide informative characters above the species level.

FUNCTIONAL MORPHOLOGY: Sexual dimorphism in the cheliceral setae is extensive but mostly unexplored. The setae of solifuges are in general more strongly developed in males than females, except for most prolateral setae, for which the opposite is true (Hewitt, 1919b: 10). Although the arrangement of prolateral setae is similar in both sexes, the individual setae are more or less differentiated between them. The prolateral setae of males are differentiated only on the distal or dorsodistal parts of the chelicera, and include the flagellum, an example of extreme setal modification in solifuges. The *pvd* and *pvsd* setae are more numerous and strongly plumose in females than males, as exemplified by Hexisopodidae, in which the plumose setae are well developed in females and absent in males of all species examined. Plumose setae are probably associated with feeding, which would explain their increased plumosity and greater density in females, which seem to eat more readily than males (e.g., Wharton, 1987). With few exceptions (cf. male in Pl. 50A, with female in Pl. 50C), the setal comb of the *pvsd* series was not found to be sexually dimorphic. The stridulatory setae, probably serving a defensive function (see section on Stridulatory Apparatus), are also similar in both sexes.

Some of the most extensive and even less studied sexual dimorphism observed among the cheliceral setae concerns the setae situated dorsally to retrolaterally on the finger (Pl. 16). The precise functions of the modified dorsal setae of male solifuges remain unknown, but they presumably play a role in mating (Table 2). Based on observations that these setae are located on the part of the chelicera that comes into close contact with the female's genital area during mating (e.g., Peretti and Willemart, 2007; Hrušková-Martišová et al., 2010a), these setae may collect chemo- or mechanoreceptory cues from the female. Another possible function of the dorsal setae, first suggested by Pocock (1895), may be to protect the flagellum. The arrangement of the dorsal setae indeed appears to be optimal for protecting some types of flagella such as those of Ceromidae (Pl. 91E, F), *Hemiblossia* Kraepelin, 1899 (Daesiidae, Pl. 139G, H), and Galeodidae (Pl. 59A–D). However, even if these setae might serve a protection function in some taxa, it is unlikely to be the only function of these setae.

In conclusion, male solifuges exhibit greater differentiation among the setae of the retrolateral and dorsal cheliceral surfaces, and the apices of the prolateral surfaces of the cheliceral fingers, but less differentiation (or a similar level of differentiation to the female) among the setae on the prolateral cheliceral surfaces. The opposite is true of females (Hewitt, 1919b). This structural difference implies a functional division between the prolateral surfaces of the chelicera used primarily for feeding (and secondarily, in at least some taxa, for defense), and the dorsal and retrolateral surfaces of the chelicera and prolateral apices of the fingers, which are modified for mating. Finally, immatures generally exhibit fewer setae, arranged in a more orderly pattern, than adults (Hewitt, 1919b: 10).

TAXONOMIC DIVERSITY OF CHELICERAL SHAPES, PROCESSES AND CHAETOTAXY

AMMOTRECHIDAE: Ammotrechid male chelicerae range from slender and relatively unmodified (Pl. 146) to highgly modified, some relatively robust. Most ammotrechid cheliceral modifications concern the mucra of the fixed and/or movable fingers, especially prominent in *Pseudocleobis* Pocock, 1900 (e.g., Pl. 146A, B; Maury, 1976: 96, figs. 13, 14, 18, 19, 21, 22; 1980b: 42, figs. 1–4). A medial notch is present in some species (Fig. 7D). Hornlike processes and **dorsal cheliceral spines** are absent. A pronounced angular process on the fixed finger of females, here referred to as a dorsal crest (Muma, 1951: 126, figs. 273–4; Maury, 1982: 141, figs. 36, 44), similar to that in some female Mummuciidae and here referred to as a dorsal crest, is common in Ammotrechidae. The crest in females is unusual among Solifugae in which females are usually more conserved in cheliceral shape than males.

CEROMIDAE: In typical ceromid male chelicerae, the fixed finger is shorter than the movable finger (except for *Ceroma inerme* Purcell, 1899) and a prolateral flange is situated parallel to the movable finger medial (MM) tooth (see section on Dentition) (Pls. 91–95). No other processes or flanges are present. The chelicerae of *Toreus* are highly modified and appear to be unlike other ceromids. Purcell's (1899: 400) description of the dorsal finger of *Toreus* as "divided into two portions" is reminiscent of *Trichotoma michaelseni*, which possesses a hornlike process fused dorsally to the fixed finger (Pls. 87A, C, 88C). However, the phylogenetic placement and even the sex of the holotype of *Toreus* are uncertain (Appendix 1; Lawrence, 1962c; Muma, 1976; Wharton, 1981).

DAESIIDAE: Daesiid male chelicerae display diverse shapes, from relatively unmodified, to bizarre modifications such as the extremely elongated fixed finger of *Ceratobiton styloceros* (Kraepelin, 1899) (Pl. 137D), and the chelicera seemingly adapted for burrowing in *Gnosippus klunzingeri* Karsch 1880 (Pls. 136C, D, 137A, B). In the latter, the *rlf* setae are short, stout and spiniform, creating a rostrum-like distal finger apparatus.

Various daesiids also exhibit cheliceral processes such as the pronounced **dorsal hornlike process** (spine) of *Ammotrechelis goetschi* Roewer, 1934 (Pls. 132F, 134A) or the short dorsal distally directed spine of various shapes as in *Biton* (*B.*) *gariesensis* (Lawrence, 1931) (Lawrence, 1931: 134, fig. 3A, B) and *Blossia echinata* Purcell, 1903 (see Purcell, 1903b: pl.1, fig. 9); a rugged retroventral lamina at the apex of the fixed finger, e.g., *Biton* (*B.*) *cataractus* Lawrence, 1968 (Lawrence, 1968: 72, fig. 4c) and *Blossia hessei* Lawrence, 1929 (Lawrence, 1929: 174, fig. 16); a marked concavity in the ventral tip of the fixed finger apparently to accommodate the distal tooth (DT) of the movable finger, e.g., *Biton* (*B*)*. ehrenbergi* Karsch, 1880 (Roewer 1934: 389, fig. 275b1, b2; El-Hennawy, 1998); and a large, concave medial tooth on the movable finger (MM) to accommodate the fixed finger medial (FM) tooth, e.g., *B.* (*B.*) *truncatidens* Lawrence, 1954 (Pl. 137C). The apices of the fixed and movable fingers of male *Namibesia pallida* are markedly concave and twisted. A broad flange which appears to be a prolaterally displaced cutting edge, situated prodistally on the fixed finger, and approximately perpendicular to the prolateral surface of the finger, forms a ventral concavity (Pls. 132A, 133A). Flanges and toothlike structures on the cutting edges of the fingers of *Blossia* are described elsewhere (see section on Dentition). The fixed finger is straight and narrow, resembling the mostly stylet-like fixed fingers of Eremobatidae, in several species of *Biton*, e.g., *Biton* (*B.*) *kraekolbei* Wharton, 1981 (Wharton, 1981: 15, fig. 8; Roewer, 1934: 389, figs. 275 $a_{1,}$ $f_{1,}$ g, h_1). As in Eremobatidae, this shape is accompanied by a reduction in the dentition, especially distally, on the fixed finger. The relatively short finger with a straight dorsal margin is a common pattern in southern African *Biton* and *Eberlanzia* Roewer, 1941 (Pl. 143). The prodorsal proximal series of setae vary from weakly to well differentiated.

EREMOBATIDAE: Eremobatid males display some of the most highly modified chelicerae among Solifugae, including a cheliceral manus that is narrowed proximally, becoming wider distally in most species. A typical eremobatid male fixed finger possesses a vertical fond with unusually well developed fondal teeth, distal to which the finger narrows abruptly into a toothless or nearly toothless, narrow, stylet (males in Pls. 65, 67, 68). A characteristic of Eremobatidae is the presence of a notch proximal to the FP (Fig. 7A, B), termed the fondal notch (FN) by Muma (1951), and used extensively in eremobatid taxonomy. The notch is usually well developed, especially in species with a narrow fixed finger (Pls. 65–68). Deviations from this distinct stylet shape are usually associated with a shorter and/or less vertical fond and a weak to absent fondal notch as in, e.g., *Eremochelis* Roewer, 1934 (Pl. 76) and *Hemerotrecha* Banks 1903 (Pls. 79, 82).

The stylet-like fixed finger of eremobatid males varies from straight to curved, the latter resulting in a slight upturn or **fixed finger crimp**, e.g., in *Eremobates corpink* Brookhart and Cushing, 2004 (Pl. 67A, B). Brookhart and Cushing (2004) noted a positive correlation between the degree of curvature and the depth of the fondal notch in the *scaber* group of *Eremobates*. A retrodorsal process (RDP) (ectodorsal process of Muma, 1951) is present at the base of the fixed finger in the *palpisetulosus* group of *Eremobates*, and varies from a low peaked ridge, barely distinguishable from the dorsal margin of the finger, e.g., in *Eremobates palpisetulosus* Fichter, 1940 (Pls. 68D, 69D) to a tall, flange-like process, e.g., in *Eremobates tuberculatus* (Kraepelin, 1899) (Pls. 68J, 69F).

The **flagellar groove** is a longitudinal prolateral groove associated with the cryptic eremobatid flagellum (Pls. 38, 39A–E, H). Variation in length (extending along the entire finger or restricted to the distal part), and shape (distinct or indistinct crease-like or cup-like concavity) is significant for the taxonomy of genera and species groups (Muma, 1951:39; Brookhart and Brookhart, 2006), e.g., widening of the base of the flagellar groove into a cup-like enlarged proximal concavity (Pl. 39B) in the *pallipes* group of *Eremobates* (*vide* Muma, 1951). Brookhart and Muma (1981: 287, 288) noted “subtle” differences among populations in the “length, width, and pitch” of the basal flange of the groove, and found these useful in separating species in combination with other characters. An oval, proventral to retroventral, well-defined cuplike concavity on the asetose area of the fixed finger of male Eremobatidae, e.g., *Eremocosta* Roewer, 1934 (Pls. 73B), is referred to here as a **ventrodistal concavity** (Pl. 37C).

Prodorsal proximal (*pdp*) setae are often very pronounced in Eremobatidae, sometimes with enlarged sockets, and an additional, more weakly developed row of setae is often situated ventral to the primary row (Pl. 73A). In addition to the "typical" eremobatid cheliceral shape, enlarged *pdp* sockets are shared by some eremobatids and the gylippines examined (Pls. 12A, 85A, C, E). Eremobatid stridulatory setae are unique in being inserted on swollen, elevated sockets, unlike the modified stridulatory setae of other taxa in which the setal bases are swollen (Pl. 11E).

GALEODIDAE: The shape of the galeodid male chelicera is relatively conserved, with modification restricted to the mucra (males in Pls. 59, 62). A small, prolateral circular blemish usually on a slight, toothlike, elevation is situated on the prolateral surface of the fixed finger near the base of the mucron (Pl. 60A). It was observed in all specimens examined and is referred to here as the **mucron organ**. A similar structure is present in Solpugidae (Pl. 27E), and Mummuciidae (Botero-Trujillo, personal commun.). No distinct processes or flanges are present on the chelicera of Galeodidae. At rest, the flagellum is surrounded by numerous erect spiniform setae on the fixed finger (Pocock, 1895) (Pl. 30G). These are similar to, but longer and more robust than the apically truncated cylindrical setae often found on the pedipalps. At least three types of stirulatory setae identified in galeodids (Fig. 9A–C, Pl. 11G–I).

GYLIPPIDAE (GYLIPPINAE): The chelicera of a typical male gylippine (Pls. 85A, B, 86A, B) resembles that of a male eremobatid with a more vertical fond, reduced dentition on a stylet-like distal half of the fixed finger, and a cheliceral manus that is narrowed proximally, becoming wider distally. The fixed finger narrows abruptly and remains stylet-like until the apex. The median series teeth are highly reduced, at most vestigial, and the fond usually vertical. (Pls. 12A, 85A, C, E). Additional structures on the prolateral surface of the male chelicera, the **dental papillae**, occur on the sclerotized area adjacent to the cutting edge of the fixed finger, at the base of the teeth in *G*. (*Anoplogylippus*) species. Unfortunately no species of this subgenus was available in the current study. The presence and number of dental papillae varies interspecifically (Birula, 1938: 93, 96, figs. 64, 61). Prominent swollen sockets of the prodorsal proximal (*pdp*) setae present in specimens examined (Pls. 8D, 12A, 85A, C, E) are similar to those of some eremobatids.

In addition to a very robust *rlm* seta in males, a group of *rlm* setae are distinctly spiniform (Pl. 85B) and treated by various authors as presumably unique in Gylippinae. These are referred to as *Spina accessoriae* by Roewer (1934: 308) and *Nebendornen* by Birula (1913: 332) who also referred to the spiniform setae associated with the galeodid flagellar complex (*fcs*) as *Nebendornen*. These “accessory spines” are probable homologs of the *rlm* setae, with similar examples of increased robustness observed in other families, e.g., Eremobatidae (Pl. 76F), Galeodidae (Pl. 62 H), and Solpugidae (Pl. 121B), and are thus not considered unique to gylippines, but as regular *rlm* setae with a strong spiniform character.

GYLIPPIDAE (LIPOPHAGINAE): The mucron of the movable finger is markedly curved dorsally in male *Lipophaga* Purcell, 1903 and *Trichotoma* Lawrence, 1968, and angulate in *Bdellophaga* Wharton, 1981 (Pls. 85G, H, 38). These mucra are deeply concave dorsally, i.e., on the cutting edge (Wharton, 1981), especially in *Trichotoma*, and this concavity is more pronounced in males than females (Pl. 87). No cuticular processes are present in Lipophaginae, except for an unusual structure, hypothesized to be a dorsal hornlike process that is fused to the dorsal finger in *Trichotoma michaelseni* (see Taxon Survey under section on Dentition).

HEXISOPODIDAE: Hexisopodid chelicerae are compact and robust in both sexes, presumably an adaptation to the exclusively fossorial existence of these solifuges (Pls. 126–130). The cheliceral fingers of hexisopodids are sexually dimorphic in shape, being more slender in males. In females, the base of the movable finger, along the granulation row, forms a blunt, angular, and longitudinal retrolateral elevation (retrolateral carina) which accommodates the base of the fixed finger (Pl. 126F–H). Similar, but more angular and less granular retrolateral carinae are present in *Dinorhax* (at least in males; Pls. 56B, 57B) and Rhagodidae (both sexes; Pl. 56D, F, H). The granular row is more densely granular below the movable finger medial (MM) tooth in females (Pl. 126F). Prominent, randomly spaced granules, in addition to the regular granular row, are also more distinct in females.

The asetose area on the fixed finger of both sexes is modified to form a lobate, sclerotized area, termed the callus (Fig. 6A; Lamoral, 1973; Wharton, 1981). The number of tubercles on the callus has been used in species diagnosis (e.g., Lawrence, 1949b; Lamoral, 1973). Tubercles on the callus may vary in size (Wharton, 1981: 52), perhaps due to wear. A well developed, longitudinal flange-like carina at the apex of the fixed finger, usually terminating in a sharp point distally, occurs in some species (Pl. 127B; Lawrence 1967: 14, fig. 7a–c), creating the unusual shape of the fixed finger in dorsal view (Fig. 6A). This carina is not considered homologous to the prodorsal flange-like carina, or the **flagellar groove process** (FGP) of Solpugidae, associated with the flagellar groove which accommodates the base of the **flagellar shaft** (see discussion on Solpugidae). Wharton (1981: 52) reported “shape of flange either variable, or subject to considerable wear.”

A small field of short, stout spiniform setae (prodorsal cluster of spiniform setae, *pdcs*) is present on the prodorsal surface of the chelicera, directly ventral to the callus and proximal to the sclerotized area of the fixed finger, in some male *Chelypus* (Pls. 32C, 130D; Hewitt, 1919b; Lamoral, 1973). The propeltidium and dorsal surfaces of the chelicerae of *Chelypus hirsti* Hewitt, 1915 are randomly covered with globular setae which have not been observed in other families (129D, E; Lawrence, 1949b; Lamoral 1973: 97, fig. 7c). Plumose setae appear to be absent on the chelicerae of male Hexisopodidae.

The unusual case of *Siloanea* Roewer, 1933 merits discussion in the context of hexisopodid cheliceral modifications. *Siloanea* was established by Roewer (1934: 339) based on several non-cheliceral characters exhibited by the holotype of *Siloanea macroceras* Roewer, 1933 (currently placed in *Chelypus*), the sex of which was uncertain. Roewer (1934) identified the holotype of *Siloanea eberlanzi* Roewer, 1941, the second species of the genus to be described, as an adult male. No flagellum is present in either specimen. However, the chelicerae of both display one or more hornlike processes dorsally on the fixed finger. Lawrence (1966: 6, fig. 3d) argued that the holotypes of *Siloanea* are merely female specimens of *Chelypus*, none of which had ever been described, and described a specimen with cuticular hornlike processes, showing close affinities with *Siloanea*, as the female holotype of *Chelypus coatoni* Lawrence, 1966 (currently in synonymy with *Chelypus lennoxae* Hewitt, 1912). Lamoral (1973) disagreed with Lawrence (1966), re-identified the holotype of *Chelypus coatoni* as a male, transferred this species to *Siloanea*, and revalidated the latter. Wharton (1981) agreed with Lawrence (1966), however, and officially synonymized *Siloanea* with *Chelypus*, proposing *Chelypus lawrencei* Wharton, 1981 as a replacement name for *Siloanea eberlanzi*, a junior secondary homonym of *Chelypus eberlanzi* Roewer, 1941.

Although the strong hornlike processes are unusual for female solifuges, the well-developed dentition (Lawrence, 1966: 6, fig. 3d), plumosity of the proventral distal setae (*pvd*), and presence of two malleoli (e.g., Lawrence, 1966) are typical characters of female Hexisopodidae. Assuming the three holotypes are indeed female, as the absence of a flagellum suggests, these species represent a rare case in which the female chelicera is modified.

KARSCHIIDAE: Male Karschiidae possess a low prolateral flange approximately parallel or distal to the medial tooth (MM) on the movable finger, creating a small trough-like concavity (“spoonshaped excavation” *sensu* Lawrence, 1954: 112). This structure may serve to protect the flagellum (Fig. 16). The dorsal mucron in both sexes of *Eusimonia* is sinuous and curved ventrally (Birula, 1938; Gromov, 2000) (Pl. 53). The fixed finger of male *Karschia* commonly exhibits a relatively straight dorsal margin, with a markedly angular ventrodistal bend in the mucron, and an almost vertical fondal area (Pls. 50B, F, 52A; Birula, 1938: fig. 20, 25; Gromov, 1998: fig. 1j) resembling that of male Eremobatidae. A small dorsoproximal toothlike protuberance (spine) occurs in some *Karschia* males (*r* and *rh sensu* Birula, 1938) and a distally directed hornlike process occurs in males of all but one species of *Eusimonia* (e.g., *rh sensu* Birula, 1938; Muma, 1982; Gromov, 2000).

The prolateral setae of Karschiidae differ from those of other Solifugae in differentiation and position. The comb of *pvsd* setae is weakly differentiated in female *Karschia* (Pl. 50C) and both sexes of *Eusimonia* (Pl. 53). The comb is often located more dorsally and arranged horizontally, rather than the typical medial position and vertical arrangement observed in most Solifugae (e.g., Pls. 52B, 54A). The various apical series of the fixed finger (*pvsd*, *pdd*, and *pm*) are not readily distinguished (e.g., Pl. 53) and the *pvd* setae greatly reduced in males (Pl. 53A, C, G).

MELANOBLOSSIIDAE (DINORHAXINAE): The cheliceral shape of *Dinorhax* Simon, 1879 with its low aspect ratio (cheliceral length / cheliceral height) resembles the chelicerae of Rhagodidae, in which *Dinorhax* was originally placed by Simon (1879a), and Hexisopodidae. The cheliceral similarity, together with the short, robust legs, are consistent with a fossorial habitus, but no life history data are available for *Dinorhax* to confirm that. The dorsal mucron is angular, pointing ventrodistally (Pls. 56A, B, 57A, B). The movable finger possesses a blunt, angular, and longitudinal retrolateral surface (retrolatral carina) into which the rounded proximal margin of the fixed finger closes (Pls. 56B, 57B), as in female and immature Rhagodidae (Pl. 56D, F, H) and a similar carina in female and immature Hexisopodidae (Pl. 126F–H).

MELANOBLOSSIIDAE (MELANOBLOSSIINAE): The chelicerae of Melanoblossiinae are long and slender in both sexes. Males possess a prolateral concavity which accommodates the setiform flagellar complex, here termed the **flagellar complex depression** (Fig. 26C, Pl. 36G–I). The ventral location of the flagellar complex creates a

medioventral excrescence (MVE) in the fixed finger which may be weak (Pl. 158C) or pronounced (Pls. 156B). Modified setae are absent on the melanoblossiine chelicera except for the setae comprising the setiform flagellar complex. Processes and flanges are also usually absent, except for an undescribed *Melanoblossia* Purcell, 1903 species with elaborate modifications distally on the fixed finger (Fig. 6B; Pls. 154G, H, 157).

MUMMUCIIDAE: Mummuciid chelicerae are fairly conserved, differing little in shape between the sexes (Pls. 149E–H, 151, 152). The most prominent modifications in the male chelicerae concern the flagellar groove, formed by prodorsal ("dorsal keel" of Botero-Trujillo, 2014: 325, fig. 16) and prolateral flange-like carinae on the fixed finger, which accommodates the flagellum (e.g., Carvalho et al., 2010: 25, figs. 13, 15, 16; Botero-Trujillo, 2014: 325, figs. 13, 15). These are here referred to as the **prodorsal carina** and **proventral carina** respectively (Pls. 34G, H, 35H, I). A low but distinct dorsal crest (carina) is present on the fixed finger of females approximately dorsal to the fixed finger distal (FD) and fixed finger medial (FM) teeth ("dorsal hump" of Iuri et al. 2014: 21; see also Botero-Trujillo, 2014: 321, 325, figs. 11, 17). A dorsal crest situated approximately opposite to the widest part of the flagellum and which forms part of the prodorsal carina (Pl. 149E, G), is also present on the fixed finger of some males, but less pronounced than in females (see Botero-Trujillo, 2014: 321, 325, fig. 16). Botero-Tujilo (personal commun.) observed structures similar to the mucron organ in Galeodidae and Solpugidae in female and juvenile mummuciids, but noted that these do not show well in scanning electron micrographs. Other modifications concern, at most, the shape of the mucra of the fingers, particularly the fixed finger.

RHAGODIDAE: Rhagodid chelicerae are robust and compact in both sexes, being slightly more slender in males (Pls. 56C–H, 57C, D, 58). A blunt, angular retrolateral surface (retrolateral carina), into which the rounded proximal margin of the fixed finger closes (Pl. 56D, F, H), is observed in both sexes, and is similar to that observed in *Dinorhax* (at least males; Pls. 56B, 57B) and female and immature Hexisopodidae (Pl. 126F–H).

Distinct macrostructures (flanges, cheliceral processes, etc.) are absent. Prodorsal setae are exceptionally robust and pronounced in most species. Stridulatory setae are similar to the Type II (*araneoides*-type) of Galeodidae (Fig. 9D, Pl. 11F), and apparently not restricted to the field between the stridulatory plate and the *pvsd* setal comb, but extend dorsal to the stridulatory plate.

SOLPUGIDAE: *Solpugema* is partly characterized by a medial notch (Fig. 7C) which is not considered homologous to the fondal notch of Eremobatidae (Fig. 7A, B). The medial notch may be strongly curved, e.g., in *S. derbiana* (Pocock, 1895) (Pl. 108F) to sublinear, e.g., *S. brachyceras* (Lawrence, 1931) (Pl. 108D). Although Roewer (1934: 466) identified the medial notch as a diagnostic character for *Solpugema*, the length of the toothless gap varies, and there is some overlap between its length in *Solpugema* and other genera. For example, the short, shallow notch of *Solpugema hamata* (Hewitt, 1914) (Pl. 106J; Hewitt, 1914b: 160, fig. 22) is not significantly different from that in *Solpugista hastata* (Pl. 110I; Kraepelin, 1901: 59, fig. 15) or *Solpuga chelicornis* Lichtenstein, 1796 (Pl. 102B, E).

The diversity of cuticular modifications associated with the tip of the male cheliceral fixed finger of Solpugidae rivals that of all other solifuge families (Pl. 20). These modifications include toothlike processes, carinae and flanges, while the mucron may also be distinctly modified. The structures appear to be associated with the insertion of the flagellar shaft into a furrow, the flagellar groove, in the fixed finger, and are referred to here as the flagellar groove processes (FGP). These structures form through a distal extension of the prolateral rim of the flagellar groove, and may be modified to form a weakly elevated carina as in *Zeria carli* (Roewer, 1933) (Pl. 20B) and *Zeria venator* (Pocock, 1897) (Pl. 20C); a long, smooth flange-like carina as in *Solpugiba lineata* (C.L. Koch, 1842) (Pl. 111A), *Solpuga chelicornis* (Pl. 20D), and *Oparba asiatica* (Turk, 1948) (Pl. 27E); a short, markedly curved carina as in *Solpugema derbiana* (Pocock, 1895) (Pl. 108E) and *Solpugema hamata* (Pls. 20G, 106I); a jagged, toothlike carina situated dorsally as in *Solpugema intermedia* (Lawrence, 1929) (Pl. 109F) and *Solpugema montana* (Lawrence, 1929) (Pl. 109E); or a jagged, ridgelike carina situated prodorsally as in *Solpugema brachyceras* (Lawrence, 1931) (Pls. 20H, 108C), *Solpugema genucornis* (Lawrece, 1935) (Pl. 20F), and *Solpugista bicolor* (Lawrence, 1953) (Pl. 20E). Even in the absence of a distinct FGP, a mucron organ (Pl. 20A), often situated on a toothlike structure (e.g., Fig. 24B, insert), is present. Pocock (1897: 264) described the medially pointed toothlike process situated prolaterally on the apex of the finger of *Solpugassa dentatidens* (Simon, 1879) as *Solpuga dentatidens* and *Zeria ferox* (Pocock, 1895) as *Solpuga ferox,* as a supernumerary tooth and hypothesized that it functions to stop the closure of the movable (ventral) finger. The flagellar groove processes (FGP) of male Solpugidae are used extensively for species diagnosis in the family (e.g., Pocock, 1897; Lawrence, 1951). The extent of intraspecific variation in these structures has never been evaluated, however, and there is some evidence that such variation exists. For example, according to Simonetta and Delle Cave (1968), prolateral “tubercles” (apparent toothlike flagellar groove process, FGP) were present in some but not all specimens of *Zeriassa lepida* Kraepelin, 1913 (*N* = 9) examined.

The prodorsal proximal setae (*pdp*) are weakly differentiated in Solpugidae, and the promedial setae (*pm*) are not modified into stridulatory setae.

SUMMARY OF GENERAL CHELICERAL MORPHOLOGY

The two-segmented solifuge chelicera comprises a paturon (manus plus fixed (dorsal) finger), that articulates with the movable (ventral) finger, and is surprisingly rich in morphological characters. Little evidence of sexual dimorphism exists in characters such as granulation on the asetose areas of the fingers, and development of stridulatory ridges and stridulatory setae. If sexual dimorphism is present, however, these characters are often more developed in females than males, which suggests non-reproductive functions such as feeding and defense.

Males have more gracile chelicerae than females, with a higher aspect ratio, likely due to reduced feeding, but differences in the shape of the male fixed finger appear more related to reproduction. Similarly, processes such as carinae, flanges, and hornlike structures are absent in females, but may be diverse in males of some families, especially Solpugidae. The mucron organ (mo) in Galeodidae and Solpugidae is, however, present in both sexes, and may be situated on a slight to prominent toothlike elevation.

The rich chaetotaxy of solifuges is also extended to the chelicera, but the retrolateral and prolateral setae on the chelicera are notably different in morphology and arrangement. Setal modifications in males compared to females indicate regional specialization on the chelicera associated with different functions. Retrolateral setae, particularly retrolateral manus setae, are more randomly distributed, whereas prolateral setae are arranged in distinct, recognizable series and setal fields. Bifid setae, common and pronounced in solifuges, appear to be absent on the prolateral surface of the chelicera whereas plumose setae are restricted to the prolateral surface. Most modifications in male setae concern the retrolateral manus (*rlm*) setae and prolateral setae towards the apices of the fingers, especially the fixed finger. In females, setae in these regions of the chelicera tend to be largely homogeneous.

The chelicerae of solifuges are unique among arachnids because they play a prominent role during mating behavior and sperm transfer, in addition to a suite of other functions such as feeding, defense and burrowing. This is reflected not only in the richness of characters on the chelicera, but also in the regional specialization of these characters on the chelicera.

DENTITION

HISTORICAL PERSPECTIVE AND BACKGROUND

The dentition pattern refers to the size, shape, position and number of teeth on the cheliceral fingers of Solifugae (Pls. 21, 22). Dufour (1861: 350) was the first to formally distinguish different types of teeth. Based on a male *Oparbella aciculata* (Simon, 1879) and a female *Galeodes olivieri* Simon, 1879 (both as *Galeodes dastuguei* Dufour, 1861) Dufour (1861) termed the larger teeth “canines,” the smaller teeth between them, “incisors,” and the two rows of basal teeth on the fixed finger, “molars.” Dufour (1861) regarded 16 teeth per chelicera (6 incisors, 4 canines and 6 molars) as typical for solifuges. Pocock (1889) referred to the large proximal tooth on the movable finger as the principal tooth.

Kraepelin (1899, 1901) proposed the first comprehensive formal terminology for the cheliceral dentition of Solifugae, and applied it to the diagnosis of species except those with highly modified dentition, e.g., *Ceratobiton styloceros* currently in synonymy with *Gnosippus*. Kraepelin (1901: 101) referred to the two large distal teeth and any smaller teeth between them, as *Vorderzahne* (“front teeth”), the large, proximal tooth, the *Hauptzahn* (“main” or “principal tooth”), the smaller teeth between them, the *Zwissenzähne* (“intermediate teeth”), and the two diverging rows of small teeth at the base of the fixed finger, the *Wangenzähne* (“cheek teeth”). Kraepelin (1901: 99, 1908b: 277) referred interchangeably to two principal teeth (similar terminology was applied by Pocock, 1900a) or to a principal and an anterior tooth on the movable finger. Kraepelin

(1901) supplemented terminology with a numbering system to specify the relative positions of teeth within the series, permitting the dentition to be more precisely defined, e.g., *4. Hauptzahn* implied that the primary tooth is the fourth from the tip of the fixed (dorsal) finger.

Except for the numbering, Kraepelin's (1899, 1901) terminology continued to be followed exactly (e.g., Roewer, 1934: 53; Kraus, 1956; Panouse, 1956, 1960a, b; Simonetta and Delle Cave, 1968; Armas 1994) or with some modifications. Early South American workers used "basal teeth" for cheek teeth (Mello-Leitão, 1938; Maury, 1970, 1984; Armas, 2002) whereas Muma (1951: 38, fig. 5), followed by other North American workers, used "fondal teeth" for cheek teeth and "medial tooth" for the middle primary tooth of the fixed finger. Nonetheless, a standard reference to the terminology of the cheliceral dentition remained elusive. Muma's (1951) modifications to Kraepelin's (1899, 1901) terminology are followed mainly by New World workers (e.g., Brookhart, 1965), often with further minor changes, e.g., Brookhart and Cushing (2004, 2008) and Catenazzi et al. (2009) used "primary tooth" instead of "principal tooth." Rocha and Carvalho (2006) followed Muma (1951) in the use of "fondal," but Kraepelin (1899, 1901) and Maury (e.g., 1970, 1982) in the use of "anterior teeth." Carvalho et al. (2010) followed Rocha and Carvalho (2006), and was the only recent study to refer to the small (submedial) tooth on the fixed finger as a "second principal tooth." Botero-Trujillo (2014) provided a recent, more comprehensive terminology, e.g., Fa_1 for the distalmost primary tooth, but did not distinguish between primary and **secondary teeth** among the three distalmost teeth on the fixed (dorsal) finger. His annotation of subscripts is, however, very useful to distinguish among individual secondary teeth within a category, e.g., two secondary teeth between the proximal and distal **primary teeth** on the movable finger.

Therefore, although Kraepelin's (1899, 1901) terminology and Muma's (1951) subsequent modifications represent a major step towards standardization of the terminology for dentition, the many inconsistent, often contradictory usages increased confusion and reduced communication. To this day, the absence of any synthesis of these subtle changes in terminology makes it difficult to correctly interpret or compare the dentition among solifuge taxa. Perhaps for this reason, past workers on the Old World solifuge fauna (e.g., Hirst, 1911a; Hewitt, 1919b; Birula, 1937a; Turk, 1960; Levy and Shulov, 1964; Lawrence, 1955; 1968; Wharton, 1981; Reddick et al., 2010) tend to partially or entirely ignore the terminology of Kraepelin (1899, 1901) and Muma (1951). Instead, as with earlier workers (e.g., Birula, 1890; Pocock, 1895; Pavesi, 1897; Purcell, 1903a; Mello-Leitão, 1924), these workers inferred no homology, implicit or explicit, for the cheliceral dentition, and used only general descriptions (Reddick et al., 2010), often numbering each tooth from distal to proximal, irrespective of size (e.g., Wharton, 1981). The avoidance of terminology may prevent assumptions in descriptions, but results in a loss of information about homology, and a reduction in the potential for comparison among teeth of the same or different individuals. For example, the third tooth in the median series of one species (or even an individual) is not necessarily homologous to the third tooth in another species (or individual). Other studies provide no descriptions of dentition whatsoever and refer only to figures (e.g., Lawrence, 1955, 1968; Lamoral, 1972, 1974), which may be misleading and fail to satisfactorily represent important details such as position, size and extent of sclerotization.

The absence of a standardized terminology can largely be attributed to the absence of explicit criteria for identifying the respective teeth and precisely defined terminology for their description and communication. The aims of the study of dentition presented below were to propose hypotheses of dental homology, based on objective criteria, and to revise and standardize the terminology of Kraepelin (1899, 1901) and Muma (1951) in light of these hypotheses.

TERMINOLOGY

Conserved dentition, historically referred to as "unmodified" and presumed to be plesiomorphic (Hewitt, 1919b; Wharton, 1981), refers to the pattern in Pl. 22B. These terms continue to be used in the present contribution merely to refer to a specific pattern of dentition and remain statements of primary homology. De Pinna's (1991) criteria of similarity, applied to other cheliceral characters in the present contribution, were refined for primary homology assessment of dentition (Appendix 3). "Reduced" or "absent" teeth refer to variation in the size and presence of teeth among chelicerae, and not to loss or damage by wear or deformity.

Discussions of terminology are concerned mainly with largely unmodified to weakly modified, i.e., conserved, patterns of dentition (Pl. 22). Solifuge dentition may be divided into series, i.e., a median and a fondal series on the fixed finger, and a median and prolateral series on the movable finger (Fig. 1A). Each of these may be further subdivided. The fixed finger bears a single row of median teeth, which usually comprises primary and secondary teeth, and two short converging rows of fondal teeth which, in Eremobatidae, Galeodidae, and Rhagodidae are often connected by a third, weakly developed row along the **basal fondal margin**. The movable finger bears a single row of median teeth, again comprising primary and secondary teeth. A second series consisting of a single tooth (movable finger prolateral tooth, MPL) and/or carina is present in most taxa. Muma's (1951) terminology is modified as follows: "proximal" replaces "principal"; "distal" replaces "anterior" on fixed finger; "medial" replaces "anterior" on movable finger; and "secondary teeth" replaces "intermediate teeth." "Retrolateral" and "prolateral" replace "ectal" and "mesal," respectively. "Proximal" and "distal" replace "posterior" and "anterior," respectively. "Proximal tooth" replaces "principal tooth" in order to describe its position. The distalmost tooth of the movable (ventral) finger is termed the "medial tooth," to match the medial tooth on the fixed (dorsal) finger, with which it may be considered serially homologous. "Terminal tooth" is introduced for the tip of the fingers. "Primary teeth" is introduced to refer to the three and two most prominent teeth in the median series of the fixed and movable fingers, respectively. "Secondary teeth" replaces "intermediate teeth" to complement the term "primary teeth." Additional terms, i.e., "subterminal," "subdistal," "submedial," and "subproximal," are proposed to distinguish among the secondary teeth.

MEDIAN SERIES: Two median series are recognized, each comprising a single row, usually of primary and secondary teeth, on the cutting edges of the fixed and movable fingers. Primary teeth are distinctly differentiated (larger and often more sclerotized) and comprise two teeth on the movable and three on the fixed finger (Pls. 21, 22 A–D). The primary teeth of the fixed finger comprise the proximal (FP) tooth, i.e. the "principal tooth" of Pocock (1889), Kraepelin (1899, 1901) and Muma (1951), the medial (FM) tooth, i.e. the "second" anterior tooth of Kraepelin (1899, 1901), and the distal (FD) tooth, i.e. the "first" or distalmost, "anterior tooth" of Kraepelin (1899, 1901) and the "anterior tooth" of Muma (1951). The primary teeth on the movable finger comprise the proximal (MP) tooth, i.e. the "principal tooth" of Kraepelin (1899, 1901) and Muma (1951), and the medial (MM) tooth, i.e. the "anterior tooth" of Kraepelin (1899, 1901) and Muma (1951). The tips of the fingers are the terminal teeth, i.e. the **fixed finger terminal (FT) tooth** and the **movable finger terminal (MT) tooth**. Secondary teeth, i.e. the "intermediate teeth" of Kraepelin (1899, 1901), collectively refers to the less differentiated (smaller, often less sclerotized) teeth. Three categories of secondary teeth are usually present and named based on their position relative to the primary teeth: **fixed finger subdistal (FSD)**, **fixed finger submedial (FSM)** and **movable finger submedial (MSM)** teeth, situated proximal to the FD, FM and MM respectively (Pls. 21, 22A). Multidentate taxa (see Denticles, Multidentate Condition, Supernumerary Teeth section below) often possess additional secondary teeth situated proximal to the MP, and proximal to the FT and MT (i.e. on the fixed and movable finger mucra), and are therefore referred to as the **fixed finger subterminal (FST), movable finger subproximal (MSP)**, and **movable finger subterminal (MST) teeth** respectively. In the present contribution, an operational assumption, supported by dentition patterns, was applied, according to which subproximal teeth are absent on the fixed finger (see Fondal Teeth below).

FONDAL SERIES, FIXED FINGER: Fondal teeth are situated on the fond, the slight broadening at the base of the fixed (dorsal) finger (Pls. 2A, B, 22E, F), proximal to the median series of teeth. Three rows of fondal teeth may be present (Pls. 21, 22) within the fixed finger fondal series. Two rows diverge distally (Kraepelin, 1901; Roewer, 1934:

58), i.e. the profondal (PF) teeth, corresponding to Muma's (1951) mesal row, and the retrofondal (RF) teeth, corresponding to Muma's (1951) ectal row. The basifondal (BF) teeth, situated along the basal margin of the fond, are usually minute, and present only in Eremobatidae (Pl. 84I, J), Galeodidae (Pl. 64K, L), and Rhagodidae (Pl. 64I, J). Muma (1951) numbered the fondal teeth from distal to proximal with Roman numerals (Muma, 1951: 38, fig. 5), a convention followed by Brookhart (e.g., 1965) and Brookhart and Cushing (e.g., 2002, 2004). This numbering was not intended to reflect homology, i.e. the same numerals assigned to teeth in different taxa did not imply that these teeth were homologous.

The profondal (PF) row generally comprises one to four teeth (Pls. 21, 22E, F, 23L). An additional, minute fifth tooth is occasionally present, often positioned to form a small bifid tooth at the proximal end of the PF row (Pls. 21A, 78A). Two conspicuous teeth, separated by a smaller tooth or a distinct gap, the “diastema” mentioned by Maury (1976), are usually evident in the PF row. These teeth are typically narrow and pointed apically, and are often the largest (tallest) in the fondal series. They were commonly mentioned in species diagnoses, e.g., Birula (1926: 196), Lawrence (1935a: 77), but homology across the order was previously unrecognized. These teeth are referred to here as the **profondal proximal (PFP) tooth** and **profondal medial (PFM) tooth**. If present, a tooth situated between the PFP and PFM teeth, and another one or two teeth situated proximal to the PFP tooth, are referred to as the profondal submedial (PFSM) tooth/teeth and the profondal subproximal (PFSP) tooth/teeth.

Although homologizing individual retrofondal (RF) teeth across the entire order proved challenging, probable homologs were often readily identified among putative phylogenetically related species, genera or even families (Pls. 21B, 22E, F, 23). The most prominent landmark tooth is referred to here as the **retrofondal proximal (RFP) tooth**. This tooth is situated towards the proximal end (usually subproximal) of the RF row, and can often be identified by its distinct shape (equilateral triangle with a simple, sharp point at the apex). It is also often, although not necessarily so, the largest RF tooth in the RF row. This tooth is especially distinct in size and shape in Lipophaginae (Pls. 87B, D, F, 88). By using the RFP tooth as a landmark, and by comparing dentition among taxa with distinct fondal dentition patterns, other probable homologs may be identified within the RF row (Pl. 23). In Solpugidae, for example, four or (rarely) five retrofondal teeth are the rule, often with subtle yet identifiable differences in size, and these may be identified as follows: The two largest teeth, i.e., an equilateral triangular retrofondal proximal (RFP) and a **retrofondal medial (RFM) tooth**, often separated by a smaller retrofondal submedial (RFSM) tooth, in addition to one, rarely two, proximally situated retrofondal subproximal (RFSP) tooth/teeth (e.g., Pls. 22B, E, 23Q, R, 90G–L, 103B, D). This approach may be extrapolated to other taxa, e.g., the three most prominent RF teeth of Galeodidae (Pls. 23M, N, 59, 64K, L) or even the three to four most pronounced RF teeth of Eremobatidae (Pls. 68B, D, 84). In male Eremobatidae, the RF teeth decrease in size proximally, such that the RFSM tooth is almost always larger than the RFP tooth, but its identity as an RFSM tooth is confirmed by comparison with females (cf. Pl. 78B with D), and males of different species with a more “typical” pattern (two large teeth alternating with two smaller teeth).

Teeth of the fondal series (RF row) may be difficult to distinguish from possible subproximal teeth of the median series on the fixed finger, especially when more than four teeth are present proximal to the fixed finger proximal (FP) tooth, as in Eremobatidae, Karschiidae, Mummuciidae, and Rhagodidae. Muma (1951: 38, fig. 6), and some New World workers (e.g., Brookhart and Cushing, 2004: 286, for Eremobatidae; Catenazzi et al., 2009: 154, as per their dental formula for a species of Ammotrechidae) recognized an "intermediate tooth", i.e., a fixed finger subproximal tooth in the terminology presented here, between the FP tooth and the fondal teeth. Examination of specimens indeed indicated that, in the presence of such a large number of teeth proximal to the FP tooth, some teeth situated directly proximal to the FP tooth, but on the cutting edge, are often more similar to median teeth than to fondal teeth (e.g., Pl. 67D, L). This similarity include level of sclerotization (e. g., in some species median series teeth are more sclerotized only towards the apices whereas fondal teeth are entirely more sclerotized) and/or structure (e.g., median series teeth are laterally compressed whereas fondal teeth are pyramidal in shape). The distinction is not always clear, however, and contradictory patterns may be apparent. In the present contribution, and pending further investigation, all teeth situated proximal to the FP tooth and distal to the RFM tooth are therefore regarded as part of the fondal series, referred to here as retrofondal apical (RFA) teeth. For example, Rhagodidae typically have six or seven teeth forming a curved row, proximal to the FP tooth, generally comprising four teeth (the RFSP, RFP, RFSM and RFM teeth) in the basal, curved part of the row, and three teeth on the cutting edge, aligned with and directly proximal to the FP tooth, and distal to the RFM tooth (Pl. 64I, J). The three teeth on the cutting edge are structurally more similar to teeth of the median series in being somewhat laterally compressed with a distinct median edge, unlike the uniformly rounded proximal teeth, but are as sclerotized as the four proximal teeth. The three teeth on the cutting edge are therefore also referred to as retrofondal apical (RFA) teeth. This interpretation is noteworthy as it is consistent with the absence of secondary teeth in Rhagodidae. Some retrofondal apical (RFA) teeth on the cutting edge are structurally similar to teeth of the median series, e.g., in Karschiidae (Pl. 64A–H), Mummuciidae (Pl. 153I, J), and female Eremobatidae (Pl. 84E, F), but again a consistent pattern could not be identified, and the term RFA is therefore retained. According to this hypothesis, small teeth and denticles in the fondal notch of male eremobatids are RFA teeth (Pl. 84G, H). Retrofondal apical teeth appear to be absent in, e.g., Ammotrechidae, Daesiidae, and Solpugidae (Pl. 23).

In addition, one or more small to minute teeth are often present at the proximal end of the PF and RF rows, merging with the basal fondal margin, and providing it with a serrate edge in some taxa (e.g., Muma, 1951: 39). Such apparently vestigial teeth blur the distinction between the presence or absence of proximally situated PF and RF teeth, and contribute to inflated estimates of variation in the number of fondal teeth. Panouse (1964) recognized the dilemma regarding whether or not to include denticles on the basal fondal margin within counts of the PF and RF rows, reluctantly following previous authors by excluding them. According to Panouse (1964: 51, fig. 1, 2E, E), however, the PF and RF counts would be stable among the four known species of *Othoes* Hirst, 1911, even if these teeth were included. In the present study, examination of different conspecifics usually facilitated identification of such vestigial teeth as either RFSP or PFSP teeth, or as crenulation fused with the basal fondal margin and therefore excluded from PF and RF counts.

The retrofondal (RF) row gradually merges with the median series and some workers (e.g., Birula, 1926: 192–3, fig. 1b; Lamoral, 1974: 267, fig. 1) regarded these teeth as a single unit, i.e. the “external row” or “outer teeth.”

The basifondal (BF) teeth represent a third row of vestigial teeth, applied to teeth situated on the basal fondal margin which do not form part of either the PF or RF rows (e.g., Aliev, 1985: 1101, fig. d). Basifondal teeth have been observed in Galeodidae (Pl. 64K, L; Sørensen, 1914; Roewer, 1934: 53) and Rhagodidae (Pocock, 1889; contra Roewer, 1934: 54; Pl. 64I, J), while weak BF teeth may be present in Eremobatidae (Pl. 84I, J).

Regularly arranged rows of bead-like denticles at the base of the fond (Fig. 2A, Pls. 2A, 131) constitute a potential synapomorphy for Hexisopodidae. These denticles may be homologous with the basifondal (BF) teeth as suggested by their partial merger with the basal fondal margin which resembles teeth in the BF row, or may have originated from the proximalmost PF and RF teeth which subsequently shifted medially along the fondal margin. The latter hypothesis is supported by similar patterns observed in Eremobatidae (Pl. 84I, J), Gylippinae (Pl. 90A, B), and Karschiidae (Pl. 64C, D) where the proximalmost teeth are denticle-like, often bead-like, and situated on the pro- and retrolateral ends of the basal fondal margin. Furthermore, in Hexisopodidae, (i) a larger number of bead-like denticles are present on the retrolateral surface than on the prolateral surface, as is often the case with the pro- and retrolateral fondal teeth; (ii) and “regular” fondal teeth are often absent (Pl. 131A–D). For these reasons, the bead-like denticles of Hexisopodidae are considered here to be pro- and retrofondal (PF and RF) teeth rather than basifondal (BF) teeth.

The distinction among the various fondal teeth, more obvious in some taxa than others, is critically important to evaluate variation in the fondal teeth. Similarly, the identification of homologous teeth in the PF and RF rows between taxa varies in difficulty and may, in some cases, be impossible with the data and specimens available. Hypotheses for the most typical RF patterns in major suprageneric taxa are proposed in Pl. 23. Such hypotheses were based on relative size, and level or pattern of sclerotization, and on comparison between related taxa. Detailed examination and comparison of an adequate number of specimens of related taxa is, however, necessary to test the hypotheses proposed concerning the homology of fondal teeth.

PROLATERAL SERIES, MOVABLE FINGER: A basal tooth on the prolateral surface of the movable finger (Pls. 15B, 22C), situated slightly below the movable finger primary (MP) tooth, and referred to here as the **movable finger prolateral (MPL) tooth**, was recorded in Ammotrechidae (Roewer, 1934: 54; Muma 1951; Armas 1994), Eremobatidae (Muma, 1951), Rhagodidae (Roewer, 1934: 54), and several species of Solpugidae (Lawrence, 1954; 1961; Roewer, 1934: 429; Wharton, 1981). In place of, or in addition to, an MPL tooth, a weakly to markedly developed longitudinal carina often extends proximally from the MPL tooth. The distinction between a tooth and a pronounced carina is a continuum and they are hypothesized here to represent different states of a single character. Brookhart and Muma (1981) considered the size of the prolateral tooth to be useful, in combination with other characters, for species identification.

CATEGORY-SPECIFIC SIZE GRADATION: When two or more teeth are present within a category of secondary teeth (i.e., FSM, FSD, and MSM categories), the teeth may progressively decrease in size, proximally or distally (Fig. 17, Table 6). These patterns are significant for homology assessment of secondary teeth. Different gradations in each category appear to be taxon-specific and may prove synapomorphic for some taxa, especially at the family level (Pls. 24, 25; Table 6). For example, Eremobatidae is the only family with teeth in all three categories, i.e., FSM, FSD and MSM teeth, increasing in size proximally (Pl. 24O). The only apparent deviation, rarely observed, concerns species with a larger number of teeth within a category compared to the general range of teeth in that family or subfamily, and where the larger number is due to the presence of small teeth, usually denticles, between the secondary teeth, e.g., three small teeth interspersed in the FSM row in *Solpugiba lineata* (Pls. 110B, 111B), and a minute third denticle between two larger FSD teeth in *Horribates bantai* Muma, 1989 (Pl. 78D). These denticles are, in general, the most labile of all teeth in size and presence/absence.

DENTICLES, MULTIDENTATE CONDITION, SUPERNUMERARY TEETH: The terms “denticles,” “multidentate,” and “supernumerary” are commonly encountered but inconsistently applied in the literature. “Denticle” has been used as a synonym for “tooth” (primary, secondary and fondal teeth; Birula, 1926), to describe the small teeth typical of the multidentate condition (Wharton, 1981), e.g., in *Lawrencega* Roewer, 1933, or to describe very minute, often intraspecifically variable teeth, as used here. For example, the movable finger of the male *Lawrencega procera* Wharton, 1981 (Pl. 154I, J) possesses a row of minute teeth (i.e., denticles) distal to a row of small, similar teeth, not denticles. Most denticles are secondary or fondal teeth.

“Multidentate,” subjectively applied in the literature, is defined here in accordance with the most common usage, to describe a pattern of dentition characterized by a row of small, similar, equally spaced teeth in the median series, with relatively homogeneous teeth in the median and retrofondal series (Pls. 24R, 154J, L, 158). Compared to taxa with “typical” dentition, taxa with the multidentate condition possess a greater number of secondary teeth, and the cutting edge of the finger tends to be sublinear, resulting in a row of small, relatively homogeneous teeth without, or with a weak, pattern of gradation. The multidentate condition occurs predominantly in Melanoblossiinae and, to a lesser extent, Karschiidae. It may be restricted to only one sex or to one cheliceral finger.

The dentition of some species of Eremobatidae, Karschiidae, Melanoblossiinae, and Mummuciidae, usually, but not always, females, exhibit some multidentate characters, e.g., increased number of secondary teeth, crenulations on the mucron (FST, MST teeth) and proximal to the movable finger medial series (MSP), and greater homogeneity among all teeth of the median series (Pls. 24O, P, 50H, 70J, 149H, 154C), but cannot be described as truly multidentate based on the abovementioned definition. In *Eusimonia divina* Birula, 1935, the fixed fingers of both sexes are multidentate, but more distinctly so in males in which the primary and secondary teeth are similar in size and regularly spaced, whereas the movable finger of the female only shows a tendency towards the multidentate condition, with greater differentiation in size between the primary and secondary teeth (Pl. 53G–J). Wharton (1981) described the dentition of *Namibesia pallida* (Pls. 132A–D, 133), which possesses an unusually large number of secondary teeth compared to other daesiid taxa, as multidentate. However, this species does not possess the multidentate characteristics redefined here, e.g., the teeth are not similar and equally spaced, and is therefore not regarded as multidentate. *Namibesia* *pallida* thus simply possesses a larger than usual number of FSD and FSM teeth, similar to the larger than usual number of MSM teeth observed in Galeodidae. Multidentate patterns of dentition, and a tendency towards such patterns, occur in taxa as diverse as Eremobatidae, Karschiidae, Mummuciidae and Melanoblossiinae, and are sometimes more pronounced in one sex or the other. Taxa with a tendency towards this pattern of dentition may provide useful insights into the evolution of the multidentate condition.

Supernumerary, defined as “exceeding the usual, stated, or prescribed number” (Grove, 1986: 2295), has been used to refer to various structures: the movable finger prolateral (MPL) tooth (Brookhart, 1965: 153); denticles situated among the fondal teeth (Muma, 1962: 11) or in the fondal notch of Eremobatidae (Brookhart and Muma, 1981: 302, fig. 73); the prolateral toothlike structure near the tip of the finger of some Solpugidae (Pocock, 1897); additional secondary teeth indicating an abnormality (Fichter, 1940: fig. 1G, H), bilateral asymmetry (e.g., Muma, 1951: 50), intraspecific variation (e.g., Muma, 1962), and interspecific variation in the median series (e.g., Muma, 1962: 10); or the retrolateral fondal series (e.g., Maury, 1980b). The use of “supernumerary” is unnecessary, however, if the abovementioned structures and “additional” teeth are more precisely defined, e.g., prolateral tooth, denticle-sized subproximal teeth, etc.

NUMBERING OF TEETH AND DENTAL FORMULAE

Numbers and formulae are commonly used to describe the dentition of solifuges. A distal to proximal numbering is conventionally used in place of terms for individual teeth (e.g., Wharton 1981). Two types of **dental formulae** are used, i.e., a dental pattern formula (Tables 7, 8) and a size grading formula. Unfortunately, dental formulae have not been standardized.

DENTAL PATTERN FORMULAE: Dental pattern formulae employ a combination of dental terms and numbers to indicate the types of teeth, and the number of each. Several formulae are currently in use (Table 7). A standardized formula, which incorporates variation in the secondary and fondal teeth, is proposed here. Notation for the fixed (dorsal) finger dentition of *Uspallata pulchra* Mello-Leitão, 1938 (Pls. 26, 152) is FD-(1)-FM-(1-2)-FP-(5-7RF)(3?PF). Numbers in parentheses indicate secondary (FSD and FSM) and fondal (RF and PF) teeth, ranges indicate variation (when applicable), underlined numbers indicate the most common pattern, and questionmarks indicate uncertainty, e.g., when teeth are obscured or a tooth or part of the chelicera is broken. Notation may be adapted to accommodate different patterns and levels of understanding, e.g., (2, 3, 4RF), or (PFM-0,1-PFP-1).

SIZE GRADING FORMULAE: Two superficially similar yet fundamentally different size grading formulae are used, illustrated here with the profondal (PF) teeth of Pl. 22C as an example. The first formula for grading fondal teeth was introduced by Muma (1951), and followed by Brookhart (1965) and Brookhart and Cushing (2002, 2004, 2008). In this system, individual fondal teeth are numbered distal to proximal with Roman letters, and then ordered from large to small. The notation I-III-IV-II for the PF teeth in Pl. 22C thus indicates the first tooth to be the largest, followed by the third, fourth and second, respectively. This formula does not allow for coding teeth of similar size, however, which requires elaboration in the text, e.g., "FT graded I, III, II, IV, FT III …large as FT I" (Brookhart and Cushing, 2004: 290). The second system (Maury, 1982) used Roman or Arabic numbers to indicate the relative sizes of teeth, e.g., for median and fondal teeth, in Roman numerals (Xavier and Rocha, 2001; Rocha and Cancello, 2002; Rocha and Carvalho, 2006; Carvalho et al., 2010) or for fondal teeth only, in Arabic numbers (Maury, 1982; Armas, 1993). Teeth are referred to in decreasing order of size, from distal to proximal, with size I (or 1) being the largest, size II (or 2) the second largest, and so on, in the order in which they are situated on the finger. According to this system, the notation for the PF teeth (Pl. 22C) would be I-IV-II-III (or 1-4-2-3) as opposed to I-III-IV-II in the notation of Muma (1951). This system assigns the same notation to teeth of similar size, e.g., II-I-III-I indicates that the second and fourth teeth are of similar size, and is therefore preferred here.

Size grading formulae are prone to error and subjectivity, and comparison between series (i.e., median and fondal series) is complicated by different shapes, but may be of value for independently communicating relative size. For example, in Carvalho et al. (2010), the retrolateral fondal teeth grading of I-III-V-II-IV does not match their line drawing (Carvalho et al., 2010: 23, fig. 9), but appears to match the scanning electron micrograph (Carvalho et al., 2010: 25, fig. 15). The size grading formula thus added a level of accuracy to the species diagnosis in the paper of Carvalho et al. (2010). It is suggested here that Arabic numbering (1, 2, 3, etc.) should be reserved for individual teeth, e.g., for distinguishing among multiple secondary teeth within a category, such as three MSM teeth, leaving Roman numerals (I, II, III, etc.) for ranking size.

LIFE STAGES AND SEXUAL DIMORPHISM

The cheliceral dentition of females and juveniles is more conserved (Hewitt, 1919b), and of females often more worn (Fichter, 1940) than that of males. Immature specimens for which reliable identifications were available are rare but, based on those that were examined, the dentition of immatures appears to be similar to that of females, except sharper, probably due to less wear, and often more pronounced. For example, in *Zeriassa* Pocock, 1897 the FM tooth is usually larger than the FD and FP teeth (Pl. 124E, H), a pattern also exaggerated in immatures (Pl. 124F).

Modifications to the dentition increase with each molt in immature males. Based on an examination of six males, one female and six immatures, Wharton (1981) documented the change with each molt from the distal (FD) and medial (FM) teeth on the fixed finger being similar in size and shape in immature *Biton* (*B.*) *striatus* (Lawrence, 1928), to the forms and shapes observed in adult males.

TAXONOMIC SIGNIFICANCE AND INTRASPECIFIC VARIATION IN DENTITION

It is well known in systematics that interspecific variation is informative for species delimitation and diagnosis, whereas intraspecific variation only contributes noise. Dentition is commonly used in solifuge taxonomy, but simultaneously criticized for unreliability. Variation in dentition, especially intraspecific, remains poorly understood.

HISTORICAL PERSPECTIVE: Cheliceral dentition has traditionally been used for solifuge systematics at all levels (Kraepelin, 1901; Birula, 1905; Hewitt, 1919b: 12; Lawrence, 1955; Muma, 1970a; Wharton, 1981; Maury, 1982, 1984), but the influential monograph of Roewer (1934) placed the greatest emphasis on this character system. Roewer (1934: 55, 509) considered dentition to be constant intraspecifically and emphasized its importance in solifuge systematics. Roewer (1934: 509) treated any variation in dentition not attributable to wear or damage, as a diagnostic character, as reflected in almost every species-level identification key to solifuges presented. Faced with an increasing number of species and genera which could not be accommodated within Roewer's (1934) classification, subsequent workers began to doubt the stability of the dentition and criticized the reliance on characters that are highly variable (e.g., Birula, 1936b; Simonetta and Delle Cave, 1968; Turk, 1960). Some species diagnosed by Roewer (1934) on the basis of dentition were subsequently synonymized (e.g., Gromov, 2000) but, for the majority of taxa, Roewer's (1934) classification prevails. Regardless of reservations concerning the value of dentition for solifuge systematics, there is a recognition that taxon-specific patterns are real, as noted in statements such as "dentition is comparatively constant within limits of any one form" (Hewitt, 1919b: 14), "dentition … apparently quite variable but in general as in … paratype" (Muma, 1962:12), "dentition of chelicerae somewhat variable but maintaining general pattern" (Muma, 1963: 2), "dentition… cannot be relied upon exclusively for generic or specific distinctions…this does not exclude their use entirely, as long as variation is taken into consideration” (Wharton, 1981: 71) and dentition is “generally species-specific” (Rocha and Carvalho, 2006: 166). The urgent need to re-evaluate inter- and intraspecific variation in dentition depends on series of adult males and females, accurate identifications, and comparability among studies.

Variation cannot be satisfactorily assessed without the availability of many specimens, especially adults, ideally from the same series (collection event). Solifugae are rarely collected in large series, however (Hewitt, 1919b; Dean & Griffin, 1993; Brookhart & Cushing, 2004). Roewer’s (1934) emphasis on stable dentition is probably an artifact of small sample sizes, a problem that continues to hinder solifuge taxonomy (Turk, 1960; Wharton, 1981). Unfortunately, even when large series are available, variation is rarely quantified, and the number of specimens designated as types is often a subset of the number collected.

Evaluations of intraspecific variation are reliable only when based on accurately identified specimens. Unfortunately, identifications are often uncertain, especially among Old World solifuges (see Harvey, 2002b) for several reasons. Descriptions of genera and species are often inadequate and sometimes contradictory (Simonetta and Delle Cave, 1968; Lawrence, 1968; Rocha, 2002). For example, see discrepancies, especially concerning the flagellum and dentition, in the descriptions of *Biton* (*B.*) *subulatus* by Purcell (1899: 389, fig. 12) and Roewer (1934: 389, fig. 275f_1). Type designations are often unclear and/or inadequate, types lost or untraceable, and the depositories unspecified (e.g., Muma, 1951, Simonetta and Delle Cave, 1968). Females or immatures, lacking relevant diagnostic characters, were often designated as holotypes, and it may be impossible to associate them with adult male conspecifics

(Turk, 1960; Simonetta and Delle Cave, 1968). Type localities are often vaguely defined and impossible to locate (Turk, 1960; Simonetta and Delle Cave, 1968). There are few revisionary syntheses.

Even when notes on variation in dentition are provided, the literature may be of limited comparative value, for several reasons. Different interpretations and terminology reduce comparability among or even within studies, such as whether a structure is interpreted as a flange or one of the regular teeth, and whether or not a denticle is counted as a tooth (e.g., Simonetta and Delle Cave, 1968). Different interpretations may have taxonomic implications, affecting how intraspecific variation is evaluated. For example, Lawrence (1949b) separated *Chelypus kalaharicus* Lawrence, 1949 from *C. hirsti*, mainly based on differences in the number of teeth on the fixed (dorsal) finger. When Lamoral (1973: 95) re-examined the holotype, identified as “definitively a juvenile or subadult male” (despite the presence of a flagellum), two denticles, not mentioned by Lawrence (1949b), were identified, on the basis of which *C. kalaharicus* was synonymized with *C. hirsti*. Lawrence (1949b) may not have regarded the denticles as taxonomically significant.

Lastly, only a handful of studies report variation in a manner that enables the identification of interspecific, intraspecific, or even intrapopulation variation, e.g., by reporting variation among individuals (e.g., Simonetta and Delle Cave, 1968; Lamoral, 1973) or within populations (e.g., Wharton, 1981; Botero-Trujillo, 2014). The few studies that report variation in detail (e.g., Maury, 1976: 94, 95), often including basic statistics (e.g., Simonetta and Delle Cave, 1968; Wharton, 1981), were intended for general descriptions of intraspecific variation, rather than for comparisons of specific teeth within and among taxa. Nonetheless, it is often possible to use such data to assess which broad categories as well as types (e.g., size) of teeth are more prone to variation among individuals (Table 9) and populations (Table 10).

FALSE INTERPRETATION OF VARIATION: Worn and damaged teeth, especially in older females and fossorial taxa (e.g., Lawrence, 1963: 5, fig. 4; Wharton 1981), are easily misinterpreted as small or absent teeth. Aberrant teeth may also be mistaken for intrinsic variation. Solifuges appear to have a propensity for aberrant characters, e.g., flagellum lost (Turk, 1960: 115) or duplicated (Wharton, 1981: 30) on one chelicera, a double unguis, or a misformed leg (e.g., Roewer, 1934: 255), and dentition is no exception. Variation in dentition is seldom as obvious as the presence of a duplicate flagellum, but just as the latter abnormality would not be indicative of variation in number of flagella on a chelicera, aberrant teeth should not be counted as intrinsic variation. Examples of aberrant teeth include a bifid FM tooth of a female *Melanoblossia braunsi* Purcell, 1903 (Pls. 154C, 155F), and a bifid FD tooth reported by Simonetta and Delle Cave (1968) in a specimen of *Solpuga* Lichtenstein, 1796, each restricted to a single chelicera. Other examples involve all teeth on the chelicera, again with some examples more clearly aberrant than others. A striking example is the “distinctive” chelicerae characterized by peculiar teeth, including the apex of the finger, on the basis of which Turk (1948: 269) diagnosed the female of *Solpugella asiatica* Roewer, 1933, but which is undoubtedly a chelicera with highly deformed or worn teeth (Fig. 18A). It is less certain whether, e.g., the dentition of the single specimen of a putative *Ferrandia robusta* Lawrence, 1954 examined in the present study (Fig. 18B) represents wear or intrinsic variation, and verifying this may require the examination of additional specimens.

Although abnormalities in dentition should not be included in estimates of variation, they are not always readily identified as such, emphasizing the need to examine series of specimens, when available. Abnormalities are often confirmed by other characters. An abnormality in one character in a particular individual (e.g. two flagella on a chelicera) may be accompanied by abnormalities in other characters (e.g., “abnormal tarsal variation,” Wharton, 1981: 30). Examples of variation in dentition concentrated in a particular specimen were observed in the present study. For example, when variation was recorded in a series of male *Bdellophaga angulata* (*N* = 53 specimens), 15 teeth were found to vary in presence/absence among the 53 individuals. Six of the 15 variable teeth were restricted to a single male, however.

PATTERNS OF INTRASPECIFIC VARIATION IN DENTITION

During the present investigation, examination of materials and review of species diagnoses revealed that intrinsic intraspecific variation in dentition, i.e., excluding wear and deformity, is common in Solifugae. However, this variation, which concerns presence/absence, relative size and shape, is largely restricted to predictable components of dentition.

The literature suggests that the fondal teeth and the secondary teeth of the median series are more prone to variation than the primary teeth (e.g., Maury 1976), in individuals (Table 9) and populations (Table 10). A summary of literature references to variation in presence/absence of primary, secondary or fondal teeth, in seven families, 23 species and 335 specimens (670 chelicerae), is provided in Table 10. These published findings, including variation in shape and relative sizes not included in the table, were compared with data collected during the present study.

PRIMARY TEETH: The study confirmed that primary teeth are fairly stable intraspecifically in presence/absence. Variation in presence or absence of a primary tooth was observed in one chelicera (an FD tooth in a female *Zeria venator*), or 0.2% (*N* = 444 chelicera; 22 species; 9 families). This is in accord with literature reports; as indicated in Table 10, primary teeth were remarkably stable, with no variation in presence/absence recorded. The only taxa in which it was uncertain whether a primary tooth was variable involved the 2–4 “very small apical [teeth]” of *Blossia sabulosa* (Lawrence, 1972) and the “3–6 small teeth on low ridge adjacent base of flagellum” in *Hexisopus pusillus* Lawrence, 1962, both reported by Wharton (1981: 31, 51). These specimens should be examined to evaluate whether variation exists in the primary or secondary teeth.

In general, the more distally situated in the median series, the more prone teeth appear to be to vary in presence/absence and relative size. Martins et al. (2004: 2367) reported that an FD tooth “may be vestigial” in different specimens of *Mummucia coaraciandu* Pinto-da-Rocha and Rocha, 2004. A specimen of *Gaucha fasciata* Mello-Leitão, 1924 examined during the present study possessed a small tooth, resembling a secondary tooth, distal to two distinct primary teeth (Pl. 151A). In his redescription of this species, Maury (1970: 359, 360) mentioned that both anterior teeth were similar in size and this was also depicted in his figs. 2 and 3 (the former reproduced in Pl. 151B). The *G. fasciata* example illustrates intraspecific variation in the size of the FD tooth, the distalmost primary tooth. It also confirms that a small tooth distal to the FM is most likely the FD, which superficially resembles a secondary tooth in those cases. Even if the illustrated specimen of Maury (1970: 359, 360, figs. 2, 3) and the specimen examined in the present study prove not to be conspecific, they are clearly closely related, and therefore still support the same conclusion of a small FD rather than a FSD present as the most distal tooth in these taxa.

Patterns of dentition are generally similar in closely related species and males and females of the same species. Increased variation in distal teeth accounts for variation among closely related species. This was also noted earlier by Maury (1980b: 41), who mentioned that interspecific variation in *Pseudocleobis* was “near exclusively” restricted to the “anterior teeth” on the fixed (dorsal) finger, where FD, FSD and FM may be reduced or absent. In Rhagodidae, the FD and MM are reportedly absent in some species (e.g., Turk, 1960: 121, fig. 9), but tend to be minute when present (Pls. 56C–H, 57), again demonstrating that interspecific, variation, and probably also intraspecific variation, occurs primarily among the distal teeth, and that size is also correlated with variation. Female *Zeriassa furcicornis* Lawrence, 1929 examined in the present study possessed three distinct primary teeth on the fixed finger whereas, in the male examined, the distalmost tooth was very small, but positionally homologous with the **fixed finger distal (FD) tooth** of the female (cf. Pl. 124B, D). If interpreted as a small FD, the general pattern of median series dentition in the male, i.e., FD-FM-(2)-FP, is identical to that of the female. This observation reinforces the identity of a distal tooth as a primary tooth, despite its superficial similarity to a secondary tooth, and the tendency for greater variation distally as opposed to proximally in the main series.

The above examples illustrate two practical implications for homology assessment (with some exceptions): (i) A small tooth with the superficial appearance of a secondary tooth, situated distal to the FM tooth or the MP tooth is more likely to be a primary tooth (FD tooth or MM tooth, respectively) than a secondary tooth (FSM tooth or MSM tooth, respectively). (ii) On the movable (ventral) finger, the medial (MM) tooth is more likely to be absent or variable in size than the proximal (MP) tooth. Similarly, on the fixed (dorsal) finger, a distal (FD) tooth is more likely to be absent or variable in size than a medial (FM) tooth, which, in turn, is more likely to be absent or variable in size than a proximal (FP) tooth.

Exceptions to the apparently greater stability of primary teeth relative to secondary teeth include cases in which a medial (FM or MM) tooth is absent and a submedial (FSM and MSM) tooth present, the latter situated very close to a proximal (FP or MP) tooth, often on the distal margin of the proximal tooth itself. Examples on the movable finger occur in Eremobatidae (e.g. Pl. 78B) and on the fixed finger in Gylippinae (e.g., Pls. 85B, 86B). The pattern may also be present in Daesiidae (e.g., Roewer, 1934: 398, fig. 278a), but requires further investigation. The identity of the secondary tooth is confirmed in these examples by the simultaneous presence, vestigial or well developed, of the primary tooth (i.e., vestigial FM and FD teeth in Gylippinae and MM tooth in Eremobatidae, respectively) in some species. These examples also indicate greater stability among secondary teeth for those situated proximally in the medial series, and close to the proximal (FP or MP) tooth.

SECONDARY TEETH: Based on a survey of the literature (Table 10), variation in the number of secondary MSM teeth was observed in three species (13.6%; *N* = 22 spp.), in number of FSM teeth in seven species (31.8%), and in number of FSD teeth in, at most, six species (27.3%). The present study also confirmed that secondary teeth, especially denticle-sized teeth, are more variable than primary teeth (e.g., Figs. 19, 20). Intraspecific variation in the presence/absence of secondary MSM teeth was observed in 13 chelicerae (3%; *N* = 426 chelicerae), of FSM teeth in 18 chelicerae (4.1%; *N* = 440), and of FSD teeth in 8 chelicerae (4.5%; *N* = 176).

Unlike primary teeth that, in general, become more stable proximally (see discussion above under Primary Teeth), based on specimens examined and the literature, the stability of individual secondary teeth is associated with the direction of size gradation. When two or more teeth are present within categories of secondary teeth (MSM, FSM, FSD), a gradation in size is observed, such that the teeth increase in size proximally or distally (Table 6). The distalmost teeth are less likely to vary if the teeth increase in size distally, whereas the proximalmost teeth are less likely to vary if the teeth increase in size proximally. Smaller teeth are therefore more likely to be variable than larger teeth. Denticles interspersed among larger secondary teeth are the most labile in presence/absence and size (e.g., Figs. 19, 20), and rarely conform to the patterns of size gradation.

Another pattern observed in the secondary teeth is that the FSD row rarely comprises more teeth than the FSM row (Fig. 17C), in accordance with the pattern that more teeth are absent distally than proximally on the finger.

Exceptions to the patterns identified in the present study are rare and usually caused by the presence of tiny denticles. For example, the absence or presence of denticles among the FSD teeth or the FSM teeth may result in more FSD teeth than

FSM teeth, and the absence of a distinct gradation in size. Although most examples concern species of Eremobatidae, taxa from other families are also represented (e.g., *Solpugiba lineata*, *Namibesia pallida*). *Horribates bantai* (Pl. 78C) possesses three FSD teeth and only two FSM teeth, and size gradation within the FSD row is confounded by a small denticle between two larger FSD teeth. A small denticle situated distally in the FSD row results in three FSD teeth and two FSM teeth in the female paratype of *Hemerotrecha hanfordana* Brookhart and Cushing, 2008 (Pl. 82D). Other examples include illustrations by Muma (1951) pertaining to species, mostly of *Hemerotrecha*, with more FSD teeth than FSM teeth. These include a male *H. denticulata* Muma, 1951, with no FSM teeth and one FSD tooth (Muma, 1951: 103, fig. 211), females of *H. banksi* Muma, 1951, *H. californica* (Banks, 1899), and *Eremochelis insignatus* Roewer, 1934 as *H. insignata* (Roewer, 1934), each with one FSM tooth and two FSD teeth (Muma, 1951: 97, fig. 191; 101, fig. 195; 109, fig. 221), and a female *H. marginata* (Kraepelin, 1911) with three FSM teeth and four FSD teeth (Muma, 1951: 101, fig. 200). In these examples, the additional secondary teeth that violate general patterns are almost always minute or the size of denticles, and thus probably very labile (e.g., Fig. 20). It should be noted the two denticle-sized FSD teeth of *H. marginata*, illustrated in Muma's (1951: 101) fig. 200, which was redrawn from Roewer's (1934: 568) fig. 327c, are absent in the female syntype (ZMUH [R8376]; Pls. 82F, 83B; also see Brookhart and Cushing, 2008: 57, fig. 29).

FONDAL TEETH: Fondal teeth have been reported to vary considerably in number and size (Tables 9, 10). According to the literature (Table 10), variation in the number of profondal (PF) teeth was found in four species (18.2%; *N* = 22 spp.), in the number of

RF teeth in six species (27.3%). In the present study, however, variation in the number of fondal teeth depended on whether a proximalmost tooth was included in the count. Variation was also more common in particular teeth.

Detailed examination of individuals within series revealed patterns not only in the number of fondal teeth, but also in their shape and, often, relative size. For example, among males of the gylippid *Bdellophaga angulata* (*N* = 53; 106 chelicerae), five teeth were counted in the retrofondal (RF) row of most specimens, each of which was individually recognizable based on relative position, size and shape. This pattern corresponds to that of the female *B. angulata*. Disregarding three chelicerae with broken teeth, the retrofondal teeth were almost identical in position, size, and shape in all but seven (94%; *N* = 103) chelicerae. Five retrofondal subdistal (RFSD) teeth and two retrofondal subproximal (RFSP) teeth were absent and one retrofondal medial (RFM) tooth was deformed. It is noteworthy that three of the absent fondal teeth and three (of five) of the absent main series teeth (FSD and FSM) belonged to a single specimen. This apparent predisposition towards abnormality, also observed in other specimens of different families, is discussed above further in the section on False Interpretation of Variation.

A similar example of variation restricted to predictable areas was observed in a series of males of the mummuciid *Uspallata pulchra* (*N* = 26; 52 chelicerae), the homologs of which were each recognizable among individuals. The RFP tooth was readily identifiable in most specimens, but the identity of other teeth in the RF series was challenging. Based on the structure of individual teeth, the most plausible hypotheses are presented here (Pls. 26, 152), with probable homologs numbered one to eight to facilitate discussion (RFA: 1, 2; RFM: 3; RFSM: 4; RFP: 5; RFSP: 6, 7, 8). Two retrofondal subproximal (RFSP) teeth were present in all except six chelicerae (i.e., in 89% of the chelicerae), which possessed one RFSP tooth instead. A third RFSP tooth was present on one chelicera only (Pl. 26B). A retrofondal submedial (RFSM) tooth was present in only five (9%) chelicerae (Pl. 26D), and the proximalmost retrofondal apical (RFA) tooth in all except one (98%) (Pl. 26E) of the chelicerae. Variation in presence/absence was thus limited and restricted to particular teeth, but in this species size variation was more extensive than in *B. angulata.* Such size variation, together with the previous inability to identify individual teeth and the difficulty in examining fondal teeth without damaging specimens, may create a false impression that there is no pattern in the fondal teeth of species such as *Uspallata pulchra*.

As with primary and secondary teeth, fondal teeth that are usually smaller are usually also more labile, especially in presence/absence. For example, the most stable profondal teeth are almost always the large profondal proximal (PFP) and profondal medial (PFM) teeth.

INTRASPECIFIC VARIATION IN SHAPE OF TEETH: As with other aspects of solifuge morphology, variation in shape has seldom been evaluated. Kraepelin (1901: 69) used shape as a diagnostic character, but added a questionmark when uncertain about its stability in a particular taxon, e.g., “*zweizackigen* (*immer*?) *Hauptzahn*”. Examples of shape in species diagnoses and identification keys (Purcell, 1899: 420; Kraepelin, 1901; Turk, 1948: 266; Wharton, 1981: 74) include the fixed finger distal (FD) and medial (FM) teeth “strongly hooked” apically in *Solpugema vincta* (C.L. Koch, 1842) as *Solpuga vincta*; a bifid FP tooth in *Zeria schweinfurthi* (Karsch, 1880) as *Solpuga schweinfurthi*;

and the FP, FM, and FD teeth recurved at the apex in the female of *Gylippus shulowi* Turk, 1948. These examples were often based on single specimens, but examination of more specimens suggests that shape may be relatively stable. Wharton (1981: 63) mentioned the distinct bifurcate MM tooth as a diagnostic character for *Solpugista hastata*. Brookhart and Cushing (2004: 286) examined many specimens, and found that the shape of the **movable finger medial (MM) tooth** of males, and the presence or absence of a small notch ("cleft") distal to the MM tooth in both sexes, could be used to diagnose species in the *scaber* group of *Eremobates*. Roewer (1934: 433, fig. 289c_1) noted the presence of a rounded, bifid FP tooth in seven males of *Zeria boehmi* (Kraepelin, 1899), as *Solpugarda boehmi*.

Even subtle shapes appear to be more consistent than generally recognized. For example, the slightly recurved tips of otherwise symmetric primary teeth were invariant in all male *Uspallata pulchra* examined (*N* = 26; 52 chelicerae) (Pl. 152) and similar in shape to the primary teeth of a potentially close relative, *Mummucia coaraciandu* (*vide* Martins et al., 2004: 2365, fig. 3A, B). In the present study, the vestigial, hypothesized FST, FD and FM teeth of all male *Melanoblossia braunsi* examined (*N* = 5; 10 chelicerae) (Fig. 21; Pl. 155E) were "folded" in shape, which correlated with shapes in an undescribed species of *Melanoblossia* (Pl. 156A) and the teeth illustrated in Wharton's (1981: 53) fig. 54 of *M. globiceps* Purcell, 1903. In male *Bdellophaga angulata* (*N* = 53; 106 chelicerae), the ventrodistally directed bifid shape, created by the narrow fixed finger distal (FD) tooth being partly fused to the fixed finger subdistal (FSD) tooth (Pls. 87H, 89C), was almost identical in all except one chelicera (99% of 98 chelicerae; *N* = 49) in which both teeth were present (the FD–FSD teeth of six chelicerae were broken and of two, intensely worn, preventing the evaluation of shape). Distinct, rounded bifid FP and FM teeth were observed in the holotype of *Oparba asiatica* and two other potentially conspecific males from different localities (Pl. 27) as well as in a male *Solpugema brachyceras* (Pl. 20H). Although prominent, this shape has not been previously noted in either species perhaps because it was misinterpreted as a worn or aberrant tooth, e.g., cf. Pl. 27A with Turk's (1948: 270) fig. 4 of the same specimen. The systematic value of shape, at least for the primary teeth, remains poorly understood, but should not be dismissed *a priori.* As the abovementioned examples illustrate, shape may prove informative for phylogenetic reconstruction or taxon diagnosis at the species level or above, but current understanding of solifuge relationships prevents further assessment.

CRITERIA FOR PRIMARY HOMOLOGY ASSESSMENT OF DENTITION

Objective, explicitly defined criteria for the identification of homologous dentition in solifuges are non-existent. Criteria for identifying homologous primary, secondary and fondal teeth are therefore proposed here, based on findings discussed in the section on Patterns of Intraspecific Variation in Dentition. Some problematic cases are also discussed.

STRUCTURAL AND POSITIONAL HOMOLOGY OF PRIMARY TEETH: In the present study, four criteria were developed and applied for the identification of homologous primary teeth. The first and second criteria are traditionally used in the solifuge literature but have not been formally stated. The third and fourth criteria were newly developed, based on synthesis of the literature and examination of material representing taxa across the order. These criteria were developed and are discussed here based on unmodified patterns of dentition (Pl. 22B), and then extrapolated to modified patterns. Reciprocal illumination (Hennig, 1966) of these criteria was essential to formulate hypotheses of homology for individual teeth in modified patterns of dentition. A summary of the criteria is provided in Appendix 3.

Criterion 1 distinguishes primary teeth from secondary teeth on the basis of structure (size and sclerotization). In the conserved dentition of most females and immatures, primary teeth are easily distinguished from secondary teeth as the largest, sometimes most sclerotized teeth on the fingers, or at least within the median series (Pl. 21). There are three primary teeth on the fixed finger and two on the movable finger. When dentition is reduced, modified or homogeneous, however, it may be difficult to separate primary from secondary teeth, resulting in primary teeth being ignored in descriptions, or miscoded as absent or as secondary teeth in character matrices. For example, the primary teeth of female Karschiidae identified by Roewer (1934: 296, fig. 223, reproduced in Pl. 28 with the interpretation presented here color coded for comparison), apparently on the basis of structural criteria, are unlikely to be homologous among species. Two corollaries of criterion 1 are therefore proposed to prevent reduced primary teeth from being mistaken for secondary teeth. These corollaries are justified by observations that primary teeth are more stable than secondary teeth, and that stability increases with proximal position (see Primary Teeth, in the section on Patterns of Intraspecific Variation in Dentition), and are supported by patterns between sexes, e.g., cf. male and female *Zeriassa* (Pl. 124B, D) and related species, e.g., cf. *Zeriassa furcicornis* (Pl. 124B) and other solpugid genera (e.g., Pl. 121H), and patterns of intraspecific variation, e.g., cf. *Gaucha fasciata* male examined (Pl. 151A) and *G. fasciata* redrawn from Maury (1970: 360, fig. 2) in Pl. 151B.

Corollary 1 states that secondary teeth are more likely to be absent than primary teeth. Therefore, when a distinct primary tooth is not evident, but a small tooth or denticle is present in the same position, the small tooth or denticle is more parsimoniously assumed to be a reduced primary tooth than a secondary tooth. For example, if a tooth is observed distal to an FM tooth, then, regardless of size, the distalmost tooth is the FD tooth, and not merely a secondary tooth.

Corollary 2 states that primary teeth are more likely to be reduced or absent from distal to proximal on the finger. Consequently, the fixed finger dorsal (FD) tooth is the first primary tooth to be reduced or absent, the fixed finger proximal (FP) tooth is the last primary tooth to be reduced or absent, the proximal (FP or MP) tooth is usually the largest tooth on a cheliceral finger and, when only two distinct primary teeth are present on the fixed finger, the FD (not FM) tooth is assumed to be absent. There are few examples in which a probable FP tooth is absent while an FM and/or FD teeth are present. In the present study, this was recorded in only a few species, mainly belonging to *Hemerotrecha* Banks, 1903 with its reduced FP tooth (Pls. 79J, 82H, 83C; Brookhart and Cushing, 2002: 94, figs. 32, 33). Corollary 2 is also true among categories of secondary teeth but not within them, i.e., a subdistal (FSD) tooth is more likely to be absent than a submedial (FSM) tooth, but within a row of FSD teeth, the tooth most likely to be absent is hypothesized to depend on the direction of size gradation within that row, the smallest being the most likely to be absent.

Corollary 2 was found to be more applicable the more proximal a tooth was situated in the median series. This is based largely on examples in which the **movable finger proximal (MP) tooth** and submedial (MSM) teeth are present, and the medial (MM) tooth absent in Eremobatidae (Pl. 78B), and a similar pattern on the fixed finger of Gylippinae where the fixed finger proximal (FP) and submedial (FSM) teeth are present, and the FM tooth absent (Pls. 85B, 86B).

Criterion 2 formalizes the intuitive method by means of which the primary teeth have traditionally been named (e.g., Roewer, 1934, 1941; Muma, 1951), based on their positional order on the cheliceral fingers. Three primary teeth are situated on the fixed (dorsal) finger, i.e. the FP, FM, and FD teeth, the FP tooth being the proximalmost primary tooth, and often the largest on the finger, followed distally by the FM and FD teeth. Two primary teeth are situated on the movable (ventral) finger, i.e., the MM and MP teeth, with the MP tooth being the proximalmost primary tooth on the finger, and the MM tooth, the distalmost. Only in rare cases was this arrangement not observed, i.e., the FP tooth was reduced to absent while the FM and/or FD tooth were present in some *Hemerotrecha* (Pls. 79J, 82H, 83C; mentioned above under corollary 2).

Criterion 3 refers to the pattern by means of which the teeth interlock and/or overlap when the cheliceral fingers are closed, i.e., the position of teeth on a finger relative to teeth on the opposite finger (Pl. 29). The fixed/movable finger articulation restricts the relative movement of the fingers, in turn constraining the dental interlock/overlap to a rigid, fixed pattern. The MP tooth typically fits between the two converging rows of fondal teeth, the FP tooth usually fits directly distal to the MP tooth, in a space provided by a smaller submedial secondary tooth/teeth, and the FM and FD teeth and any subdistal teeth, if present, fit into the space created by the usually toothless mucron.

The more conserved the dentition (as in Pl. 22B), the more precise the interlock of the FP tooth distal to the MP tooth, and the FM tooth distal to the MM tooth, and the less the overlap between the teeth on the fixed and movable fingers. The extent of overlap increases with greater modification of the dentition, but these patterns of interlock generally remain even when the dentition is greatly modified (Pl. 29G–I). Closure of the FP tooth proximal to its homolog on the movable finger was not observed in the present study and there are few examples in the literature, e.g., *Biton* (*B.*) *kraekolbei* (Wharton, 1981: 15, fig. 8). Closure of the FP tooth well distal to its homolog on the movable finger is a more common occurrence, e.g., in *Trichotoma michaelseni* (Pl. 88E) and an undescribed species of *Melanoblossia* (Pl. 156C). In the latter species, the FP tooth even closes distal to the MM tooth (see section on Melanoblossiinae in Taxonomic Diversity of Cheliceral Dentition). It should be noted, however, that evaluating patterns of dental overlap from published illustrations, especially those portraying open cheliceral fingers, may be misleading (Pl. 29A–C).

Criterion 4 states that similar patterns, e.g., relative position, size and shape of teeth, and the presence of other toothlike structures, are observed in conspecifics of the opposite sex and closely related heterospecifics. Examples include the parallel toothlike flanges on the movable finger of all species of Ceromidae (e.g., Pl. 92A) and the “fourth tooth” (**subterminal flange, STF**) on the fixed (dorsal) finger of four species in the *tricolor* group of *Blossia* (Pls. 144B, D, 145B, D) and on the movable (ventral) finger and in some species on the movable finger in the *setigera* group of *Blossia* (e.g. Pls. 144E, 145E).

Biton (*B.*) *rossicus* (Birula, 1905) (Pls. 136E–H, 138) provides a convenient example of how the abovementioned criteria contribute to identify structures of unclear affinity. Individual teeth and toothlike structures are numbered (1–5) to facilitate discussion. In males of this species, the most distinct structures observed on the cutting edge of the fixed finger in retrolateral view, are a flange-like structure (1) and the three largest teeth (2, 4, 5). Two alternative approaches to naming these teeth are apparent: (i) 5 as the FP tooth, 4 as the FM tooth, 2 as the FD tooth, and an additional toothlike flange distally, or (ii) 4 as the FP tooth, 2 as the FM tooth, and the flange-like 1 as a modified FD tooth, leaving 5 as the apical fondal tooth. The extent of sclerotization of the flange, as well as the pattern of dental overlap, suggests that the flange is a primary tooth (FD). This hypothesis is further supported by comparing the modified male dentition with the unmodified conspecific female dentition, which possesses the same number and similar relative sizes of teeth, and with the dentition of related congeners, e.g., *Biton* (*B.*) *browni* (Lawrence, 1963), the dentition of which is similar except for the more distinctly toothlike, less flange-like, FD tooth (Pl. 136I, J).

Single criteria become less reliable as dentition becomes more markedly modified, requiring greater reliance on reciprocal illumination by multiple criteria. Further examples concerning Ceromidae, *Trichotoma michaelseni* (Gylippinae), and a species of *Melanoblossia* (Melanoblossiinae) are provided in the taxon survey.

POSITIONAL HOMOLOGY OF SECONDARY TEETH: Hypotheses of primary homology concerning individual secondary teeth are difficult to propose across the order. Unlike primary teeth, there is no fixed number of secondary teeth within a category, e.g., zero

(Pl. 58) to four (Pl. 158) movable finger submedial (MSM) teeth, no obvious landmark tooth within a category such as the proximal (FP or MP) teeth on the fixed and movable fingers, respectively, no particular pattern of overlap, and the positions of secondary teeth relative to the two primary teeth may vary. Secondary teeth may, however, exhibit a gradation in size (Fig. 17A, B; Table 6), increasing distally or proximally within a category (FSM, FSD, MSM). Should only one tooth be present within the category, it is assumed to be the tooth at the large end of the size gradation in conspecifics or congeners with more than one tooth in the category. This assumption is supported by observations, e.g., a single MSM tooth is situated closer to the MM tooth in Galeodidae and Karschiidae, in both of which the teeth increase in size distally, but closer to the MP tooth in Eremobatidae and Solpugidae, in both of which the teeth increase in size proximally. A single tooth in a category of secondary teeth is therefore considered homologous in two species if the direction of gradation of the secondary teeth is the same in both species, i.e. both increasing in size proximally or distally.

Primary homology assessment may be confounded when the direction of gradation is not obvious, e.g., due to small teeth, usually denticles, situated between larger secondary teeth. When two secondary teeth are present in some conspecifics and absent in others, gaps indicating the positions of absent teeth may imply homology with teeth that are present in other individuals.

HOMOLOGY OF FONDAL TEETH: Unlike secondary teeth, several landmark fondal teeth may be identified, i.e., the profondal medial (PFM), profondal proximal (PFP), and (usually) retrofondal proximal (RFP) teeth, on the basis of which other homologs may be inferred. The profondal (PF) row usually possesses at most four teeth (a second small profondal subproximal (PFSP) tooth is rarely present), of which the PFM and PFP teeth are quite stable, allowing probable homologs to be readily identified in most species. The retrofondal (RF) row is more challenging to homologize, but the RFP tooth constitutes a distinct landmark, based on shape (equilateral triangular) and position (usually subproximal or proximalmost tooth in the RF row) in many species (Pl. 23), which may be used to identify other homologs, although this is sometimes possible only in conspecifics or congeners.

Supraspecific Patterns of Dentition

Typical patterns of dentition are recurrent above the species level across the order. The profondal medial (PFM) and profondal proximal (PFP) teeth are usually large, tall and slender whereas the retrofondal proximal (RFP) tooth is equilateral triangular. Primary teeth of the fixed (dorsal) finger are often identical in size and shape. For example, all three primary teeth are identical in size and shape in some Mummuciidae (Pl. 26), the distal (FD) tooth is identical to the medial (FM) tooth in male Ceromidae (Pl. 91), and the medial (FM) tooth is identical to the proximal (FP) tooth in various male Solpugidae (Pl. 118D, H). Other structures are restricted to specific taxa. These include two parallel flanges situated distal to the MM tooth in male Ceromidae (e.g., Pl. 92A), an additional toothlike subterminal flange (STF) situated distal to the fixed finger distal (FD) tooth in male *Solpugema* (Pls. 106E, F, 107B, 109E, F) and males of the *tricolor* group of *Blossia* (Pls. 144B, D, 145B, D), or distal to the movable finger medial (MM) tooth in males of the *crepidulifera* group of *Blossia* (e.g., Wharton, 1981: 23, 24, figs. 15, 23), or on the fixed finger and in some species on the movable finger in the *setigera* group of *Blossia* (e.g. Pls. 144E, 145E). These and other similar patterns may represent potential synapomorphies. Furthermore, patterns observed in both sexes and all lifestages may enable females and juveniles to be assigned to families, subfamilies or genera, as in the case of an exceptionally large RFP tooth in both sexes of Lipophaginae, the medial (FM and MM) teeth much larger than other primary teeth in Hexisopodidae, and the FM tooth often being distinctly larger than the FP and FD in *Zeriassa*.

FUNCTIONAL MORPHOLOGY OF DENTITION

SEXUAL DIMORPHISM, PLESIOMORPHIC CONDITION, AND FEEDING: As with other cheliceral characters such as shape, the pronounced sexual dimorphism in solifuge dentition reflects the function of dentition in the sexes (Roewer, 1934: 56; Lawrence, 1965b). The brief lifespan of males, indicated by numerous life history studies and observations (e.g., Heymons, 1902; Amitai et al., 1962; Muma, 1966b; Wharton, 1987), appears to be associated with a reduction in feeding, at least in some species. Whereas some male solifuges feed readily (Cloudsley-Thompson, 1961; Muma, 1966b), others appear to feed rarely, opportunistically, or selectively (Junqua, 1962; Wharton, 1987; Hrušková-Martišová et al., 2010b). The connection between reduced cheliceral dentition in male solifuges (“smaller, blunter and/or less numerous teeth”), a short lifespan with less emphasis on feeding, and adaptation towards mating, was first suggested by Wharton (1987: 372).

Feeding is clearly the primary function of the cheliceral dentition of females. Except for a few termitophagous species, solifuges appear to be generalist predators (e.g., Muma, 1966c; Wharton and Reddick, 2014). There is therefore little pressure for interspecific differentiation of the chelicera except in the adult males, in which differentiation is driven by sexual, rather than natural selection. The number, size and shape of the dentition of female and immature solifuges is remarkably uniform interspecifically, and thus probably represents the plesiomorphic condition (Wharton, 1981). According to Wharton (1981), the putative plesiomorphic condition for southern African solifuges (Daesiidae, Hexisopodidae, Lipophaginae, Melanoblossiinae and Solpugidae) comprises five primary (FD, FM, FP, MM, MP) teeth, two submedial (FSM, MSM) teeth, and three or four fondal teeth in the PF and RF rows (Pl. 22B). Based on the present study, this pattern appears to be conserved in females and immatures across the order. By definition, the plesiomorphic pattern therefore does not include a subdistal (FSD) tooth. An FSD tooth is, however, a relatively common addition to this otherwise conserved pattern. The putatively plesiomorphic dentition of the movable (ventral) finger is also supported by the fossil record. The enigmatic solifuge-like arachnid *Schneidarachne saganii* Dunlop and Rössler, 2003 possesses three teeth on the movable finger (Dunlop and Rössler, 2003: 397, fig. 6).

Although dentition is conserved in most females, there are exceptions, notably the multidentate chelicerae of Karschiidae and Melanoblossiinae. These suprageneric taxa tend to comprise small, microphagous species and the multidentate condition is probably an adaptation to microphagy, involving small, fast running prey. Little or no sexual dimorphism in dentition is evident in the larger, termitophagous *Solpugiba lineata*

(Solpugidae), in which the dentition of both sexes is slightly reduced in size, with an increased number of secondary teeth, resembling the multidentate condition (Pls. 110A–D, 111). Species of *Hemiblossia* (Daesiidae), also known to be termitophagous (Lawrence, 1963; Wharton, 1981), display little sexual dimorphism and, especially in the *australis* group, the primary and secondary teeth are relatively homogeneous in size (Pl. 139J), resembling the multidentate condition.

Although reduction in the size and/or number of teeth, and blunting of the terminal teeth in males are usually interpreted as adaptations for sexual reproduction (e.g., Wharton, 1987), slight differences between the sexes might be more parsimoniously explained by reduced feeding in males (Roewer, 1934: 56; Lawrence, 1965b). The diet of males might be limited to less sclerotized prey (Lawrence, 1965b), a hypothesis confirmed by some laboratory observations (Hrušková-Martišová et al., 2010a). A similar argument was advanced above to account for the gracile shape of the male cheliceral manus (see Functional Morphology in the section on Chelicerae).

REPRODUCTION: Even when the dentition is similar in both sexes, as in *Solpugiba lineata*, the chelicerae are dimorphic in other respects, e.g., the fingers are longer, the mucra more strongly curved, and the distal teeth of the fixed finger (FM, FSD, FD) more distally directed in the male. Reduced male dentition and more distally directed teeth may reduce injury to the female during violent and forceful chewing of the female prosoma and/or opisthosoma by the male, and/or reduce damage during the genital contact phase which prepares the female for sperm transfer and often involves vigorous chewing actions of the genital opening and surrounding area by the male (Heymons, 1902; Muma, 1966b). Indeed, opisthosomal kneading was not reported in an ammotrechid, *Oltacola chacoensis*, with pronounced teeth (Peretti and Willemart, 2007), whereas forceful kneading of the female was reported in two galeodids with very blunt teeth (Heymons, 1902; Amitai et al., 1962; Hrušková-Martišová et al., 2008a, 2010a) and a solpugid with small, reduced teeth (Wharton, 1987). Reduced teeth were, however, similarly common in families and species for which light kneading was reported, such as in several eremobatids, which are toothless (Muma, 1996b: 347; Punzo, 1998b), a daesiid, *Gluvia dorsalis*, in which the finger is toothless distally but armed with pronounced median teeth proximally (Hrušková-Martišová et al., 2010), and at least one galeodid with blunt teeth (Cloudsley-Thompson, 1961). There is thus no obvious correlation between heavy kneading and reduced dentition, even within genera, and reduced dentition may not function to reduce injury to females. Forced copulation (coercion) has also been documented in solifuges (Peretti and Willemart, 2007; Hrušková-Martišová et al., 2010a).

There is also no apparent correlation between the development of dentition and the insertion of the fixed finger into the female genital tract during the genital contact phase. For example, the fixed finger is largely toothless in Eremobatidae, where the male “thrusts the needle-like fixed fingers of his chelicera deep into [the female genital tract]” (Muma, 1966b: 347), whereas teeth are well developed on the fixed finger of Ammotrechidae for which a similar “rapid intromission” of the fixed finger in the female reproductive tract has been reported (Peretti and Willemart, 2007: 33). It may be significant that modification of the fixed finger into an elongated stylet, abruptly attached to the fondal area, is usually associated with greatly reduced or absent dentition. This morphology, first noted by Kraepelin (1908a), and predominant in Eremobatidae, is also observed in *Biton* (Daesiidae) and *Gylippus* Simon, 1879 (Gylippinae).

The limited data available do not suggest an obvious connection between reduced male dentition and any aspect of mating, including behavior, which risks injuring females. Alternatively, reduced dentition may limit injury to males during mating. Hrušková-Martišová et al. (2010a: 95, fig. 3) reported that some teeth, including the terminal teeth, of a male daesiid broke off during post-insemination behavior. In such comparisons it should be noted, however, that behavioral observations remain subjective, and descriptions are unstandardized between studies. For example, what is meant by “deep” if the finger is reported to be inserted deeply into the female genital tract? Reports of mating behavior may, therefore, not be fully comparable.

Although the psammophilous, fossorial adaptations of Hexisopodidae are reflected in their chelicerae, habitat alone is insufficient to explain the modified dentition of males. As both sexes are fossorial and thus subjected to similar selection pressures, the sexual dimorphism of dentition is probably related to reproductive behavior, which may involve encircling the entire body of the female with the greatly curved fixed and movable fingers and reduced dentition, during the somatic copulatory phase (Pls. 126-130).

In contrast to the widespread pattern of reduced male dentition, some males possess additional toothlike structures or some exceptionally enlarged, rather than reduced, teeth. Examples of subterminal flanges distal to the distal (FD and/or MD) teeth are observed in various species of *Solpugema* (Pl. 109F) and *Blossia* Simon, 1880 (Pl. 144C–F). Examples of exceptionally large teeth are observed mostly in Daesiidae, and usually restricted to the movable finger, e.g., in *Biton* (*B.*) *truncatidens*

(Pl. 137C), the FM tooth appears to close into the large, concave MM tooth. The functions of these modifications are unknown, and remain rare with movable finger dentition usually fairly conserved in male solifuges.

TAXONOMIC DIVERSITY OF CHELICERAL DENTITION

AMMOTRECHIDAE: The typical ammotrechid fixed finger possesses three distinct primary teeth and a single submedial tooth (Pls. 23W, X, 24L, M, 25M, 146–148, 149A–D, 150, 153G, H). A subdistal tooth may be absent or present. A movable finger prolateral (MPL) tooth may also be present (e.g., Pl. 147E; Muma, 1951; Maury, 1984). As with cheliceral shape, however, sexual dimorphism in ammotrechid dentition varies from weak to strong, depending on the species, and concerns the size and positions of teeth. Examples of such dimorphism include vestigial teeth associated with a finger that approaches a stylet in shape, e.g., *Ammotrechula mulaiki* Muma, 1951; a distinct, albeit weakly developed medial notch, e.g., *Branchia angustus* Muma, 1951; and a proximal shift in the teeth of the median series, e.g., *Procleobis patagonicus* (Holmberg, 1876) (Fig. 7D, Pl. 150C; Muma, 1951: 131, figs. 291–292; Muma, 1951: 136, fig. 305).

CEROMIDAE: The pattern of dentition in Ceromidae is complicated (Pls. 23O, P, 24D, 25E, 91–96) and emphasizes the importance of comparison between sexes and among taxa (criterion 4; Appendix 3), inference based on large series, and the need to identify dentition from specimens rather than images. Roewer (1934: 323) recognized the three primary teeth on the fixed finger of male *Ceromella* Roewer, 1933, an interpretation adopted in the present study (Pl. 95), but interpreted the fixed (dorsal) finger dentition of *Ceroma*, as “two anterior teeth” (FD and FM), situated directly distal to the fondal teeth, implying the absence of secondary teeth (FSD and FSM) and a proximal (FP) tooth (Pl. 92B). Two alternative interpretations of fixed finger dentition are therefore (i) two large, similar, distally situated FP and FM teeth, with the FD tooth absent (Pl. 92B) or (ii) two large, similar, distally situated FM and FD teeth, with a small, insignificant FP tooth situated proximally (Pl. 92C). The more conserved dentition of the female of *Ceroma inerme* (Pl. 92D, E) and the related *Ceromella* (Pl. 95) supports the second interpretation (Pl. 92C, indicated with a check mark) rather than the first (Pl. 92B, indicated with an X). The absence of a proximal (FP) tooth, together with the presence of the medial (FM) and distal (FD) teeth on the fixed finger, contradicts corollary 2 of criterion 1 (Appendix 3), and further supports the second interpretation. Roewer’s (1934) interpretation of the dentition of *Ceroma* is therefore dismissed and the second interpretation applied to other ceromid species (Pls. 93, 94).

The movable (ventral) finger dentition was fairly conserved in *Ceroma inerme* and the *Ceromella* species examined during the present study. Distinct, movable finger proximal (MP) and medial (MM) teeth are separated by a small submedial (MSM) tooth (Pls. 92, 95). A prominent prolateral flange-like carina, described by Purcell (1899: 399) as “inner keel sub-dentiform,” parallel to a pronounced raised, flange-like cutting edge, is situated distal to the MM tooth. This pair of carinae distal to the MM tooth creates a deep sulcus (Purcell, 1899). The movable finger dentition of *Ceroma swierstrae* Lawrence, 1935 (Pls. 91G, H, 94) and, to a greater extent, *Ceroma ornatum* Karsch, 1885 (Pls. 91E, F, 93) is more complicated, and two interpretations are proposed: (i) an MP tooth and a modified, bicuspid MM tooth, separated by a secondary tooth of similar size, and without a flange distal to the MM tooth (Pl. 94E) or (ii) MP and MM teeth of similar size, not separated by a secondary tooth, and situated proximal to a toothlike structure comprising a compressed, prolateral flange-like carina parallel to an equally compressed, raised, flange-like cutting edge (Pl. 94B). The first interpretation, according to which the distalmost structure is interpreted as a modified MM tooth rather than as parallel flange-like carinae, is less parsimonious as it implies firstly that the submedial tooth is approximately the same size as the primary tooth, whereas the pattern in other ceromids suggests a greatly reduced secondary tooth, and secondly that the flange-like carinae have either been lost or fused with an MM tooth. The second interpretation, according to which the MP and MM teeth are situated proximal to a flange-like carina, agrees with the more conserved dentition patterns of other ceromids and is therefore followed here (Pl. 94B, indicated with a check mark, over Pl. 94E, indicated with a X). This interpretation implies absence of the submedial (MSM) tooth, which is consistent with the observation that the secondary teeth are more labile. For example, an MSM tooth was recorded on only one chelicera in one of the two *Ceroma inerme* males examined by Purcell (1899: 396, fig. 14). Both Purcell (1899: 396, fig. 14) and Roewer (1934: 324, fig. 238c) illustrated the *C. inerme* chelicera without an MSM tooth.

The typical ceromid dentition, excluding *Toreus*, the taxonomic affinities of which are uncertain (Appendix 1), therefore comprises a relatively small to moderately sized fixed finger proximal (FP) tooth compared to the larger medial (FM) and distal (FD) teeth which are identical in size and shape. Secondary teeth are commonly absent on the fixed finger. The movable finger dentition comprises a proximal (MP) tooth and a similar or slightly smaller medial (MM) tooth, sometimes separated by an insignificant, submedial (MSM) tooth (Table 8). Distinct parallel flange-like carinae, situated distal to the MM tooth, one on the prolateral surface and another on the cutting edge, together forming a sulcus, are characteristic of *Ceroma* and *Ceromella*. The abovementioned interpretations differ from previously published opinions that the tooth, interpreted here as the FP tooth, belongs to the retrofondal (RF) series, and the flange-like carinae on the movable finger represent a modified MM tooth in some species (Purcell, 1899; Roewer, 1934: 323; Wharton, 1981).

The FP tooth of ceromids, especially *Ceroma*, is small in comparison to the rather large FM and FD teeth, an unusual pattern for Solifugae, in which the FP tooth is usually the largest on the finger. The primary teeth are easier to distinguish in *Ceromella*, although they are relatively small, because the FM and FD primary teeth are not as enlarged and the size difference between them and the FP tooth is therefore less distinct.

A transition appears to be evident from a relatively conserved pattern, with distinct flanges situated distal to the FM tooth, e.g., *C. inerme*, to an increasingly proximal shift in the flange-like carinae, e.g., *C. swierstrae*, and ultimately a pattern in which the carinae are greatly compressed and situated close to the movable finger median series teeth, superficially resembling a bicuspid tooth instead of parallel flange-like carinae, e.g., *C. ornatum*. The proximal shift of the two carinae in *C. ornatum* might be associated with the short chelicera and, particularly, the short movable finger of this species.

DAESIIDAE EXCLUDING NAMIBESIINAE, *SYNDAESIA* AND *AMMOTRECHELIS*: Given the diverse cheliceral morphology of Daesiidae, often involving remarkable modifications (e.g., Pl. 137), only the most prominent and potentially problematic patterns are discussed here (Pls. 23S–V, 24K, 25L, 132I, J, 135–145). Based on a survey of the literature, fixed finger subdistal (FSD) teeth and a second submedial (FSM) tooth are rare in the family, with few exceptions (e.g., Pl. 143D, E; Table 8). Wharton (1981) questioned the stability of a second FSM tooth in *Biton* (*B.*) *pearsoni* Hewitt, 1914, used by Hewitt (1914a) to distinguish this species from others in the *hottentottus* group.

Hemiblossia, a termitophagous genus, is unusual among Daesiidae due to the limited modification of its dentition, especially in the *australis* group (Pl. 139I, J). Male *Hemiblossia* possess a relatively conserved pattern of pronounced teeth (Pls. 139G–J, 141, 142A–D). The medial (FM) and distal (FD) teeth of the fixed finger are similar in shape, and slightly larger than the proximal (FP) tooth in the *bouvieri* group (Pl. 139G, H, 141,142).

Extremely modified chelicerae confound hypotheses of dental homology in two species of Daesiidae. The chelicerae of *Gnosippus klunzingeri* appears to be adapted for burrowing (Pls. 136C, D, 137A, B) although the female chelicera and dentition remain unmodified (Kraepelin, 1901). The teeth of the movable finger are greatly enlarged, the terminal (FT) and distal (FD) teeth of the fixed finger flattened and scoop-like, with a cheliceral projection prodorsal to the terminal tooth, referred to by Kraepelin (1908a) as a forked fixed finger. The fixed finger of the unique chelicerae of *Ceratobiton styloceros* is greatly elongated to form a long, slender distal projection, with the FD tooth situated approximately medially on the projection, and aligned with the apex of the movable finger (Pl. 137D).

Biton is a speciose genus, expressing some of the most highly modified dentition in Solifugae (for examples see Roewer, 1934: 389, figs. 275–279). In some species the FD tooth is flange-like rather than toothlike (e.g., Pls. 136F, J, 143H, I, J). Other notable modifications include an extremely large, modified movable finger medial (MM) tooth, as in *B.* (*B.*) *crassidens* Lawrence, 1935, *B.* (*B.*) *ragazzii* (Kraepelin, 1899), *B.* (*B.*) *simoni* (Kraepelin, 1899) and *B.* (*B.*) *truncatidens* (*vide* Kraepelin, 1899: pl. 1, fig. 12a, 13; Lawrence, 1935a: 72, fig. 1a; Lawrence, 1954: 115, fig. 3D; Delle Cave and Simonetta, 1971: 50, fig. 4) and a ventrally concave mucron of the fixed finger, with the teeth situated on the prolateral margin as in *B.* (*B.*) *zederbaueri*, *B.* (*B.*) *ehrenbergi*, and *B.* (*B.*) *bellulus* (Pocock, 1902) (see Pl. 139B; Kraepelin, 1901: 96, fig. 66; Roewer, 1934: 389, fig. 275c). The primary teeth are often reported as absent in *Biton* (e.g., Roewer, 1934: 389, fig. 275) but should be re-examined for primary teeth reduced to denticles as recognized, e.g., by Lawrence (1962: 197), regarding *B.* (*B.*) *tenuifalcis* Lawrence, 1962: “[a]nterior teeth of dorsal jaw absent or represented in front of the first tooth by 2 or 3 obsolete, indistinct granules.” In other *Biton* species, only the FD tooth is greatly reduced, e.g., in *Gluvia dorsalis* (Pl. 135A).

In several southern African *Blossia* species, additional flange-like or small toothlike structures, often characterizing species groups or subgroups (Hewitt, 1919b; Wharton, 1981), are present on the cutting sufaces of the mucron distal to the fixed finger distal (FD) tooth and/or the movable finger medial (MM) tooth (Pls. 144, 145). Applying the homology criteria for dentition (Appendix 3) suggests that these structures do not belong to any of the usual primary teeth hence they are termed subterminal flanges (STF), similar to, but more toothlike than, those on, e.g., the ceromid movable finger mucron.

In the *setifera* group of *Blossia* (e.g., Pl. 144E), a flange on the cutting edge of the movable finger with a prolateral lamelliform carina situated parallel to it ("median lamella" *sensu* Wharton, 1981: 20), both situated distal to the movable finger medial tooth (MM), resemble an additional bicuspid tooth. This structure has been variously described as a bifid fourth tooth on the movable finger, e.g., *B. filicornis* Hewitt, 1914, *B. pringlei* (Lamoral, 1974), and *B. setifera* Pocock, 1900 (Pocock, 1900a: 302, fig. 6a; Hewitt, 1914a: 158, fig. 21; Lamoral, 1974: fig. 2); as a fourth "obsolete" tooth "with a transparent lamina on the outer side of the jaw," e.g., *B. lapidicola* (Lawrence, 1935) (*vide* Lawrence, 1935a: 75, fig. 3); as part of the distal tooth forming a single trifid tooth, e.g., *B. falcifera* Kraepelin, 1908 (*vide* Kraepelin, 1908 b); or as a cleft lamella distal to the median series, e.g., *B. singularis* Lawrence, 1965 (*vide* Lawrence, 1965a: 56, fig. 3A). Further examples of taxa possessing this structure include *Blossia echinata*, *B. lapidicola*, *B. orangica* (Lawrence, 1935), *B. rooica* Wharton, 1981, *B. singularis*, and various subspecies of *B. falcifera* (Pls. 144E, 145E; Purcell, 1903b: pl. 1, fig. 10; Lawrence, 1935a: 80, figs. 6, 7, 8; 1965a: 56, fig. 3A).

Additional toothlike subterminal flanges may be present on the fixed or movable fingers, distal to the FD and MM teeth, respectively, in some species of the *crepidulifera* group of *Blossia* (Roewer, 1934: 359; Wharton 1981). These structures may form a rounded to "talus-like" prominence on the movable finger (Lawrence, 1929: 171). Examples of species possessing this structure include *B. alticursor* Lawrence, 1929, *B. crepidulifera* Purcell, 1902, *B. litoralis* Purcell, 1903, *B. planicursor* Wharton, 1981, and *B. scapicornis* (Lawrence, 1972) (Purcell, 1902: 215, fig. 4; 1903a: 5, fig. 3; Lawrence, 1929: 171, fig. 14; 1972: 115, fig. 5D; Wharton, 1981: 24, fig. 23). The subterminal flange on the cutting edge of the fixed finger is usually toothlike. Examples of species possessing this structure include *B. alticursor*, *B. crepidulifera*, and *B. planicursor* (*vide* Purcell, 1902: 214, fig. 4; Lawrence, 1929: 171, fig. 14; Wharton, 1981: 24, fig. 23). A parallel, prolateral toothlike carina may be present adjacent to the flange, e.g., in *B. litoralis* (Purcell: 1903a: 5, fig. 3).

In the *tricolor* group of *Blossia*, a subterminal flange on the cutting edge of the fixed finger, resembling a small tooth or tubercle, is present in *B. gaerdesi* (Lawrence, 1972), *B. purpurea* Wharton, 1981, *B. spinicornis* Lawrence, 1928) and *B. tricolor* Hewitt, 1914 (Pls. 144B, D, 145B, D; Hewitt, 1914a: 157, fig. 20; Lawrence, 1928: pl. 23, fig. 49; 1972: 114, fig. 4f; Wharton, 1981: 23, fig. 17).

Some *Blossia* species, such as those belonging to the *namaquensis* group and a few others of uncertain affinity (Wharton, 1981), e.g., *B. grandicornis* Lawrence, 1929, do not possess flange-like or toothlike structures in addition to the usual primary teeth (Pl. 139D).

DAESIIDAE (NAMIBESIINAE, *SYNDAESIA* AND *AMMOTRECHELIS*): *Namibesia pallida* is unique among Daesiidae in several of cheliceral characters, including dentition (Pls. 24I, 25J, 132A–D, 133) and was therefore assigned to a monobasic subfamily, Namibesiinae Wharton, 1981. The movable finger dentition is unmodified in both sexes, with a single movable finger submedial (MSM) tooth situated between pronounced proximal (MP) and medial (MM) teeth. However, an unusually large number of secondary teeth (FSM, FSD) are present on the fixed finger in both sexes. The male and female examined each possessed three fixed finger subdistal (FSD) and one (male) or two (female) fixed finger medial (FSM) teeth (Pl. 133). These counts fall within the range of two or three subdistal (FSD) and submedial (FSM) teeth reported by Maury (1985) for one male and three females, the three submedial and three subdistal teeth reported by Lawrence (1962a: 216) for *N. purpurea* Lawrence, 1962 (currently in synonymy with *N. pallida*), who noted that "one of these intermediate teeth may be extremely small, granuliform or absent, but usually 9 teeth in all," and the average of four secondary teeth on the fixed finger (*N* = 11 males; range of secondary teeth three to six) reported by Wharton (1981: 40, fig. 35).

The male chelicera of *Ammotrechelis goetschi*, another enigmatic, monobasic daesiid species is modified in various respects, but dentition remains readily identifiable (Pls. 24J, 25K, 132E–H, 134). The female dentition of this species is the typical plesiomorphic condition with a single submedial tooth (FSM, MSM) on the fixed and movable fingers. The same pattern is evident in males, although more reduced. In males, the movable finger bears distinct proximal (MP) and medial (MM) teeth separated by a small submedial (MSM) tooth. The MM tooth is a bicuspid (Pl. 134A), parallel and retrolateral to which is situated an additional granular tubercle, approximately within the row of granules running retrolaterally along the finger (Pl. 134B, D, arrows). Maury's (1985: 5, fig. 3) figure of a *Syndaesia mastix* Maury, 1980 male indicates similar structures, i.e., a bicuspid movable finger medial (MM) tooth and a blunt, granular process (the *diente parietal externo* of Maury, 1980a: 62), situated retrolateral to the MM tooth, suggesting that *Syndaesia* and *Ammotrechelis* may be closely related. Unfortunately, specimens of *Syndaesia* were unavailable for examination.

EREMOBATIDAE: Eremobatid dentition (Pls. 24O, 25P, Q, 65–84) are strongly modified in males, while females exhibit well defined dentition patterns, often with additional secondary teeth. Secondary teeth increase in size proximally within each category (Pl. 24O; Table 6). Greatly reduced or absent median series teeth and pronounced fondal teeth are common in males. Weak basifondal (BF) teeth are present in some taxa (Pl. 84C, D, I, J). The retrofondal row (RF) commonly terminates in bead-like crenulations on the basal fondal margin. A movable finger prolateral (MPL) tooth is often present, regardless of sex (e.g., Pl. 66C).

The typical eremobatid dentition as exemplified by females includes one or two movable finger submedial (MSM) teeth, one fixed finger subdistal (FSD) tooth, two fixed finger submedial (FSM) teeth and one or two retrofondal apical (RFA) teeth (Table 8). The absence of a fixed finger distal (FD) tooth and the presence of “one [intermediate tooth] in front of the medial tooth” was previously indicated as a diagnostic character for the *magnus* group of *Eremorhax* Roewer, 1934 (*vide* Muma, 1951: 43). Species with a distinct FD tooth formerly accommodated within *Eremorhax* are currently placed in *Eremocosta* (see Harvey, 2002a) resulting in “FD absent” as a diagnostic character for *Eremorhax* (*vide* Brookhart and Brookhart, 2006: 301). As interpreted in the present study, the “intermediate tooth” in question is a reduced distal (FD) tooth, and the diagnostic character is therefore revised to FD tooth reduced, not absent, as in *Eremorhax magnus* (Hancock, 1888) (Pl. 72H). Some characters approaching the multidentate condition are often observed in eremobatid females. These include a row of indistinct (e.g., Pl. 67D) to pronounced (e.g., Pl. 70J) crenulations, referred to as *Sägezänchen* (saw denticles) by Roewer (1934: 571) situated on the fixed and movable finger mucra, proximal to the MP tooth, and an increased number of secondary (FSD, FSM, MSM) teeth (Muma, 1951: 39) and retrofondal (RF) teeth.

Fixed finger median series dentition reduced or absent, with four large, distinct retrofondal (RFM, RFSM, RFP, RFSP) teeth is typical of most eremobatid males (FIg. 25P). The retrofondal (RF) teeth decrease in size proximally, such that the retrofondal proximal (RFP) tooth are smaller than the RFM and RFSM in many males, especially in *Eremobates* and *Eremochelis* (Pl. 78B). Other typical characters are a large movable finger proximal (MP) tooth with a distinct submedial (MSM) tooth distally at the base of the MP tooth, and the movable finger medial (MM) tooth almost absent, or modified and flange-like in males (Pls. 65, 67, 68). Although the absence of an MM tooth violates corollary 1 of criterion 1 (Appendix 3), the identification of a small submedial (FSM) tooth (not an MM tooth) at the distal base of the proximal (MP) tooth is supported by comparisons of congeners bearing distinct MM and MSM teeth, similarly arranged at the base of the MP tooth, e.g., *Eremobates pallipes* (Say, 1823) (Pl. 68F). The pattern of dentition in males is corroborated by that in females (Pl. 68F). The position of the MSM tooth at the base of the MP tooth or on the margin of the MP tooth itself (e.g., Muma 1951: 68, fig. 95) indicates that it is a secondary tooth rather than a primary tooth. This interpretation of the eremobatid dentition agrees with the literature (e.g., Fichter, 1941; Muma, 1951). An additional process, situated distal to the MM tooth on the cutting edge of the movable finger is evident in some males, e.g., *Eremocosta gigas* Roewer, 1934 as *Eremorhax gigas*, *Eremocosta striata* (Putnam, 1883) as *Eremorhax striatus*, and *Eremochelis imperalis* (Muma, 1951) as *Therobates imperialis* (Muma, 1951: 46, fig. 26; 46, fig. 32; 95, fig. 174, 175).

The retrofondal (RF) teeth often appear to include additional retrofondal teeth between the retrofondal medial (RFM) and fixed finger proximal (FP) teeth in males and females. These are situated on the cutting edge and often show greater similarity in sclerotization and shape with the median series than the fondal series (e.g., Pl. 70, 71). These teeth were interpreted as fixed finger subproximal (FSP) teeth by Muma (1951: 47) and Brookhart and Cushing (2004: 285, 286), but are referred to here as retrofondal apical (RFA) teeth (see Fondal Teeth, Fixed Finger under Terminology).

Small teeth and denticles are situated in the fondal notch in many eremobatid males (Pls. 2B, 4E, 84G, H). These denticles are either ignored in the literature (e.g., Fichter, 1941) or referred to without being assigned to specific categories, e.g., described as “modified teeth in the fondal notch” (Muma, 1951: 61, 108), “aborted teeth of the fixed finger” (Muma, 1951: 108), “supernumerary teeth” (Brookhart and Muma, 1981), or “accessory teeth” (Brookhart and Muma, 1987). According to Muma (1951: 108), Roewer (1934: 570) mistakenly interpreted these denticles as teeth of the retrofondal series. The affinities of the fondal notch denticles remain ambiguous, however. These denticles may be reduced primary teeth that shifted proximally, reduced fondal teeth, subproximal secondary teeth, or additional denticle-like teeth without homologs in females or non-eremobatids. Their identity has implications for the position of the fondal notch relative to particular teeth, and therefore whether the fondal notch of eremobatids is homologous with the medial notch of other taxa (e.g., *Solpugema*). The presence, in some eremobatid males, of highly vestigial, equally spaced primary teeth along the length of the stylet of the fixed finger, e.g., *Eremochelis albaventralis* Brookhart & Cushing, 2005 and *Eremochelis andreasana* (Muma, 1962) (Pl. 76C, D), does not support the hypothesis that the primary teeth shifted proximally, regardless of the extent of modification of the fixed finger, therefore rejecting the hypothesis that the fondal notch denticles are reduced primary teeth. This is further supported by the coincidence of vestigial primary teeth together with the fondal notch denticles (e.g., Pls. 76C, 77D). Whether the denticles in the fondal notch are homologous to the retrofondal apical (RFA) teeth in females, or independently derived serially homologous apical teeth, remains unclear, however. Although usually exceeding the maximum number of two RFA teeth recorded in females, the fondal notch teeth and denticles of males are similar positionally to the RFA teeth in females. Until evidence is available to the contrary, the fondal notch teeth/denticles are considered to be retrofondal apical (RFA) teeth. It seems clear, however, that they do not include the primary teeth of the median series on the fixed finger. Consequently, it may be concluded that the fondal notch of eremobatids (Fig. 7A, B) is not homologous with the medial notch in, e.g., Ammotrechidae and Solpugidae (Fig. 7C, D).

GALEODIDAE: The teeth on the fixed (dorsal) finger of male Galeodidae usually appear worn, often merging into a low, crenulate margin, or “lobulate crest” (Pls. 62B, 63A; Pocock, 1900b; Kraepelin, 1908a). Even when “weak or almost obsolete” (Pocock, 1900b: 136), individual teeth may be identified in most species, especially by application of the criteria in Appendix 3.

The typical galeodid dentition (PLS. 23M, N, 24C, 25D, 59–63, 64K, L) comprises all primary teeth and one or two submedial (FSM) teeth and a single subdistal (FSD) tooth on the fixed finger (Table 8). In males, the FSD tooth may be difficult to distinguish from the FD and FM teeth when all three are reduced to a crenulate margin. One to four submedial (MSM) teeth occur on the movable finger (e.g., Roewer, 1934: 511, 521;

Birula, 1938: 116, fig. 75) which is a large number for a taxon that does not display any multidentate characters. Both the FSM and MSM teeth increase in size proximally (Table 6). Panouse (1964) observed that the number of fondal teeth in both sexes of *Othoes* species is stable interspecifically, with two teeth in the profondal (PF) series and four in the retrofondal (RF) series, the latter including a small proximal tooth on the basifondal margin. The same pattern was observed in *Galeodes* and *Paragaleodes* Kraepelin, 1899 specimens examined during the present study. The basifondal (BF) teeth of galeodids are relatively well developed (Pl. 64K, L; Panouse 1964: 51, fig. 1). Unlike male dentition, female dentition in galeodids remains distinctly differentiated, but wear may be very pronounced in older specimens (Pl. 60E).

Galeodid dentition patterns were incorporated in species diagnoses by various authors (e.g., Caporiacco, 1944) and rigidly applied by Roewer (1934: 509), who regarded the number of secondary teeth as a criterion for separating species, a view largely abandoned by later authors (e.g., Turk, 1960), as here. The general uniformity in galeodid chelicerae (Panouse, 1964) has resulted in a limited number of illustrations and often very broad descriptions. Consequently, the literature was of limited utility for evaluating dentition patterns or comparison with material examined in the present study.

GYLIPPIDAE (GYLIPPINAE): In Gylippinae a distinct dentition pattern is evident (Pls. 23G, H, 24E, 25F, 85A–F, 85, A, B). The male chelicerae of central Asian *Gylippus* and *Acanthogylippus* Birula, 1913 superficially resemble those of typical male Eremobatidae in shape of the manus and fixed (dorsal) finger, vertical position of the fondal teeth, and reduced dentition on the fixed finger. A fixed finger proximal (FP) tooth is evident in *Gylippus* (*P.*) *monoceros* Werner, 1905, with a distinct, but smaller tooth situated distal to, and directly adjacent to the FP tooth, at its base. Two reduced teeth, barely visible in *G.* (*P.*) *monoceros*, are situated distal to these two teeth. Patterns of dental overlap suggest that these reduced teeth are the fixed finger medial (FM) and fixed finger distal (FD) teeth (Pl. 86C, D). This is supported by juvenile and female dentition patterns (e.g., Pl. 85C–F), in which regular FP and FM teeth are present on the fixed finger, separated by a small submedial (FSM) tooth situated close to the FP tooth and resembling the tooth at the base of the FP tooth in males. The latter tooth is therefore referred to as the fixed finger submedial (FSM) tooth, which is in a position that suggests homology with the FSM tooth situated in a similar position in many male Solpugidae (e.g., Pl. 109). This fixed finger dentition pattern comprising a distinct FP tooth with a distinct FSM tooth at its base, and with vestigial FM and FD teeth situated distal to the FSM tooth, is typical of Gylippinae (e.g., Roewer, 1934: 311–318; Birula, 1938; Gromov, 1998).

GYLIPPIDAE (LIPOPHAGINAE): The dentition of Lipophaginae (Pls. 23I–L, 24F, 25G, 87–89, 90C–F) is complex and challenging to interpret, for several reasons. An unusually large retrofondal proximal (RFP) tooth, often similar to or larger than the primary teeth (e.g., Wharton, 1981) may be synapomorphic for lipophagines. In addition, the similar size of the fixed finger proximal (FP) tooth and the apical tooth in the retrofondal (RF) row, and the closure of both of teeth distal to the movable finger proximal (MP) tooth, obscures the boundary between the median and fondal series, as observed by Wharton (1981: 39), who stated “apical teeth in outer cheek series not readily distinguishable from main series in some species.” Another perculiar structure is the large structure situated distally on the modified fixed finger of *Trichotoma michaelseni*, which may be interpreted in different ways (cf. Pl. 88B and 88C). The traditional interpretation of the large distal structure on the cutting edge of the fixed finger as a large, distally directed distal tooth (e.g., Roewer, 1941; Wharton, 1981), is illustrated in Pl. 88B (indicated with a X). In the present study, this structure is reinterpreted as the terminal tooth at the tip of the fixed finger, with a dorsal hornlike process fused to the dorsal surface of the fixed finger (Pl. 88C, indicated with a check mark). This interpretation is briefly discussed, with the teeth and toothlike structures labeled 1–6 from distal to proximal on the illustration of the chelicera of the male *T. michaelseni* (Pl. 88B). Teeth 3, 5 and 6 are similar in size, with 3 and 5 separated by a small tooth (4). Patterns of overlap with teeth of the movable finger (criterion 3) suggest that tooth 6 is the FP tooth. This interpretation disagrees, however, with the conserved pattern of the relative size and number of teeth observed in both the median and fondal series of the female. The most parsimonious interpretation is therefore that tooth 5, rather than 6, is the FP. This differs from previous interpretations which identified tooth 6 as part of the median series (e.g., Wharton, 1981).

Having identified the FP tooth, the remaining teeth of the median series are readily identified in most species except *T. michaelseni*, for which two alternative hypotheses may be considered: (i) tooth 2 is a subdistal secondary (FSD) tooth and structure 1 is a large distally directed distal (FD) tooth (Pl. 88B) or (ii) tooth 2 is an FD tooth and structure 1 a large distally projecting process in addition to the regular teeth of the median series (Pl. 88C). Neither hypothesis is supported by the pattern of dental overlap (criterion 3) but the second hypothesis is consistent with the female dentition of *T. michaelseni* and *T. brunnea* (Pl. 88F, G) and is therefore adopted in the present study. This hypothesis is further supported by an observation of Wharton (1981) that the submedial tooth was absent in one of the four males examined. If tooth 2 is interpreted as a subdistal tooth, this would imply that a subdistal tooth was present in the absence of a submedial tooth, a pattern not observed in the present study. According to this reinterpretation, the structure previously identified as a large distally directed distal tooth in *T. michaelseni* (Kraepelin 1914: 132; Hewitt, 1919b: 65; Roewer, 1941: 115) and *T. fusca* Roewer, 1941 (Wharton, 1981: 43) is actually the fixed finger terminal (FT) tooth, i.e. the apex of the fixed finger, the tooth traditionally identified as a secondary (FSD) tooth is the distal (FD) tooth (Pl. 88C), and what appears to be the apex of the fixed finger is a cuticular outgrowth of the dorsal surface of the chelicera, similar to the dorsal hornlike processes on the fixed fingers of male Karschiidae. The conclusion that the apparent “apex” of the fixed finger is a separate structure, fused to the dorsal surface of the finger is further supported by the presence of a longitudinal groove separating it from the main tooth on the pro- and retrolateral sides. Further support is provided by the ventral surface of the terminal tooth (FT) which possesses the typical cutting edge carina flanked by the pro- and retrofondal carinae characteristic of the mucra of the fingers whereas the fused hornlike process is smooth all around. According to this interpretation, the diagnostic character separating *Lipophaga* and *Trichotoma* is therefore not a smaller distal tooth (Wharton, 1981), but rather the absence of a hornlike process fused to the dorsal surface of the fixed finger.

It may therefore be concluded that the typical pattern of dentition in Lipophaginae includes a single FSM tooth and one (*Bdellophaga* and *Lipophaga*) or no (*Trichotoma*) FSD teeth on the fixed finger, and a single medial (MSM) tooth on the movable finger (Pls. 24F, 25G; Table 8).

HEXISOPODIDAE: No attempt has previously been made to identify or homologize the dentition of Hexisopodidae (Pls. 24B, 25C, 128–131). Male dentition is highly modified and reduced. Whereas the median series of the fixed finger is situated on a distinct, narrow cutting edge in all female and all non-hexisopodid male solifuges, the "cutting edge" of the fixed finger is a broad, blunt surface in male Hexisopodidae (Pl. 167C). In some males, two parallel teethlike rows are present, one at the base of the flagellum and another on the retrolateral surface. In addition to considerable intrinsic variation in the number of smaller teeth or denticles on both fingers, wear induced by burrowing may further contribute to intraspecific variation in dentition (e.g., Wharton, 1981).

Female dentition may assist in understanding the dentition of male hexisopodids. In females and juveniles, secondary teeth are absent on the fixed finger and, if present, vestigial on the movable finger (Pls. 126F–H, 128D–F). Although the dentition of females is more conserved than that of males, it is unique within the order in bearing a large medial tooth on both the fixed (FM) and movable (MM) fingers, which is at least twice the size of the other primary teeth on each finger.

As a consequence of what appears to be a proximal shift, the median series teeth of male hexisopodids are situated towards the fondal area. In the male *Chelypus hirsti*, three distinct primary teeth are situated close together near the base of the flagellum, towards the retrolateral side of the cutting edge (Pls. 129C–F, 130A–C). The hypothesized fixed finger medial (FM) tooth is the largest, in accordance with the patterns of females and juveniles. A smaller but distinct Fixed finger distal (FD) tooth is situated distal to the FM tooth, with three equally spaced subterminal (FST) denticles situated distal to that. Parallel to the "regular" teeth which are situated on the retrolateral side of the cutting edge, a prolateral toothlike ridge, referred to here as the **prolateral dental process (PLDP)**, is situated near the base of the flagellum (Pl. 130A). This prominent process, recognized by Hewitt (1931) as the functional row of teeth, restricts movement of the flagellum past a certain point of rotation. The positions of the primary teeth (on the retrolateral side of the cutting edge) and the presence of a dental process near the base of the flagellum (on the prolateral side of the cutting edge) were similar in other *Chelypus* species examined: *C. hirsti*, *C. lennoxae*, *C. shortridgei* Hewitt, 1931, and two unidentified species. The dentition was generally less developed in *C. shortridgei* (Pl. 129G, H), which differed further in the shape of the prolateral dental process. Manual rotation of the flagellum of the specimen revealed that the process completely prevents rotation past a certain point, suggesting that the dental process functions to prevent rotation and damage to the flagellum during burrowing.

The fixed finger dentition of male *Hexisopus* Karsch, 1879 species examined in the present study, i.e., *H. aureopilosus* Lawrence, 1968, *H. lanatus* (C.L. Koch, 1842), *H. moiseli* Lamoral, 1972, and *H. pusillus*, was more reduced than that observed in species of *Chelypus* (Pls. 127A, B, D, 128B, C). This may, however, not be true for all *Hexisopus* species, e.g., Wharton (1981: 48) described the dentition of the fixed (dorsal) finger of *H. fumosus* Lawrence, 1967 as "relatively well developed." Fixed finger primary teeth may be identified in *Hexisopus* by comparison with the positions of the primary teeth and the relative size of the FM tooth in *Chelypus*. A ridge-like process at the base of the flagellum, similar to the prolateral dental process (PLDP) of *Chelypus*, observed in all *Hexisopus* specimens examined, was variously referred to as a protuberance bearing teeth (e.g., Lamoral, 1972; Wharton, 1981) or as a single tooth (e.g., Wharton, 1981), and is interpreted here as homologous to the prolateral dental process (PLDP) in *Chelypus*. This dental process differs from the PLDP of *Chelypus* because it appears to be more distinctly composed of individual teeth (Fig. 2A, Pls. 2A, 127D) and does not appear to restrict movement of the flagellum. Also unlike *Chelypus*, no teeth are present on the retrolateral side of the broad cutting edge. It is hypothesized that the primary teeth of *Hexisopus* are situated on the prolateral side of the cutting edge, rather than on the retrolateral side as in *Chelypus*, and fused to the positionally homologous dental process (PLDP) of *Chelypus*. This hypothesis is supported by the observation that one tooth on the dental process of *Hexisopus* is more prominent, and situated in a similar position to the FM tooth of *Chelypus*, suggesting that it may be homologous with the FM tooth of *Chelypus*. The prolateral dental process (PLDP) appears to comprise many teeth, e.g., "...series of 3–6 small teeth on low ridge adjacent base of flagellum, number and size of teeth variable" (Wharton, 1981: 51), two of which are here interpreted as the FM and FP teeth.

One to three clearly identifiable teeth are present on the movable (ventral) finger of hexisopodids (Pls. 126D, E, 127E, 128A, 129, 130F, G; Wharton, 1981). *Hexisopus* males appear to possess fewer teeth, "at most two" compared to *Chelypus* males with "at least three," according to Wharton (1981: 45, 48), but these may be very reduced and the patterns and numbers of teeth are not always clear. A **prodorsal serrate carina** or **prodorsal granular tooth**, in *Chelypus* and *Hexisopus*, respectively, is slightly offset prolaterally from the cutting edge of the movable finger, and might prove to be synapomorphic for the respective genera, or at least species groups within these. The serrate carina of *Chelypus* is slightly more distally located with respect to the teeth on the cutting edge, and often situated parallel to a cutting edge serrate carina. The prodorsal serrate carina bears denticulate projections with various degrees of differentiation (Pl. 130F, G), which have been referred to as a “row of minute inner teeth” (Purcell, 1902: 225), “row of minute teeth forming serrate ridge,” or “inner side of lower jaw near fang tip with a row of 4 small teeth” (Lawrence, 1955: 173), “keel bearing four to six very small teeth” (Lamoral, 1973: 96), and “distally placed mesal row of denticles” (Wharton, 1981: 45). The status of this structure as a generic level diagnostic character (Wharton, 1981), and its homology among different species should be further examined. An additional granular tooth situated prodorsally opposite the medial (MM) tooth in some species of *Hexisopus* (Pls.127E, 128A; Wharton, 1981), was observed in all *Hexisopus* examined in the present study. Although usually referred to as a tooth, this structure is not homologous with the median series of the movable finger. Its position and granular character suggest that it is not homologous with the serrate prolateral carina of *Chelypus* either.

The two hexisopodid genera, *Chelypus* and *Hexisopus*, can therefore be separated based on two distinct characters of cheliceral dentition. In *Chelypus*, the median series on the fixed finger is situated on the retrolateral side of the cutting edge, parallel to a prolateral dental process (PLDP) at the base of the flagellum whereas, in *Hexisopus*, the median series teeth are hypothesized to be fused with the PLDP (Pl. 131). A prodorsal serrate carina or prodorsal granular tooth is present on the movable finger, in addition to the median series teeth, in *Chelypus* and *Hexisopus*, respectively.

A characteristic row of small, regularly spaced, bead-like denticles lining most of the ventral edge of the basal fondal margin may prove to be a unique synapomorphy for Hexisopodidae, although these denticles bear some resemblance to the serrations at the base of the eremobatid fondal series. Until evidence is presented to the contrary, these bead-like denticles are interpreted here as reduced retrofondal teeth (Pl. 131).

KARSCHIIDAE: Karschiidae (Pls. 23A–D, 24P, 25R, S, 50–55, 64A–H) contains species with truly multidentate chelicerae (Pl. 53), typified by male *Eusimonia*, and many species of *Karschia* with a tendency towards a multidentate condition. Fixed and movable finger subterminal (FST, MST) denticle-like teeth and movable finger subproximal (MSP) denticle-like teeth are common among karschiids, especially females (Pls. 50G, H, 51D, 52C, D). According to Gromov (1998a), the teeth of Karschiidae are of limited taxonomic value due to variation in number, size and shape within series. Gromov (2003a) therefore described the dental patterns of karschiids broadly, in terms of the range in number of teeth. Irrespective of whether Gromov's (1998a) assertion proves valid, it can only be evaluated when primary and secondary teeth are identified, a task more achievable for multidentate taxa than generally thought.

Roewer (1934: 296, fig. 223, reproduced in Pl. 28) apparently identified the primary teeth of female Karschiidae on the basis of size, and numbered them I–V. Based on relative size and sclerotization, and supported by reciprocal illumination of criteria 1–4 (Appendix 3), a different interpretation is proposed here for many of the species illustrated by Roewer, e.g., *Karschia* (*K.*) *mastigofera* Birula, 1890. For details, compare Roewer's (1934: 296) fig. 223K, reproduced and color coded in Pl. 28K with Pl. 51E.

The typical pattern in Karschiidae includes one or two subdistal (FSD) teeth and one or two submedial (FSM) teeth on the fixed finger. Additional labile, seemingly “randomly” situated denticles may be present in *Eusimonia* (Figs. 19, 20). Up to three FSM teeth can be present in *Karschia* (Birula, 1938: 57, 66, figs. 32, 42, 48). The most common pattern, however, is a single FSD tooth and two FSM teeth. Up to three movable finger submedial (MSM) teeth are present, although the MSM teeth of males are often reduced or indistinct (Table 8; Birula, 1938). Size gradations are evident in the secondary teeth on the fixed finger, which increase in size proximally, and the movable finger, which increase in size distally (Table 6). Unlike the pronounced profondal (PFM and PFP) teeth in multidentate Melanoblossiinae (Pl. 159), the profondal (PF) teeth tend to be reduced in multidentate Karschiidae (Pl. 64A–H). For example, examination of both chelicerae in three male specimens of *Eusimonia divina* revealed that the profondal teeth are absent in two, and represented by a single denticle in the third. The number of retrofondal (RF) teeth is generally at the upper end of the range for the order (Pls. 23A–D, 64A–H), but varies among species.

Female dentition is relatively similar among karschiid genera, but male dentition differs between *Karschia* and the other genera, *Barrus* Simon, 1880, *Barrussus* Roewer, 1928 and *Eusimonia* (Pls. 50–55). The primary, secondary and fondal teeth are more differentiated and the spacing among the teeth more irregular on the fixed finger in male *Karschia* (Pl. 50B, F), unlike the other genera, which exhibit a typical multidentate fixed finger.

MELANOBLOSSIIDAE (DINORHAXINAE): The fixed (dorsal) finger teeth of the male of *Dinorhax rostrumpsittaci* (Pls. 23d, 25A, 56A, B, 57A, B) are apically rounded, dome-shaped, and more distinctly differentiated than the dentition of the movable finger. The fixed finger proximal (FP) and medial (FM) teeth are readily recognized as primary teeth, but the FD tooth is reduced. The dentition on the movable finger comprises a sharp, jagged cutting edge; the distinct proximal toothlike structure probably represents the movable finger proximal (MP) tooth, and the vestigial distal tooth the movable finger medial (MM) tooth. The anterior surface of the MP tooth is notched to form a separate toothlike structure, the position of which resembles the characteristic placement of the submedial (MSM) tooth on the movable finger of male Eremobatidae, suggesting that it may be a precursor to the MSM tooth. Similarly, denticle-like serrations on the proximal surface of the MP tooth could be precursors to subproximal (MSP) teeth. The large, jagged MP tooth with a probable MSM tooth on its distal margin is similar to published illustrations (Simon, 1879: pl. 3, fig. 16; Kraepelin, 1901: 41, fig. 12). Differences include a more distinct MM tooth and two additional distinct submedial (MSM) teeth in the published illustrations, and might indicate intraspecific variation. The jagged movable finger cutting edge, combined with the dome-shaped fixed finger teeth are unique among Solifugae.

MELANOBLOSSIIDAE (MELANOBLOSSIINAE): Melanoblossiinae dentition (Pls. 23b, c, 24Q, R, 25T, U, 154–159) include the best examples of multidentate dentition, e.g., the fixed finger of female *Lawrencega minuta* Wharton, 1981 (Pls. 154L, 158F), and a tendency towards multidentate dentition, e.g., the subterminal (MST) denticles of female *Melanoblossia braunsi* (Pl. 155F), occur in Melanoblossiinae. The profondal (PF) teeth are more pronounced than the retrofondal (RF) teeth in melanoblossiines (Pl. 159), unlike karschiids which are multidentate or exhibit a tendency towards the multidentate condition, in which the retrofondal teeth (RF) are more pronounced. Although it may be difficult to distinguish between primary and secondary teeth in multidentate taxa, especially species in which teeth are absent on one of the fingers, structural and positional criteria (Appendix 3) may be applied to formulate hypotheses concerning the identity of the primary teeth as described above for Karschiidae. Criterion 1 (relative size and sclerotization) is the most useful for species in which teeth are absent on one of the fingers, e.g., the female of *L. minuta* (Pls. 154L, 158F).

Not all melanoblossiines are multidentate or display a tendency towards the multidentate condition, but male dentition remains challenging to understand, even in these taxa, as it is usually greatly reduced. The approach followed for identifying homologous teeth in melanoblossiine males is illustrated here in two species, i.e., *Melanoblossia braunsi* (Pl. 155, with teeth labelled 1–7) and an undescribed species of *Melanoblossia* (Pl. 156). The fixed finger dentition is much reduced in both species, and the movable finger dentition relatively distinct with a proximal (MP) tooth and a medial (MM) tooth separated by a smaller submedial (MSM) tooth. Homologous teeth on the fixed fingers of *M. braunsi* and *Melanoblossia* sp. may be identified by their unique morphology, cf. teeth 2, 3 and 4, which all resemble a fold in the surface of the laterally compressed finger, and tooth 6 that is distinctly pointed (Fig. 21A). Tooth 6 of *M. braunsi* is hypothesized to be the FP tooth, based on the pattern of overlap of the teeth on the fixed and movable fingers (Pl. 155D), and corroborated by the female dentition (Pl. 155F, G). In the *Melanoblossia* sp., however, the movable finger teeth are concentrated proximally on the finger, and the pattern of overlap suggests that 6 and 7 might be the FM and FP teeth, respectively (Pl. 156A, C). The dentition of *M. braunsi* is more conserved hence tooth 6 in the *Melanoblossia* sp. is more likely to be the FP tooth, despite closing far distal to the MP tooth. If the *Melanoblossia* sp. were examined without comparison to *M. braunsi*, tooth 7, rather than tooth 6, would seem more likely to be an FP tooth, emphasizing the value of taxonomic comparisons (criterion 4). Although the identification of primary teeth is difficult in melanoblossiines, it is possible to formulate hypotheses of dental homology, even in species with complex dentition, by reciprocal illumination of criteria outlined in the present study.

MUMMUCIIDAE: Mummuciidae dentition (Pls. 23Y–a, 24N, 25N, O, 26, 149E–H, 151, 152, 153I, J) display the usual compliment of primary teeth, although either the distal tooth on the fixed finger (FD), e.g., in *Mummucina colinalis* Kraus, 1966, or the medial tooth on the movable finger (MM), e.g., in *Mummucia mauryi* Rocha, 2001 may be reduced (Pl. 149F; Kraus, 1966: 183, figs. 2, 3; Xavier and Rocha, 2001: 130, fig 3). One or two submedial (FSM and MSM) teeth are present on the fixed and movable fingers. A subdistal tooth (FSD) may be present or absent (Pls. 26, 151–153). In a series of *Uspallata pulchra* males examined during the present study (Pls. 26, 152), the primary teeth were observed to be stable in position, size, and shape (e.g., consistent proximal curvature of the apices of individual teeth), with variation limited to the secondary and fondal teeth (see discussion under Intraspecific Variation in Dentition). Unlike Ammotrechidae, a movable finger prolateral (MPL) tooth is absent in Mummuciidae (Maury, 1984).

Mummuciidae includes species that share a tendency towards the multidentate condition, i.e., relative homogeneity in size of the primary and secondary teeth, and regular spacing between the teeth. Examples include *Mummucia coaraciandu*, *M. mendoza* Roewer, 1934, *M. taiete* Rocha and Carvalho, 2006, *Mummucina masculina*

Lawrence, 1954, and *Uspallata pulchra*. Besides sharing features similar to multidentate taxa, these species share similarities in the shape of the dentition, especially concerning the proximal curvature of the apices of individual teeth. Such similarities, evident, e.g., in *U. pulchra* (Pls. 26, 152) from Chile and *M. coaraciandu* from Brazil (Martins et al., 2004: 2365, fig. 3A), might be due to convergent evolution, perhaps related to microphagy, or to phylogenetic relationship, but this cannot be evaluated because mummuciid taxonomy is in disarray (Maury, 1998; Xavier and Rocha, 2001; Martins et al. 2004; Rocha and Carvalho, 2006; Botero-Trujillo, 2014).

RHAGODIDAE: The typical rhagodid dentition (Pls. 23E, F, 24A, 25B, 56C–H, 57C, D, 58, 64I, J) comprises all primary teeth, i.e., three teeth (FP, FM, FD) on the fixed finger and two teeth (MP, MM) on the movable finger. Whereas the proximal teeth are well developed on both fingers (FP, MP), the distal tooth on the fixed finger (FD) and the medial tooth on the movable finger (MM) are greatly reduced (Pl. 57C, D) or absent (e.g., Turk, 1960: 121, fig. 9). Due to its small size, the MM tooth superficially resembles a secondary tooth, but positional criteria, specifically the pattern of dental overlap (Pl. 58D) and corollaries of criterion 1 (secondary teeth are more likely to be absent than primary teeth) suggest that it is a primary tooth. The interpretation of a large MP tooth and a very small MM tooth as the only teeth on the movable finger is followed by most workers (e.g., Birula, 1905; Roewer, 1934: 264) but not all, e.g., Kraepelin (1901: 30). Consequently, secondary teeth are absent in rhagodids. Rhagodids possess five to seven retrofondal (RF) teeth (Pls. 23E, F, 64I, J). Individual RF teeth are readily homologized across the family. A few small, distinct basifondal medial (BFM) teeth are usually present (Pl. 64I, J; Pocock, 1889). A distinct prolateral (MPL) tooth occurs on the movable finger in both sexes of all species (Roewer, 1934: 264). As with Galeodidae, but to an even greater extent, the uniformity in rhagodid chelicerae has resulted in very few published illustrations, greatly limiting a literature survey of the dentition patterns in this family.

SOLPUGIDAE: Dentition in Solpugidae is relatively conserved compared to other Solifugae families (Pls. 23Q, R, 24G, H, 25H, I, 90G–L, 97–125). Sexual dimorphism varies from minor with dentition reduced in both sexes, e.g., *Solpugiba lineata* (Pl. 110A–D), through minor with dentition barely reduced in males, e.g., *Zeria sericea* (Pocock, 1897) (Pl. 116E–H), to major with dentition modified and greatly reduced in males, e.g., *Solpugista bicolor* (Pl. 110E–H). Modifications in male dentition concern the size, shape, and relative positions of teeth. Regardless of the extent of modification, however, five primary teeth are always present and easily identified, usually with some agreement in the number and relative sizes of teeth between sexes in many taxa, although there are exceptions.

The dentition on the movable (ventral) finger of Solpugidae comprises a proximal (MP) tooth and a medial (MM) tooth. The MM tooth is usually only slightly smaller than the MP tooth. One to three submedial (MSM) teeth separate the MP and MM teeth. The most common pattern on the movable finger is a single submedial (MSM) tooth (Table 8), situated closer and usually directly adjacent to the MP tooth. Two or three MSM teeth are present in a few species, e.g., *Solpuga bovicornis* Lawrence, 1929, *Zeria fusca* (C.L. Koch, 1842) and *Zeria zebrina* (Pocock, 1898) (Pl. 116D; Roewer 1934: 445, fig. 293a; 448, fig. 295b; 496, fig. 310d). In specimens with three MSM teeth, these secondary teeth are situated in a row along the distal margin of the MP tooth (Pls. 116D, 117C).

The typical dentition on the fixed finger of Solpugidae usually comprises one or sometimes two submedial (FSM) teeth and no (rarely one) subdistal (FSD) teeth (Table 8). For example, within a population of *Metasolpuga picta* (Kraepelin, 1899), Wharton (1981: 67) reported “at least one” small FSD tooth in 50% of females (*N* = 18). Wharton (1981) recorded variation in the fixed finger dentition of *Solpugista bicolor* (*N* = 12 females; *N* = 21 males) and observed one FSD tooth and two FSM teeth in all females and seven males, but with the second FSM tooth in males often restricted to one chelicera, one FSD tooth, and one FSM tooth in three males, and no FSD teeth and one FSM tooth in 11 males. The male depicted in Pl. 110F bears no FSD teeth and one FSM tooth, whereas the immature depicted in Pl. 110H displays the same pattern as the females reported by Wharton (1981). Sexual dimorphism in the “typical” dentition pattern therefore appears to be present in *S. bicolor*. The termitophagous *Solpugiba* Roewer, 1934 is unique among Solpugidae due to its large number of fixed finger secondary teeth. Both sexes of *Solpugiba lineata* depicted in the present study (Pls. 110A–D, 111) bear two FSD teeth and five FSM teeth, two of which are denticles. The counts for this species fall within the intrapopulation ranges of one to three FSD teeth, and two to four FSM teeth, reported by Wharton (1981). The additional denticles were found to be less common in seven juvenile *S. lineata*, five in the 3-malleoli stage, for which the most common pattern in the fixed finger median series was 1-(1)-1-(2)-1. Exceptions were present in two of these specimens. The second FSM tooth was absent from both chelicerae of one specimen whereas a denticle proximal to a larger FSD tooth was present on both chelicerae of a second specimen.

FSD teeth are rare in Solpugidae and usually comprises small, variable teeth or denticles. In the few species with more than one MSM or FSM teeth, these teeth increased in size distally in both categories (Table 6). Largely due to the presence of denticles in the FSM and FSD rows, no gradation in the size of the teeth within categories was observed in *S. lineata*, however.

Whereas the fixed finger proximal (FP) tooth is usually the largest, or nearly so, primary tooth on the fixed finger in Solifugae (but see Ceromidae and Hexisopodidae), the fixed finger medial (FM) tooth is often distinctly larger than the other primary teeth in the solpugid genus *Zeriassa*. The FM tooth is especially pronounced in females and juveniles (Pl. 124E,F). Simonetta and Delle Cave (1968: 171, fig. 6) also mentioned a large FM tooth in various species of *Zeriassa*. A similarly large FM tooth occurs in *Solpugisticella* Turk, 1960 (Pl. 124G, H) which appears to be closely related to *Zeriassa* (*vide* Turk, 1960).

A prolateral tooth on the movable finger (MPL) has only been recorded in a few solpugid species, i.e., the female of *Ferrandia robusta*, *Zeriassa furcicornis* Lawrence, 1929, and several species of *Solpugassa* Roewer, 1933 including *S. furcifera* (Kraepelin, 1899) and *S. rudebecki* Lawrence, 1961 (Pls. 104A, C, E, 105A, C, 124C, 125C; Roewer, 134: 429; Lawrence, 1954: 117, fig. 4C; Lawrence, 1961). An MPL tooth is absent in the male of *Z. furcicornis*. Wharton (1981) recorded an MPL tooth in a male *Solpugassa furcifera*, and a distinct MPL tooth was observed in females of this species in the present study (Pl. 104C).

Solpugema is characterized partly by the large toothless medial notch on the fixed finger (Roewer 1934: 420), between the proximal (FP) and submedial (FSM) teeth

(Fig. 7C). A typical dentition pattern associated with the medial notch is a large proximal (FP) tooth, situated directly proximal to a much smaller submedial (FSM) tooth, which is sometimes situated on the base of the FP tooth, e.g., *S. derbiana* Pocock, 1895 (Pl. 108F). The FP tooth and its associated FSM tooth are situated proximal on the finger, whereas the two distal primary teeth (FM and FD) are situated relatively close to one another, more distally towards the apex of the finger.

A small to significant subterminal flange (STF) is situated on the cutting edge of the fixed finger, towards the distal end of the mucron, in many *Solpugema* (Pls. 107A, 109B, D, E). This flange may resemble a tooth and is often interpreted as such (e.g., Kraepelin, 1900; Lawrence, 1931: 133). Application of the criteria in Appendix 3 suggests that this flange does not belong to the median series teeth. Kraepelin (1901: 61) also excluded it from the regular set of teeth and referred to it as an additional *Höckerzahn* [tooth cusp] in *Solpugema lateralis* (C.L. Koch, 1842).

SUMMARY OF DENTITION

The appearance of variation caused by wear, abnormalities, or misidentifications, should not be misconstrued as intrinsic (inherent) variation. Although relatively common in Solifugae, intrinsic variation in dentition or, occasionally, bilateral asymmetry in a single individual is largely predictable whereas wear, or abnormalitiesare usually random. Various authors recognized that secondary and fondal teeth are more likely to vary than primary teeth, but the extent of variation appears to be taxon-specific. The present contribution is the first to formally identify areas of variation in teeth and analyze where variation within categories can be expected, e.g., fondal teeth, primary teeth, and different categories of secondary teeth. Variation was found to be more common among secondary teeth and fondal teeth than among primary teeth, among small rather than large teeth, and, within the median series, among distal rather than proximal teeth. Within the sexes of any particular taxon, primary teeth appear to be largely stable in number, relative size, shape and, often, position, except when these teeth are mostly vestigial in that taxon, whereas some species also appear to have a greater propensity for variation than others. Although variable in size and number, fondal teeth were more consistent intraspecifically than expected based on the literature, with variation restricted largely to specific teeth, in particular the retrofondal submedial (RFSM), retrofondal subproximal (RFSP), profondal submedial (PFSM) and profondal subproximal (PFSP) teeth. Within categories of secondary teeth (FSM, FSD, MSM), teeth increase in size either distally or proximally, creating taxon-specific gradation patterns (Table 6). Recognizing these patterns within the FSM, FSD and MSM categories may be of value for evaluating variation among, and proposing hypotheses of primary homology for the secondary teeth.

Classifying teeth as primary, secondary and fondal, and evaluating each type independently for intrinsic variation (excluding wear and abnormalities) reveals more stable patterns than suggested in the literature, with implications for taxon diagnosis, species identification, and phylogenetic analysis. Except in rare cases, e.g., *Lawrencega minuta*, dentition of females is too conserved to provide sufficient characters for species, or even generic diagnosis. Unique patterns, in male but also female dentition have been identified in some or all members of certain families (Pls. 23, 24; Tables 6, 8), however, providing potentially informative higher-level characters, especially in conjunction with characters concerning cheliceral shape and size gradation patterns. Examples are the medial (FM and MM) teeth which are the most prominent primary teeth in Hexisopodidae (Pls. 126–130); a large retrofondal proximal (RFP) tooth, often larger than the primary teeth, in Lipophaginae (Pls. 87–89, 90C, D); tendency towards multidentate such as a greater number of secondary teeth and the presence of subterminal teeth on the mucra in some Eremobatidae (Pl. 70J); and the absence of secondary teeth in the main series combined with a larger number of fondal teeth in Rhagodidae (Pls. 56C–D, 58, 64I, J).

Taxon-specific trends, often applicable to both sexes, may be identified, including (i) the multidentate condition predominant in Melanoblossiinae and Karschiidae; (ii) the interspecifically uniform dentition and absence of secondary teeth in Rhagodidae; (iii) the “worn” appearance of the dentition of males in most species of Galeodidae; (iv) the tendency towards a multidentate condition, including a relatively large number of secondary teeth, in Eremobatidae; (v) two flange-like carinae with various degrees of modification, situated parallel to each other and distal to the movable finger medial (MM) tooth in male Ceromidae; and (vi) large, well developed fixed finger medial (FM) and movable finger medial (MM) teeth, relative to the other primary teeth, on both fingers, and a prolateral dental process (PLPD) in Hexisopodidae.

Intraspecific variation is prevalent in solifuge morphology, but largely restricted to the secondary and fondal teeth. Delimiting species based on the secondary or fondal teeth of singletons should be avoided. In the presence of large series, however, dentition patterns, including placement and number of secondary teeth, and size gradation of teeth within a category, may provide valuable diagnostic characters, from species to family level.

The attempt to identify and define homologous teeth through explicit, objective criteria, presented here, offers several advantages. It will (i) reduce conflicting and/or subjective coding of morphological characters, resulting in more informative matrices; ii) facilitate more concise, accurate and comparable descriptions of species and supraspecific taxa; and (iii) provide landmarks for other hypotheses based on positional homology concerning, e.g., the male flagellum, or flagellar complex, an important character system in all aspects of solifuge systematics.

MALE FLAGELLUM AND FLAGELLAR COMPLEX

MALE FLAGELLUM

The solifuge flagellum, situated on the fixed (dorsal) finger of the chelicera of the adult male (Kraepelin, 1901), is a highly modified seta (Bernard, 1896; Sørensen, 1914; Hewitt, 1919b; Roewer, 1934: 135; Lamoral, 1974), which may take many forms. A **primary flagellum** and a **secondary flagellum**, defined here as a modified ventral flagellar seta (*vfs*) and dorsal flagellar seta (*dfs*) respectively, may be present. Flagella have taxon-specific shapes, including membranous bowl-, husk-, or vesicular-shaped, chitinous filiform, modified setiform, and leaf-shaped. The flagellum was discussed in various levels of detail by Kraepelin (1908a), Sørensen (1914), Hewitt (1919b), Roewer (1934: 135–155), and Lamoral (1975). Roewer (1934: 135–155) presented the most detailed study of flagellar morphology across all solifuge families, and discussed possible mechanisms of flagellar operation through hemolymph pressure. The precise function of the flagellum remains unknown, however. Despite a brief period of doubt (Pocock, 1895; Bernard, 1896), it has long been known that the flagellum is unique to adult males (e.g., Fabricius, 1781, Savigny, 1809: 178; Pocock, 1897: 264; Kraepelin, 1899; Purcell, 1903a; Sørensen 1914: 161; Lamoral, 1975) and this was confirmed by dissections (Dufour, 1861). Dunlop et al. (2004) mistakenly mentioned that the flagellum occurs in both subadult and adult males. The absence of a flagellum in a subadult *Blossia* was reported by Hewitt (1919b: 10). According to Lamoral (1975), the flagellum is formed during the final ecdysis before becoming adult. Levy and Shulov (1964: 105) observed that the appearance of a flagellum, and the transformation from a “normal” cheliceral shape to the elongated beak-like fixed finger of adult male *Ceratobiton styloceros* occurred in a single molt from subadult to adult male (Pl. 137D).

HISTORICAL REFERENCE TO THE “FLAGELLUM”

The term “flagellum” is consistently used in the literature to refer to the single, distinct structure present in male Ammotrechidae, Ceromidae, Daesiidae, Galeodidae, Gylippinae, Hexisopodidae, Mummuciidae and Solpugidae (Pls. 30A, E, G, 32A–G, 34), but is inconsistently applied when more than one distinctly modified structure is present (Pl. 30A–D, F). For example, among Karschiidae, a distinct flagellum is usually recognized in *Karschia* (Pl. 30A), and referred to as such (e.g., Sørensen, 1914: 174; Roewer, 1934: 146; Gromov, 1998) whereas, in *Eusimonia* and *Barrussus* (Pl. 30D), either the dorsal or the ventral structures on the male fixed finger are referred to as “the flagellum” (Table 11). In Rhagodidae (Pl. 30F), “the flagellum” describes two separate structures with lamellae that overlap to form a unit (Roewer 1934: 55, fig. 50). In Melanoblossiinae (Pl. 36G–I), an entire cluster of modified setae is often collectively referred to as “flagellum” (Lawrence, 1972: 98; Wharton, 1981: 53; Gromov, 2003b: 199) or else “flagellum” refers to an individual seta which is slightly more differentiated within the cluster (Purcell, 1903a: 7, fig. 4B; Lawrence, 1935: 86). Roewer (1941: 125) identified a “Flagellum” within the melanoblossiine “Flagellum-Komplex.” In Lipophaginae (Pl. 36A–C), the strongly to weakly (depending on the species) modified group of setae at the apex of the fixed finger is collectively described as “the flagellum”

(Roewer, 1934: 309; 1941: 115; Wharton, 1981: 39), or as either “flagellum absent” (Kraepelin, 1908b: 281; Birula, 1913: 320), or “flagellum not distinguishable” (Purcell, 1903a: 10) when setae of the flagellar complex are barely modified. The cluster of modified setae observed in male Eremobatidae (Pls. 37–39) has been described in numerous ways. “The flagellum” may refer to two setae (Banks, 1903: 78) or to a cluster of setae (e.g., El-Hennawy, 1990: 26). Kraepelin (1908a: 223) was the first to recognize a flagellum proper in some Eremobatidae but the term “flagellum” has rarely been used to refer to a single, distinct seta since then (e.g., Fichter, 1941). More recent workers referred to the eremobatid flagellum as apical plumose seta, bristle or spine (e.g., Muma, 1951, 1970a; Brookhart and Muma, 1981; Brookhart and Cushing, 2002), adding descriptive terms such as “apical plumose bristle,” or “subapical plumose bristle” (Table 12; Muma, 1951: 61). Muma (1976: 3) identified specific “flagellar setae…usually 1 or 2” hidden among associated setae.

The inconsistent use of flagellum led Selden and Shear (1996: 596) to describe “the flagellum” as:

> “... a complex of structures ... In some, the dorsal side of the base of the fixed finger bears a curious horn or projections. In others, there is a bunch of large setae, which may be plumose or distally expanded, and such setae may extend onto the movable finger. In many genera there is a single organ (flagellum proper, presumably a highly modified seta) which is commonly associated with groups of modified setae.”

The absence of an unambiguous definition for the flagellum confounds the question as to whether it is a single, homologous structure in all solifuges or multiple structures, some with independent origins, and has implications for describing and coding morphological characters for diagnoses, descriptions and phylogenetic analyses from the species level on up. An unambiguous definition of the flagellum and its component structures, however, requires a framework of testable hypotheses of homology, both among its components and across the order.

FLAGELLAR ANATOMY

The only histological study of the flagellum, by Lamoral (1975), was based on four species of Solpugidae. Two canals, extending along the shaft of the flagellum, were identified (Pl. 41). The first, referred to as the **flagellar hemolymph lumen** (hemolymph canal), is connected proximally to the hemolymph, and blind ending apically. A connection between the hemolymph and flagellum, through a longitudinal **atrium** at the base of the flagellum, was described by Sørensen (1914: 168, fig. 11c), and depicted in cross section by Roewer (1934: 154, fig. 156; reproduced here in Fig. 22D). The second, referred to as the **alembic lumen**, comprises the alembic canal in the flagellar shaft, which, at least in Solpugidae, terminates proximally in a blind pouch, the alembic pouch. The pouch transitions into the canal resulting in a characteristic flask shape which is visible through the cuticle of the **bulbous base** of the flagellum of Solpugidae (Pls. 33K, L, 45A). The alembic canal is lined by epicuticle and is hypothesized to have formed through "longitudinal invagination" (Lamoral, 1975: 139) of the seta. There appears to be no connection between the alembic canal and any part of the hemolymph.

With the possible exception of *Karschia*, all flagella comprising a shaft may prove to contain an alembic canal and a hemolymph canal. Two canals, one clear and often appearing to contain what appear to be specs of dirt suggesting an opening to the exterior, the other opaque, often containing patches of a milky, viscous substance, are visible in Ammotrechidae, Ceromidae, Hexisopodidae, Solpugidae, and the daesiids, *Ammotrechelis* and *Namibesia*. In cross sections of the flagellar shaft of two solpugid species, the alembic canal is clearly visible as a well defined circular, empty canal, whereas the hemolymh canal is compressed between the alembic canal and the flagellar cuticle, and is apparently filled with a yellowish, viscous substance (Pl. 41A), confirming the observations of Lamoral (1975). A cross section of a ceromid flagellar shaft reveals a similar pattern (Pl. 41B).

Roewer (1934: 135–155) reported that the **flagellar tip** is closed, but Lamoral (1975) was the first to provide evidence for the presence of an opening to the exterior of the alembic canal at the tip of the flagellum in Solpugidae. Indications of an opening in a ceromid were also found in the present study (Pl. 41E, arrow). Maury (1980a) indicated two openings in the flagellum, one near the base and one at the apex of the shaft, connected by a tube, in *Amacata penai* Muma, 1971, currently in synonymy with *Ammotrechelis goetschi* (Maury, 1980a: 64, fig. 11), and in *Syndaesia mastix* Maury, 1980 (Maury, 1980a: 64, figs. 3, 4). When the flagellum of *Ammotrechelis goetschi* was examined in the present study, the external opening at the apex of the flagellar shaft (Pls. 32F, 33H, arrows) and a broad, clear alembic canal (Pl. 32F), were distinctly visible. An opening could not be found at the base of the flagellum (Pl. 40G), however, and the shaft may connect to a blind-ending pouch.

According to Lamoral (1975: 139) “[e]xamination of a large selection of representative species from [Ceromidae, Daesiidae, Hexisopodidae, Lipophaginae, Solpugidae and Melanoblossiinae] revealed that all have an alembic canal connected to a basal pouch, thus strongly suggesting that this cuticular structure prevails in all species." Lamoral (1975) only discussed and provided longitudinal and cross-section illustrations of the flagellum of Solpugidae, however, and it is unclear how the flagella of Daesiidae (excluding *Ammotrechelis*, *Namibesia*, and *Syndaesia*), Lipophaginae and Melanoblossiinae would accommodate an alembic canal. Only the whip-like flagella exhibit openings to the exterior, and no fluid other than the milky hemolymph is visible in, e.g., the narrow lumen of the membranous secondary flagellum of *Eusimonia* (Pl. 30D). Roewer (1934: 135–155) illustrated cross-sections of most flagellar types (some reproduced in Fig. 22), but none of his figures indicate a possible alembic lumen.

Lamoral (1975: 139) hypothesized that the alembic fluid is secreted by modified epidermal cells during ecdysis, and the fluid is trapped in the basal pouch (alembic pouch) by invagination of the flagellar cuticle during the final ecdysis.

In summary, an alembic canal, opening externally and connecting basally to a blind ending pouch, is probably present in all whip-like flagella, i.e., in Ceromidae, Hexisopodidae, Solpugidae, and some daesiids, i.e., *Ammotrechelis*, *Namibesia*, and *Syndaesia*. The function of the alembic fluid is unknown, however. A hemolymph canal, situated parallel to the alembic canal, is also present in the shaft of the whip-like flagella. Only a hemolymph lumen is present in the membranous flagella (Ammotrechidae, Mummuciidae, and Daesiidae other than *Ammotrechelis*, *Namibesia*, and *Syndaesia*), the primary and secondary flagella of Rhagodidae, *Barrus*, *Barrussus* and *Eusimonia*, and the flagella of *Karschia*, and Galeodidae. The hemolymph canal or lumen probably functions to change the shape or direction of the flagellum.

FLAGELLAR MORPHOLOGY AND TERMINOLOGY

No attempt has been made to unify the terminology for different components of a single flagellum. Homologous components, and associated terminology, are here proposed based on structural and positional similarity between different sections of the flagellum, and comparisons with apparent transitional forms (e.g., *Ammotrechelis goetschi*). Three types of flagella, i.e., setiform, sessile, and composite types (Table 13), may be identified based on the extent or manner of modification, whether or not the flagellum is subdivided into components, and whether or not it can change direction (i.e., rotate) or shape by, e.g., hemolymph pressure.

SETIFORM FLAGELLUM: The setiform flagellum is relatively uniform throughout, and retains a strong setiform character and affinities with plumose setae. It is present in Eremobatidae (Pls. 38, 39A–F) and Melanoblossiinae (Pls. 36G, I). The flagellum emerges and projects directly from the chelicera without a distinct **flagellar stalk** and base to change its direction, and is unable to change shape by hemolymph pressure.

SESSILE FLAGELLUM: The sessile flagellum is clearly modified from its original form (i.e., it is not setiform), but the modification does not appear to involve a longitudinal invagination along the seta (Pls. 30, 31). With the possible exception of the karschiid, *Karschia*, it also bears no obvious homologs to the parts of the composite flagellum (see below), and an alembic canal appears to be absent, based on the absence of an external opening. Most sessile flagella are not able to rotate at its attachment point. The sessile flagellum includes the spoonshaped flagellum of Galeodidae and both the primary and secondary flagella of Rhagodidae and the karschiids, *Barrus*, *Barrussus* and *Eusimonia*. The filiform flagella of *Dinorhax* (Dinorhaxinae) and *Karschia* are tentatively considered to be sessile flagella because both appear to have formed by infurling longitudinally, rather than invaginating, and an alembic canal is not evident in either. The sessile flagellum emerges and projects directly from the chelicera without a distinct stalk, except in *Karschia*. It is able to change direction only in Galeodidae (Roewer, 1934: 149), but apparently, based on hemolymph remains visible in the flagellum of some specimens (e.g., Pl. 30G, H; Roewer, 1934: 143–144) is able to change in shape in *Eusimonia*, and Rhagodidae. The spiraling flagellum of *Karschia* and the ventrally directed flagellum of *Dinorhax* are probably also able to straighten with hemolymph pressure based on remnants of hemolymph in these flagella (Pl. 30A, E).

COMPOSITE FLAGELLUM: A composite flagellum comprises a stalk, base and shaft, although some flagellar components may be secondarily lost. All composite flagella are probably able to change direction and/or shape, most plausibly through hemolymph pressure (Sørensen, 1914: 167, 169; Roewer, 1934: 135–155; Lamoral, 1975). All three sections (stalk, base, and shaft) occur in the flagellum of Ceromidae, some Daesiidae (*Ammotrechelis*, *Namibesia*, *Syndaesia*), Hexisopodidae, and Solpugidae (e.g., Pls. 32A–G, 33A–H, K–M; Table 13).

The flagellar shaft, when present, is markedly sclerotized, long, and round to laterally compressed and whip-like in composite flagella, with few exceptions. In *Ceromella* the shaft is wide and membranous (Pl. 33B). A broad, laterally compressed membranous shaft is also present in *Ammotrechelis*. The whip-like shape appears to be secondarily modified in a few Solpugidae (e.g., Pl. 49A–C), taking on claw-like or angular forms. The shaft of these taxa almost certainly contains a hemolymph and an alembic canal, the latter opening to the exterior at the tip of the shaft (Pl. 41; Lamoral, 1975; Maury, 1980a: 64, fig. 11). The fusion of the flagellum to the dorsal surface of the fixed finger in Gylippinae (Pl. 32H, 33J) resembles the fusion of the shaft of the flagellum to the fixed finger, between its emergence from the bulbous base until it curves dorsally, in Solpugidae (e.g., Pl. 32G). The flagellum of Gylippinae is therefore hypothesized to comprise a modified shaft, with the base and stalk lost.

The **flagellar base** is an enlarged section from which the shaft emerges. It is swollen and bulbous in Solpugidae (Pl. 40D), vesicular in Ceromidae (Pls. 32B, 33B, C), and cup-shaped in Hexisopodidae (Pl. 40F) and two daesiid genera, *Namibesia* (Pl. 40E) and *Syndaesia*. In *Ammotrechelis* (Pls. 32F, 33H, 40G), the base is membranous and bowl-shaped, resembling the flagellum of ammotrechids (Pls. 34E, F, 35F, G), other daesiids (Pls. 34A–D, 35A–E) and, to an extent, mummuciids (Pls. 34G, H, 35H, I). The membranous bowl- or husk-shaped flagella of these taxa are therefore considered homologous with the base of the flagellum of *Ammotrechelis* and taxa with whip-like flagella, a hypothesis first proposed by Hewitt (1919b) and Roewer (1934: 155). The shaft is therefore hypothesized to be absent in Ammotrechidae, Daesiidae (excluding *Namibesia*, *Syndaesia* and *Ammotrechelis*) and Mummuciiidae (Pls. 34, 35).

A short flagellar stalk connects the flagellar base to the cheliceral finger (e. g., Pl. 40C, F). The stalk varies from relatively distinct, e.g., in Ceromidae, Hexisopodidae, and *Namibesia*, to short and barely identifiable, e.g., in Ammotrechidae, Mummuciidae and Daesiidae with membranous flagella. In the daesiid genera, *Ammotrechelis*, *Biton*, and

Gluvia C.L. Koch 1842, the membranous stalk was found to attach to the base in such a manner that a hairpin shape, the “rotatory axis” visible as a “triangular” marking, according to Lawrence (1928: 267, plate XXIII, fig. 48) was visible through the transparent base (Pl. 40G, H, I). The “hairpin” changes direction with the movement of the flagellum because it is located at the transition from the stalk to the base of the flagellum, cf. the “stalk” of a dorsally rotated flagellum (Pl. 40H) with the “stalk” of a flagellum in the rest position (Pl. 40I). The flagellum of some species of *Blossia*, e.g., *Blossia rosea* (Lawrence, 1935) (Pl. 145F), resembles the **peduncle** and **scapus** of the flagellum of Galeodidae (Lawrence, 1935: 76, fig. 4) (Pl. 31E). The similarity is superficial, however, because both the **flagellar stem**, commonly referred to as the stalk (Purcell, 1903a: 5; Wharton, 1981: 28), and the broadened leaflike section of the daesiid flagellum, represent the base of the composite flagellum, whereas the flagellum of Galeodidae, comprising peduncle and scapus, is a sessile flagellum. The “stalk” of the flagellum of Daesiidae is not homologous to the stalk of the whip-like flagella, and the term “stem” is therefore preferred for such types of daesiid flagella.

The collar at the base of the flagellum of Galeodidae may be homologous with the base of the composite flagellum, and the stem (peduncle) + blade (scapus) with the shaft of the composite flagellum (Pl. 30G, H). However, unlike the composite flagella, there is no indication of a stalk in the flagellum of Galeodidae, which retains a basic setal morphology, without any indication of longitudinal invagination, hence probably without an alembic canal.

MANNER OF FLAGELLAR ATTACHMENT: The point of flagellar attachment to the fixed (dorsal) finger is distinctly socket-like and rotatable in Ceromidae, Daesiidae (including

Ammotrechelis, *Namibesia*, and *Syndaesia*), Galeodidae, and Hexisopodidae, and socket-like and non-rotatable in the filiform flagella of *Karschia* and *Dinorhax* and the setiform flagella of Eremobatidae and Melanoblossiinae (Pl. 40). The point of attachment is obscured in Solpugidae (Pl. 40D) and apparently lost in Gylippinae. The flagellum is immovably inserted parallel to the chelicera in Rhagodidae (Pl. 40B) and the karschiids, *Barrussus* and *Eusimonia*. The flagella of Ammotrechidae (Pl. 40J, K) and Mummuciidae (Pl. 40L) are also non-rotatable and attached to the round to oval, sclerotized inner margin of the socket. The inner margin of the flagellar socket is often more strongly sclerotized, especially in Ammotrechidae, Ceromidae, Daesiidae, Hexisopodidae, Mummuciidae, and *Karschia*.

The stalk of the composite flagellum is inserted perpendicular to the chelicera and connects perpendicular to the flagellar base, thus enabling the flagellum to be situated parallel to the fixed finger on the prolateral or prodorsal surface of the chelicera. The stalk is fused to the chelicera in Solpugidae and its position parallel to the longitudinal axis of the chelicera is facilitated by the deep insertion of its base into the dorsal surface thereof (Pl. 24B). A stalk is absent in the setiform (Eremobatidae, Melanoblossiinae), and most sessile (*Barrus*, *Barrussus*, *Dinorhax*, *Eusimonia*, Galeodidae and Rhagodidae) flagella, and parallel insertion of the flagellum into the fixed finger is accomplished by originating from a slightly elevated area (e.g., *Dinorhax*, *Eusimonia*) (Pl. 30D, E), or originating from (e.g., Galeodidae, Rhagodidae) or into (e.g., Eremobatidae, Melanoblossiinae) a depression, which may take the form of a deep socket, the alveolus (e.g., Galeodidae, Rhagodidae) (Pl. 30F, H), a groove, the flagellar groove (e.g., Eremobatidae) (Pl. 38), or a shallow depression, the flagellar complex depression (e.g., Melanoblossiinae) (Pl. 36G–I).

ORIGIN OF THE FLAGELLUM

As first proposed by Bernard (1896), the flagellum is broadly accepted to be a modified seta (Sørensen, 1914; Hewitt, 1919b; Roewer, 1934: 135; Lamoral, 1974). Its distinct setal character is evident in some taxa but not others, although even in strongly modified flagella, e.g., in Daesiidae, the presumed plesiomorphic plumosity is often retained. Whether there is a single origin for the flagellum, i.e., whether it is homologous across the order, or multiple origins, remains unknown. Hypotheses concerning flagellar homology are complicated by its great diversity in structure and position, probably associated with different reproductive pressures (Tables 1–4).

LITERATURE: Kraepelin (1908a) and Roewer (1934) each proposed multiple origins of the male flagellum, whereas Hewitt (1919b) proposed a single origin for southern African taxa. Hewitt (1919b) argued that the seta giving rise to the flagellum is homologous across taxa, an idea first put forth by Sørensen (1914), and largely adopted here (Pl. 43). Hypotheses of setal modification include thickening of the seta, invagination of the seta, or fusion of two setae.

Kraepelin (1908a: 220) proposed at least two origins of the flagellum, involving the two basic structures (or setae) that comprise the compound rhagodid flagellum, which was interpreted as the "most primitive," namely the *Stab* ("rod," i.e., the dorsal unit of the rhagodid flagellum) and *Schuppe* ("flake," i.e., the ventral unit) (Pl. 42A). Largely based on the shape of these two structures, Kraepelin (1908a) proposed a transformation series for the flagellum of Solifugae (Pl. 42). According to Kraepelin (1908a), the dorsal unit (*Stab*) is homologous to the rodlike flagellum of Galeodidae (Pl. 42B), and the ventral unit (*Schuppe*) to the husklike flagellum of Daesiidae (Pl. 42C). According to Kraepelin (1908a), both structures are present in Solpugidae (Pl. 42D), but fused into a single structure composed of a bulbous base (*Schuppe*) and a shaft (*Stab*). In *Dinorhax* (Pl. 42I) and Hexisopodidae (Pl. 42G), the *Schuppe* is reduced, leaving only the filamentous *Stab* to form the flagellum. Both *Stab* and *Schuppe* are represented in the flagellar complex of Karschiidae*,* in *Eusimonia* (Pl. 42E) by the upper membranous structure labeled as *Plättchen* and the ventral structure generally referred to as flagellum, and in *Karschia* (Pl. 42F) by the filiform flagellum and modified setae labeled as *Säbelborsten*. It is difficult to hypothesize whether the flagella in Eremobatidae (Pl. 42K), Gylippidae, and Melanoblossiinae (Pl. 42J) are homologs of the *Stab* or *Schuppe*. The lamelliform flagellum (*Läppchen*) of *Gylippus* (Pl. 42L) is situated towards the apex of the fixed finger, but is connected through a ribbon-like extension to the “normal attachment point” (“*normalen Insertionsstelle*” of Kraepelin, 1908a: 222) of the flagellum, thus linking its origin to either (*Stab* or *Schuppe*) of the flagellar components. The flagellum of *Melanoblossia*, a short robust seta within a cluster of modified plumose setae, and Eremobatidae, obscured in a deep longitudinal furrow with differently modified setae on either side, may be either *Stab* or *Schuppe* components, situated within a cluster of coarse, modified setae. The flagellum of *Lipophaga* (Lipophaginae) appears to be absent but coarse modified setae remain. Kraepelin (1908b) emphasized, however, that it would be more correct to refer to the reversal of one or both of the original (*Stab* or *Schuppe*) flagellar components, rather than to refer to absence of the flagellum in any given taxon.

Roewer (1934: 135–155, figs. 126–56) proposed multiple origins of the flagellum, based on an elaborate interpretation of transformation series, often within the framework of other morphological characters (e.g., presence or absence of claws on tarsus I, number of leg IV tarsal segments), and within the context of New and Old World taxa. In many parts of the discussion, Roewer (1934) only alluded to similarities between flagella of different taxa without actually proposing hypotheses of transition. A summary follows (for illustrations see Roewer, 1934: 136–154, figs. 126–56): Among New World taxa, similar positions of setae in the eremobatid flagellar complex suggests a transition from a brush of setae at the base of the fixed finger, to a row of modified dorsal setae, eventually resulting in two enlarged but barely sclerotized, finely fringed setae situated close together and parallel on the fixed finger. One of these setae widens and the margins curl slightly inwards to form the flagella of Ammotrechidae and Mummuciidae.

Roewer (1934: 138) proposed various pathways among Old World taxa: The slightly modified setae of Lipophaginae gave rise to the well defined flagellar complex of Melanoblossiinae. The two flagella of Rhagodidae underwent various transformations. Firstly, based on the interpretation of an apparently bifid flagellum in *Gylippus* (*Anoplogylippus*) *ferganensis* Birula, 1893, as *G. rickmersi* (Gylippinae), the two rhagodid flagella gave rise to the two papillae of *G.* (*A.*) *ferganensis*, which eventually fused into the single flagellum of other Gylippinae. Secondly, the two rhagodid flagella are homologous to the two flagella of *Eusimonia* (Karschiidae).

Roewer (1934) pointed out various similarities that might indicate affinities among different flagella: For example, the flagellum and associated setae of *Dinorhax* are similar to the flagella of Rhagodidae and additional proventral distal setae. The row of setae covering the base of the flagellum of Ceromidae resembles the flagellum of Melanoblossiinae. The base of the flagellum of Ceromidae is similar to the small swelling, or **basal peg** (*Zapfen* of Roewer, 1934), at the base of the *Karschia* flagellum. The field of short setae dorsal to the attachment point of the flagellum of Hexisopodidae resembles the setae at the base of the flagellum of Ceromidae. The narrow lumen in the scapus of the flagellum of Galeodidae bears some similarity with the flat apex of the flagellum of some Ceromidae. Alternatively, the flagellum of Galeodidae could be derived from that of Daesiidae, which also possesses a narrow lumen. The flagellum of Solpugidae is the most derived, related to the flagella of either Daesiidae or Ceromidae, the latter based on similarity in the flagellar base.

Hewitt (1919b: 10), focusing only on southern African taxa, hypothesized a single origin of the flagellum, based on its putative origin from a socketed bristle, which, it was argued, would imply that a rotatable flagellum is “more primitive” than the fixed flagellum of Solpugidae. Hewitt (1919b) described the “primitive” flagellum of Daesiidae as a membrane with “more or less infolded edges,” which gave rise to the flagella of Ceromidae and Hexisopodidae by further infolding and extensive fusion along its length to form a flattened shaft. Hewitt (1919b) also hypothesized that the bulbous base of the flagellum of Solpugidae is homologous with the “cup-like base” in *Blossia* (Daesiidae).

SINGLE OR MULTIPLE ORIGINS OF THE FLAGELLUM: The evidence supporting single vs. multiple origins of the male flagellum is summarized below. The potential for setae to be modified appears to be particularly strong among setae situated apically on the chelicera as is especially evident in the wide array of setal forms associated with the flagellum of *Karschia* (Pl. 30A–C). This might indicate that any of these setae could be a precursor to the flagellum, an argument for multiple origins. However, this wide array of setal modification is also consistent with a single origin of the flagellum, as it may explain how the diversity in flagellar form could be derived from a similar original form, a possibility already suggested by Kraepelin (1908a: 223).

Positional homology of the attachment points of the flagellum on different parts of the fixed finger among taxa may appear to support multiple origins of the flagellum, e.g., the distally situated flagellum of Gylippinae (Pl. 32H) versus the proximally situated flagellum of Hexisopodidae (Pl. 32C). However, the diversity of cheliceral shapes is likely to affect not only where on the prolateral side of the fixed (dorsal) finger the flagellum is attached, but also how the teeth are distributed along the cutting edge of the finger. When homologous teeth were used as landmarks for evaluating the position of the flagellum (Pl. 44), flagella which appeared to be located in very different positions on the prolateral surface of the chelicera, were found to be situated near the same landmark tooth (Pl. 44). For example, the flagella of Hexisopodidae, Solpugidae, and *Namibesia* (Daesiidae) provide examples of flagella attached at very different positions on the chelicera: dorsodistal in Solpugidae, medial in *Namibesia*, and ventroproximal on the finger in Hexisopodidae. However, the points of flagellar attachment are approximately aligned with the **fixed finger medial (FM) tooth** in all three taxa and presumably shifted in association with changes in the shape of the chelicera. This example illustrates that apparent differences in the position of the flagellum on the chelicerae do not necessarily contradict the criteria of positional homology. The hypothesis that the flagella of Hexisopodidae, Solpugidae, and *Namibesia* are homologous is further supported by their structural similarity.

If a homologous seta gives rise to the flagellum, in accordance with the hypothesis of a single origin thereof, the **flagellar attachment point** may be expected to retain the same position relative to unmodified setae in the series from which the flagellum was derived. This does not appear to be the case, however, as noted also by Hewitt (1919b: 9), potentially supporting the hypothesis of multiple origins of the flagellum. On the other hand, this variation in flagellar position, relative to unmodified setae in the series from which the flagellum was derived is observed even among taxa for which the flagellum may reasonably be assumed to be homologous, e.g., within Solpugidae. For example, the point of flagellar attachment is approximately aligned with the apicalmost proventral distal (*pvd*) seta in *Zeria carli* (Pl. 45A), the most common position in Solpugidae (Hewitt, 1919b: 11, fig. 1bC), but remote from the apicalmost *pvd* seta in *Oparba asiatica* (Pl. 44D). Hewitt (1919b: 9) mentioned similar examples concerning differences in the relative positions of flagellar attachment points within Daesiidae, but noted that the “original relation” to the row of *pvd* setae was retained within the *Blossia* species discussed. In the present study, the point of flagellar attachment in taxa with broad, membranous flagella, e.g., the bowl-, husk-, or vesicle-shaped flagella of Ammotrechidae, some Daesiidae (e.g., *Biton*) and some Mummuciidae (Pls. 136A, E, I, 146A, E, G, I) was usually further from the *pvd* series than in taxa with a stem or basally tapering flagellum, e.g., some *Blossia* and *Hemiblossia* (Pl. 139C, G, I), suggesting a shift in attachment point influenced by the shape of the flagellum. Apparent differences in the position of flagellar attachment relative to the *pdd* and *pvd* setae are therefore unreliable indicators of flagellar homology.

FLAGELLAR PRECURSORS: Sørensen (1914: 177) observed that all modified spiniform setae situated dorsal to the flagellum, i.e., the flagellar complex subspiniform and spiniform (*fcs*) setae, are non-plumose, whereas all those situated proximal, e.g., the long plumose setae (**flagellar complex plumose setae, or *fcp*)** in *Karschia* (Pls. 30A, 31A), or distal, e.g., the *fcp* seta/e in Solpugidae (Pls. 45B; Sørensen, 1914: 212, fig. 10), to it are plumose. Sørensen (1914) thus concluded that the flagellum originated from the distalmost plumose seta or, in the case of Rhagodidae, the two distalmost plumose setae. Hewitt (1919b) agreed with Sørensen (1914), based on a study of developmental stages: a three-malleoli stage juvenile, a subadult male and an adult male Solpugidae. The juvenile possessed a single row of plumose setae ending in a distal non-plumose, slightly longer seta, whereas the subadult male possessed "several simple bristles of which one is markedly stouter than the rest and strongly curved like the feather bristles" near the distal end of the plumose series (Hewitt, 1919b: 11, fig. 1bA, B). Hewitt (1919b) concluded that the apicalmost of the plumose setae (plumose proventral distal, *pvd* row) is the precursor to the flagellum of adult males, and referred to it as the "flagellar bristle." In the present study, a similar enlarged seta was observed in a subadult male *Metasolpuga picta* (Pl. 46C), consistent with Hewitt's (1919b) observation that this seta is the precursor of the flagellum, at least in Solpugidae (Pl. 46C), and this unmodified seta is referred to here as the ventral flagellar seta (*vfs*). The *vfs* can thus be defined as the apicalmost seta in the proventral distal (*pvd*) series, usually also the apicalmost in the setose area of the fixed (dorsal) finger, and the seta on which both the *pdd* and *pvd* series converge (Pl. 12, 47). The *vfs* is hypothesized to be the precursor of the primary (ventral) flagellum, and this is supported by the position of the flagellum relative to adjacent setae (Pl. 46A, B). Directly dorsoproximal to the *vfs*, and belonging to the prodorsal distal (*pdd*) series based on its position, is the dorsal flagellar seta (*dfs*), which is hypothesized to be the precursor of the secondary (dorsal) flagellum of *Barrussus*, *Eusimonia,* and the rhagodids. This differs from Sørensen's (1914) hypothesis according to which the seta ventral to *vfs* is the precursor of the ventral flagellum of *Barrussus*, *Eusimonia* and the rhagodids.

A broad survey of setation in female solifuges, based on 45 species representing all families, was undertaken during the present study to investigate the differentiation and structure of the flagellar seta across the order (Pl. 47). The identity of the *vfs* as the apicalmost *pvd* seta was observed to be relatively obvious when the various prolateral series of setae (especially the *pvd* and *pdd* series), are well differentiated, e.g., in *Hemerotrecha branchi* Muma, 1951 (Pl. 12), but not when apical setae on the finger are relatively homogeneous, e.g., in *Eremorhax joshui* (Brookhart and Muma, 1987) (Pl. 72G). The *vfs* in Solpugidae are non-plumose (Pl. 47C). In addition to its position relative to the *vfs* and *pdd* setae, a "typical" *dfs*, e.g., in *Hemerotrecha branchi* (Pl. 12), is pronounced in length, shape and, often, girth: it is usually the longest seta in the area, is usually gently recurved ventrally and is more robust than the other *pdd* setae. It is therefore usually readily identifiable except in the presence of an additional and similarly modified seta, the longest of which is often situated dorsal or dorsoproximal to the shorter of the two, which confused the identity of the *dfs* in a few species, especially among some species of Daesiidae (Pl. 47D). These cases are, however, irrelevant to discussion of primary flagellar homology, which pertains to the *vfs*. The identity of the *dfs* is also somewhat ambiguous when the apical setae are homogeneous.

The position of the flagellar attachment point relative to the **proventral distal (*pvd*) setae** in Ceromidae and Galeodidae, and relative to the hypothesized prodorsal distal (*pdd*) setae in Daesiidae may at first appear to contradict the hypothesis that the flagellum is derived from the apicalmost setae of the *pvd* series. The point of attachment appears to be situated within the *pdd*, not *pvd,* series in Galeodidae (Pl. 59A, C, G), whereas the **flagellar base** is situated distal to, i.e., not aligned with, and partly obscured by several modified *pvd* setae (the flagellar complex plumose setae, or *fcp*) in Ceromidae (Pl. 32A, B), and proximal to a regularly spaced row of what appear to be *pdd* setae in Daesiidae (Pl. 34C). However, structures on the chelicera appear prone to shifts in position, and these examples could plausibly be explained by a shift in the flagellum relative to the *pdd* or *pvd* setae, or vice versa, allowing the point of flagellar attachment to remain next to the margin of the asetose area. Among the material examined during the present study, the male flagellum was, without exception, situated next to the margin of the asetose area of the fixed (dorsal) finger (e.g., Pl. 4C), be it the **prodorsal distal margin (pddm)** or the **proventral distal margin (pvdm)**, whereas the *pvd* and *pdd* setae were often found to be situated slightly more medioproximal on the chelicera when the flagellum was present. For example, in Galeodidae, the presence of one or two distinct plumose setae, situated proximoventral to the base of the flagellum and referred to here as the flagellar complex plumose (*fcp*) seta(e) (Pls. 30H, 61C), appears to locate the flagellum within the *pvd* series, on the basis of which it would be derived from *either* the second (if only one *fcp*) or third (if two) distalmost seta of the *pvd* series. This hypothesis, unrealistically, implies that the flagellum originated twice, from different setae in Galeodidae. It is more parsimonious to interpret the apparent position of the flagellum of galeodids within the *pvd* series as a consequence of a shift of the flagellum and the rest of the *pvd* series relative to one other. Similar hypotheses may be postulated for the setae at the base of the flagella of Ceromidae and Daesiidae. Accordingly, observations of flagella situated out of alignment with the *pvd* and *pdd* setae do not falsify the hypothesis of primary homology of the flagellum.

Homology of the Flagellum

A single origin for the primary (ventral) flagellum of Solifugae is proposed here (see Pl. 43 for summary). The hypothesis of primary homology is based on Remane's (1952) criteria of topographical and structural similarity, and intermediate forms, and builds upon the earlier hypotheses of flagellar homology by Kraepelin (1908a), Hewitt (1919b), and Roewer (1934: 135–155), augmented by an examination of specimens representing the diversity of flagellar morphology.

Composite Flagella: The modified *vfs* of the subadult *Metasolpuga picta* indicates that the *vfs* is the precursor of the primary flagellum of Solpugidae (Pl. 46C). Structural similarity among the flagella of Solpugidae, Ceromidae, Hexisopodidae, and the daesiids, *Namibesia* and *Syndaesia*, i.e., composite flagella comprising a stalk, base and shaft, with the latter being predominantly chitinous, and usually whip-like, suggests that these flagella are homologous (Pls. 32A–E, G, 43A–D). The membranous, straplike flagellum of Gylippinae, specifically the short shaft fused dorsally to the fixed finger, appears structurally similar to the part of the flagellar shaft of Solpugidae which is fused to the fixed finger, suggesting that the flagella of these families are also homologous (Pls. 32F, 43F).

Males of the daesiid, *Ammotrechelis*, possess a unique flagellum (Pls. 32F, 43E), which appears to represent a structurally intermediate form between the whip-like flagella of the taxa discussed above (Ceromidae, Gylippinae, Hexisopodidae, Solpugidae, and the daesiids, *Namibesia* and *Syndaesia*), and the membranous bowl-shaped flagella of, e.g., Ammotrechidae (Pls.34E, F, 43H). The flagellum of *Ammotrechelis* comprises two distinct components. An elongated shaft resembles the shafts of the whip-like flagella, including the presence of two canals, the contents of which also appear to be similar. The base is broad and membranous, however, resembling the membranous flagella of Ammotrechidae. The latter in turn is similar to the membranous flagella of most Daesiidae (i.e., excluding *Namibesia* and *Syndaesia*), and Mummuciidae (Pls. 34A–D, G, H, 43G, I). Based on these structural similarities, the flagellar base of *Ammotrechelis* is therefore hypothesized to be homologous with the, bowl-, husk-, or vesicle-shaped membranous flagella of Ammotrechidae, most Daesiidae, and Mummuciidae, while the shaft is hypothesized to be homologous to the shaft of Ceromidae, Gylippinae, Hexisopodidae, Solpugidae and the daesiids, *Namibesia* and *Syndaesia*. The hypothesis that the shaft is homologous to the whip-like flagella is supported by new evidence of a possible phylogenetic relationship between *Ammotrechelis* and *Syndaesia*, i.e., the retrolateral granular tooth and the bifurcated movable finger medial (MM) tooth (cf. Pl. 134B, D and fig. 3 in Maury, 1985: 5). The probable homology of the *Ammotrechelis* flagellum and the membranous flagellum of most Daesiidae is further supported by the similar hairpin-shaped transition of the short stalk into the flagellar base in these taxa (Pl. 40G–I). The *Ammotrechelis* flagellum therefore supports the homology of the base of the chitinous whip-like flagellum with the membranous bowl-, husk-, or vesicle-shaped flagella.

SESSILE (PRIMARY AND SECONDARY) FLAGELLA: The sessile flagellum of the karschiid, *Karschia*, is hypothesized to be homologous with the composite flagella based on its filiform structure and the swelling at its base (Pls. 30A, 40C), which resembles the base of the whip-like flagella, as suggested by Roewer (1934) in his comparison of *Karschia* and Ceromidae (Pl. 43J). The position of the flagellum of *Karschia* relative to the *pvd* setae, which are greatly modified and thus termed flagellar complex plumose (*fcp*) setae, further supports its derivation from the apicalmost *pvd* seta, i.e., the *vfs*. The flagella of *Karschia* and *Dinorhax* share structural similarities, implying homology, e.g., both are long and filiform and appear to have been modified longitudinally as indicated by a longitudinal plumose fringe in the flagellum of *Karschia* and a longitudinal sulcus along the flagellum of *Dinorhax*. The flagellum of *Karschia* also shares positional and structural similarities with the sessile flagella of *Barrussus*, *Eusimonia*, Galeodidae, and Rhagodidae, i.e., a similar origin relative to the proventral distal (*pvd*) and probable prodorsal distal (*pdd*) setae as in *Eusimonia*, probably in *Barrussus*, and in Rhagodidae, and a deep socket (alveolus) with a distinct elevation on the socket margin, as *Eusimonia*, Galeodidae and Rhagodidae (Pls. 30B, D, F, H; 40J, K, L, arrows).

Positional similarities are also evident between the flagellum and adjacent dorsal and ventral setae of *Dinorhax* (Pl. 30E, 43N) and the flagellar complex of Eremobatidae

(Pls. 38, 39, 46A): the flagellum is situated distally on the fixed (dorsal) finger, in a relatively narrow asetose area, and the associated modified setae are inserted directly dorsoproximal and ventroproximal to the flagellum, in both taxa. Two sources of evidence therefore support the hypothesis that the flagellum of *Dinorhax* is homologous with the flagella of *Karschia* and Eremobatidae and, by extension, the flagella of all other taxa with which these are homologous.

Two groups of Solifugae, i.e., Rhagodidae and the karschiid genera, *Barrussus* and *Eusimonia*, possess two distinct flagella, the ventral and dorsal flagellar structures referred to, respectively, as the primary and secondary flagella (Pls. 30D, F, 31B, D). A third karschiid genus, *Barrus* apparently possesses a single flagellum (Roewer, 1934: 305, fig. 227A), the structure of which indicates homology with the secondary flagellum of the other three taxa. The flagella of both groups are fairly stable in structure, particularly in Rhagodidae, and position of attachment. The primary flagellum of most *Barrussus* and *Eusimonia* resemble that of Rhagodidae in structure and position (Pls. 30D, F, 31B, D). The attachment points of the primary flagella of Rhagodidae, *Barrussus* and *Eusimonia* are clearly aligned with, and situated at the distal end of the row of *pvd* setae, suggesting they developed from the *vfs* and are therefore homologous to the whip-like flagella of Ceromidae, Gylippinae, Hexisopodidae, Solpugidae, and the daesiids, *Namibesia* and *Syndaesia*, and hence the membranous bowl-, husk-, or vesicle-shaped flagella of Ammotrechidae, most Daesiidae, and Mummuciidae. The secondary flagellum, situated directly dorsal to the primary flagellum, is thus likely derived from the *dfs*, and therefore also assumed to be homologous in *Barrussus, Eusimonia,* and Rhagodidae based on their similar positions, and to *Barrus* based on structural similarity between this genus and the other two previously mentioned karschiid genera.

The flagellum of Galeodidae (Pls. 30G, 31E, F, 43M) is more dorsoproximally situated than the flagella of other solifuge taxa, but the presence of one or two distinct plumose setae at its base (*fcp*) suggests a dorsoproximal shift in the *pvd* series (described under Flagellar Precursors), implying that the flagellum of Galeodidae is derived from the *vfs*, and thus homologous to the primary flagellum of Rhagodidae, *Barrussus* and *Eusimonia*, as well as the whip-like and membranous bowl-, husk-, or vesicle-shaped flagella of the other taxa previously discussed.

An alternative hypothesis concerning the homology of the sessile flagella of *Barrussus, Eusimonia*, Galeodidae, Rhagodidae, may be considered, however. A curved, elevated socket margin of striking similarity is evident at the proximal or dorsoproximal margin of the socket of the (primary) flagellum of *Karschia*, the secondary (dorsal) flagellum of Rhagodidae, the primary (ventral) flagellum of *Eusimonia*, and probably *Barrussus* and the base of the flagellum of Galeodidae (Pls. 30B, D, F, H; 40J, K, L, arrows). If this feature were homologous in all four taxa, it might imply that the dorsal flagellum of Rhagodidae, the ventral flagellum of *Barrussus* and *Eusimonia*, and the flagella of Galeodidae and *Karschia* are homologous to the primary flagellum, thus leaving the ventral flagellum of Rhagodidae without a flagellar homolog in solifuges, while the dorsal flagella of *Barrussus* and *Eusimonia* remain homologous to secondary flagella. On the other hand, the sockets of the primary and secondary flagella may have fused, shifting the curved raised area on the socket margin to the dorsal position it occupies in the secondary (dorsal) flagellum in rhagodids. This possibility is supported by the structural similarity of the deep depression into which both flagella are attached in rhagodids and the alveolus, the deep socket of the flagellum of galeodids, and pending evidence to the contrary, the flagellum of Galeodidae is considered homologous to the *Karschia* flagellum and the primary (ventral) flagellum of *Barrussus, Eusimonia* and Rhagodidae, in accord with the main hypothesis initially set out in the present study.

SETIFORM FLAGELLA: The setiform flagella of Eremobatidae (Pls. 38, 39) and Melanoblossiinae (Pl. 36G, I) are more challenging to homologize with other primary flagella. However, the flagellum and the flagellar groove in which it is situated are positionally homologous in Eremobatidae and Mummuciidae. The flagellar groove of Eremobatidae (e.g., Brookhart and Muma, 181: 291, figs. 2, 3) and Mummuciidae (e.g., Botero-Trujillo, 2014: 325, figs. 13, 15) are both demarcated by strong borders and open towards the distal end of the fixed (dorsal) finger. The position of flagellar attachment, relative to the groove, is also similar in the two families, although the possibility that this position is due to convergent evolution, the flagellum emerging at the base of the groove which protects it, should not be disregarded. Nonetheless, these similarities suggest that the eremobatid and mummuciid flagella are homologous, implying that the eremobatid flagellum is a primary flagellum. Further support is provided by the similarity in position of the flagellum relative to the prodorsal distal (*pdd*) and proventral distal (*pvd*) setae, and relative to a small setose area on the finger, in various taxa, notably *Dinorhax*.

The setiform character of the flagellum is probably secondarily and independently derived in Eremobatidae and Melanoblossiinae. The setiform flagellar complex of

Melanoblossiinae is greatly modified, obscuring the underlying pattern of the *pvd* series. Furthermore, the most differentiated seta in the flagellar complex (*sfc*), presumed to be the flagellum of *Lawrencega*, differs structurally and positionally from the most differentiated seta, presumed to be the flagellum of *Melanoblossia*, which in turn appears to be vestigially present in *Lawrencega*. This is further confounded by the simultaneous presence of both setae in the flagellar complex of an undescribed species of *Melanoblossia*. Consequently, it is impossible to unequivocally identify the flagellum of Melanoblossiinae (Pl. 36G–I).

FLAGELLUM OF *XENOTRECHA HUEBNERI*: Kraepelin (1908a) hypothesized that the flagellum of Solpugidae comprises two setae fused into a single structure. The single differentiated seta, i.e., the *vfs*, of the subadult male *Metasolpuga* Roewer, 1934, regarded here as the precursor of the flagellum (Pl. 46C), does not support Kraepelin's (1908a) hypothesis for the Solpugidae flagellum, however, as discussed above. The only example of a flagellum which could potentially comprise two fused setae is that described for *Xenotrecha huebneri* (Kraepelin, 1899). Maury (1982: 137, fig. 22, 27, 28) described and illustrated a plumose seta arising from near the center of the flagellum of *X. huebneri*, and extending almost to its tip. This seta was described as being similar to the *pvd* setae, although it appears to possess a broad base in the illustrations. A configuration in which a seta perforates the base of the broad membranous flagellum might be the precursor for a combined, transitional type of flagellum as in *Ammotrechelis*. The male of *X. huebneri* is, however, known from only a single specimen and the possibility that its flagellum is an abnormality cannot be disregarded. The most parsimonious hypothesis remains a single setal origin for the primary flagellum, as discussed above.

SETAL TRANSFORMATION HYPOTHESES: The structure of the flagellum allows hypotheses for the transformation from seta to flagellum to be postulated. Lamoral's (1975) histological studies indicated that the alembic lumen of the flagellum of Solpugidae is lined by epicuticle (Pls. 32G, 41A), which would most likely be achieved by longitudinal invagination of the seta. This is probably also true for the flagella of ceromids (Pls. 32A, B, 41B–E), hexisopodids (Pl. 32C, D), and two daesiid genera, *Namibesia* (Pl. 32E) and *Syndaesia*, based on external and internal similarities in the flagellar shaft, e.g., indications of canals, in these taxa. The flagellum of Gylippinae (Pl. 32H) is probably a remnant of the composite flagellum, formed in a similar manner, but without the base, stalk and possibly the alembic canal. There are two most plausible pathways by means of which the membranous, usually bowl-, husk-, or vesicle-shaped flagella of ammotrechids, most daesiids, and mummuciids (Pls. 34, 35) might be formed. (i) Roewer (1934: 138) suggested the membranous flagella may have formed by simple flattening and broadening of the seta. (ii) Alternatively, the membranous flagella might have been secondarily derived from the chitinous whip-like flagella, by unfolding of the base, loss of the shaft and, possibly, the alembic canal. This hypothesis is suggested by the flagellum of *Ammotrechelis* (Pl. 32F), which is intermediate in form between the whip-like and membranous flagella and may have formed by invagination to create the elongated shaft, and subsequent opening (secondary unfolding) of the base.

Roewer (1934: 145, 154, fig. 156; reproduced here as Fig. 22A) hypothesized that the flagellum of *Karschia* originated as a seta that broadened and rolled in on itself along its length, resulting in a double membraned flagellum with hemolymph restricted to the lumen between the membranes. As such, the flagellum of *Karschia* may represent a precursor to the alembic canal observed in the flagella of other taxa, but formed in a different manner, i.e., by the seta rolling in on itself rather than by longitudinal invagination as proposed for Solpugidae by Lamoral (1975). Although hemolymph was observed in the flagellum of *Karschia* (Pl. 30A), it was impossible to verify whether hemolymph is restricted to its outer double wall in the present study. The composite flagella of Ceromidae (Pls. 32A, B, 33A–C), Gylippinae (Pls. 32H, 33J), Hexisopodidae (Pls. 32C, D, 33D–F), Solpugidae (Pls. 32G, 33K–M), and the daesiid genera, *Namibesia* (Pls. 32E, 33G) and *Syndaesia*, share a similar basic structure comprising a stalk, base, and shaft, suggesting a transformation series. The flagellum of *Karschia* (Pls. 29A, 30A) may therefore be intermediate between the typical composite flagella, i.e., the whip-like flagella, and the sessile flagella.

The flagella of Karschiidae (Pls. 30A, D, 31A, B), Galeodidae (Pls. 30G, 31F). Rhagodidae (Pls. 30F, 31D) and *Dinorhax* (Pls. 30E, 31C) appear to have altered shape without longitudinal invagination, in *Karschia* and *Dirohax* probably by longitudinal infolding; in Galeodidae by simple compression of the distal part of a seta (although it is difficult to explain the plumosity restricted to the internal surface of the scapus); and in *Barrus*, *Barrussus*, *Eusimonia* and Rhagodidae by, e.g., broadening of the seta.

The flagella of Eremobatidae (Pls. 38, 39) and Melanoblossiinae (Pl. 36G–I) are probably secondarily setiform. This hypothesis is partly supported by the atypical position of the prolateral setae which form the flagellar complexes characteristic of both families, and especially the melanoblossiines.

Other modified setae of solifuge males are more common and pronounced in the prodorsal distal (*pdd*) series and the ventral flagellar (*vfs*) seta. Examples include the subspiniform *pdd* setae of some *Hemerotrecha* (e.g., Pl. 37D) and the flagellar complex subspiniform or spiniform (*fcs*) setae of Ceromidae, Galeodidae, Gylippidae, and Karschiidae. Contrary to Sørensen's (1914: 177) initial assessment, the *pdd* setae may also be plumose, as in *Dinorhax* (Pl. 30E), although this is uncommon. Plumosity is not necessarily restricted to the proventral distal (*pvd*) setae.

FLAGELLAR COMPLEX

The male flagellum is often associated with various modified spiniform and setiform setae. These include the flagellar complex subspiniform or spiniform setae (*fcs*), i.e., the one to four spiniform setae situated at the base of the flagellum of Ceromidae (Pl. 93B, C), Galeodidae (Pl. 63A, D), Karschiidae (Pls. 51B, 55A) and Gylippidae (Pl. 86A), and the flagellar complex plumose setae (*fcp*), including the suite of variously modified setae situated dorsal and ventral to the flagellum in *Karschia* (Pl. 51A), the one or two plumose setae situated proximoventral to the base of the flagellum of Galeodidae (Pl. 63A, D), and the often pipette-shaped *pvd* setae arranged in a row at the base of the flagellum of Ceromidae. This combination of modified setae constitutes the flagellar complex of a male solifuge.

The spiniform to subspiniform (*fcs*) setae of Ceromidae, Galeodidae, Gylippidae and Karschiidae are invariably situated dorsally. Although the dorsal position obscures their origin, their location relative to the flagellum and the prodorsal distal margin (pddm) of the fixed finger asetose area suggests that they are probably modified *pdd* setae (Pls. 30A–D, G, H, 32B, H,). One to four *fcs* setae appear to originate proximal to the flagellum next to the margin of the asetose area in galeodids (Pls. 4C, 30G, H). The relative positions of these setae are similar in *Ceroma* (Pl. 32B). The positions of the robust *fcs* setae of *Gylippus* (Pl. 32H) are, in turn, similar to the *fcs* setae of *Ceroma*, suggesting that the *fcs* setae of Ceromidae, Galeodidae, and Gylippinae are homologous. The subspiniform (*fcs*) setae of *Karschia* (Pl. 30A) are situated directly dorsoproximal to the flagellum, resembling the position of the dorsal flagellar seta (*dfs*) relative to the ventral flagellar seta (*vfs*). Although the *fcs* setae are more dorsally situated in *Eusimonia* (Pl. 30D) than in *Karschia* (Pl. 30A), these setae are probably homologous given the frequency with which structures shift on the chelicera and the putatively close phylogenetic relationship between the two genera.

The flagellar complex plumose (*fcp*) setae, as defined here, include modified plumose setae belonging to the *pvd* series. The flagellar complex of *Karschia* includes highly modified *pvd* setae, the *Säbelborsten of* Kraepelin (1908a: 222), which become increasingly modified distally (30A, 31A). A row of *pvd* setae, often pipette-shaped and smooth or plumose, inserted at the base of the flagellum (Pls. 32A, B, 33A–C) may constitute a synapomorphy for Ceromidae (excluding *Toreus*). The presence of one (usually) or two, stout, plumose setae situated directly proximoventral to the base of the flagellum (*fcp* in Pl. 30G, H; Birula, 1936a: 48, fig., 1937a,b, 1938; Panouse, 1960b: 178, fig. 4) is a potential synapomophy for Galeodidae. Although not obviously connected to the *pvd* row, these setae appear to be homologous with the one or two subdistal *pvd* setae (the distalmost *pvd* seta is the flagellum itself).

The flagellar complex of Eremobatidae, Lipophaginae and Melanoblossiinae, referred to here as the **setiform flagellar complex (*sfc*)**, differs fundamentally from the flagellar complexes of other taxa, which comprise a distinct flagellum associated with well differentiated, modified setiform and spiniform setae, in comprising a suite of slightly to markedly modified setae, all of which, including the flagellum if present, are setiform.

The **type A setiform flagellar complex (*sfc*)** of eremobatids (Pls. 37–38) consists of modified *pdd* setae. Proventral distal (*pvd*) setae may or may not be modified to form part of the *sfc*. Similarly, a flagellum may be present or absent, but is always setiform when present and partly or fully obscured by the remaining *sfc* setae. The flagellum may be associated with a well defined (e.g., *Eremobates*) to weakly defинded (e.g., many *Eremochelis*) flagellar groove. The type A *sfc* may be a heterogeneous (e.g., *Eremobates*, Pl 38A) or homogeneous (e.g., *Eremorhax joshui*, Pl.37C) cluster of setae (table 13).

A flagellum is absent in the **type B setiform flagellar complex (*sfc*)** of Lipophaginae (Pl. 36A–F), and all setae in the flagellar complex tend to be similarly modified *pvd* setae, as observed, e.g., in *Lipophaga trispinosa*, or two types of modified *pvd* setae in *Bdellophaga angulata* (Pl. 36D–F). The extent of differentiation of the flagellar complex in *Trichotoma michaelseni*, which comprises slightly elongated and slightly more robust *pvd*, *pdd* and probably also *pvsd* setae, is so minor that it can barely be considered a flagellar complex.

The **type C setiform flagellar complex (*sfc*)** of Melanoblossiinae (Pl. 36G–I) is unique in various ways. Firstly, setae in the complex are arranged in a compact cluster forming a well-defined unit. The setae are more distally directed and more linearly arranged in *Melanoblossia* than in *Lawrencega*, in which the arrangement is more curved. The dorsalmost seta in the flagellar complex is long in *Melanoblossia* and short in *Lawrencega*. Secondly, the setae forming the flagellar complex are situated in a broad, shallow depression, referred to here as the flagellar complex depression (cf. the flagellar groove which accommodates the flagellum in several other taxa). Thirdly, the setae of the flagellar complex, including the flagellum, appear to be derived from the *pvd* series. A setiform flagellum seems to be present in some species or genera, but remains uncertain: two modified setae have been identified as flagella by various authors, but probably only one of these is homologous with the primary flagellum (Pl. 36G–I).

The setiform flagellar complexes of Eremobatidae (type A), Lipophaginae (type B) and Melanoblossiinae (type C) thus share few similarities. According to the interpretation proposed here, the type B setiform flagellar complex (*sfc*) of Lipophaginae, derived from *pvd* setae, is homologous to the ventral series of the type A *sfc*, characteristic of eremobatids such as *Eremobates*, which is also derived from *pvd* setae. The flagellar complex of Lipophaginae may be homologous to the type C *sfc* of Melanoblossiinae, also hypothesized to be derived from *pvd* setae, but differs greatly in the arrangement and structure of individual setae. Unlike the type B and C *sfc*, no example of an eremobatid type A *sfc* was found to be entirely comprised of *pvd* setae.

ABSENCE OF THE FLAGELLUM

The absence of a definition for flagellum and flagellar complex led to confusion regarding whether a flagellum is present in all male solifuges. For example, a flagellum has been reported to be present in all known species (e.g., Lamoral, 1975), in most species (Hewitt, 1919b), or in all except Eremobatidae (e.g., Punzo, 1998a; Dunlop et al., 2004; Bayram et al., 2011). In character 34 of their morphological character matrix, Pepato et al. (2010) coded the flagellum present in *Chanbria* Muma, 1952, the known species of which do not possess a flagellum as defined here, and absent in *Eremobates*, in which a flagellum is present.

Most of the confusion concerns Eremobatidae. There is a mistaken perception that eremobatids are unique among Solifugae in lacking a flagellum (Kraepelin, 1901: 6, but not Kraepelin, 1908a: 223; Punzo, 1998a; Bayram et al., 2011) or in having the flagellum replaced by a suit of modified setae, i.e., a flagellar complex (e.g., Klann, 2009). Rocha (2002: 441) stated that "(t)he most distinctive shape of the flagellum is present in Eremobatidae, the only family with hairy flagella (which) consist of a complex of modified bristles." Statements such as these and Punzo's (1998a: 17, 100) "all families bar one" are misleading. Firstly, a distinctly modified seta that satisfies the definition of a flagellum may be present, e.g., in *Eremobates* (Pls. 38, 39A–F) or absent, e.g., in *Eremocosta* (Pls. 37C, 39G–J), in the family. Secondly, the setal flagellar complex is formed by relatively undifferentiated setae, without a flagellum, in some Eremobatidae, e.g., *Eremocosta titania* (Muma, 1951) (Pls. 37C, 39I), as in some Lipophaginae, e.g., *Trichotoma michaelseni* (Pl. 36A). Previous references to "flagellar complex," instead of "flagellum" are more descriptive of the suit of modified setae in eremobatids. However, the use of "flagellar complex" to refer to the flagellum and all modified setae associated with it in Ceromidae, Karschiidae, and Melanoblossiinae (Roewer, 1934: 144; 1941: 117, 127; Pieper, 1977), does not differentiate the eremobatid flagellar complex from these other examples. The term setal flagellar complex was introduced here to refer to the cluster of modified setae in Eremobatidae, Lipophaginae, and Melanoblossiinae, which may (some Eremobatidae, Melanoblossiinae) or may not (some Eremobatidae, Lipophaginae) possess a flagellum as part of the flagellar complex.

By defining the flagellum in terms of setal modification, the presence of a flagellum becomes a character state of "ventral flagellar seta (*vfs*) modified and differentiated from surrounding setae," as opposed to "*vfs* unmodified," which would apply to females and immature males, or "*vfs* modified similarly to surrounding setae," which would apply, e.g., to Lipophaginae.

In addition to the suprageneric taxa in which a flagellum is absent (Lipophaginae and some Eremobatidae), a few other, mostly monotypic genera belonging to families in which a distinct flagellum is usually present, were diagnosed partly or entirely on the absence of a flagellum. Examples are *Toreus* (Ceromidae), *Microblossia* Roewer, 1941 (Melanoblossiinae), *Siloanea* (Hexisopodidae), and *Rhinippus* Werner, 1905 (Karschiidae). The validity of several of these genera was later questioned, and some were synonymized. *Rhinippus* was based on the absence of a flagellum (Werner, 1905). Roewer (1934) synonymized *Rhinippus* with *Barrussus* after recognizing a flagellum upon inspection of the type. In the others, the identification of the type specimens as adult males was called into question (e.g., *Siloanea*), or the species was considered a potential transitional form between taxa (e.g., *Microblossia*). *Siloanea* was synonymized with *Chelypus* by Wharton, 1981. Lawrence (1962b) questioned the sex of *Toreus* (Ceromidae). If the holotype of *Toreus* is indeed male, this species might be more closely related to Lipophaginae, in which the flagellum is absent, rather than Ceromidae. Similarly, for *Microblossia* (Melanoblossiinae), Wharton (1981: 60) mentioned that "if the holotype … is actually an adult male, a detailed examination of the specimen should reveal relationships between Melanoblossiidae and other solifuge families." However, both *Toreus* and *Microblossia* are known only from the holotypes. More material, including series containing both sexes, is needed to resolve these questions.

Finally, Warren (1939) reported the absence of a flagellum in apparently aberrant adult male Solpugidae. These abnormal males possessed a swollen opisthosoma, giving the appearance of gravid females. Despite the absence of a flagellum, the reproductive organs were clearly male, albeit "represented by the merest rudiments," and their genital plates (opercula) remained "in a more or less juvenile condition" (Warren, 1939: 140, 141). According to Warren (1939) the incidence of this condition, referred to as gigantism, was relatively high in the two populations examined (20% in *Solpugema hostilis* White, 1846 and 13% in *Solpuga chelicornis*), but lower in other specimens examined. Warren (1939) considered the possibility of parasitism as a causal factor, but found no evidence thereof. No further reference to this or any similar gigantism was encountered during the present study.

FLAGELLAR VARIATION AND TAXONOMIC SIGNIFICANCE

The flagellum plays an important role in the taxonomy of Solpugidae at the species level. However, an apparently limited amount of variation among what were assumed to be closely related species prompted Hewitt (1919b) to suggest that the flagellum is of little value at the generic level. Considering that many solpugid genera may not be monophyletic, Hewitt's (1919b) opinion may be misleading.

Few data are available concerning intraspecific variation in aspects of the solifuge flagellum. Wharton (1981: 52) reported "considerable variation" in the shape of the cup-shaped flagellar base of *Hexisopus pusillus*. The morphologically uniform group of large nocturnal *Zeria* Simon, 1879 species with a long flagellar shaft in southern Africa are distinguished largely on the basis of the relative length of the shaft and microstructures thereon (Hewitt, 1919b; Wharton, 1981). These characters, sometimes representing minor differences such as the shape of the tip of the shaft, e.g., in *Zeria obliqua* (Roewer, 1933), or a paler area subapically on the shaft, e.g., in Namibian *Zeria monteiri* (Pocock, 1895) (*vide* Wharton, 1981), are often corroborated by dentition and geographical distribution, thus providing some basis for stability in flagellar morphology at the species level. Wharton (1981) presented a detailed investigation of intraspecific variation in the flagellar shaft of a series of *Metasolpuga picta.* Subapical denticles (serrations) on the shaft varied in the level of differentiation, from fairly distinct to absent. Wharton (1981) speculated that variation in curvature of the shaft near its base might be related to the male's mating history. Of particular interest is a negative correlation between the size of the male and the relative length of its flagellum.

The general absence of revisionary studies on solifuges seldom permits evaluation of intraspecific variation, especially regarding geographically widespread species. For example, Purcell (1899) reported variation in flagellar length of more than 1.3 times the width of the ocular tubercle for specimens of the widely distributed *Zeria venator* as *Solpuga venator* from different localities. Purcell (1899) found no reliable character by means of which the species might be subdivided but Hewitt (1919b: 13) noted that this range in flagellar length might indicate “several races or local forms” if intermediate forms proved to be absent. Hewitt (1934) reported variation in the “slenderness of the flagellum” of *Blossia falcifera,* coincident with variation in other characters such as the relative length of the terminal tooth. Wharton (1981) pointed out that Lawrence (1928, 1953, 1959, 1961) described several species and subspecies of *Solpugassa* based on flagellar proportions. Wharton (1981) argued that these characters might be allometric, noted the presence of minute spicules on the forks at the tip of the shafts in all specimens examined, and emphasized the need for more specimens to study flagellar variation within and among populations. Hewitt (1919b: 13) mentioned that the tip of the flagellum of *Solugema hostilis* is “quite constant”, but variable in *S. derbiana* and therefore cannot be used “as an absolute unit character.”

Interspecific similarity in flagellar morphology concerning the sharp, blade-like tip of the flagellum in various species of *Solpuga* now mostly placed in *Solpugema*, i.e., *Solpugema derbiana*, *S. hamata*, *S. hostilis*, *S. tookei* (Hewitt, 1919), and *Solpuga bechuanica* Hewitt, 1914, was noted by Hewitt (1919b: 14). Such interspecific similarity in flagellar morphology might be indicative of monophyletic groups. As with dentition, however, the lack of a robust systematic framework hampers evaluation of the value of flagella in solifuge taxonomy at the species or generic level.

Structures associated with the flagellum should also be evaluated for variation. For example, Brookhart and Muma (1981) reported that variation in the mesoventral groove and its basal flange was “subtle but consistent ... among populations examined.”

FUNCTIONAL MORPHOLOGY OF THE FLAGELLUM

The precise functions of the flagellum remain elusive. Earlier speculated to be a sensory seta (Bernard 1896), it has since been shown that no nerves are associated with the flagellum of Solpugidae (Lamoral, 1975). Warren (1939) proposed that the flagellum is used to stimulate the female. Heymons (1902) and Junqua (1962) observed that copulation was unaffected when the flagellum was removed in two species of Galeodidae (whether these copulations resulted in fertilized eggs is unknown, however), prompting some workers (e.g., Cloudsley-Thompson, 1961; Lawrence, 1963) to state that the flagellum plays little or no role in reproductive success. On the other hand, Sørensen (1914: 170) stated that the flagellum is unquestionably a copulatory organ developed to collect (*Rhagodes* Pocock, 1897) or retain (*Galeodes*, *Solpuga*) seminal fluid, i.e., *une masse visquese*. To date, its function as an organ that holds sperm proved true only for the bowl-shaped flagellum of the ammotrechid *Oltacola chacoensis* (*vide* Peretti and Willemart, 2007). Only three observations support the hypothesis that the flagellum has some function during copulation itself, although the details appear to differ among taxa (Table 2).

A possible mechanical function of the flagellum is likely facilitated by hemolymph action. Despite the great diversity in flagellar morphology, all flagella are either inserted into the chelicera in a distally directed position, as in Ammotrechidae, Eremobatidae, Gylippinae, Rhagodidae, Melanoblossiinae, Mummuciidae, and the karschiid genera, *Barrus, Barrussus* and *Eusimonia*, or are able, probably by means of hemolymph pressure, to be directed distally by rotation in the socket, as in Ceromidae, Daesiidae, Galeodidae, and Hexisopodidae, or by extension, as in Solpugidae and the karschiid genus, *Karschia*. This commonality was first noted by Sørensen (1914: 165), who identified a more weakly sclerotized section at the base of the flagellum of some Solpugidae, where the flagellum “articulates” during forward movement. In the present study, this apparently weaker section was confirmed in Solpugidae, the only family which possess a proximally directed flagellum that is fixed to the chelicera but able to be distally directed presumably by means of hemolymph pressure. A distally directed flagellum would place the flagellum, and particularly its apex, closer to, and deeper into the female reproductive tract during the female genital contact phase (Table 2). Hemolymph pressure might also improve the function of a membranous flagellum as an intromittent organ by increasing its girth and rigidity, and hence its ability to retain and transfer sperm. The flagellum may also assist movement of the aflagellate spermatozoa of Solifugae (Klann et al., 2009) by inducing the muscles around the female reproductive tract to move the spermatozoa along. Strong muscles surrounding the female reproductive tract were observed in a galeodid studied by Klann (2009: 164), suggesting a mechanical displacement of sperm packages within the female genital system. The flagellum may also function to break up the sheath surrounding individual spermatozoa or groups of spermatozoa in some taxa. Among six families studied by

Klann (2009), only Eremobatidae and Solpugidae possessed separate, non-bound spermatozoa that do not need to be freed from a cluster, package or surrounding sheath, prior to fertilization, suggesting that the type of sperm packaging possessed by a solifuge taxon may be related to its flagellar morphology (Table 3).

The diversity in flagellar morphology may indicate different, taxon-specific functions. For example, the uniform **diploflagellum** of different species of Rhagodidae, and probably also the largely similar flagella of, e.g., different species of Ammotrechidae and Galeodidae, suggest a general functionality for the flagellum, which may or may not be in addition to species-specific functions. For example, the ubiquitous bowl-shape of the flagellum among different species of Ammotrechidae suggests a general function for sperm retention and transfer, as confirmed in one species of Ammotrechidae (Peretti and Willemart, 2007), whereas the species-specific variation in shape, e.g., in the apex of the flagellum (e.g., truncated to spouted) suggests a function in specific-mate recognition or sexual selection through cryptic female choice.

Species specific modifications to the flagellum of Solpugidae typically involve microstructures (denticles, hooks, lamellae, etc.) concentrated on the distal end of the flagellar shaft. These microstructures present the greatest diversity in form and position among the flagella of Solpugidae. The only area in which these microstructures come into sufficiently close contact with the female during mating is in her reproductive tract (Table 2). The female reproductive system comprises two ovaries, each connected to a relatively short oviduct, which open into a single genital chamber, variously referred to as the copulatory pocket or seminal reservoir (Dufour, 1861: 434), the “uterus and vagina” (Birula, 1892) or the “genital vestibule” (Warren, 1939), connected to the exterior via a gonopore situated on the second abdominal segment (Klann, 2009). The lumen of the genital chamber is lined with a thick but flexible, chitinous layer (Warren, 1939; Vachon, 1945; Klann, 2009). Subdivision of the oviduct of Solpugidae into the oviduct proper and the oviducal chamber (Warren, 1939) may be of relevance to the shape of the flagellum in this family. After passing through the oviduct proper with its thick lining of chitin, the long whip-like flagellum would enter the oviducal chamber through a very narrow duct that bends back upon itself before entering the chamber, as illustrated by Warren (1939: 143, fig. 2d), bringing the distal part of the flagellar shaft, with its species-specific microstructures very close to the sides of the duct. The most likely area for species specific mate recognition or cryptic female choice may therefore be the part of the female oviduct which connects with the oviducal chamber. Similar female reproductive tract anatomy may exist in other taxa with long whip-like flagella, but no data are available. It is noteworthy, however, that denticle-like microstructures on the whip-like flagellum of Hexisopodidae are weakly developed or absent, suggesting that the whip-like flagellum might fulfill at least partly different functions in different taxa.

Two canals are present in the whip-like flagella of Solpugidae (Lamoral, 1975) and probably also in Ceromidae, Hexisopodidae, and the daesiid genera *Ammotrechelis*, *Namibesia*, and *Syndaesia*. Whereas the hemolymph canal is closed to the exterior, the alembic canal opens to the exterior at the flagellar apex, suggesting a possible exocrine function for the alembic fluid. Lamoral (1975) hypothesized that the secretion serves as a pheromone but this is unlikely if it is excreted within the female reproductive tract as indicated by circumstantial evidence for Solpugidae, at least. For example, a glistening at the apex of the flagellum of a male *Metasolpuga picta* when withdrawn from the female genitalia (R.A. Wharton, personal obs.) suggests that secretion occurred during insemination or post-insemination genital chewing (alternatively, the glistening substance represents the remnants of seminal fluid). In these observations, the only observations involving a whip-like flagellum, the entire shaft was inserted into the female (Wharton, 1987, personal obs.). The flagellum of *M. picta* is almost the length of its chelicera (Pl. 97B) and can thus be inserted deep into the female genital tract, most likely extending along the oviduct proper and into the oviducal chamber (Table 4) where it may secrete the alembic fluid. The thick cuticular lining of the oviduct proper would protect it from being ruptured by the sclerotized male flagellum during insertion. Some dirt, which is often observed in the alembic lumen, sometimes far down the shaft, may have entered after the alembic fluid was dispelled, indicating that the male has mated. More data are needed to shed light on the functional morphology of the flagellum, including measurements (different aspects of the flagellar shaft, depth of shaft insertion, length of different parts of the female reproductive tract), comparative reproductive tract morphology (representative of different flagellar types), sperm morphology, and additional observations of mating behavior in a range of taxa.

The function of the spiniform setae associated with the flagellum in some taxa, as well as additional processes and flanges on the male chelicera, especially apically, are unknown, but given their diversity across the order, are most likely sexually selected (Hewitt, 1919b: 15).

Modified setae in the setiform flagellar complex (*sfc*) of Eremobatidae, may function to detect the presence of, and/or remove sperm from a previous mating. Indeed, remnants of seminal fluid were observed on the fingers of males post-mating

(Muma, 1966b). According to Muma (1966b), copulation among eremobatids is only complete after the male chelicera has made contact with a seminal globule, which is supported by the observation of an aberrant mating in which a male mounted a female 50 times in the course of 40 minutes, in an endless loop of "sperm transfer" and genital prodding until the pair were separated. Muma (1966b: 348) reported that "the male did not appear to accomplish emission [of sperm] throughout the abortive procedure". The importance of the flagellum during sperm transfer is emphasized by the comparison between the weakly modified, relatively uniform flagellum of Eremobatidae, with direct sperm transfer, and the highly modified flagellum of taxa, e.g., Solpugidae, with indirect sperm transfer. Unfortunately, no relevant data are available for other taxa with a setiform flagellar complex and flagella that are reduced or absent (i.e., Lipophaginae and Melanoblossiinae).

TAXONOMIC DIVERSITY OF THE FLAGELLAR COMPLEX

AMMOTRECHIDAE: The flagellum of Ammotrechidae (Pls. 34E, F, 35F, G, 40J, K) is a fixed (non-rotatable) membranous, oval bowl-shaped structure (Muma, 1976). A short stalk ("base" in composite flagellar terminology, Table 13) connects the flagellum to the cheliceral finger prodorsally. The stalk attaches and is fixed to the sclerotized oval internal margin of the socket such that the apex of the flagellum is distally directed (Pl.146A, E, G, I). The margins of the flagellum are usually slightly curled inwards and minutely fringed, often more so where the bowl-shaped structure opens distally. According to Roewer (1934: 138, fig. 133b, c, reproduced here in Fig. 22E), the flagellum comprises a narrow lumen between two membranous walls, derived from a plumose seta that broadened, the edges curling inwards (see also Setal Transformation Hypothesis in section Homology of the Flagellum). This double-sided character disappears towards the tip of the flagellum, restricting the lumen to the very proximal part of the flagellum. The lumen is presumably connected to the hemolymph in the chelicera via the attachment point and hemolymphic pressure in the flagellum is presumed to increase by contraction of muscles in the cheliceral manus during copulation (Roewer, 1934: 138). Maury (1984: 756, fig. 3) neither indicated a double-sided character in his cross-section of an ammotrechid flagellum, nor provided a description thereof. No modified spiniform setae are associated with the flagellum of Ammotrechidae and, except for the flagellum itself, the proventral distal setae (*pvd*) are undifferentiated.

CEROMIDAE: Except for *Toreus*, in which the flagellum is apparently absent, the flagella of Ceromidae (Pls. 32A, B, 33A–C, 91A, C, G, I) can rotate paraxially through 180°, with the apex directed proximally in the resting position. The flagellum was erroneously described as “immovably fixed” by Purcell (1899: 395). The shaft is sclerotized and rod-shaped, e.g., in *Ceroma*, to membranous and partially rod-shaped (in *Ceromella*) and, as in Solpugidae, minutely serrate along the shaft (Pl. 41D), especially towards the apex. The base is swollen (capsular) with a longitudinal membranous section prolaterally which appears to hold the alembic fluid and may be homologous to the alembic pouch in Solpugidae. A similarity between the swollen base of the flagellum of Ceromidae and the bulbous base of the flagellum of Solpugidae was first noted by Pocock (1897), whereas Roewer (1934: 148) suggested that the small enlargement at the base of the flagellum (the basal peg) of *Karschia* is similar to the base of the flagellum of Ceromidae. The base of the flagellum of Ceromidae is attached to the cheliceral fixed finger via a short but distinct stalk situated in a strongly sclerotized socket (Pl. 96). The flagellum probably formed by longitudinal invagination of a seta, as with the formation of the flagellar shaft of Solpugidae described by Lamoral (1975). A cross-section of the flagellum of *Ceroma inerme* prepared during the present study appears to show two canals, an alembic canal and a hemolymph canal (Pl. 41B–E). Roewer (1934: 140) reported that the shaft is blind-ending apically. However, if an alembic canal is present, it would be connected to the exterior via an apical pore, indications of which were found in *Ceroma inerme* (Pl. 41E). The hemolymph canal narrows and eventually disappears towards the apex (Pl. 41C). Hemolymph in the shaft does not connect to the exterior, and hemolymphic pressure is thought to cause the flagellum to rotate through 180° (Roewer, 1934: 148).

The base of the flagellum of Ceromidae is obscured behind a fan-like array of three to eight (depending on species and on which setae are included in the count) rigid flagellar complex plumose (*fcp*) setae arising from a small elevation. These setae, which may protect the base of the flagellum (Purcell, 1899; Hewitt, 1935), tend to be distinctly narrowed apically, and often shaped like a pipette, comprising a long, broad, markedly sclerotized cylindrical base, and a narrow, extended and weakly sclerotized apical section which may be smooth or plumose. Two or three flagellar complex spiniform (*fcs*) setae (*Oberfingerdornen sensu* Roewer, 1934: 148) situated dorsolaterally on the cheliceral fixed finger near the base of the flagellum, characterize some species. For example, two *fcs* setae are present in *Ceroma langi* Hewitt 1935 and *Ceroma ornatum*

(Pl. 93B, C) whereas three are present in *Ceroma sylvestris* Lawrence, 1938 and *Ceromella focki* (Kraepelin, 1914).

DAESIIDAE: The flagellum is used extensively in the systematics of Daesiidae. The flagella of Daesiidae can rotate paraxially through 180°, with the apex directed posteriorly in the resting position. The diversity of form in this family is reflected in the flagellar shapes. Except for *Ammotrechelis* (Pls. 32F, 33H), *Syndaesia*, and the Namibesiine, *Namibesia* (Pls. 32E, 33G), a shaft is absent, and the flagellum is typically membranous. In the membranous flagella, the sides of the flagellum may be shallowly curved inwards, forming a bowl-shaped structure, or deeply curved inwards, forming a husk- or capsule-shaped structure, and various modifications thereof. As opposed to the mummuciid flagellum, in daesiid taxa which possess a vesicular flagellum, the longitudinal aperture, where the two margins of the flagellum converge, faces away from the surface of the chelicera. The edges of the flagellum of Daesiidae are usually fringed, especially towards the apex, and fine hairs or spicules, important for species diagnosis, cover the surface of the flagellum in many species. A midrib, which may terminate in a distal hooklet, extends medially along the length of the flagellum in some species of *Blossia* (Pl. 35C). The flagellum of Mummuciidae is fixed prodorsally to the fixed (dorsal) finger and, as in Ammotrechidae, In the rest position, the apex of the flagellum is proximally directed in Daesiidae as opposed to the distally directed flagellar apex in Mummuciidae and Ammotrechidae.

Based on the absence of a shaft, the membranous flagellum of Daesiidae, i.e., excluding daesiids with a shaft present (*Ammotrechelis, Namibesia*, and *Syndaesia*) is hypothesized to be homologous with the base of the composite flagellum (Table 13). It is connected to the flagellar socket via a stalk that is usually very short and indistinct. The stalk is gradually attached to the base, e.g., in *Ammotrechelis*, *Biton*, and *Gluvia*, in such a manner that the attachment superficially represents a hairpin to kidney shape (e.g., Pl. 40G–I). The flagella of *Blossia* and *Hemiblossia* are attached to the chelicera at the proximal end of the flagellum (Pl. 34C, D). The flagellar stalk is situated more medially on the membranous flagella of other Daesiidae, e.g., in *Biton* and *Gluvia* (Pl. 34A, B). The point of attachment may be phylogenetically informative. Roewer (1934) did not illustrate the flagellum of Daesiidae in cross section but, based on its similarity to the flagellum of Ammotrechidae (Roewer, 1934: 138, fig. 133b, c), it presumably evolved in a similar manner, by broadening of a seta and subsequent slight to marked inward curving of the margins (see also Setal Transformation Hypothesis in section Homology of the Flagellum). The lumen is probably also connected to the hemolymph, and the flagellum may function when hemolymph pressure increases by contraction of the muscles in the cheliceral manus during copulation. No sign of hemolymph was seen in the present study, however.

Spiniform setae associated with the flagellar complex (*fcs*) are absent in Daesiidae. The modified spiniform setae of *Gnosippus klunzingeri* are unlikely to be part of the flagellar complex, but may be associated with its psammophilus habitus. Setiform setae, on the other hand, are commonly more differentiated in male *Blossia*. The three distalmost proventral distal (*pvd*) setae are slightly more robust, and arranged into a cluster, slightly separated from the rest of the *pvd* series, in males of some species of *Blossia*, e.g., *Blossia falcifera dolichognathus* Hewitt, 1921 currently in synonymy with *B. falcifera* Kraepelin, 1908, *B. filicornis*, and *B. grandicornis* (e.g., Pl. 139C; Hewitt

1921: 10, fig. 4). Hewitt (1921) noted a similarity between these setae and the setae situated at the base of the flagellum of Ceromidae, and suggested that they may protect the flagellum in the resting position. Among the setae of the retrolateral finger (*rlf*) series, one or two of the dorsodistal setae, situated slightly below the upper margin of the chelicera on the retrolateral surface, are thicker, less filiform, and differ in presence/absence and extent of spicules. These modified setae in *Blossia* are termed the *principal rlf* setae (Fig. 14B). The number of *principal rlf* setae, and the extent and position of spicules on these setae are important in *Blossia* systematics (e.g., Hewitt, 1919b: 58, fig. 10; Lawrence, 1935, and figures therein).

The monotypic genera, *Namibesia* (Namibesiinae) (Pl. 132A) and *Syndaesia*, are unique among Daesiidae in possessing flagella which are long, sclerotized and whip-like, more closely resembling the flagella of Ceromidae, Hexisopodidae, and Solpugidae than those of other daesiids. The base, stalk and manner of the attachment of the flagellum of *Namibesia*, and probably that of *Syndaesia* (*vide* Maury, 1985), is particularly similar to that of Hexisopodidae (Pl. 40E, F).

The flagellum of *Ammotrechelis goetschi* appears to be intermediate in form between the whip-like and membranous flagella, possessing both bowl-shaped and whip-like sections (Pl. 32F). The bowl-shaped section, or base, is considered homologous to the membranous flagellum of most Daesiidae, Ammotrechidae, and Mummuciidae, and to the base of, e.g., Ceromidae and Solpugidae. The broad shaft is considered homologous to the shaft of Ceromidae, Hexisopodidae, Solpugidae, and the daesiids, *Namibesia* and *Syndaesia*. The *Ammotrechelis* flagellum therefore supports the hypothesis that the base of the whip-like flagellum is homologous to the various shapes of membranous flagella.

EREMOBATIDAE: The type A setiform flagellar complex (*sfc*) of Eremobatidae is a heterogeneous assemblage of modified setae belonging to the proventral distal (*pvd*), or *pvd* and prodorsal distal (*pdd*) series, and, if present, a setiform flagellum (Pls. 37–39). The type A *sfc* differs from the type B and type C *sfc* in that it does not appear to ever comprise *pvd* setae *only*. The various forms of *sfc* in eremobatids are well documented by Muma (1951, 1970a, 1989) and summarized in Table 12. The *sfc* of *Eremobates* and, often to a lesser extent, *Eremochelis* comprise a modified apical seta, hypothesized to be the modified ventral flagellar seta (*vfs*), or “flagellum,” which demarcates the boundary between the **dorsal** and **ventral series of the setiform flagellar complex** (Pls. 38A, B, 39A–F). Both series are situated in a narrow recess of the asetose area. The flagellum originates distalmost, consistent with its origin from the ventral flagellar seta (*vfs*) (Pl. 46A). The dorsal and ventral series are respectively hypothesized to be homologous to the prodorsal distal (*pdd*) and proventral distal (*pvd*) series of setae. The setiform flagellum ranges from a flat, membranous, blade-like structure, fringed at the margins, e.g., in *Eremobates* (Pl. 39A–E; Muma 1951;53, fig. 46), to a short, barely visible plumose seta, e.g., in *Eremochelis insignatus* (Pl. 76E), but is never prominent, and is concealed by other modified and unmodified setae which form a cluster. In *Eremobates* and some species of *Eremochelis*, the flagellum is situated within a groove extending along the prolateral surface of the fixed finger (Pls. 38, 39A–E). In other taxa, the prolateral groove is absent, or differs in position, shape and length, characters used extensively in eremobatid systematics (Muma 1951: 39).

In *Eremocosta*, the *sfc* is weakly differentiated, with minor modifications to setae of the *pdd* and *pvd* series involving slight increases in length and robustness, and a flagellum is absent. For example, the *sfc* of *Eremocosta titania* (Pls. 37C, 39I) is vaguely reminiscent of the weak *sfc* of the lipophagine, *Trichotoma michaelseni* (Pl. 36A). A flagellar groove is absent, but a deep, ovate retroventral to ventral concavity, referred to here as the ventrodistal concavity, is present (Pls. 37C, 73B).

Species of *Eremothera* Muma, 1951, e.g., *E. sculpturata* Muma, 1951 (Pls. 37B, 39J, 74A) are unique in possessing markedly prolaterally projecting setae in the ventral series, which not only comprise proventral distal (*pvd*) setae, but also include the comb of the proventral subdistal (*pvsd*) series. A flagellum appears to be absent but the dorsal series, comprising modified *pdd* setae, consists of stiff, tubular bristles as well as two broad and flat setae situated apically in the *pdd* series.

The *sfc* of several other eremobatid genera mainly comprise modified *pdd* setae, without a flagellum. Species of *Eremorhax*, e.g., *Eremorhax joshui*, possess a homogeneous cluster of setae in the *sfc* that appears to consist only of *pdd* setae, although the affinity of the different setae in the *sfc* is unclear, and it may also include *pvd* setae modified similarly to the *pdd* setae. The *sfc* of *Chanbria* comprises elongated, weakly striated *pdd* setae and similarly elongated *pvd* setae, without a flagellum in all described species. The *sfc* of *Hemerotrecha* is characterized by weak to strongly modified *pdd* setae in the dorsal series. These may be homogeneously modified, forming a row of three or four modified setae, e.g., in *Hemerotrecha hanfordana* (Pl. 37D), or a row of heterogeneously modified setae such as the two clavate distal seta followed by a row of less modified *pdd* setae in *Hemerotrecha branchi*. Although situated distally in the *pdd* row, none of these more distinct setae are situated apically, implying that none is a modified *vfs* and a flagellum is therefore absent. A small ventrodistal concavity, the mesal ventral groove *sensu* Brookhart and Cushing (2008: 50, fig. 3), is present in some *Hemerotrecha*.

Setae within the complex differ in shape (round or flat, curved or straight, etc.), plumosity/striation, and robustness. Setae of the ventral series, derived from the *pvd* series, are slightly to moderately modified and usually homogeneous within species whereas setae of the dorsal series, derived from the *pdd* series, on the other hand, are often more markedly, and not necessarily uniformly, modified.

References to apical plumose bristles (e.g., Muma, 1951: 51, 99), setae (e.g., Muma, 1951: 110), or spines (e.g., Muma, 1951: 82), indicating distal setae differentiated from other setae in the complex, typically refer, albeit unintentionally, to the flagellum. A second modified seta situated ventral to the flagellum and usually very indistinct, referred to as subapical plumose seta (subapical plumose bristle in the literature, e.g., Muma, 1951: 51, 99), may be present, e.g., in *Eremobates chihuaensis* Brookhart and Cushing 2002 (Pl. 39E).

New World workers place more emphasis on the shape of the flagellar groove than on the flagellum, which is seldom depicted in figures, except in a few cases, e.g., Muma (1951: 53, fig. 46) and Brookhart and Muma (1981: 291, figs. 2, 3). A detailed survey with modern imaging techniques may reveal the flagellum to be of more significance in eremobatid systematics. Indeed, Muma (1970a) used broad differences in apical setal morphology to distinguish between *Eremobates* and *Eremorhax*.

GALEODIDAE: The flagellum of Galeodidae has variously been described as ramiform, spoonshaped (*cuilleriforme*), capitate, and leaf-like (Pls. 30G, 31E; Sørensen, 1914: 34; Birula, 1929; Roewer, 1934: 149; Muma, 1976). The stem or peduncle flattens distally into a blade or scapus (Birula, 1916, 1925), the concave inner surface of which is finely plumose. Interspecific variation in the flagellum of Galeodidae is subtle and includes such characters as the peduncle to scapus ratio, the shape of the base of the scapus (asymmetric versus symmetric), and/or the manner in which the flagellum transitions apically into a point (e.g., Birula, 1936a, 1938: 111, fig. 74). The terms stalk and stem, although often used as synonyms of peduncle, are not assumed to be homologous to the stalk as defined here (Table 13). The flagellum is paraxially or diaxially rotatable, and has been described as “extremely” mobile, and able to turn 180º (Sørensen, 1914: 34; Roewer, 1934: 145; Muma, 1976: 4). The flagellar socket of Galeodidae is situated in a deep depression (alveolus) which permits movement in a paraxial to slightly diaxial manner. Unlike the rotatable flagellum of other taxa, i.e., of Ceromidae, Daesiidae, and Hexisopodidae, the flagellum of galeodid specimens preserved in 90% ethanol were found to be immovable, consistent with descriptions that it is non-rotatable (e.g., Klann, 2009). This may indicate some difference between the attachment of the flagellum of Galeodidae versus the rotatable flagella of other taxa (e.g., Daesiidae), which retain the ability to rotate after fixation.

The flagellum of Galeodidae appears to have altered little from its original setal form. Roewer (1934: 150, fig. 147) provided cross sections, which indicate a hollow shaft in the peduncle and a small, retrolaterally compressed lumen in the scapus (blade). Hemolymph pressure inside the lumen of the flagellum was suggested to cause it to rotate forward (Sørensen, 1914: 167; Roewer, 1934: 149).

One to four flagellar complex spiniform setae (*fcs*), usually blunt and apically flattened, are situated proximoventral to the base of the flagellum of Galeodidae (Birula, 1929a: 164, fig. 1; 1929b: 276, fig. 2; 1937a: 595, fig. 17; 1938: 155, fig. 87). These setae appear to be modified prodorsal distal (*pdd*) setae, based on their insertion adjacent to the prodorsal distal margin (pddm) of the fixed finger (Pl. 4C). Variation in number up to two *fcs* setae have been reported on the same individual (Lawrence, 1954) or among different conspecifics (e.g., Lawrence, 1956: 132; Birula, 1937b: 584), and is therefore not very useful in delimiting species. The *fcs* setae of galeodids usually decrease in size proximally (Birula, 1936a, 1937a: 594).

A well differentiated, stout flagellar complex plumose (*fcp*) seta, and occasionally a second weaker plumose seta, are situated directly proximoventral to the base of the flagellum in Galeodidae (Pls. 4C, 63A, D). This seta was first mentioned by Birula (1937a, b; 1938). The *fcp* seta probably belongs to the *pvd* series and assumed a more dorsal position due to a shift in the position of the flagellum and the remaining *pvd* setae.

GYLIPPIDAE (GYLIPPINAE): The flagellar complex of Gylippinae was discussed by Birula (1913). The flagellum of Gylippinae is unique in being situated entirely on the sclerotized area of the fixed finger, to which it is fused (Pls. 4D, 32H, 33I). The section of the flagellum that remains free is strap-like, but the apex varies (Gromov, 1998: 181, fig. 1s; Birula, 1938: fig. 62c), e.g., it is jagged in *Gylippus* (*Anoplogylippus*) *pectinifer* Birula, 1906 or pointed in *G.* (*Hemigylippus*) *krivokhatskyi* Gromov, 1998. The apex of the flagellum is reportedly bifid (Birula, 1938: fig. 58e) in *G.* (*A.*) *rickmersi* Kraepelin, 1899, currently in synonymy with *G.* (*A.*) *ferganensis* Birula, 1893. Roewer (1934: 141) interpreted the bifid apex as “two papillae,” each representing a separate flagellum homologous to the two rhagodid flagella. However, the putative “papillae” originate from the same base, consistent with a single flagellum.

The flagellum of Gylippinae may have developed from a seta that became broad and flattened. Alternatively, similarities with the basal part of the flagellar shaft of Solpugidae suggest a secondary simplification from a composite flagellum formed by infolding of a seta, which would imply that the alembic canal may have been secondarily lost in Gylippinae. If it is indeed a composite flagellum, as hypothesized here (Table 13), it is unique in the absence of a base. It appears that the lumen of the flagellum is connected to the hemolymph in the cheliceral manus, the hydraulic pressure of which is assumed to straighten the flagellum during mating (Roewer, 1934: 142).

A prominent, robust spiniform macroseta is situated prodorsally near the base of the fixed (dorsal) finger of adult male *Gylippus* (*Gylippus*) and *Gylippus* (*Paragylippus*) (Pls. 85A, B, 86A, B). This flagellar complex spiniform (*fcs*) seta, the *Oberfingerdorn* of Birula (1913: 322) and *Spina digitalis* of Roewer (1934: 308), is hypothesized to be a modified prodorsodistal (*pdd*) seta.

Another large, robust spiniform macroseta is situated on the retrolateral surface of the cheliceral manus of male Gylippinae. This seta, the *Mandibulardorn* of Birula (1913: 322), the *Spina principalis* of Roewer (1934: 308), and the mandibular spine of Gromov (1998: 184) is referred to here as the **retrolateral manus spiniform (*rlms*) seta** (Pls. 85B, 86A, B).

The flagellar complex spiniform (*fcs*) seta and the retrolateral manus spiniform (*rlms*) seta of Gylippinae are the largest, most robust setae on the chelicerae of solifuges. The position of such highly modified setae on the retrolateral surface of the chelicera is also unique because distinct modifications of one or two setae are usually restricted to the prolateral or prodorsal surfaces of the chelicera in solifuges, the only exceptions being some modified retrolateral finger setae (the *principal rlf* setae) in other families, especially Daesiidae. A possible homolog of the *rlms* seta of male Gylippinae may also be identified in females (Pl. 85D, F, arrows; Birula, 1913: pl. VIII, fig. 1).

The *rlms* and *fcs* setae are used extensively in the systematics of Gylippinae (Birula, 1913) and appear to be stable in number, position, and shape. Indications of variation in the literature may be misleading. For example, a single *rlms* seta was reported in *Gylippus* (*P.*) *monoceros* by Birula (1913) and Roewer (1933: 314, fig. 229B), as in the specimen examined in the present study (Pl. 85B), whereas two *rlms* setae were depicted by Koç (2011: 120, fig. 3). However, other differences between the specimen illustrated by Koç (2011: 120, fig. 3) and in Pl. 85B suggest they are not conspecific and that differences in the number of *rlms* may not be indicative of intraspecific variation.

Different interpretations of the spiniform setae may also account for the apparent variation. For example, Roewer (1934: 308) distinguished *Gylippus* from other gylippid genera by the presence of two *rlms* setae and one *fcs* seta, whereas Birula (1913: 322) diagnosed it on the basis of one *rlms* seta and “one or two” *fcs* setae. Based on Roewer’s (1934: 311) figs. 228$A_{1,2,}$ B_1, the second *rlms* seta reported by Roewer (1934) and the second *fcs* seta reported by Birula (1913) appear to be the same seta, interpreted differently by the two authors, thus accounting for the different numbers provided in the generic diagnosis.

GYLIPPIDAE (LIPOPHAGINAE): Southern African gylippids possess a weakly to strongly differentiated type B setiform flagellar complex (*sfc*) without a flagellum, i.e., no seta in the complex is clearly differentiated from the others (Pl. 36A–F). Unlike the type A setiform flagellar complex of Eremobatidae, the flagellar complex of Lipophaginae appears to only comprise setae of the proventral distal (*pvd*) series, which have shifted dorsally and are usually uniformly modified, i.e., all setae in the complex are similar, or nearly so, in shape, length, etc. Three or four plumose setae are more robust and distinctly more plumose compared to the other *pvd* setae in *Lipophaga trispinosa* (Pls. 36B, 89A). In *Bdellophaga angulata*, the *pvd* setae appear to have shifted dorsally and the *sfc* consists of the apicalmost eight *pvd* setae which form a brush-like cluster, intertwined apically into a “fused concave cushion” (Pl. 36C, D; Wharton, 1981: 41), directly ventral to which, approximately four regular *pvd* setae are modified and apically angular (Pl. 36C, E, F). The *pvd* setae are unmodified in *Trichotoma michaelseni* (Pl. 36A). Although some *pdd* setae are slightly more robust in male *T. michaelseni* than in females (Pl. 87A–F), they do not form a distinctly differentiated setal cluster. Therefore, the setiform flagellar complex, as well as the flagellum, are interpreted as weak to absent in *T. michaelseni*.

HEXISOPODIDAE: Although reported as immovable by Muma (1976, 1982), the flagellum of Hexisopodidae is paraxially rotatable, probably rotating by hemolymph pressure (Pls. 32C, D, 33D–F, 129). The rod-shaped, strongly curved shaft originates from a cup-shaped base, attached near the base of the fixed (dorsal) finger via a short but distinct stalk (Pl. 32D). It is largely hidden between the two chelicerae. Interspecific differences concern the apex and degree of expansion of the laterally compressed shaft (Pl. 33D, E). The shape of the cuplike base may vary intraspecifically in *Hexisopus* *pusillus* (*vide* Wharton, 1981) and *Hexisopus lanatus* (*vide* Purcell, 1902). The swollen capsular base of the flagellum resembles the base of the flagellum of Ceromidae, but differs in being open, forming a cup-shaped structure, rather than a capsular base. The cup-shaped flagellar base of the daesiid genus, *Namibesia*, is very similar to that of Hexisopodidae (Pl. 32E, F). Roewer (1934: 148) did not provide a cross section of the flagellum of Hexisopodidae, but noted its similarity to the flagellum of Ceromidae. The similarity of the flagella of Ceromidae, Hexisopodidae, Solpugidae, and *Namibesia* suggests a common origin. According to Roewer (1934: 140), the flagellum of Hexisopodidae is blind ending apically, but this should be reinvestigated if an alembic canal is present, as proposed by Lamoral (1975) and evident in Pl. 32C, D.

KARSCHIIDAE: Two very different flagellar complexes occur in Karschiidae. The flagellar complex of *Karschia* (Pls. 30A, 31A, 50–52) comprises various structures comprehensively labelled by Birula (1938: 46: fig. 20): a long, usually coiled, filiform flagellum; plumose setae situated directly ventral to the flagellum and modified to various degrees including broadening (*Säbelborsten* of Kraepelin, 1908a: 222; Birula, 1938; Gromov, 1998: 181, figs 1f-I), referred to here as the flagellar complex plumose (*fcp*) setae; and one or two acuminate subspiniform setae, typically swollen basally and situated dorsoproximal to the flagellar base, labeled, distal to proximal, *k* and *c* by Birula (1938), and referred to here as the flagellar complex subspiniform (*fcs*) setae. Based on their position relative to the flagellum in species such as *Karschia* (*K.*) *tibetana* Hirst, 1907, Hirst (1907) and Kraepelin (1908a: 221, fig. 57) suggested that the *fcs* setae function to stabilize the coiled structure of the flagellum.

The flagellum of *Karschia* resembles both the sessile flagellum and the composite flagellum. It retains a basic resemblance to a plumose seta, often with a fine fringe of hairs, mistakenly termed “cilia” by Lawrence (1954: 112) along one side (Roewer, 1934: 142), or other microstructures on the shaft, labeled *uc* in Birula (1938). This coiled, filiform flagellum has been described as an elongated double-walled tube-like structure, formed by a seta that broadened along its length, and the margins of which rolled inwards, almost forming a closed canal, with hemolymph restricted to the double walls of its shaft (Roewer, 1934: 145, fig. 143 A_1, reproduced here as Fig. 22A). Roewer’s (1934) interpretation could neither be verified nor refuted in the present study, and is accepted pending further investigation. Until more data regarding the presence of an alembic canal becomes available, the flagellum of *Karschia* is considered to be sessile, even though a stem, base and stalk are present. The base of the flagellum of *Karschia* comprises a slight swelling from which a small excrescence, the basal peg (*Zapfen* of Roewer, 1934: 148) emerges (Pls. 30A–C, 40C; Birula, 1938: fig. 20). The basal peg may function to halt the flagellum during the putatively rapid forwards straightening movement of the flagellum caused by hemolymph pressure (Roewer, 1934: 146).

Barrussus and *Eusimonia* each bear two distinct, interspecifically variable, membranous or weakly sclerotized flagella (Pls. 30D, 31B, 53–55): a broad, thin, leaf-like dorsal secondary flagellum and a tube-like ventral primary flagellum. The literature is inconsistent, however, concerning which structure is interpreted as the flagellum (Table 11). The ventral (primary) flagellum often closely resembles that of rhagodids. Panouse (1955: 347) also suggested a resemblance between the primary flagellum of *Eusimonia cornigera* Panouse, 1955 and the flagellum of galeodids. The primary and secondary flagella of *Barrussus* and *Eusimonia* arise close to one another on the finger, but remain distinct. Both flagella are blind-ending apically, and indications of a viscous milky substance suggest the lumen of each is connected to the hemolymph (Pl. 30D). Both flagella appear to be immovably fixed to the finger. According to Panouse (1955), however, they are able to move through 90° from vertical to horizontal. This could not be verified in the present study. *Barrus* appears to possess a secondary flagellum but the literature is contradictory concerning whether a primary flagellum is present (Kraepelin, 1901: 140) or absent (Roewer, 1934: 306, fig. 227A).

Panouse (1955) identified a third structure in the flagellar complex of *Eusimonia cornigera* in addition to the primary and secondary flagella, i.e., a long, distally directed spiniform seta inserted prolaterally on the fixed (dorsal) finger. One or two modified subspiniform setae situated dorsally on the fixed finger of some species of *Eusimonia* are hypothesized to be modified prodorsodistal (*pdd*) setae, and referred to here as flagellar complex subspiniform (*fcs*) setae (Pls. 30D, 31B). Additional setae may be modified in some species (Roewer, 1934: 143, fig. 141C), e.g., *Eusimonia mirabilis* Roewer, 1932.

MELANOBLOSSIIDAE (DINORHAXINAE): The flagellum of *Dinorhax* is a thin, straight, and semi-sclerotized structure with a markedly setal appearance (Pls. 30E, 31C). It is unique among the flagella of solifuges in being oriented perpendicular to the fixed finger, pointing ventrally, although it is distally directed at the point of attachment. At the base, it is inserted in a small, swollen protrusion of the finger, allowing it to be placed parallel to the finger in the absence of a stalk. The entire surface of the flagellum is covered in minute spicules. Its filiform shape and the row of minute denticles on the suture along its length resemble the flagellum of the karschiid, *Karschia*, and both are regarded as sessile flagella. The flagellum of *Dinorhax* probably evolved in a similar manner to that of *Karschia* but whether it functions in a similar manner, by means of hemolymph pressure, remains to be investigated. Two or three setae situated dorsal and ventral to the base of the flagellum are slightly more differentiated from the remaining setae near the apex of the finger. The setae situated dorsal to the flagellum are probably homologous to the apicalmost *pdd* setae (Roewer 1934: 146), those situated ventral to it, to the proventral distal (*pvd*) setae.

MELANOBLOSSIIDAE (MELANOBLOSSIINAE): Melanoblossiinae possess a type C setiform flagellar complex, comprising several modified setae situated on a shallow elevation, and clustered to form a distinct unit (Purcell, 1903a; Wharton, 1981) situated in a broad, shallow depression, referred to here as the flagellar complex depression (Fig. 26C, Pl. 36G–I). References to “alveoli” in the keys of Muma (1976) and Gromov (2003b) appear to refer to the sockets of each seta, and not to the flagellar complex depression. As with the type B flagellar complex of Lipophaginae, all setae in the flagellar complex of Melanoblossiinae appear to be derived from the *pvd* series. The setae of the flagellar complex of Melanoblossiinae are often collectively referred to as a flagellum consisting of modified setae, as in Eremobatidae (e.g., Muma, 1976: 3; Wharton, 1981: 53; El-Hennaway, 1990: 24; Harvey, 2003: 199). However, only one of these setae is assumed to be homologous to the flagellum, as defined in the present contribution. Purcell (1903a: 6) was the first to identify a flagellum in *Melanoblossia*, i.e., the dorsalmost seta in the flagellar complex (equivalent to “b” in Pl. 36G–I): “(f)lagellum not rotatable, consisting of a flexible, densely hairy rod directed forwards and lying against the inner surface of the jaw, and so completely hidden between the chelicerae." Roewer (1941: 124) referred to this seta as the *seta principalis* of the flagellar complex.

Identification of the flagella of Melanoblossiinae has always been challenging. According to Purcell (1903a: 7, 8, figs. 4, 6), the seta considered homologous with the flagellum is distinct in *Melanoblossia globiceps* Purcell, 1903, but less so in *Melanoblossia braunsi*. Lawrence (1929: 176) noted that the flagellum is "not apparent" in *Melanoblossia*? *hewitti*, currently *Lawrencega hewitti* (Lawrence, 1929), the type species of *Lawrencega.*

The problem is complicated because the most obviously modified setae identified as the flagellum of *Lawrencega* ("a" in Pl. 36G) and *Melanoblossia* ("b" in Pl. 36G, I) are not homologous. The distinctly modified seta ("a") in *Lawrencega procera* (Pl. 36G), probably homologous with the primary flagellum of other solifuge families, is absent in *Melanoblossia braunsi* (Pl. 36H), in which another seta ("b"), although shorter and less conspicuous in *L. procera*, is distinctly modified, and therefore also potentially homologous with the primary flagellum of other solifuge families. An undescribed melanoblossiid species examined in the present study possesses a typical *Melanoblossia* type of *sfc*, but appears to possess both the modified *L. procera* ("a") seta and the modified *M. braunsi* ("b") seta (Pl. 36I). Despite the considerable modification of the flagellar complex of Melanoblossiinae, the uniquely different structure of the modified seta ("a") of *Lawrencega* and the medially situated seta ("a") in the undescribed *Melanoblossia*, which comprises a smooth shaft with apically restricted plumosity, suggests that seta "a" is most likely homologous with the primary flagellum of other solifuge families. This hypothesis is further supported by the position of this seta relative to the other *pvd* setae in the flagellar complex based on similar patterns of flagellar insertion relative to the *pvd* setae in other families, e.g., Daesiidae and Galeodidae.

Although Muma (1976: 3), followed by Gromov (2003b: 199), suggested that the setae in the flagellar complex of Melanoblossiinae are “slightly movable,” these setae do not appear to possess a greater ability to move than other unmodified setae. Each seta in the flagellar complex of Melanoblossiinae retains a fundamentally setal character, with the socket visible, albeit modified. The only study that alludes to the internal morphology of the flagellum of Melanoblossiinae, by Lamoral (1975), reported the presence of an alembic canal. This seems unlikely, however, because the alembic canal is a distinct, separate canal within the flagellum, with an external opening, which would be difficult to accommodate in a setiform flagellum of the type observed in Melanoblossiinae (Table 13). The presence/absence of an alembic canal in the setiform flagellum needs further investigation.

MUMMUCIIDAE: The flagellum of Mummuciidae is a membranous, roughly ovoid structure (Pls. 34G, H, 35H, I) generally similar to the flagella of Ammotrechidae and most Daesiidae. As with Ammotrechidae and unlike Daesiidae, the flagellum of Mummuciidae is fixed (non-rotatable). The flagellum of Mummuciidae is vesicular and often retrolaterally compressed, whereas the flagellum of Ammotrechidae is a more open, bowl-shaped structure. The margins of the flagellum curve prolaterally (i.e., away from the prolateral surface of the chelicera) in Ammotrechidae and Daesiidae with a membranous flagellum, whereas they curve ipsilaterally (i.e., towards the prolateral surface of the chelicera) in Mummuciidae. The capsule of Mummuciidae thus possesses a small opening ipsilaterally, which may extend to form a distal opening (Maury, 1984; El-Hennawy, 1990; González Reyes and Corronca, 2013). Xavier and Rocha (2001) were the first to report a broad opening ipsilaterally along the length of the flagellum of Mummuciidae, which was subsequently reported by others (Rocha and Cancello, 2002: 105, fig. 6; Martins et al., 2004; Carvalho et al., 2010). The flagellum of Mummuciidae is fixed through a very short stalk into a circular flagellar socket inner margin (Pl. 40L). The flagellum of Mummuciidae is fixed prodorsally to the fixed (dorsal) finger and, as in Ammotrechidae, the apex projects distally, whereas in Daesiidae the apex of the flagellum projects proximally (Pl. 35G, H). As in Ammotrechidae and Daesiidae (excluding Namibesiinae, *Syndaesia*, and *Ammotrechelis*), the flagellum of Mummuciidae is considered to be composite, the shaft being absent.

A broad flagellar groove, situated longitudinally along the fixed finger, accommodates most of the flagellum. This groove was present in mummuciids examined during the present study (Pls. 34G, H, 35H, I) and is evident in SEM images provided by Carvalho et al. (2010: 25, figs. 13, 15, 16), González Reyes and Corronca (2013: 542, fig. 5), and Botero-Trujillo (2014: 324, figs. 12, 13). The groove is created by the compressed dorsal margin of the finger being slightly curved prolaterally to form a narrow carina dorsally (the “dorsal keel” of Botero-Trujillo, 2014: 324), and a similar but less prominent, and more gradual, carina ventrally.

The flagellum of Mummuciidae is usually covered with spicules and fringed apically. As with Ammotrechidae and most Daesiidae, the flagellum of Mummuciidae was hypothesized to be derived from a broadened plumose seta, the edges of which curled inwards, resulting in a partially or completely closed vesicle, with membranous, double-walled sides enclosing a narrow lumen (Roewer, 1934: 138). Rocha and Cancello (2002) noted a “white viscous substance,” presumed to be hemolymph, filling the lumen. Therefore, as with the membranous flagella of Ammotrechidae and most Daesiidae, the narrow lumen of the flagellum of Mummuciidae is probably connected to the hemolymph in the chelicera.

RHAGODIDAE: As in the karschiid genera, *Barrussus* and *Eusimonia*, two flagellar structures, one ventral, the other dorsal, herein referred to respectively as the primary and secondary flagella, are present in Rhagodidae (Pls. 30F, 31D). The two flagella are situated close to one other in a distinct depression (the alveolus) in the fixed (dorsal) finger. The flagella are weakly plumose distally and each bears a membranous lamella, extending along its length. The manner in which each lamella is situated relative to the lamella on the adjacent flagellum creates a diploflagellum that superficially resembles a single concave, tube-like structure, the dual nature of which is only visible when the two flagella are pried apart. Each flagellum is, at the same time, tube-like, with a longitudinal inner lumen extending along its entire length, presumably connected to the hemolymph (Roewer, 1934: 140, fig. 137, reproduced here as Fig. 22B, C). Hemolymph pressure in the lumen was suggested to cause the tube composed of the two flagella to open slightly (Sørensen, 1914: 167; Roewer, 1934: 141). Although flexible, the two flagella are immovable at the base, and Sørensen’s (1914: 165) statement that they are “*très mobile*” refers to the pliability of the flagella rather than to their movement.

SOLPUGIDAE: Although very diverse in form (Hewitt, 1919b), the flagella of all Solpugidae are characterized by a distinctly bulbous base, immovably attached prodorsally to the fixed (dorsal) finger, with a more sclerotized shaft emerging distally from the base (Pls. 32G, 33K–M). A dorsal cuticular elevation of the paturon, here termed a **retrolateral convexity**, covers part of the bulbous base retrolaterally (Fig. 25A, visible through the transparent bulbous base of the flagellum). The fixed finger possesses a flagellar groove dorsally or prodorsally, to which the base of the shaft is attached and extends distally from the flagellar base for a short distance, before curving dorsally, and then curving slightly or markedly proximally (Pl. 48). The length of the recurved shaft varies from very short, not surpassing the proximal margin of the bulbous base, to very long, surpassing the ocular tubercle. The shaft is usually a sclerotized cylindrical (rod-like or whip-like) or flattened (strap- or ribbon-like) structure, with various modifications (Pl. 49A–C). The flagellum of *Solpuguna* Roewer, 1934 is unique because it does not curve dorsally, but follows the fixed finger for a distance before terminating apically in three or four fingerlike projections resembling a claw (Pls. 48G–I, 49C), the alembic canal opening externally at the tip of one of the projections (Pl. 48I, arrow).

Although highly sclerotized, the flagellum of Solpugidae remains flexible. The bulbous base varies interspecifically in position, size, shape (e.g., from round to elliptical in prolateral view), extent of sclerotization, and disposition of the dorsal carina (Fig. 25, Pl. 45). The sides of the base are semi-transparent and flexible (Roewer, 1934: 153), flat to concave prolaterally and slightly convex retrolaterally. Although immovably fixed to the fixed (dorsal) finger, Sørensen (1914: 165) identified a section at the base of the shaft in *Zeria keyserlingi* (Pocock, 1895) comprising more pliable dorsal cuticle situated slightly distal to more pliable ventral cuticle. Similar weakened areas observed in the present study, e.g., in *Solpugema genucornis* (Pl. 49B), suggest a point of “articulation” during the forward movement of the flagellum under hemolymph pressure during copulation. Sørensen's (1914: 165) reference to "articulation" of the flagellum of Solpugidae does not imply an ability to rotate within a socket, but to the flexibility of the shaft itself. A dorsal carina on the bulbous base of the flagellum, referred to as the **bulbous base carina**, may prevent the base from yielding under hemolymph pressure, ensuring that pressure is distributed into the shaft, and in turn causing it to extend distally (Sørensen, 1914: 168). A suture on the prolateral side of the base extends approximately parallel to the carina and may be the site of longitudinal infolding of the original seta to form the flagellum. Sørensen (1914: 171, 172) suggested that the size of the bulbous base may be correlated with the size of the shaft, but no correlation between the size and shape of the base and shaft was evident in the material examined in the present study.

The atrium (Sørensen, 1914: 168, fig. 11, labeled "c") is a longitudinal space situated ventral to and separated from the lumen by a chitinous membrane (Roewer, 1934) comprising dorsal and ventral lamellae extending longitudinally, and apparently together functioning as a valve which opens under strong hemolymph pressure but prevents backflow. This mostly unidirectional valve may allow the flagellum to retain pressure in the shaft even after the muscles which cause the hemolymph to move into and remain in the shaft have ceased contracting. Roewer (1934: 154, fig. 156, reproduced here as Fig. 22D) provided a cross-section of the bulbous base whereas Lamoral (1975) provided longitudinal sections of the base and cross sections of the shaft, based on histological investigations. Lamoral (1975) identified two canals extending through the flagellum: an alembic canal (or lumen), often visible through the cuticle of the base, terminating proximally in a pouch, and opening apically (in the shaft) to the exterior, and a blind-ending hemolymph canal (or lumen) connected proximally to the hemolymph in the fixed finger. Similar canals were observed in cross sections of the flagellar shaft of the solpugid, *Zeria venator*, in the present study (Pl. 41A). According to Lamoral (1975), the alembic canal is lined with epicuticle, implying that it formed by longitudinal invagination. Minute denticles are often present on the shaft, usually situated distally rather than proximally (Pl. 49L). Spiniform to sub-spiniform setae associated with the flagellum (*fcs*) are absent in Solpugidae. Setal modifications on the prolateral surface of the chelicera are limited to slightly more differentiated plumose setae near the bulbous base (Pl. 45B), or three or four markedly differentiated proventral distal (*pvd*) setae, e.g., in *Oparba asiatica* (Pls. 27, 45D) and *Solpugisticella kenyae* (Pl. 124G), and/or movable finger proventral (*mpv*) setae, e.g., in *Solpugiba lineata* (Fig. 13), *Zeria carli* (Pl. 121A), and *Zeria keyserlingi* (Pl. 118G). The distalmost modified setae on the movable finger are the most robust, gradually becoming less modified proximally. Modified fixed finger *pvd* setae may or may not exhibit remnants of plumosity.

Summary of the Flagellar Complex

A cheliceral flagellum is restricted to adult males and present in all suprageneric taxa except Lipophaginae (Gylippidae) and some Eremobatidae. Two flagella, a primary and secondary flagellum, are present in Rhagodidae and at least two genera of Karschiidae (*Barrussus*, *Eusimonia*,). They are situated close together, forming a diploflagellum, in Rhagodidae. The primary flagellum may be defined as a modified ventral flagellar seta, and the secondary flagellum as a modified dorsal flagellar seta. Three types of primary flagella may be identified: setiform, sessile, and composite.

Flagella may be immovably fixed (Ammotrechidae, Gylippinae, Karschiidae, Rhagodidae, Melanoblossiidae, Mummuciidae, Solpugidae, and Eremobatidae) or rotatable paraxially (Ceromidae, Daesiidae, Hexisopodidae) or slightly diaxially (Galeodidae). In the resting position, the apex of the flagellum may be directed distally (Ammotrechidae, Eremobatidae, Gylippidae, Melanoblossiidae, and Mummuciidae), distodorsally (Rhagodidae, Karschiidae excluding *Karschia*), proximally (Daesiidae, Ceromidae, Hexisopodidae, Solpugidae) or dorsoproximally (Galeodidae). All rotatable flagella are thus proximally directed, and fixed flagella distally directed except for Solpugidae, which are proximally directed. Although the solpugid flagellum is fixed to the finger, the flagellum can most likely be projected distally by hemolymph pressure and an “articulation point” at the base of the shaft (Sørensen, 1914), or along the shaft (Pl. 49B).

Various cheliceral processes and modified flagellar complex plumose (*fcp*) setae and flagellar complex subspiniform and spiniform (*fcs*) setae may be associated with the flagellum. These include a fan of stiff, often pipette-shaped *fcp* setae at the base of the flagellum characteristic of Ceromidae, a distinct plumose *fcp* seta and one to four robust spiniform *fcs* setae at the base of the flagellum of Galeodidae, and one or two dorsally situated spiniform *fcs* setae (in Ceromidae and Gylippidae) or subspiniform *fcs* setae (in Karschiidae). Modified plumose setae become increasingly modified the more distally situated, e.g., the increasingly longer plumose setae of *Karschia* and the more robust *pvd* setae near the apex of the fixed (dorsal) finger of some Solpugidae. Dorsal cheliceral spines are rare in solifuges, but, when present, form horn-like or toothlike processes, especially in Karschiidae, but also in some Daesiidae (e.g., *Ammotrechelis goetschi*) and Lipophaginae (*Trichotoma michaelseni*).

The function of the male flagellum remains equivocal, and several possibilities have been suggested in the present contribution. The only unequivocal observation of a flagellum apparently functioning as an intromittent organ, with the cheliceral fingers not handling the sperm during indirect sperm transfer, was the bowl-shaped flagellum of Ammotrechidae. During flagellar insertion in the female genital tract, alembic fluid appears to be secreted by all whip-like flagella through a pore at the apex. The species-specific nature of the flagellum of many families will remain difficult to explain until more observations of mating behavior, studies on female genital tract morphology and on details of flagellar mophosculpture (spicules, etc.) and intraspecific variability thereof, become available.

CONCLUSIONS

The enormous chelicerae relative to body size is the most prominent feature of the arachnid order Solifugae. The chelicerae of solifuges, especially of the males, are particularly rich in characters for solifuge systematics. Except for the tarsal setae and the number of tarsal segments, almost the entire foundation of solifuge systematics is based on cheliceral characters. In most solifuge families, species delimitation is based primarily on cheliceral dentition and the male flagellum, yet no comprehensive survey of these character systems has ever been undertaken. Terminology has remained unstandardized, confusing and even contradictory. The poor understanding of cheliceral characters, together with the unsatisfactory terminology applied to them, has hindered the systematics of Solifugae, compared to other arachnid orders, e.g. Araneae, the major character systems of which are well understood and described with a unified terminology. The present study is the first comprehensive synthesis of solifuge cheliceral morphology, which attempts to homologize cheliceral characters across the order based on a survey of exemplar species representing all major solifuge lineages.

This survey of the chelicerae discovered many novel characters, e.g., the movable finger fondal (*mff*) setae, the mucron organ (mo), and the medioventral organ. Many other characters were reinterpreted, e.g., the fused horn-like process previously interpreted as a large tooth in the gylippine, *Trichotoma michaelseni*. Numerous potential suprageneric synapomorphies were identified, including broad patterns in taxonomically restricted character systems, such as the stridulatory apparatus, and ubiquitous character systems, such as dentition.

Identification of the homologs of individual teeth, including the first hypotheses regarding fondal teeth, facilitated the discovery of patterns, e.g., direction of size increase in categories of secondary teeth, as well as evaluation of intraspecific variation in dentition and hence the justification for using dentition in solifuge systematics. Solifuges were found to possess a relatively high propensity for variation, but, with respect to dentition, variation was largely restricted to predictable areas. For example, the secondary teeth and the fondal teeth were more variable than the primary teeth and the distal teeth more variable than the proximal teeth, especially concerning the primary teeth. Particular fondal teeth were more prone to variation. The shape of teeth was much conserved in some taxa, but not others.

Terminology for cheliceral chaetotaxy was completely overhauled, by distinguishing between different series and fields of setae. The concept of primary and secondary male flagella was introduced and the distalmost seta in the proventral distal (*pvd*) series, i.e., the ventral flagellar seta (*vfs*), was hypothesized to be the precursor to the primary flagellum, and the distalmost prodorsal distal (*pdd*) seta, i.e., the dorsal flagellar seta (*dfs*), the precursor to the secondary flagellum.

The male flagellum, which manifests a diversity of forms, is unique to solifuges. A single origin for the flagellum was hypothesized with alternative interpretations proposed for further testing. The terminology for the flagella was standardized and three types, i.e., setiform, sessile and composite flagella, identified. Parts of the flagellum in the composite types were homologized, i.e., the stalk, base and shaft.

This study has broad implications for solifuge systematics and functional morphology. It increases the number of characters for solifuge systematics, and provides a new framework for taxonomic and phylogenetic studies on the order in the form of a revised terminology and character definitions. It is the first study to propose hypotheses of primary homology for phylogenetically and taxonomically useful cheliceral structures across Solifugae, observations which can be coded into characters and tested for secondary homology in phylogenetic analyses, providing synapomorphies for the higher classification of the order.

The literature on behavior and functional morphology of the chelicerae was reviewed and interpreted in light of the present study. The conserved female chelicera, with its robust shape, putatively plesiomorphic dentition and chaetotaxy including increased plumosity of the *pvd* setae, appears to reflect its primary functions for feeding and, probably, defense. Sexually dimorphic modifications of the male chelicerae, e.g., gracile shape, modified, often reduced dentition, modified setae forming the flagellar complex and, in most species, the flagellum itself, function in mating. Mating behavior in solifuges was divided into three phases, i.e., somatic contact, genital contact and release phases, and the relevance of cheliceral modifications to each phase discussed. Increased standardization and more detailed description of mating behavior, studies on the internal anatomy of the female reproductive system, and histological studies of the male flagellum are needed to improve understanding of the function of cheliceral modifications in solifuge mating.

TABLE 1

Mode of sperm transfer in families of Solifugae for which data available, based on Heymons (1902), Cloudsley-Thompson (1961, 1967a,b), Amitai et al. (1962), Junqua (1962), Muma (1966b), Wharton (1987), Punzo (1998b), Peretti and Willemart (2007), Hrušková-Martišová et al. (2010a)

	Direct	Flagellum	Finger(s)
Ammotrechidae		x	
Daesiidae			x
Eremobatidae	x		
Galeodidae			x
Solpugidae			x

TABLE 2

Reproductive behavior associated with cheliceral structures of male Solifugae, based on observations of species in five families: Ammotrechidae Roewer, 1934: *Oltacola chacoensis* Roewer, 1934 in Peretti and Willemart (2007); Daesiidae Kraepelin, 1899: *Gluvia dorsalis* (Latreille, 1817) in Hrušková-Martišová et al. (2010a); Eremobatidae Kraepelin, 1899: *Eremobates durangonus* Roewer, 1934, *E. palpisetulosus* Fichter, 1941 and *E. nodularis* Muma, 1951 in Muma (1966b), and *E. marathoni* Muma, 1951 in Punzo (1998b); Galeodidae Sundevall, 1833: *Galeodes caspius* Birula, 1890 in Heymons (1902), *G. caspius subfuscus* Birula, 1937 in Hrušková-Martišová et al. (2008a, 2010a), *G. granti* Pocock, 1903 (misidentified as *G. arabs*), in Cloudsley-Thompson (1961, 1967a,b), *G. sulfuripes* Roewer, 1934 in Amitai et al. (1962), and *Othoes saharae* Panouse,1960 in Junqua (1962); Solpugidae Leach, 1815: *Metasolpuga picta* (Kraepelin, 1899) in Wharton (1987)

Abbreviations: GP, gonopore; FF, fixed finger; MF, movable finger.

Phase		Dentition, mucron	Chelicera shape	Fixed finger shape	Dorsal macrosetae	Flagellum
Somatic contact	initial grabbing of ♀	grasp, bite, pinch abdomen, legs, peltidia				
	somatic massage	chew abdomen, propeltidium, chelicerae (lightly or fiercely)				
	move ♀	lift, run with ♀; drag ♀ by GP up vertical surface				
Genital contact[a]	pre-insemination	knead, pinch, chew ♀ operculum, surrounds; FF into ♀ GP, grip abdomen with MF	chelicera in, out of GP	FF into GP	press setae against genital region	
	insemination	collect/lift, chew sperm droplet; open opercula; insert sperm		insert FF into GP		place sperm in flagellum, insert into GP (Ammotrechidae)[b]
	post-insemination	prod GP with tips of fingers	insert chelicera deeply into, or in, out of GP		press dorsal chelicera against ♀ genital area (Galeodidae)	insert flagellum fully into ♀ genitalia (Solpugidae)[c]
Release		pinch sides of GP opening together				close GP (Galeodidae)[d]

[a] Genital contact phase, especially pre- and post-insemination actions generally violent, described using phrases such as “deeply inserted [cheliceral fingers]…rub intensely” (Hrušková-Martišová et al., 2010a: 95) and *grofser Gewalttätigkeit* [great violence]/vigorous]” (Heymons, 1902: 42); exceptions during insemination phase, described using words such as “gently” (Cloudsley-Thompson, 1961: 160) and “inserted cheliceral tips” (Wharton, 1987: 376).

[b] The male *O. chacoensis* picked up the sperm with the tarsi of his first pair of legs, placed it “between the [spoon-like] flagella”, and inserted finger and flagellum into the female genital tract (Peretti and Willemart, 2006: 34).

[c] The male *M. picta* inserted flagellum and chelicera into the female genital tract, with the flagellar shaft held at an angle of 45–90° relative to its normal resting position (Wharton, 1987). The flagellum was completely inserted into the female; the tip was glistening on removal (R.A. Wharton, personal obs.).

[d] The genital opening of the female *G. caspius subfuscus* was closed as follows: “using two cheliceral fingers and flagella, [the male] gripped the soft cuticle of the female's abdomen and pulled it towards the operculum” (Hrušková-Martišová et al., 2010a: 95). It is unclear how the flagellum was involved.

TABLE 3

Sperm packaging in families of Solifugae for which data available (based on Klann et al., 2009; see also Warren, 1939; Klann, 2009; and Klann et al., 2011)

	Single cells[a]	Groups of cells[b]	Cleistospermia[c]	Coenospermia[d]
Ammotrechidae Roewer, 1934		x		
Daesiidae Kraepelin, 1899	x (*Biton* Karsch, 1880)			x (*Blossia* Simon, 1880)
Eremobatidae Kraepelin, 1899	x			
Galeodidae Sundevall, 1833				x
Hexisopodidae Pocock, 1897			x	
Karschiidae Kraepelin, 1899		x		
Solpugidae Leach, 1815	x			

[a] Spermatozoa remain as single cells.

[b] Spermatozoa clumped together as groups of loose knit (Ammotrechidae) or highly ordered (Karschiidae) cells.

[c] Individual spermatozoa surrounded by a thin secretion sheath.

[d] Several sperm cells surrounded by a thick (Galeodidae) or thin (*Blossia*) secretion sheath in the testis or vasa differentia.

[b–d] Not to be confused with spermatophores, i.e., sperm packages, which formed through secretions of the accessory glands (Klann et al., 2009); based on this definition, spermatophores have not been observed in Solifugae (Warren, 1939; Klann, 2009; Klann et al., 2009) and references to spermatophores in solifuges (e.g. Kaestner, 1965; Cloudsley-Thompson, 1961; Wharton, 1987) probably referred to the viscous sperm mass (Klann et al., 2009).

TABLE 4

Female reproductive tract morphology in families of Solifugae for which data available (based on Dufour, 1861: 433; Birula, 1892; Bernard, 1896; Warren, 1939; Vachon, 1945; Klann, 2009)

	Pouches on genital chamber[a]	Oviduct	Ovary
Ammotrechidae Roewer, 1934	laterally	diameter approximately uniform along oviduct	oocytes develop outside ovary, lateral side only
Eremobatidae Kraepelin, 1899	absent	strongly narrows before entering genital chamber	*ibid*.
Galeodidae Sundevall, 1833[b]	small; distally on chamber, between oviduct entry points	diameter relatively uniform along oviduct	*ibid*.
Rhagodidae Pocock, 1897	glands present, homologous with pouches?	unknown	*ibid*.
Solpugidae Leach, 1815[c]	absent?	comprises: oviduct proper[d], oviducal chamber[e], narrow connecting tube, glandular tube	*ibid*.

[a] Genital chamber and oviduct surrounded by strong longitudinal and transverse muscles; pouches surrounded by thin muscle layer (Vachon, 1958; Klann, 2009).

[b] Also see Dufour (1861: 433, plate 4, fig. 26)

[c] Dufour's (1861: plate 4, fig. 27b) figure does not agree with the figures and discussions of Warren (1939: 143, fig. 2) and Vachon (1945: 478, fig. 1).

[d] Oviduct proper enters oviducal chamber by curving back on itself and opening into chamber through comparatively small, anteriorly-directed tube (see Warren, 1939: 143, fig. 2 d, e).

[e] Oviducal chamber holds seminal fluid (Vachon, 1945) and is lined with thin layer of ectodermal epithelium (Warren, 1939).

TABLE 5

Synonyms for cheliceral fingers used in the literature

Cheliceral finger	Dorsal/fixed finger; ventral/movable finger	Reference
	article cubital (d); *article digital mobile* (f)	Savigny (1809: 178, plate 8, fig. 1c)
mors [jaw]	*mors immobile*	Dufour (1861)
jaw	*Unbeweglichen Kinnladen* [immovable jaw]; *Unterkiefer*	Koch(1842)
jaws	upper/dorsal jaw[a]; lower/ventral jaw	Pocock (1895a); Purcell (1899: 393); Hewitt (1913, 1919b); Hirst (1916b); Lawrence (1927); Lamoral (1972)
crochet [fang]	*crochet fixe en dessus/supérieur*; *crochet mobile/inférieur*	Simon (1872, 1879: 126, 1880)
fang	apophysis of penultimate[a,b] segment; terminal segment/fang	Pocock (1893: 10)
fang	upper/immovable fang; lower fang	Birula (1915:4, 1916: 73)
dactylus/digit	upper digit/immovable dactylus; lower/movable digit	Pocock (1895a, 1889)
digit	fixed digit; movable digit	Turk (1960); Levy and Shulov (1964)
Kinnlade	*obere/untere Kinnlade*	Birula (1929b: 279, fig. 5)
Oberkieferfinger [maxillary finger]	*dorsaler/ventraler Oberkieferfinger*	Kraepelin (1899)
Mandibularfinger (Mdbfgr.)	*dorsale/unbewegliche Mandibularfinger*; *ventraler Mandibularfinger*	Kraepelin (1901)
fingers	upper/fixed finger; lower/movable finger	Putnam (1883: 255–257); Banks (1900); Hewitt (1912); Muma, (1970b)
doigt [finger]	*l'article basilaire[a]/doigt fixe, doigt mobile*	Sørensen (1914); Panouse (1960b)
Chelicerenfinger/ digitus	*dorsalen unbeweglichen chelicerenfinger; ventralen beweglichen chelicerenfinger*	Roewer (1932: 53)
digitus	*digitus fixus/immobilis; digitus mobilis*	Roewer (1934: 53); Klann (2009); Klann and Alberti (2010); Van der Meijden et al. (2012)
Finger, *Oberkiefer*	*Oberfinger/Oberkiefer*; *Unterfinger/Beweglicher Finger*	Birula (1937a)
dedo [finger]	*dedo immóvil; dedo móvil*	Mello-Leitao (1938); Maury (1970); Armas (1994)
finger	immobile/fixed finger; mobile finger	Klann (2009)
ramus/podomere	fixed ramus[a]; free ramus	Dunlop (2000)

[a] Use of "penultimate segment" (Pocock, 1893: 10) , "upper jaw" (Hewitt, 1919b: 33), *l'article basilaire* (Sørensen, 1914: 158), and "fixed ramus" (Dunlop, 2000: 69) included both fixed finger and manus (i.e., paturon).

[b] Pocock (1893) interpreted chelicera as three-segmented structure: lateral lobe of propeltidium as first segment, manus and upper finger as second or "penultimate" segment, and movable finger as third or "terminal" segment.

TABLE 6

Size gradation within categories (MSM, FSM and FSD) of secondary teeth based on material examined as well as images and species diagnoses from the literature, indicating whether teeth increase in size distally (D) or proximally (P) in row[a]

Abbreviations: D, distally; FSD, fixed finger subdistal teeth; FSM, fixed finger submedial teeth; MSM, movable finger submedial teeth; P, proximally

Family	MSM	FSM	FSD
Ammotrechidae Roewer, 1934	n.a.	n. a.	n. a.
Ammotrechidae (*Sedna* Muma, 1971)[b]	P	P	n.a.
Ceromidae Roewer, 1933	n.a.	n.a.	n.a.
Daesiidae Kraepelin, 1899 (*Namibesia* Lawrence, 1962)	n.a.	D	P
Daesiidae (excl. *Namibesia*)	n.a.	n.a.	n.a.
Eremobatidae Kraepelin, 1899	P	P	P
Galeodidae Sundevall, 1833[c]	D	D?	n.a
Gylippidae Roewer, 1933[d]	n.a.	n.a.	n.a.
Karschiidae Kraepelin, 1899	D	P	P
Melanoblossiidae Roewer, 1933[e]	n.a.	n.a.	n.a.
Mummuciidae Roewer, 1934[f]	P	P	n.a.
Rhagodidae Pocock, 1897	n.a.	n.a.	n.a.
Solpugidae Leach, 1815	P	P	n.a.
Solpugidae (*Solpugiba* Roewer, 1934)[g]	n.a.	P	n.a.

[a] Taxa with fewer than two teeth in category, or more than one tooth only in apparent aberrant specimens, coupled with insufficient data, cannot be evaluated for size gradation, hence "n.a."

[b] Single MSM in Muma (1971: 7, figs. 1, 2)

[c] Contradictory patterns, e.g., Pl. 60A.

[d] FSM increase in size distally in, e.g., *Galeodes araneoides* (Pallas, 1772) (Pls, 59G–J, 60), but proximally in, e.g., *Paragaleodes pallidus* (Birula, 1890) (Pl. 59C, D, 60A–C).

[e] Teeth either too small and vestigial to evaluate for relative size, or all teeth within series of equal size (i.e., multidentate patterns).

[f] E.g., *Mummucina titschacki* Roewer, 1934 (*vide* Botero-Trujillo, 2014: 325, fig. 17).

[g] Labile denticles interspersed with "regular" secondary teeth ignored.

TABLE 7

Dental pattern formulae in the literature and new formula proposed here. Formulas adapted to describe dentition pattern illustrated in Pl. 22A with hypothetical presence of additional third fixed finger submedial (FSM) tooth and one retrofondal (RF) tooth present or absent, depending on specimen

Abbreviations: A, *anterior*; AT, anterior teeth; BE, *basal externo*; BI, *basal interno*; DA, *dent antérieure*; DI, *dent intermédiaire*; DP, *dent principale*; DJ'ext, *dent jugale externe*; DJ'int, *dent jugale interne*; PF, profondal teeth; RF, retrofondal teeth; FD, fixed finger distal tooth; FM, fixed finger medial tooth; FP, fixed finger proximal tooth; I, *intermedio*; M, medial teeth; P, *principal*.

Dental formula	Reference
3DA+2DI+1DP+5DJ'ext+4DJint	Panouse (1960b)
3A, 2-3I, 1P, 5BE, 4BI[a]	Maury (1984, 1985a)
3A, 2I, 1P, 5BE, 4BI	Armas (1993)
PT-1-2-MT-1-AT (alternating with P-1-2-M-1-A)[b]	Catenazzi et al. (2009)
FD-(1)-FM-(<u>2</u>-3)-FP-(4-5RF)(4PF)[c]	here

[a] 2-3I = intraspecific and/or individual variation in count of submedial (FSM) teeth.

[b] 1-2: implies two submedial teeth, numbered "1" and "2" respectively; Catenazzi et al. (2009) cited Maury (1982) but probably based on Maury (1984), with modifications.

[c] ( ) = secondary teeth; (<u>2</u>-3) = variation, intraspecific and/or within specimen, in count of secondary teeth; predominant count underlined. Notation may be adapted to accommodate different patterns of variation, e.g., (2, <u>3</u>,4).

TABLE 8

Common-most dentition patterns in families of Solifugae, excluding highly modified male dentition

Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; RF, retrofondal teeth; RFA, retrofondal apical teeth. Parentheses indicate secondary teeth. Ranges indicate predominant intraspecific variation. Underlined indicate most common pattern. Only general patterns, not minor intraspecific variation, indicated.

	Fixed finger	Movable finger
Ammotrechidae Roewer, 1934[a]	FD-(0,1)-FM-(1,2)-FP-(3,4RF)	MM-(0,1,2,3)-MP
Ceromidae Roewer, 1933 (excl. *Toreus* Purcell, 1903)	FD-FM-(0,1)-FP-(2-5RF)	MM-(0,1)-MP + 2 flanges
Daesiidae Kraepelin, 1899 (*Namibesia* Lawrence, 1962)[c]	FD-(1,2,3)-FM-(1,2)-FP-(4RF)	MM-(1)-MP
Daesiidae (excl. *Namibesia*)[b]	FD-(0,1)-FM-(1,2)-FP-(3,4RF)	MM-(0?,1)-MP
Dinorhaxinae Roewer, 1933	FD-(1)-FM-(1)-FP-(4RF)	MM-(1)-MP
Eremobatidae Kraepelin, 1899[d]	FD-(0,1,2,3)-FM-(1,2,3)-FP-(3-5RF)	MM-(1,2)-MP
Galeodidae Sundevall, 1833[e]	FD-(0,1)-FM-(1,2)-FP-(3RF)	MM-(1-4)-MP
Gylippidae Roewer, 1933, Gylippinae	FD-FM-(1)-FP-(4RF)	MM-(1)-MP
Gylippidae, Lipophaginae Wharton, 1981[f]	FD-(0,1)-FM-(1-)-FP	MM-(1)-MP
Karschiidae Kraepelin, 1899[g]	FD-(1,2)-FM-(1,2,3)-FP-(6-8RF)	MM-(2-3)-MP
Melanoblossiinae Roewer, 1933[h]	FD-(1-3)-FM-(1-4)-FP	MM-(1-5?)-MP
Mummuciidae Roewer, 1934[i]	FD-(0,1)-FM-(1,2)-FP	MM-(1-2)-MP
Rhagodidae Pocock, 1897[j]	FD-FM-FP-(5-6RF)	MM-MP
Solpugidae Leach, 1815 (excl. *Solpugiba* Roewer, 1934)[k]	FD-(0,1)-FM-(1,2)-FP-(4RF)[d]	MM-(1-3)-M
Solpugidae (*Solpugiba*)[l]	FD-(1,2,3)-FM-(1,2,3-5)-FP(4RF)[d]	MM-(1)-MP

[a] Larger number of secondary teeth uncommon, but present in, e.g., *Sedna pirata* Muma, 1971 with FSD, two FSM, up to two MSM (Pl. 149D), *Pseudocleobis andinus* (Pocock, 1899) with FSD present, up to three MSM (Muma, 1971: 15, fig. 24), *Pseudocleobis chilensis* Roewer, 1934 with FSD present, two FSM (Muma, 1971: 19, fig. 31). *Nothopuga* Maury, 1976 partly characterized by absence of MSM and FSD, MSM present in *N. cuyana* examined in present study (Pls. 146G, H, 147G, H).

[b] As per specimens examined (Pls. 132, 133) and Wharton (1981: 40, fig. 35),

[c] FSD rarely present, e.g. *Hemiblossiola kraepelini* Roewer 1933 and *Gluvia dorsalis* (Latreille, 1817) as *G. chapmani*, second FSM rarely present, e.g. *Bitonella roeweri* Lawrence, 1935 and *Blossiola longipalpis* Lawrence 1935, and MSM rarely absent, e.g., *Blossiola fimbriata* (Roewer, 1934) (Roewer, 1934: 258, fig. 261h, 353, fig. 256a, 385, fig. 273b; Lawrence, 1935a: 73, fig. 2, 78, fig. 5). Fixed (dorsal) finger STF present in some *Blossia* sp. (Pl. 147). Most common pattern: FD-FM-(1)-FP; MM-(1)-MP.

[d] FSD absent, FD reduced in *Eremorhax* Roewer, 1934 (Pl. 72H); second FSD in different genera, e.g., *Hemerotrecha marginata* (Kraepelin, 1911) (Pl. 82E, F), *Horribates bantai* Muma, 1989 (Pl. 70J, 78C); more than two FSD and FSM rare, largely restricted to species of *Hemerotrecha* Banks,

1903 and *Chanbria* Muma, 1951(*vide* figures in Muma, 1951). Most common median series pattern: FD-(1)-FM-(2)-FP. RFA denticles in fondal notch not included in RF count

[e] FSD rarely absent, e.g., *Othoes floweri* Hirst, 1911 (Panouse 1964, 52, fig. 2A,B). One, e.g., *Galeodes* sp. (Pl. 62I, J), up to four MSM observed, e.g. *Galeodes araneoides* (Pallas, 1972) (Birula, 1938: 116, fig. 75a). Number of MSM apparently highly variable intraspecifically, e.g., *Othoes saharae* with one to three MSM (Panouse, 1964: 65).

[f] FSD absent in *Trichotoma* Lawrence, 1968; single FSD in *Bdellophaga* Wharton, 1981 and *Lipophaga* Purcell, 1903.

[g] A third FSM usually a labile denticle.

[h] Melanoblossiidae includes multidentate species and species with a tendency towards the multidentate condition, and considerable interspecific variation in secondary teeth. Large number of secondary teeth, e.g., in female *Lawrencega longitarsis* Lawrence, 1967 with three FSD, four FSM, and five MSM indicated by Lawrence (1967: 7, fig. 4f).

[i] Second MSM rare (e.g., Pl. 26F). See counts in Botero-Trujillo (2014: 322).

[j] Rhagodidae: MM usually small, reported absent in some (e.g., Turk, 1960: 121, fig. 9).

[k] Single FSD present only in few taxa, notably *Solpugista* Roewer, 1934, but also reported in some specimens of, e.g., *Metasolpuga picta* (Kraepelin, 1899) (Wharton, 1981: 67) and Solpu*gema aethiops* Lawrence, 1967 described from one female (Lawrence, 1967: 6, fig. 3a). Three FSM reported only in *Solpuga bovicornis* Lawrence, 1929, with distalmost “either low and rounded or else toothlike and resembling the two succeeding teeth and smaller than them” (Lawrence, 1929: 156, fig. 2b, 157). More than one MSM rare, with two reported in *Zeriassa purcelli* Hewitt, 1914, based on a single male, the distalmost of the two “being very small” (Hewitt, 1914: 163, fig. 25), and two MSM not mentioned in original description but illustrated by Roewer (1934: 448, figs. 295b, d) for *Zeria celeripes* (Hirst, 1911) and *Zeria zebrina* (Pocock, 1898), both as *Solpuga* Lichtenstein, 1796. Three MSM reported in *Solpuga bovicornis*, *Zeria antelopicornis* (Lawrence, 1929) with distalmost a “hardly perceptible granule,” and *Zeria fusca* (C. L. Koch, 1842) (Pls. 116A–D, 117; Lawrence, 1929: 154, 156, fig. 2b; Roewer, 1934: 445, fig. 293a); if three MSM, these are situated on distal margin of MP.

[l] Apparently labile denticles common, especially in later stage juveniles and adults (Pl. 110B). Most typical *Solpugiba* pattern based on juveniles and discarding apparent labile denticles, is FD-(1)-FM-(2)-FP.

TABLE 9

Bilateral asymmetry in cheliceral dentition (secondary and fondal teeth)

Abbreviations: FSM, fixed finger submedial tooth; MSM, movable finger submedial tooth; PF, profondal teeth; RF, retrofondal teeth.

Family	Species	Sex	Left	Right	References
Ceromidae Roewer, 1933	*Ceroma inerme* Purcell, 1899	♂	1MSM	2MSM[a]	Purcell (1899)
Galeodidae Sundevall, 1833	*Galeodes afghanus* Pocock, 1895	♂	2MSM	3MSM[b]	Pocock (1895a)
	Galeodes bactrianus Birula, 1937	♀	1MSM	2MSM	Birula (1937a)
	Galeodes lycaonis[c] Turk, 1960	♀	2FSM	3FSM[a]	Turk (1960)
	Galeodopsis strandi (Birula 1936)	♂	1MSM	2MSM[a]	Birula (1936a)
Daesiidae Kraepelin, 1899	*Neocleobis solitarius* (Banks, 1902)	♂	1MSM	2MSM[a]	Muma (1970b)
Solpugidae Leach, 1815	*Zeria fordi* (Hirst, 1907)	♂	1MSM	2MSM	Simonetta and Della Cave (1968)
	Zeriassa pardii[c] Simonetta and Cave, 1968	♂	2RF	3RF[d]	Simonetta and Della Cave (1968)

[a] additional tooth indicated as “very small” or “minute”

[b] if absent, space of third tooth left open

[c] holotype

[d] N = 8; asymmetry in six specimens; two specimens with three retrofondal (RF) teeth on both chelicerae

TABLE 10

Variation in patterns of dentition in Solifugae based on the literature[a]

Only teeth which could be unambiguously identified were included in the assessment. Abbreviations: add, additional toothlike structure (flanges, etc.); Amm, Ammotrechidae Roewer, 1934; Dae, Daesiidae Kraepelin, 1899; Ere, Eremobatidae Kraepelin, 1899; FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial tooth; Gal, Galeodidae Sundevall, 1833; Gyl, Gylippidae Roewer, 1933; Kar, Karschiidae Kraepelin, 1899; Lip, Lipophaginae Wharton, 1981; Mel, Melanoblossiinae Roewer, 1933; Mum, Mummuciidae Roewer, 1934; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PF, profondal teeth; RF, retrofondal teeth; Sol, Solpugidae Leach, 1815.

Fam	Species	MM	MSM	MP	FD	FSD	FM	FSM	FP	RF	PF	N	Citation
Amm	*Ammotrechella geniculata* (C.L. Koch, 1842)	1	1	1	1	0	1	1	1	4	4	1 ♂	Maury (1982)
		1	1	1	1	0	1	1	1	5	4	1 ♀	Maury (1982)
Dae	*Biton* (*Biton*) *rossicus* (Birula, 1905)[b]	1	1	1	1	0	1	1	1	?	3–4	11 ♂	Birula (1936b)
	Biton (*Bitonissus*) *schelkovnikovi* (Birula, 1938)	1	1	1	1	0	1	1	1	?	3	5 ♂	Birula (1936b)
	Blossia planicursor Wharton, 1981	1	1	1	1	0	1	1	1	3	3	9 ♂	Wharton (1981)
	Blossia purpurea Wharton, 1981	1	1	1	1	0	1	1	1	3	3	12 ♂	Wharton (1981)
	Blossia rooica Wharton, 1981	1	1	1	1	0	1	1	1	3	3	5 ♂	Wharton (1981)
	Namibesia pallida Lawrence, 1962[c]	1	1	1	1		1		1	4–5	2–5	11 ♂	Wharton (1981)
Ere	*Eremochelis bilobatus* (Muma, 1951)[d]	1	1–2	1	-	-	-	-	-	?	?	12 ♂	Muma (1951)
Gal	*Galeodes setulosus* Birula, 1937	1	3–4	1	1	0	1	2	1	?	?	1 ♂?	Birula (1937a)
		1	3	1	1	0	1	2	1	?	?	9 ♀	Birula (1937a)
		1	2–3	1	1	0	1	2	1	?	?	7♀	Birula (1937a)
Gyl	*Trichotoma fusca* (Roewer, 1941)	1	1?	1	1	1	1	1–2	1	5–6	?	4 ♂	Wharton (1981)
	Trichotoma michaelseni (Kraepelin, 1914)[e]	1	1	1	1	0	1	0–1	1	6–8	?	4 ♂	Wharton (1981)
		1	1	1	1	0	1	0–1	1	5-6l	?	6 ♀	Wharton (1981)
Mum	*Mummucia ibirapemussu* Carvalho et. al. 2010	1	1	1	1	0	1	1	1	5	3	16 ♂	Carvalho et al. (2010)
		1	1	1	1	0	1	1	1	5	2–3	3 ♀	Carvalho et al. (2010)
	Mummucina puna González Reyes & Corronca, 2013	1	1	1	1	1	1	1	1	4–7	3	18 ♂, 4 ♀, 1juv.	González Reyes & Corronca (2013)
	Mummucina titschacki Roewer, 1934	1	1–2	1	1	0–1	1	1–2	1	5–7	2–4	61 ♂	Botero-Trujillo

													(2014)
	Mummucina titschacki Roewer, 1934	1	1–2	1	1	1–2	1	2	1	6–7	3	8♀	Botero-Trujillo (2014)
Sol	*Metasolpuga picta* (Kraepelin, 1899)	1	1	1	1	0–?	1	1	1	?	?	18 ♀	Wharton (1981)
		1	1	1	1	0–?	1	1	1	?	?	18 ♀	Wharton (1981)
	Solpugista hastata (Kraepelin, 1899)[f]	1	1	1	1	1	1	1–2	1	4	3	4 ♂	Hewitt (1914a)
	Solpugema genucornis Lawrence, 1935)	1	1	1	1	0	1	0–1	1	?	?	13 ♂	Wharton (1981)
		1	1	1	1	0–1	1	1	1	?	?	6 ♀	Wharton (1981)
	Solpugiba lineata (C.L. Koch, 1842)	1	1	1	1	1–3	1	2–4	1	?	?	?	Wharton (1981)
	Solpugista bicolor (Lawrence, 1953)	1	1	1	1	1	1	2	1	?	?	12 ♀	Wharton (1981)
		1	1	1	1	0–1	1	1–2	1	?	?	21 ♂	Wharton (1981)
	Zeriassa lepida Kraepelin, 1913	1	1	1	1	0	1	1	1	3	2	9 ♂	Simonetta & Delle Cave (1968)
	Zeriassa pardii Simonetta and Cave, 1914	1	1	1	1	0	1	2	1	2–3	2	8 ♂	Simonetta & Delle Cave (1968)
	Zeriassa ruspolii (Pavesi, 1897)	1	1	1	1	0	1	2	1	?	?	12 ♂, 6 ♀	Simonetta & Delle Cave (1968)

[a] Studies that base species identifications on the “number of intermediate [secondary] teeth” are excluded to avoid circular reasoning. Terminology is retrospectively assigned based on descriptions and figures provided by authors, and adapted to fit interpretations in the present manuscript.

[b] As *Daesia rossica* Birula, 1905.

[c] Total of three to six secondary teeth in FSM plus FSD.

[d] As *Therobates bilobatus* Muma, 1951.

[e] Second retrofondal tooth large, “followed by cluster or 3-4 small teeth”.

[f] As *Solpuga ornithorhyncha* Hewitt, 1914.

TABLE 11

Alternative interpretations and terminology of the flagellar structures of *Eusimonia* Kraepelin, 1899

Abbreviations: 1°, primary; 2°, secondary.

1° flagellum (ventral)	2° flagellum (dorsal)	Dorsal hornlike process	References
flagellum (*F*)	*lamelle* (*L*)	*crochet fixe*, *profondément bifurqué*	*E. furcillata* (Simon, 1872): Simon (1879: 128, 153, plate 3, fig. 21)
lame transparente	*flagellum*	n.a.	*E. kabiliana* (Simon, 1879)[a]: Simon (1879a: 128,131, plate 3, fig. 24)
Flagellum	*das Plättchen*	*Horn des dosalen finger*	Kraepelin (1901)
Chitinstab/Horn (*Flagellum*)	*das Plättchen* (*Flagellum*)	*Horn des dosalen finger*	Kraepelin (1908a)
flagellum	vertical lamella	dorsal horn	Hirst (1908: 247)
un procès conique	plaque		Sørensen (1914: 174)
flagellum ("*kurz, hornartig*")	*einem durchsichtigen senkrechten Plättchen*		Birula (1913: 321)
Haken	*flagellum/ flagellumplättchen*	*Horn* (*processus rostralis*)	Birula (1935a)
un	fl	rh	Birula (1938: fig. 47)
Viertelkreishorn	*Bläschenflagellum*	*Gabelhaken/ Chelicerenfingergabel*	Roewer (1934)
	lame		Panouse (1955, 1956, 1957)[b]
Viertelkreishorn	*Bläschen-Flagellum*	*Finger ist gegabelt*	Pieper (1977)

[a] Flagellar arrangement of *E. kabiliana* (Simon, 1879) differs from that of other species of *Eusimonia*. The arched structure situated dorsomedially on the fixed (dorsal) finger, illustrated by Simon (1870a: plate 3, figs 23, 24), is termed the flagellum by Simon (1879a). This species was not examined in the present study.

[b] Panouse (1955: 346) did not provide a specific term for the primary flagellum, but described it as "*un organe egalement mobile*". Panouse (1956, 1957) regarded this as the same structure referred to by Roewer (1934) as the *Horn* or *Viertelkreishorn*, terms he considered misleading.

TABLE 12

Morphology of the flagellar complex in genera of Eremobatidae Kraepelin, 1899 in which adult males are known, based on Muma (1951, 1989), Brookhart and Muma (1987), Brookhart and Brookhart (2006), Brookhart and Cushing (2008) and the present study

Abbreviations: *pvsd*, proventral subdistal setae; *vfs*, ventral flagellar seta; fg, flagellar groove

Genus	dorsal series (*pdd*)	ventral series (*pvd*)	*vfs*	*pvsd*	groove structure	groove position	groove length
Chanbria Muma, 1951	homogeneous; striate, weakly flattened	homogeneous; plumose; elongated	undifferentiated		absent	n.a.	n.a.
Eremobates Banks, 1900	homogeneous simple, tubular; sometimes striate	homogeneous; plumose; elongated, cover basal part of fg	plumose; conspicuous, flattened; in fg[a]		distinct	promedial to proventral	length of finger
Eremochelis[b] Roewer, 1934	homogeneous simple, tubular	homogeneous; plumose; elongated, cover basal part of fg	plumose; enlarged, flattened (*branchi* group), not conspicuously enlarged (*bilobatus* and *imperialis* groups)		deep narrow slot, without carinae (*branchi* group); distinct, enlarged basally, with distinct carinae (*bilobatus* group); indistinct series of carinae (*imperialis* group)	promedial to proventral	not to base of finger (*branchi* group); length of finger (*bilobatus* and *imperialis* groups)
Eremocosta Roewer, 1934	homogeneous, unmodified	homogeneous; plumose; unmodified	undifferentiated		deep oval concavity	proventral/ ventral/ retroventral	short, not extending to base
Eremorhax Roewer, 1934[a]	homogeneous; simple tubular	homogeneous; plumose; unmodified, or simple tubular	undifferentiated		indistinct hollow or crease	ventral to proventral	not extending to base
Eremothera Muma, 1951	heterogeneous; incl. 2 flattened	homogeneous; plumose; short	undifferentiated	simple, tubular		promedial	short, weak
Hemerotrecha Banks, 1903	homogeneous/ heterogeneous; can be subspiniform	homogeneous	undifferentiated or differentiated		absent	n.a.	n.a.

[a] Muma (1951: 53, fig. 46); Brookhart and Muma (1981: 291, figs. 2, 3).

[b] As *Therobates* Muma, 1951, in Muma (1951).

TABLE 13

Components and types of flagella in Solifugae based on hypotheses of homology proposed in the present study

Abbreviations: 1°, primary flagellum; 2°, secondary flagellum.

Taxon	Flagellum	Stalk	Base	Shaft
Lipophaginae Wharton, 1981	absent	n. a.	n. a.	n. a.
Eremobatidae Kraepelin, 1899 (when present)	setiform	n. a.	n. a.	n. a.
Melanoblossiinae Roewer, 1933	setiform	n. a.	n. a.	n. a.
Dinorhaxinae Roewer, 1933	sessile	n. a.	n. a.	n. a.
Galeodidae Sundevall, 1833	sessile	n. a.	n. a.	n. a.
Rhagodidae Pocock, 1897 (1° & 2°)	sessile	n. a.	n. a.	n. a.
Karschiidae Kraepelin, 1899 (except *Karschia* Walter, 1889) (1° & 2°)	sessile	n. a.	n. a.	n. a.
Ceromidae Roewer, 1933 (excl. *Toreus* Purcell, 1903)	composite	present	present	present
Namibesia Lawrence, 1962, *Syndaesia* Maury, 1980, *Ammotrechelis* Roewer, 1934	composite	present	present	present
Karschiidae (*Karschia*)	composite	present	present	present
Hexisopodidae Pocock, 1897	composite	present	present	present
Solpugidae Leach, 1815	composite	present	present	present
Gylippinae Roewer, 1933	composite	absent	absent	present
Ammotrechidae Roewer, 1934	composite	present	present	absent
Daesiidae Kraepelin, 1899 (membranous types)	composite	present	present	absent
Mummuciidae Roewer, 1934	composite	present	present	absent

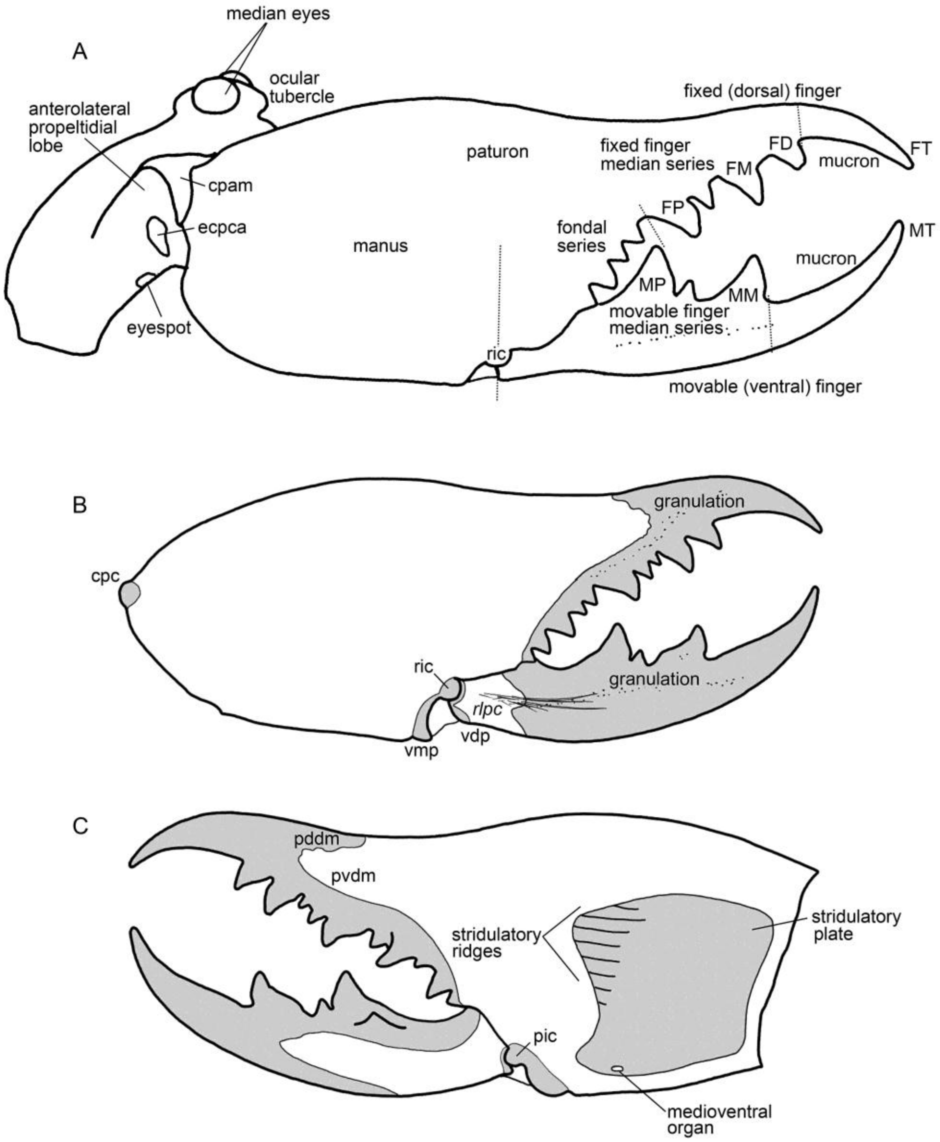

Fig. 1. Solpugidae Leach, 1815, female cheliceral morphology. **A.** *Zeria lawrencei* (Roewer, 1933), ♀ (NMNW 13820), chelicera and propeltidium, lateral view, illustrating attachment to propeltidium via cheliceropeltidial articulation site involving cheliceropeltidial condyle (visible as pale spot on retrolateral surface) and articular membrane. **B, C.** *Solpugassa furcifera* (Kraepelin, 1899), ♀ (AMNH [LP 3632]), chelicerae, retrolateral (**B**) and prolateral (**C**) views. Grey shading denotes asetose areas. Abbreviations: cpc, cheliceropeltidial condyle; cpam, cheliceropeltidial articular membrane; ecpca, external cheliceropeltidial condylar attachment; FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FT, movable finger, terminal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MT, movable finger, terminal tooth; pic, prolateral interdigital condyle; pddm, prodorsal distal margin of asetose area; pvdm, proventral distal margin of asetose area; ric, retrolateral interdigital condyle; *rlpc*, retrolateral proximal cluster of setae; vdp, ventral digital plagula; vmp, ventral manus plagula

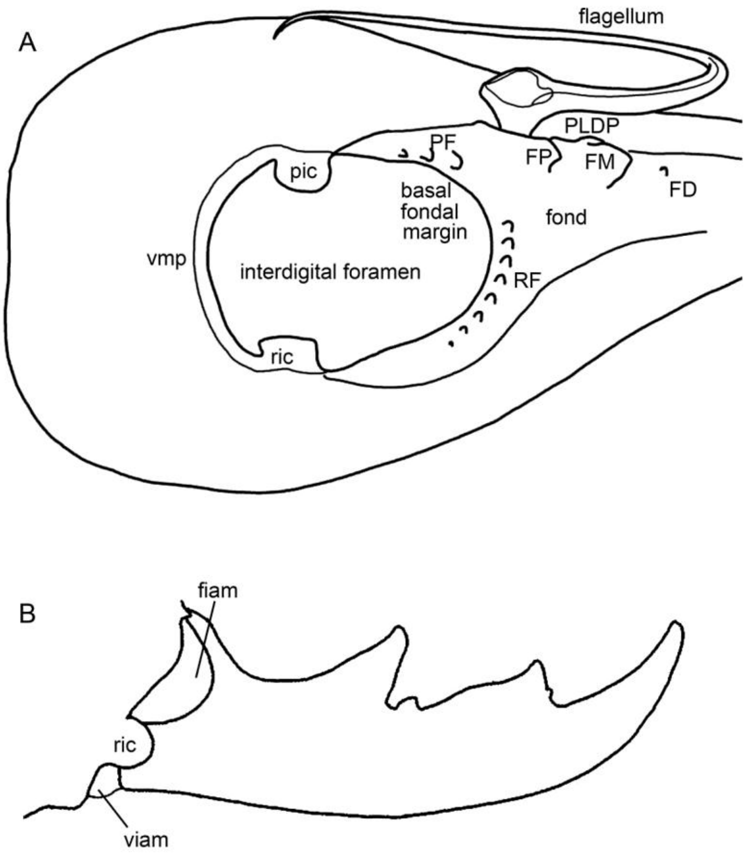

Fig. 2. Hexisopodidae Pocock, 1897 (**A**) and Daesiidae Kraepelin, 1899 (**B**), cheliceral interdigital articulation and attachment sites, illustrating condyli and articular membranes. **A.** *Hexisopus lanatus* (C.L. Koch, 1942), ♂ (NMNW 10795), fixed (dorsal) finger, ventral view, illustrating row of bead-like denticles at base of fond. **B.** *Biton* (*B.*) sp. 6 (*namaqua* group), ♂ (NMNW), Namibia: Windhoek, Auas Mountains, movable (ventral) finger, retrolateral view. Abbreviations: FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; PF, profondal teeth; RF, retrofondal teeth; *mff*, movable finger fondal setae; pic, prolateral interdigital condyle; fiam, fondal interdigital articular membrane; ric, retrolateral interdigital condyle; viam, ventral interdigital articular membrane; vdp, ventral digital plagula; vmp; ventral manus plagula.

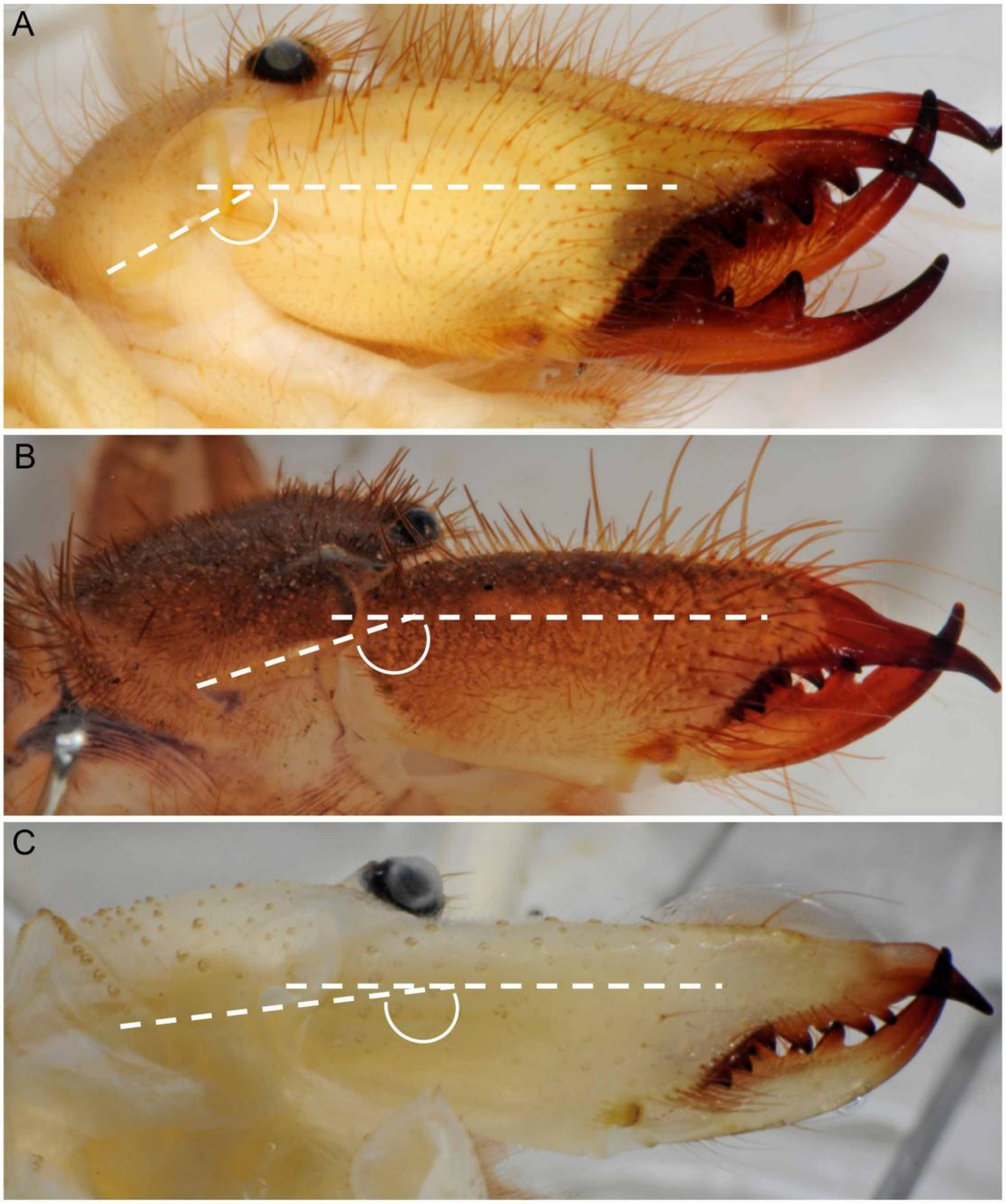

Fig. 3. Solpugidae Leach, 1815 (**A**), Daesiidae Kraepelin, 1899 (**B**), and Ammotrechidae Roewer, 1934 (**C**), cheliceral attachment to propeltidium, lateral views, illustrating increasingly obtuse angle formed by ventral margin of anterolateral propeltidial lobe with chelicera. **A.** *Zeria lawrencei* (Roewer, 1933), ♀ (NMNW 13820). **B.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]). **C.** *Nothopuga cuyana* Maury, 1976, ♂ (AMNH [LP 2263]).

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Fig. 4. Daesiidae Kraepelin, 1899, *Ammotrechelis goetschi* Roewer, 1934, chelicerae and propeltidium, dorsal views, illustrating sexual dimorphism (greater aspect ratio in ♂ than ♀). **A.** ♂ (AMNH [LP 10673]). **B.** ♀ (AMNH [LP 10673]).

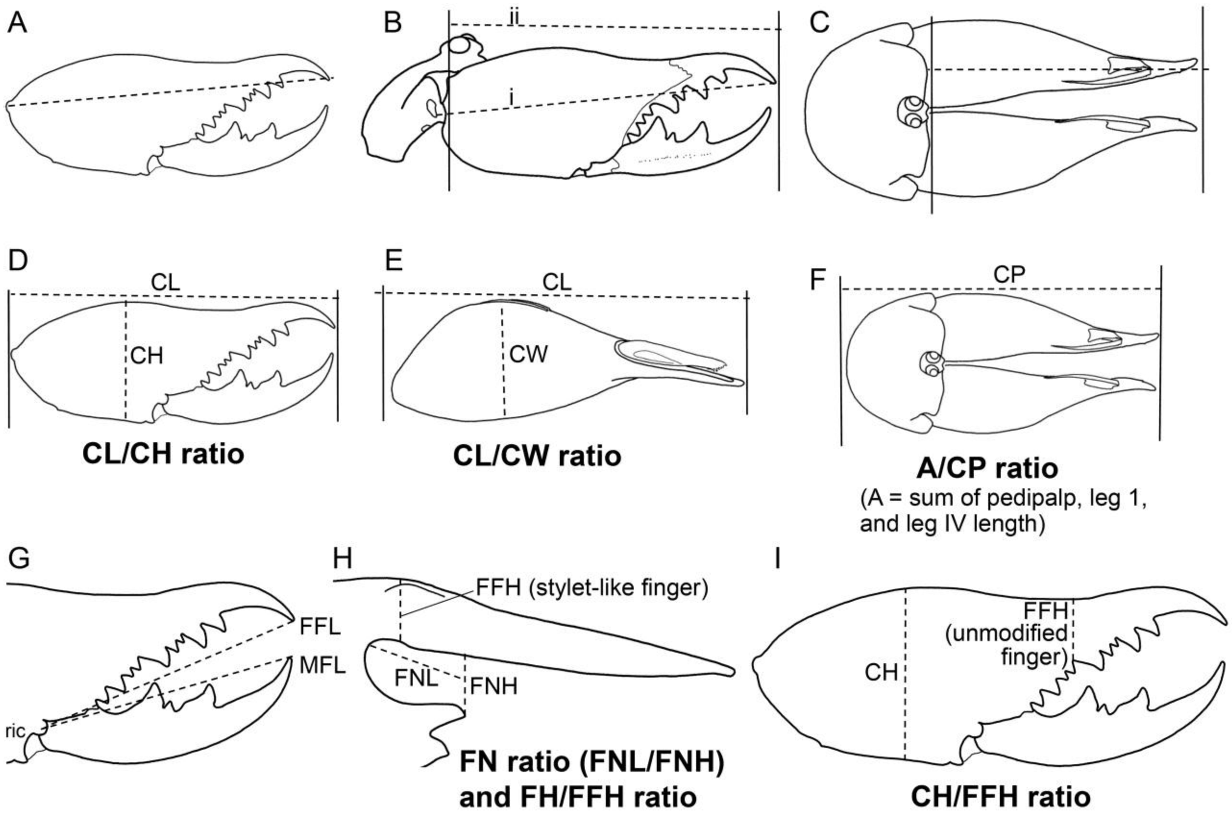

Fig. 5. Solifugae, cheliceral measurements and ratios. **A–C.** Landmarks used to measure cheliceral length (CL). **A.** Fixed (dorsal) finger, apex to cheliceropeltidial condyle, retrolateral view (Muma, 1951; Brookhart and Cushing, 2004). **B.** Fixed finger apex to anterolateral propeltidial lobe anterior margin, in a direct line (line i) or parallel to longitudinal axis of chelicera (line ii), retrolateral view. **C.** Fixed finger to propeltidium anterior margin, dorsal view. **D.** CL/CH ratio (Cloudsley-Thompson, 1961a). **E.** CL/CW ratio. **F.** A/CP index (Brookhart and Muma, 1981, 1987; Muma and Brookhart, 1988). **G.** Fixed and movable (ventral) finger lengths from retrolateral interdigital condyle (ric) center to (applicable) finger apex, retrolateral view. **H.** FN ratio (FNL/FNH), i.e., fondal notch L/W or FN ratio *sensu* Brookhart and Muma (1981, 1987) and Muma and Brookhart (1988), FL/FW ratio *sensu* Brookhart and Cushing (2004) and FNH/FFH index (FW/FFW) *sensu* Brookhart and Cushing (2004), based on finger to notch ratio (FF/FN) of Brookhart and Muma (1987), with numerator and denominator switched. Abbreviations: CH, cheliceral height; CL, cheliceral length; CP, chelicera-propeltidium length; FFH, fixed finger width; FFL, fixed finger length; FN, fondal notch; FNL, fondal notch length; FNH, fondal notch width; MFL, movable finger length; ric, retrolateral interdigital condyle.

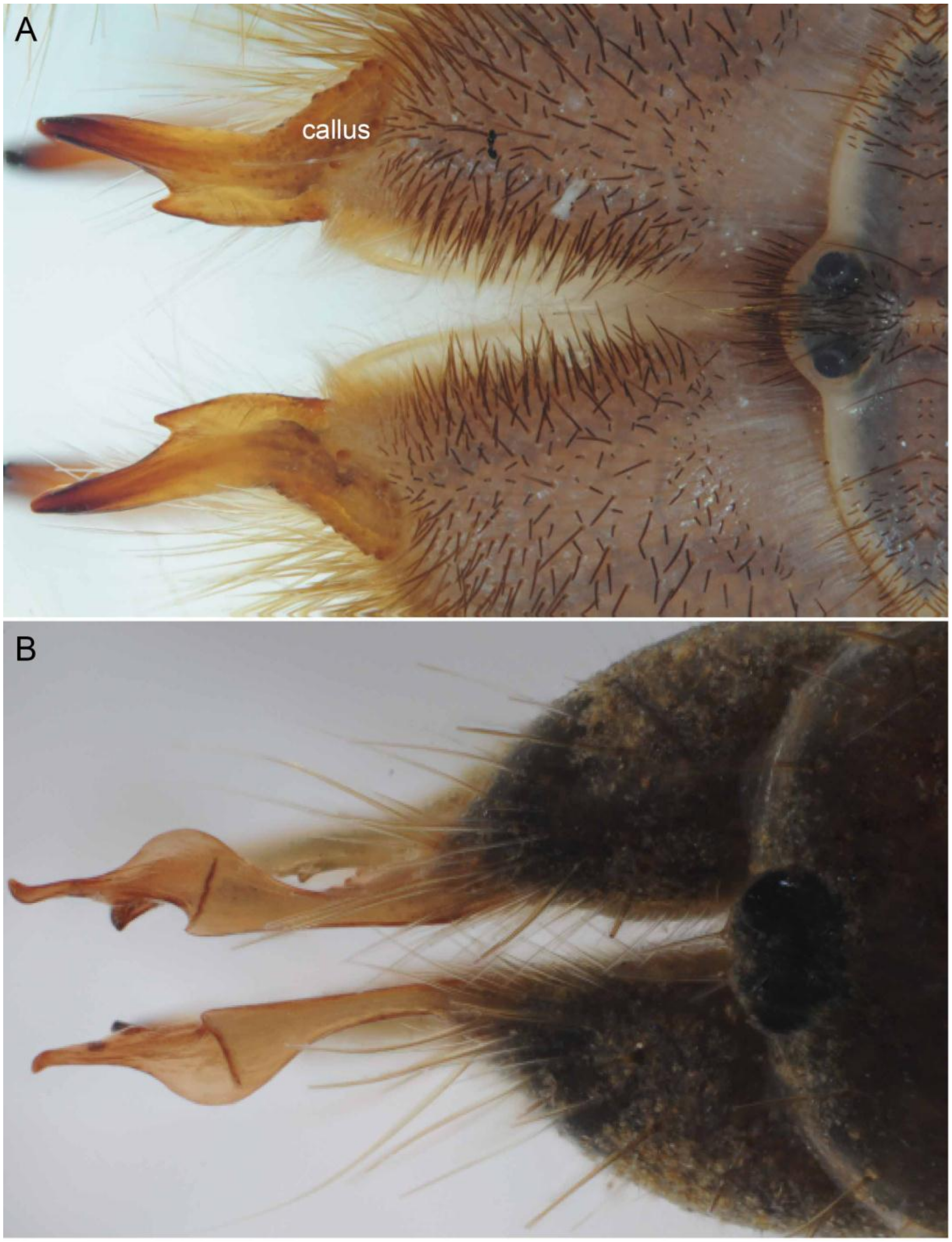

Fig. 6. Hexisopodidae Pocock, 1897 (**A**) and Melanoblossiidae Roewer, 1933, Melanoblossiinae (**B**), modified cheliceral finger apices, dorsal views. **A.** *Hexisopus pusillus* Lawrence, 1962, ♂ (NMNW 11426), illustrating callus, distinct asetose area on fixed (dorsal) finger. **B.** *Melanoblossia* sp., ♂ (AMNH [LP 9857]).

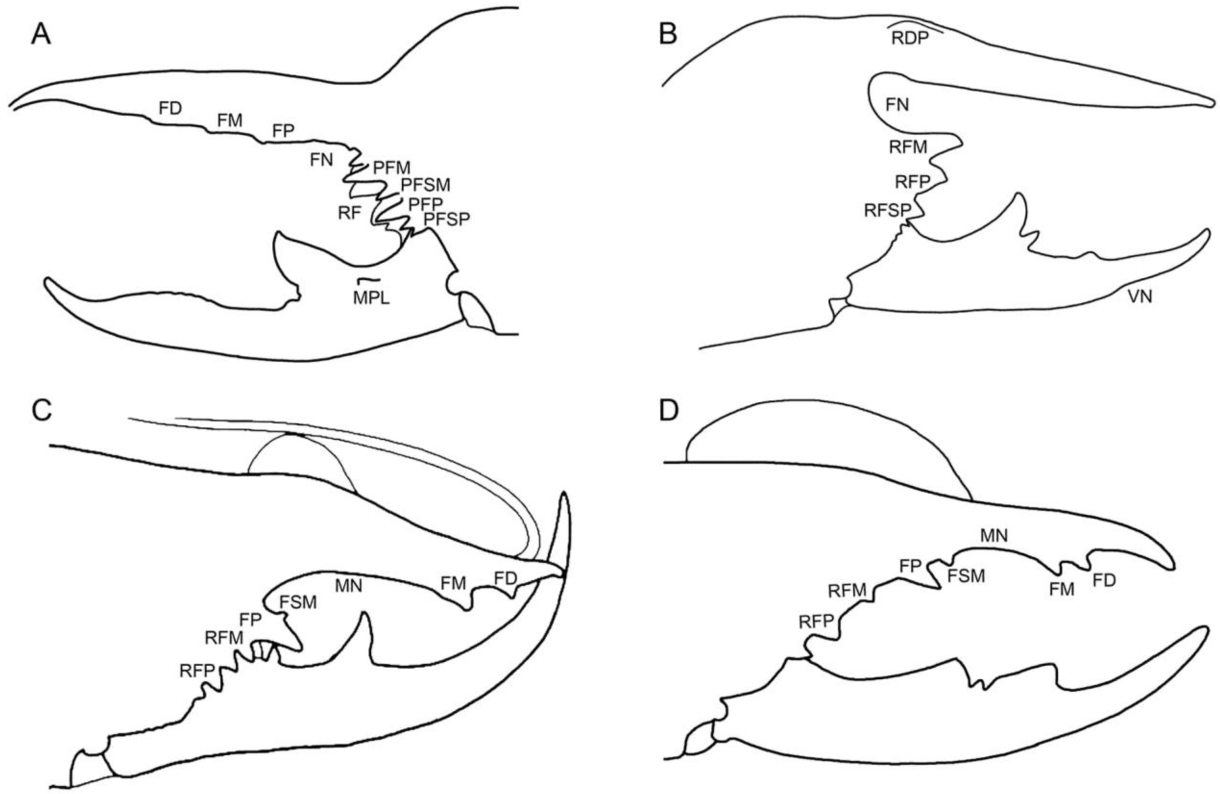

Fig. 7. Eremobatidae Kraepelin, 1899 (**A**, **B**), Solpugidae Leach, 1815 (**C**), and Ammotrechidae Roewer, 1934 (**D**), cheliceral shape modifications and positional comparison of fondal notch and medial notch, prolateral (**A**) and retrolateral (**B–D**) views. **A.** *Eremochelis andreasana* (Muma, 1962), holotype ♂ (AMNH), shallow fondal notch, illustrating proximal position, relative to reduced median series dentition. **B.** *Eremobates bajadae* Muma & Brookhart, 1988, ♂ (AMNH [LP 5740]), deep fondal notch. **C.** *Solpugema derbiana* (Pocock, 1895), ♂ (AMNH [LP 7709]), illustrating medial notch situated within median series dentition, distal to FP. **D.** *Branchia angustus* Muma, 1951, ♂, adapted from Muma (1951: 136, fig. 305), illustrating medial notch situated within median series dentition. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FN, fondal notch; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MN, medial notch; MPL, movable finger, prolateral tooth; PF, profondal medial tooth; PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFSM, retrofondal submedial tooth; RFP, retrofondal proximal tooth; RDP, retrodorsal process; VN, ventral notch.

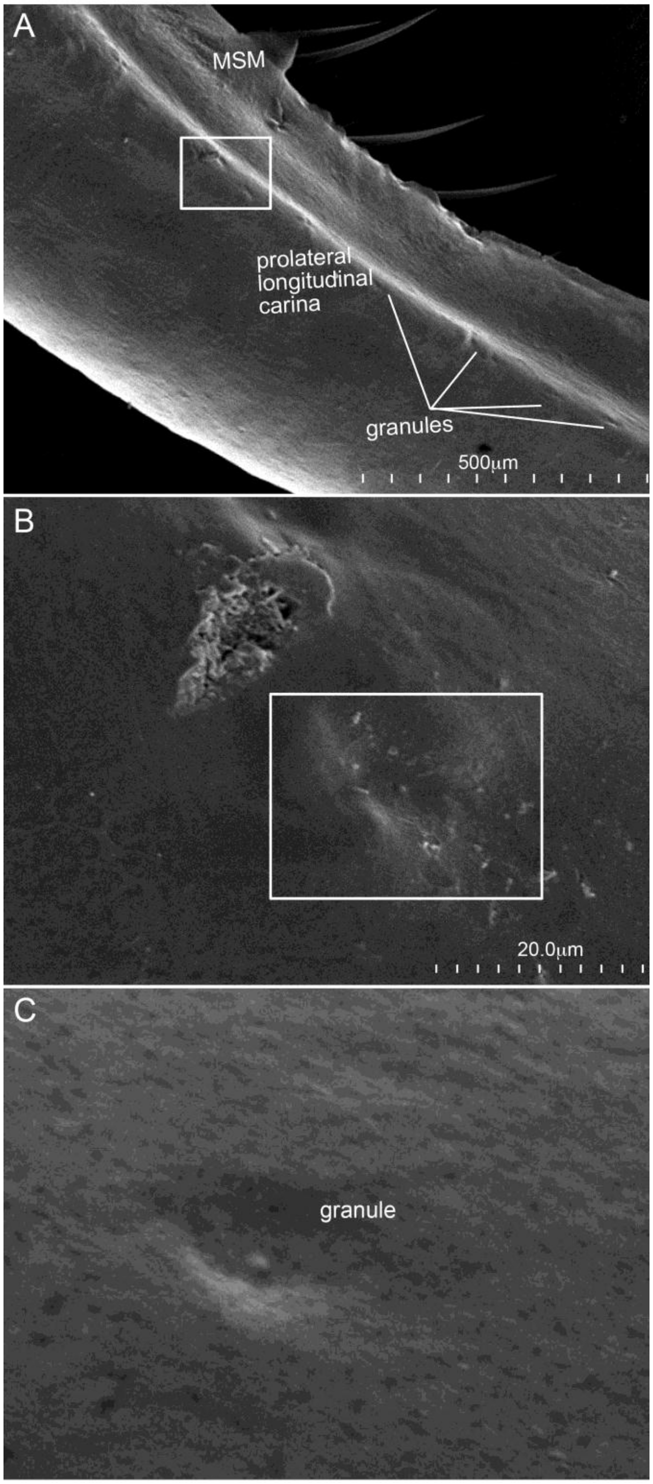

Fig. 8. Solpugidae Leach, 1815, *Solpugiba lineata* (C.L. Koch, 1842), ♂ (AMNH [LP 5919]), cheliceral movable (ventral) finger, retrolateral view, illustrating granulation on longitudinal ridge (**A**), enlargement of individual granule (**B**), and close-up, illustrating apparent absence of external pore (**C**). Abbreviations: MSM, movable finger, submedial tooth..

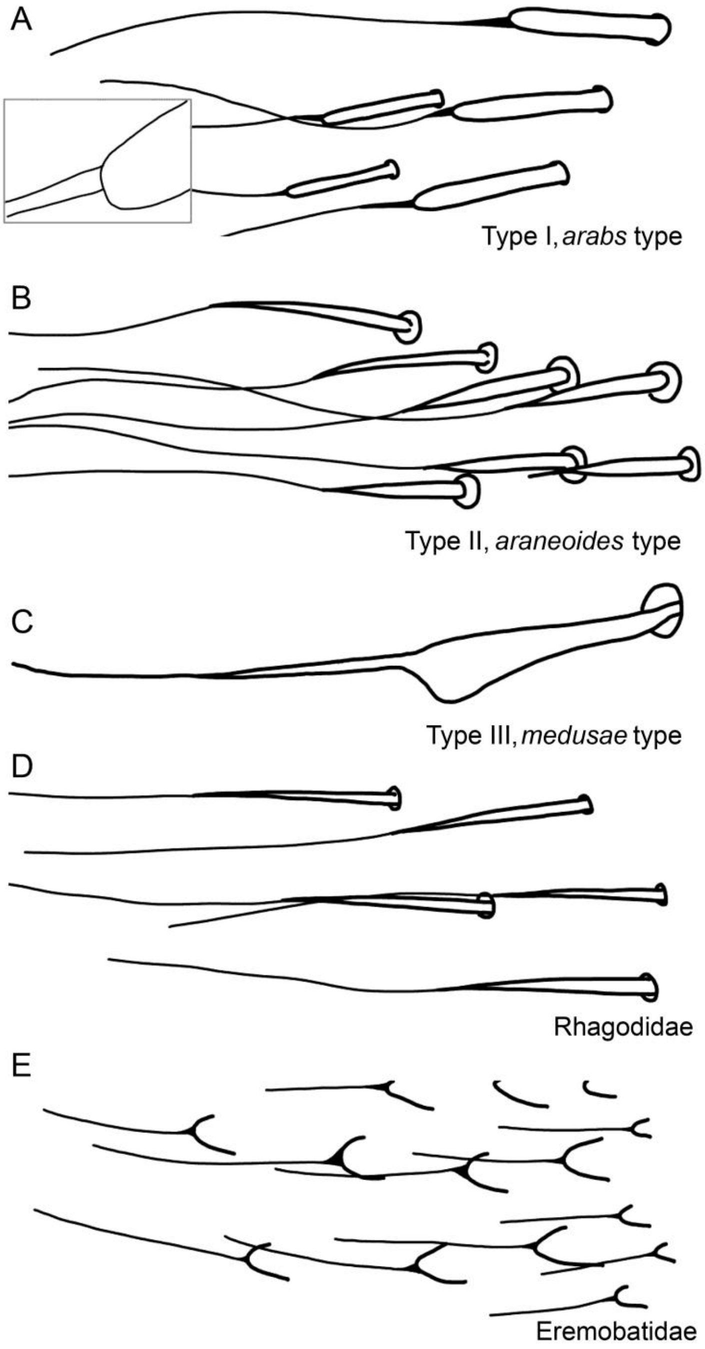

Fig. 9. Galeodidae Sundevall, 1833 (**A–C**), Rhagodidae Pocock, 1897 (**D**), and Eremobatidae Kraepelin, 1899 (**E**), modified cheliceral stridulatory setae. **A.** *Galeodes* sp., ♂ (AMNH [LP 11204]), type I (*arabs* type) setae. Inset: apex of setal base, adapted from Cloudsley-Thompson and Constantinou (1984: 366, fig. 1d). **B.** *Paragaleodes nesterovi* Birula, 1916, ♂ (AMNH [LP 7480]), type II (*araneoides* type) setae. **C.** *Galeodes medusae* Turk, 1960, ♂, type III (*medusae* type) setae, adapted from Turk (1960: 115, fig. 4). **D.** *Rhagoderma tricolor* Roewer, 1941, ♂ (AMNH [LP 5435]). **E.** *Eremocosta titania* (Muma, 1951), ♂ (AMNH [LP 5035]).

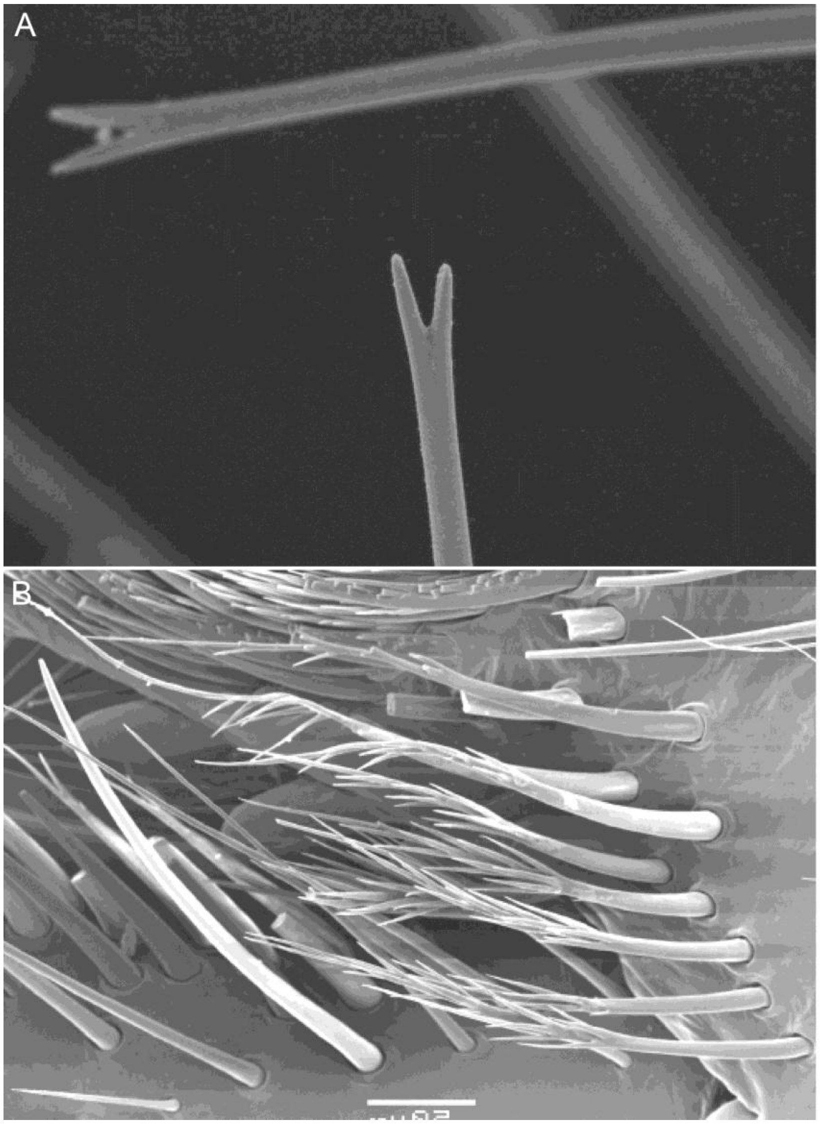

Fig. 10. Gylippidae Roewer, 1933, Lipophaginae Wharton, 1981, *Bdellophaga angulata* Wharton, 1981 ♂ (NMNW 11601), chelicerae, retrolateral surface, bifid setae (**A).** Melanoblossiidae Roewer, 1933, Melanoblossiinae, *Melanoblossia* sp. ♂ (NMNW 13396)**,** prolateral surface, plumose setae (**B**).

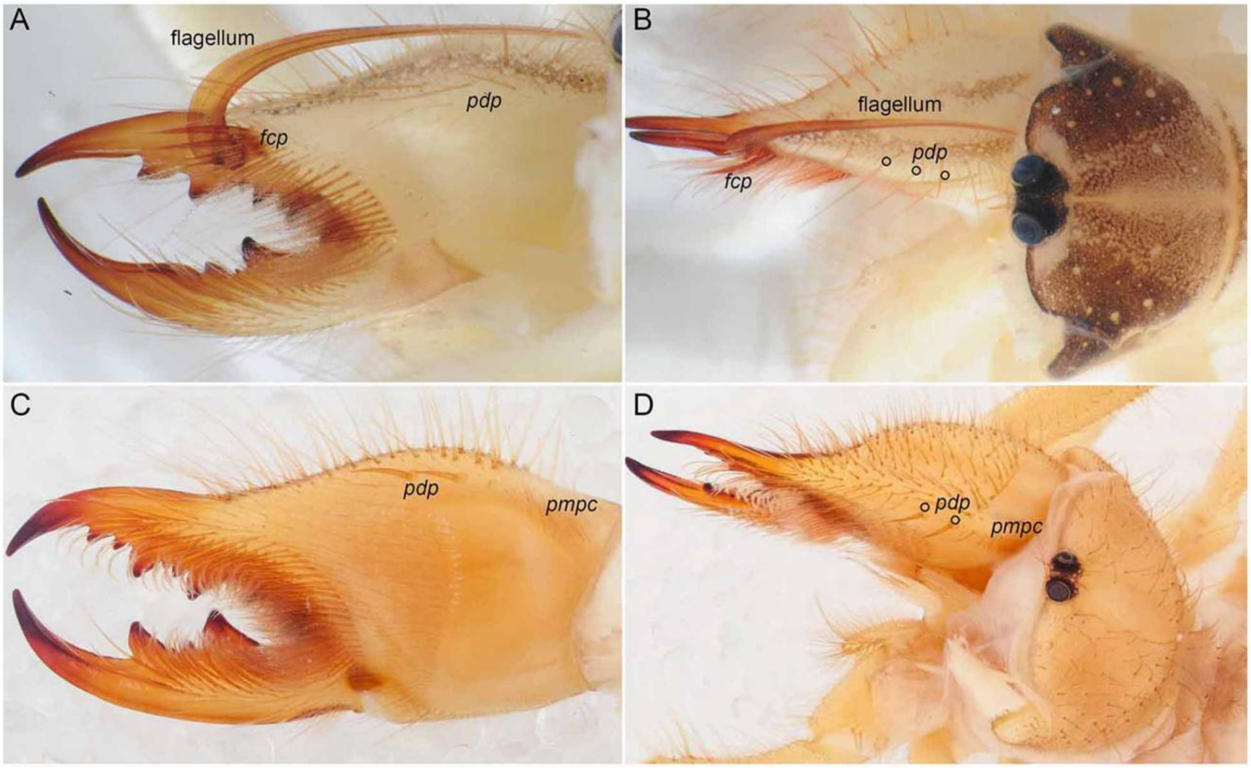

Fig. 11. Ceromidae Roewer, 1933 (**A, B**) and Eremobatidae Kraepelin, 1899 (**C, D**), chelicera and propeltidium, prolateral (**A, C**) and prodorsal (**B, D**) views, illustrating prodorsal setae. **A, B.** *Ceroma inerme* Purcell, 1899, ♂ (AMNH [LP 9864]). **C, D.** *Eremobates inkopaensis* Brookhart & Cushing, 2005, paratype ♀ (DMNS ZA.17310). Abbreviations: *pdp*, prodorsal proximal setae; *pmpc*, promedial proximal cluster of setae.

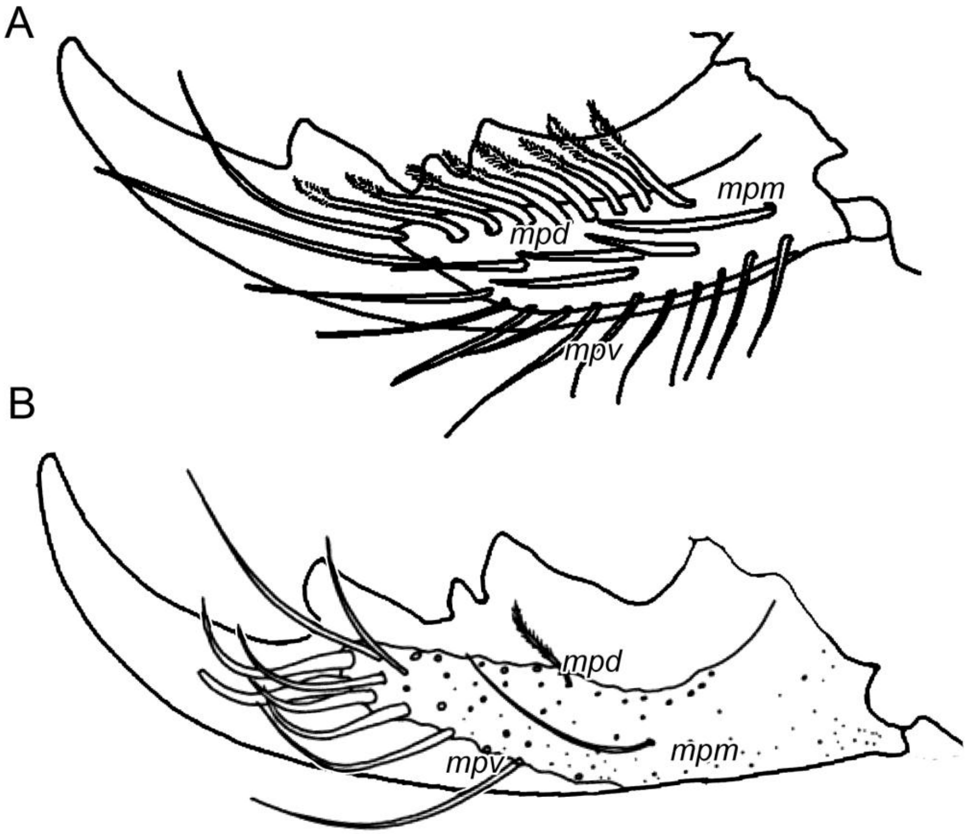

Fig. 12. Daesiidae Kraepelin, 1899 (**A**) and Solpugidae Leach, 1815 (**B**), cheliceral movable fingers, prolateral views, illustrating setae. **A.** *Blossia spinicornis* Lawrence, 1928, ♂ (NMNW), Namibia: Windhoek (NARREC). **B.** *Solpugyla* sp., ♂ (AMNH [LP 10764]). Circles represent setal sockets. Abbreviations: *mpd*, movable finger, prodorsal setae; *mpm*, movable finger, promedial setae; *mpv*, movable finger, proventral setae.

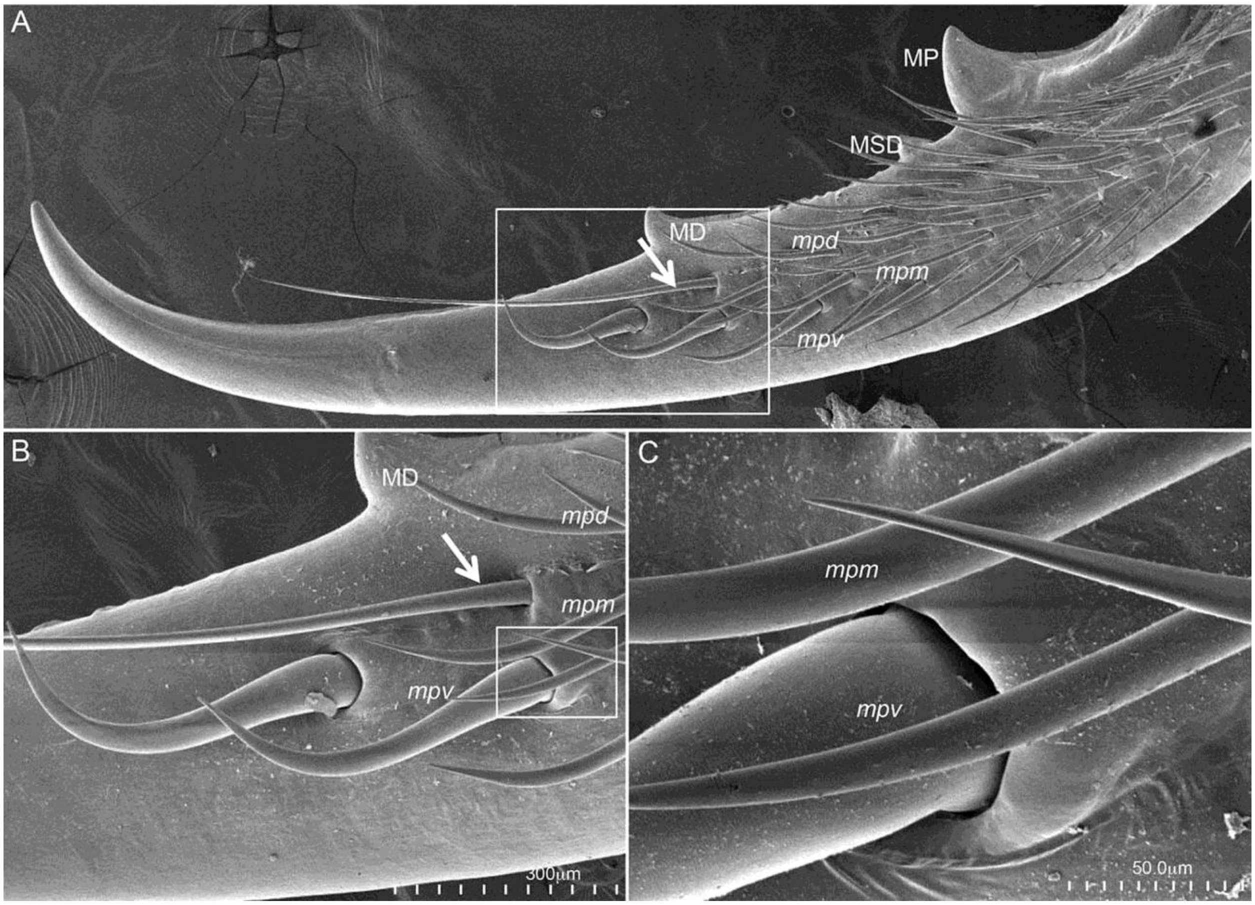

Fig. 13. Solpugidae Leach, 1815, *Solpugiba lineata* (C.L. Koch, 1842), ♂ (NMNW 13814), cheliceral movable finger, prolateral view, illustrating dorsodistally directed prodorsal setae (*mpd*), distally directed promedian setae (*mpm*), and ventrodistally directed proventral setae (*mpv*) (**A**); closeup of distal setal area illustrating long apical *mpd* seta and modified distal *mpv* setae (**B**); and closeup of socket of modified subapical *mpv* seta with distally directed insertion (**C**). Arrows indicate apicalmost *mpd* seta. Abbreviations: MP, movable finger, proximal tooth; MD, movable finger, distal tooth; MSD, movable finger, subdistal tooth.

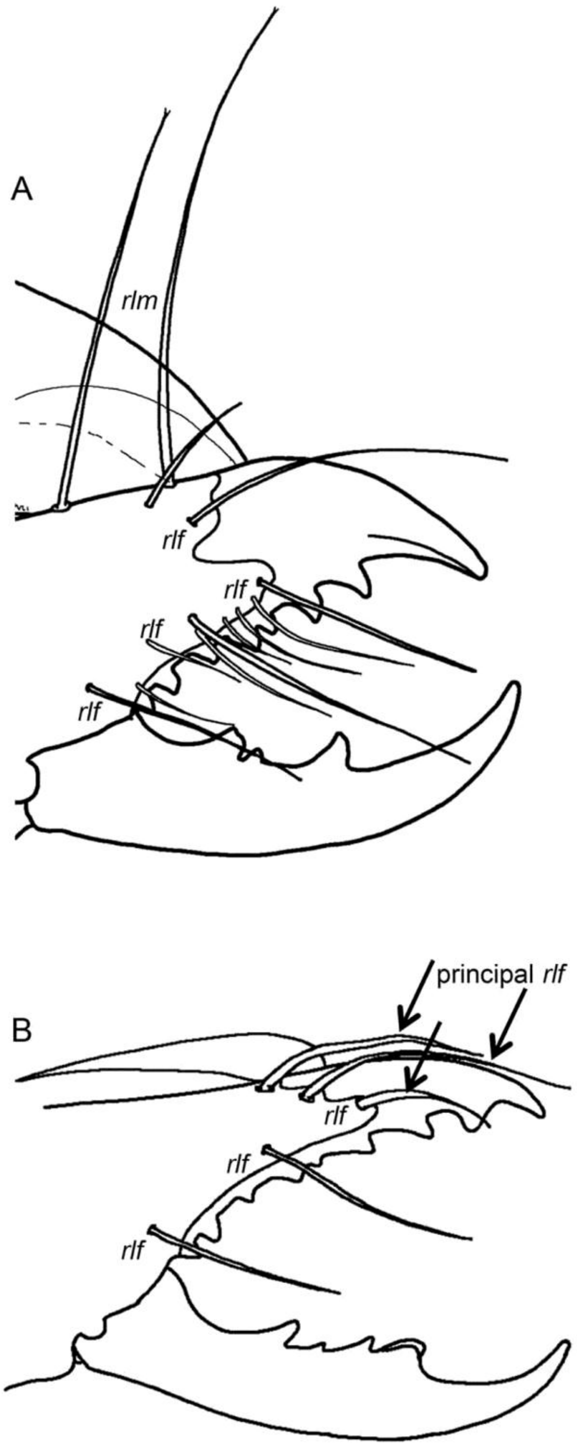

Fig. 14. Daesiidae Kraepelin, 1899, chelicerae, retrolateral views, illustrating positions of some *rlf* setae. **A.** *Hemiblossia etosha* Lawrence, 1927, ♂ (AMNH [LP 9854]), illustrating arrangement of *rlf* setae in rows, and dorsally situated, bifid *rlm* setae. **B.** *Blossia* cf. *rooica*, ♂ (NMNW), Namibia: Gondwana Cañon Park (SNAP; Site G29), illustrating unmodified *rlf* and modified *principal rlf* setae. Abbreviations: *rlf*, retrolateral finger setae; *rlm*, retrolateral manus setae.

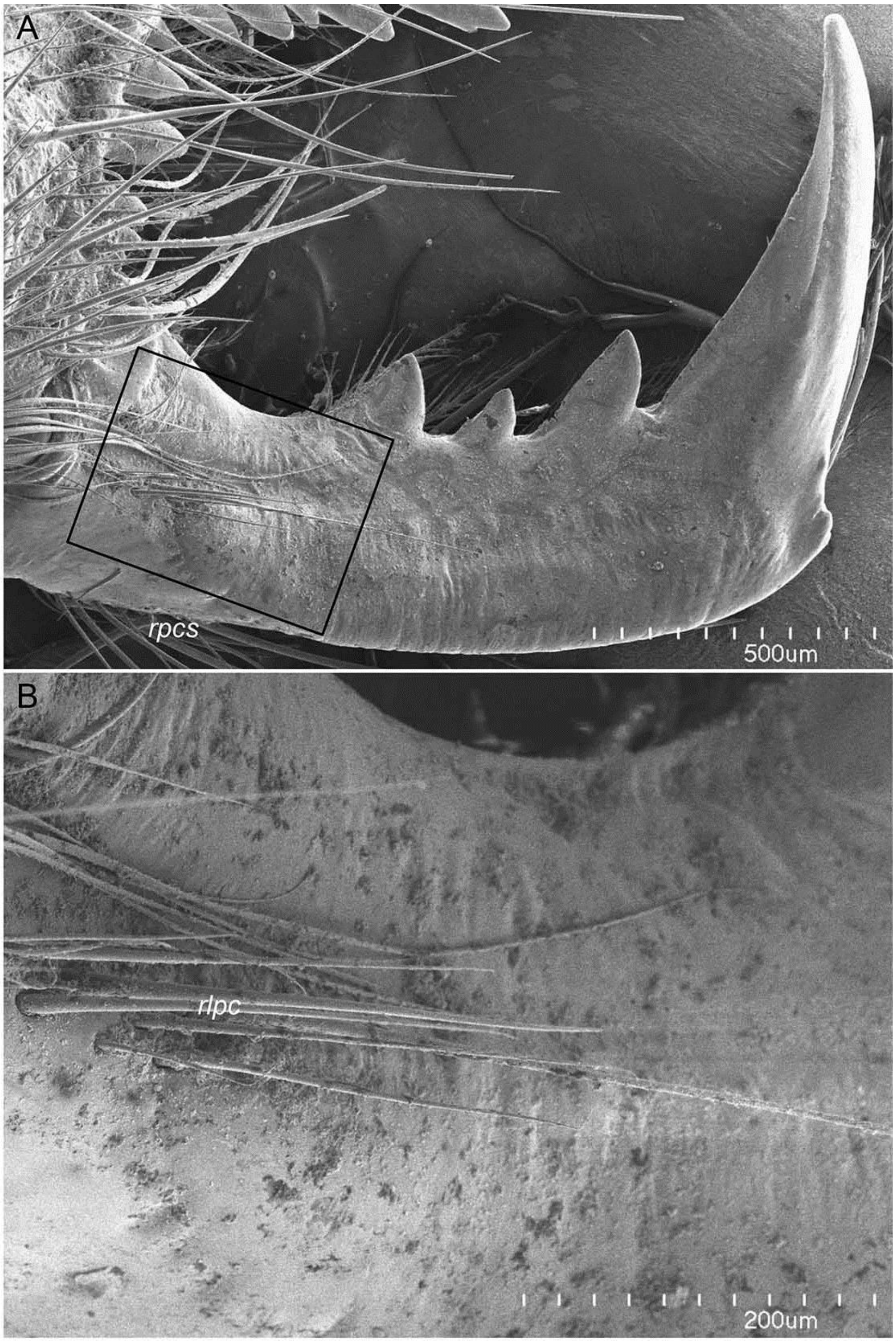

Fig. 15. Gylippidae Roewer, 1933, Lipophaginae Wharton, 1981, *Bdellophaga angulata* Wharton, 1981, ♂ (NMNW 11601), cheliceral movable finger, retrolateral view, illustrating retrolateral proximal cluster (*rlpc*) of setae and position of asetose area. Rectangle in **A** indicates area in **B**..

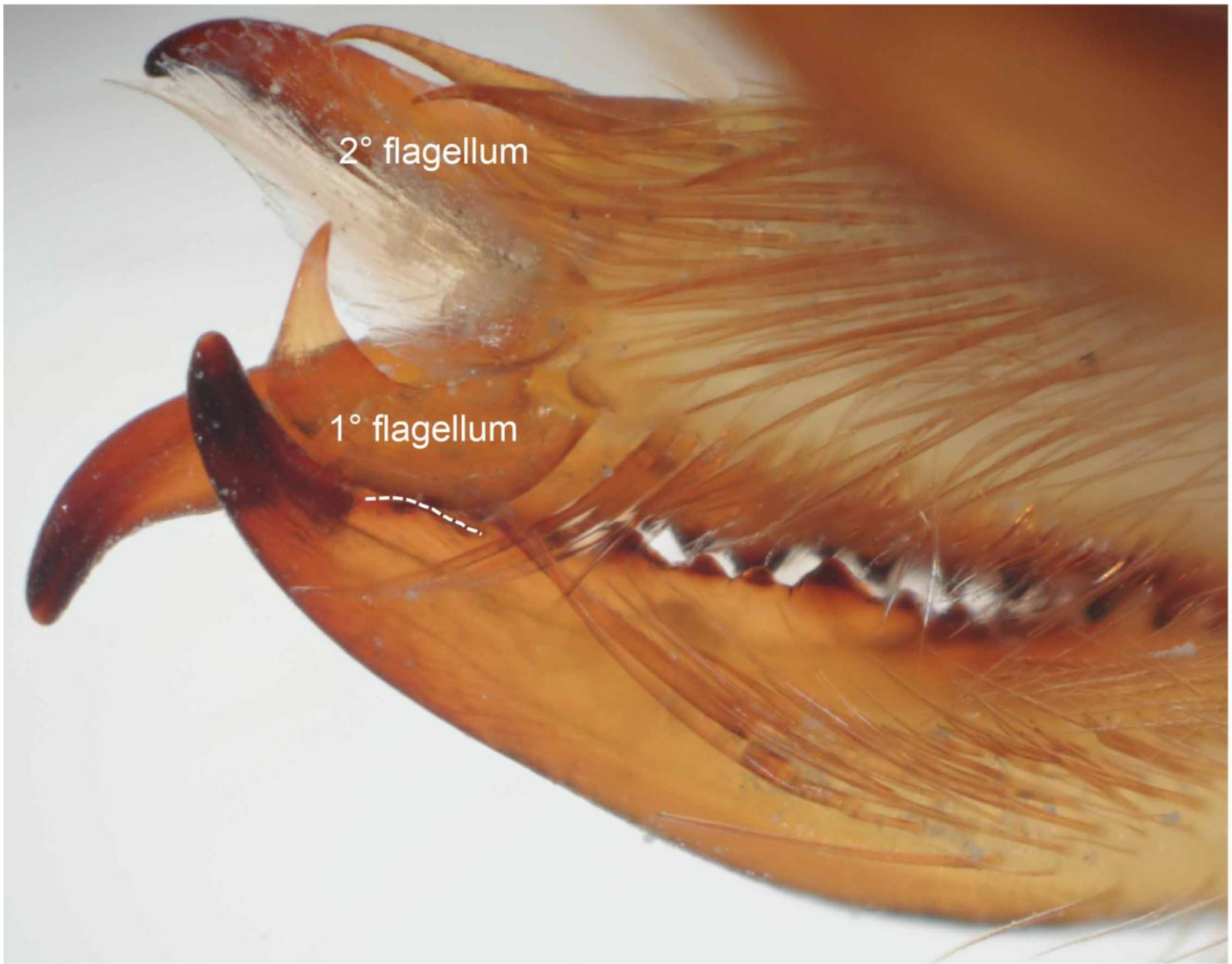

Fig. 16. Karschiidae Kraepelin, 1899, *Karschia* (*K.*) *mastigofera* Birula, 1890, ♂ (AMNH [LP 7474]), closed cheliceral fingers, prolateral view, illustrating location of flagellum in trough-like depression between prolateral flange and cutting edge of movable finger.

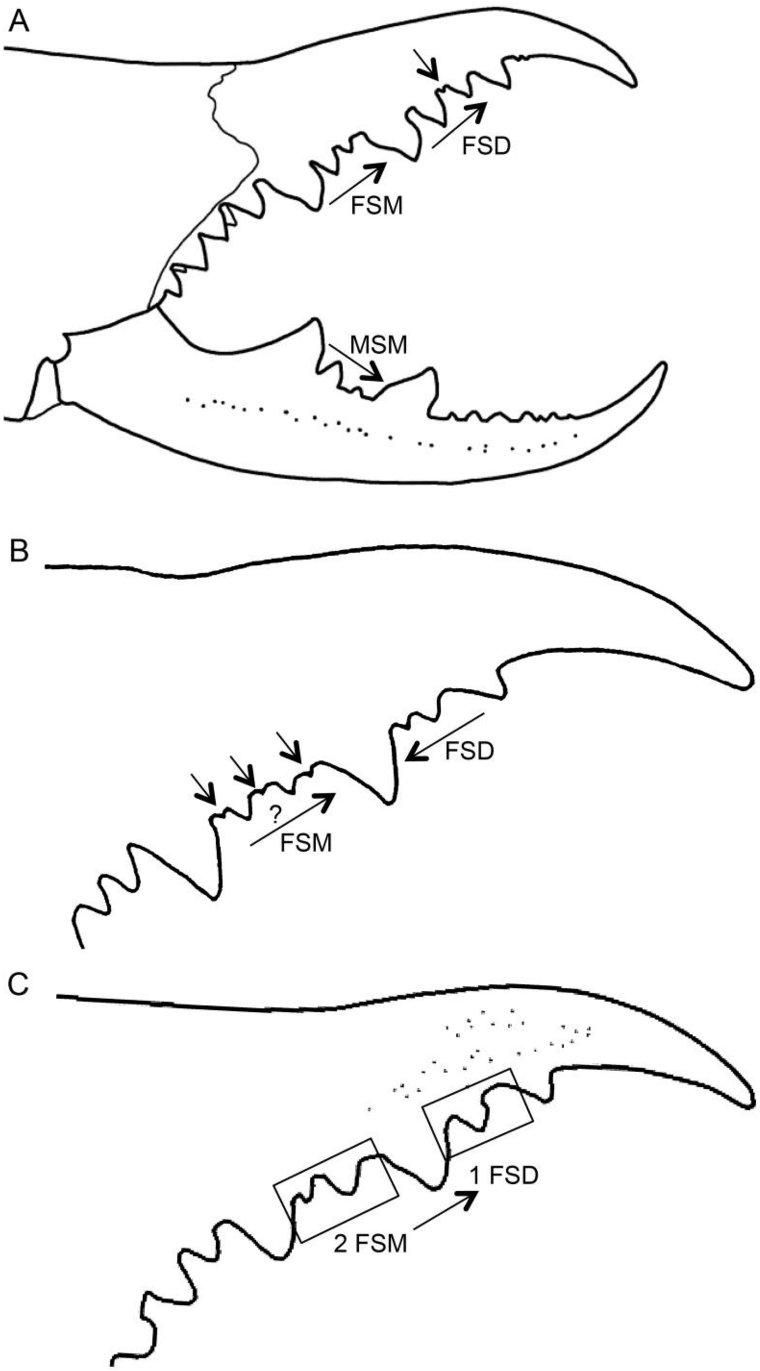

Fig. 17. Eremobatidae Kraepelin, 1899 (**A**), Solpugidae Leach, 1815 (**B**), and Galeodidae Sundevall, 1833 (**C**), chelicera (**A**) and fixed (dorsal) finger (**B, C**), retrolateral views, indicating patterns of size gradation apparent (**A, B**), and decreasing number of FSM to FSD teeth (**C**). **A.** *Horribates bantai* Muma, 1989, ♀ (DMNS ZA.17691). **B.** *Galeodes araneoides* (Pallas, 1772), ♀ (AMNH), Turkey: Gurgen. **C.** *Solpugiba lineata* (C.L. Koch, 1842), ♀ (AMNH [LP 5919]). Abbreviations: FSD, fixed finger, subdistal teeth; FSM, fixed finger, submedial teeth; MSM, movable finger, submedial teeth. Arrows indicate labile denticles not following gradation patterns.

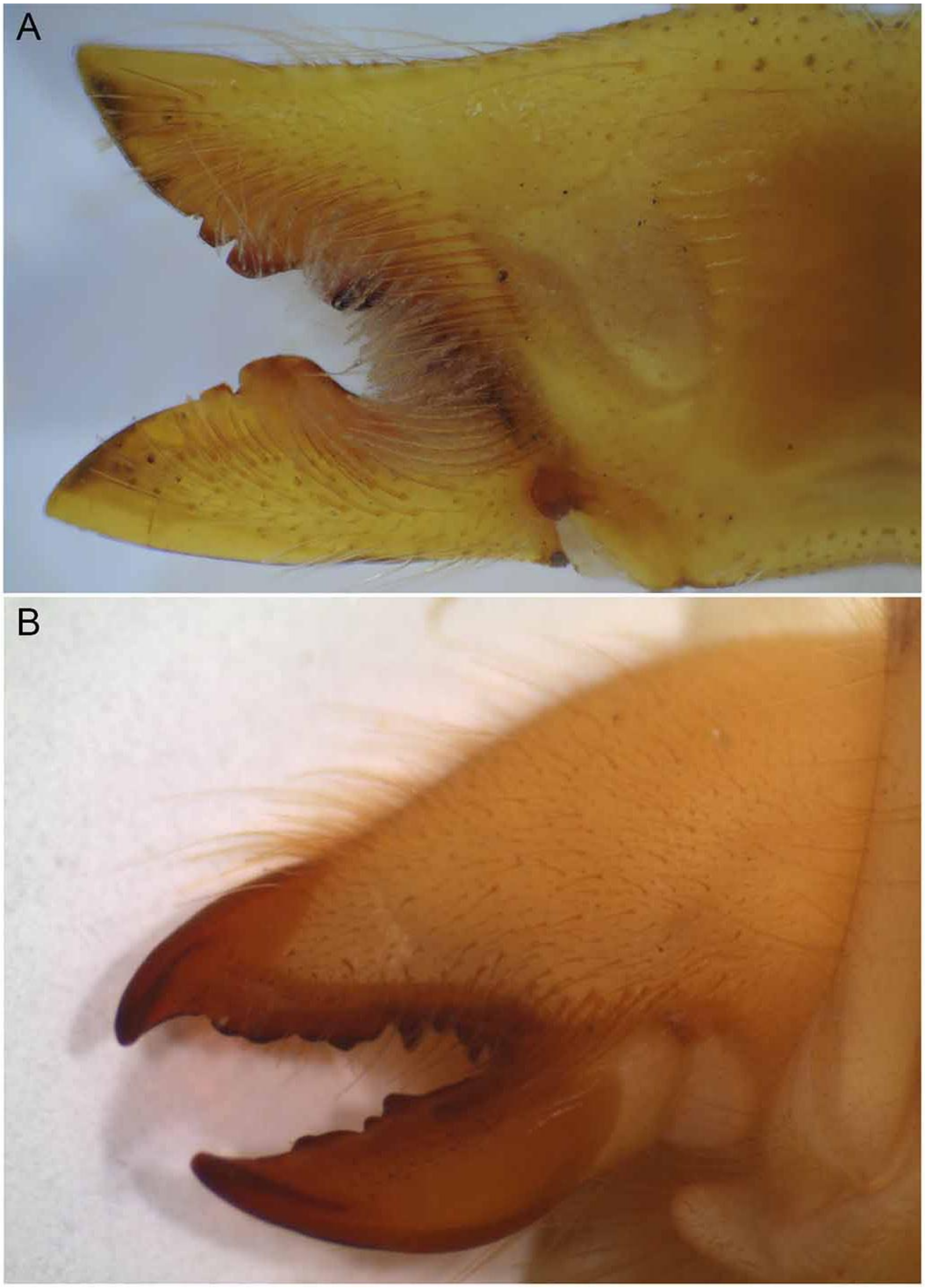

Fig. 18. Solpugidae Leach, 1815, Solpuginae (**A**) and Ferrandiinae Roewer, 1933 (**B**), chelicerae, retrolateral views, illustrating examples of unambiguously deformed or excessively worn dentition (**A**) and seemingly deformed or worn dentition (**B**). **A.** *Solpugella asiatica* Roewer, 1933, ♀ (HUJI). **B.** *Ferrandia robusta* Lawrence, 1954, ♀ (MCZ 126329).

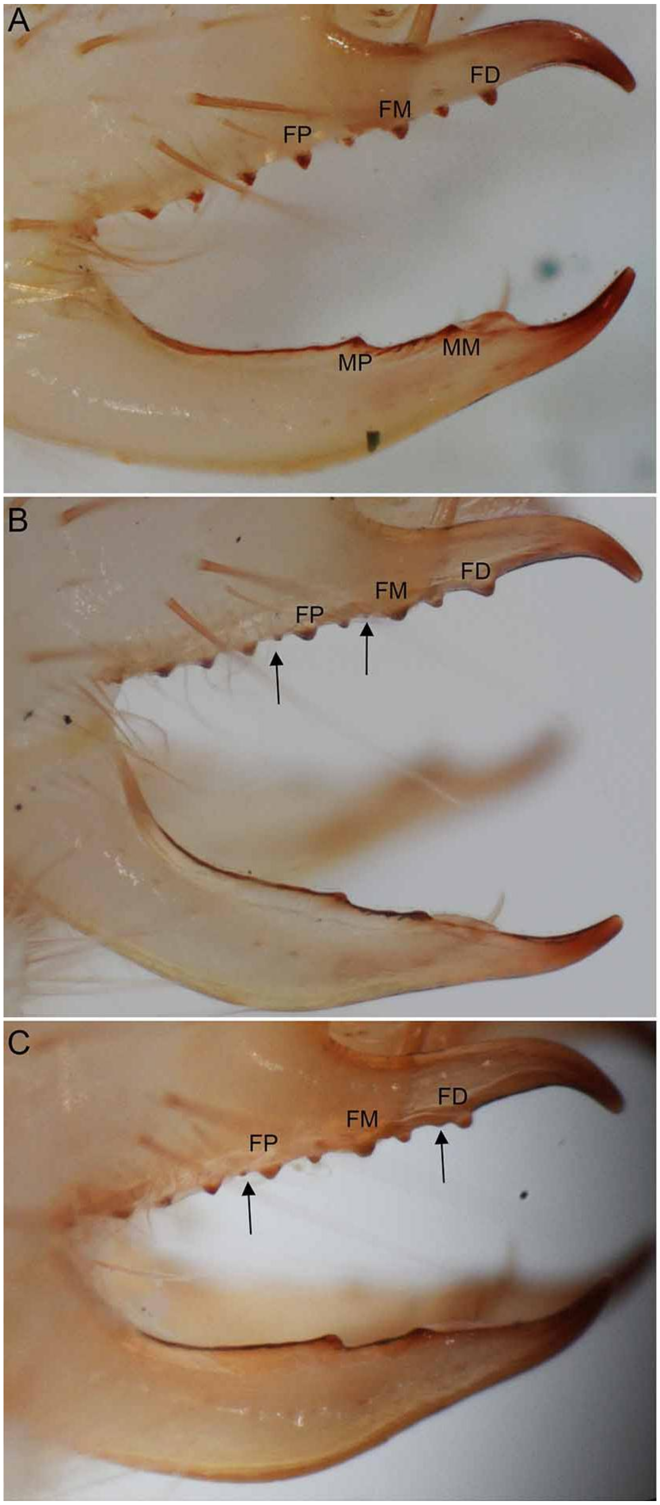

Fig. 19. Karschiidae Kraepelin, 1899, *Eusimonia divina* Birula, 1935, ♂♂ (AMNH [LP 4098]), chelicerae, retrolateral views, indicating intrapopulation variation. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth, MM, movable finger, medial tooth; MP, movable finger, proximal tooth. Arrows indicate variable teeth.

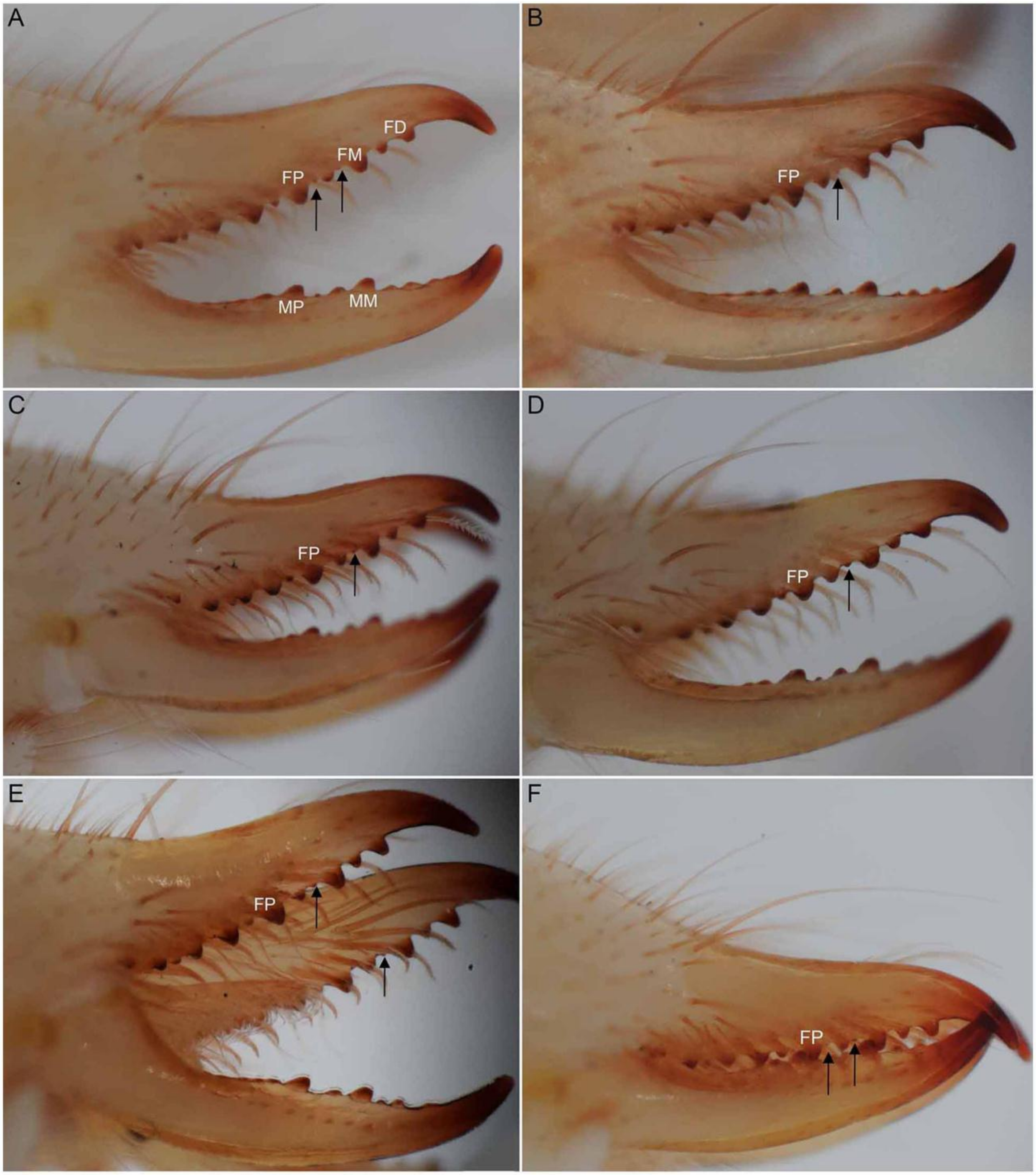

Fig. 20. Karschiidae Kraepelin, 1899, *Eusimonia divina* Birula, 1935, ♀♀ (AMNH [LP 4098]), chelicerae, retrolateral views, indicating intrapopulation variation. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth, MM, movable finger, medial tooth; MP, movable finger, proximal tooth. Arrows indicate variable teeth.

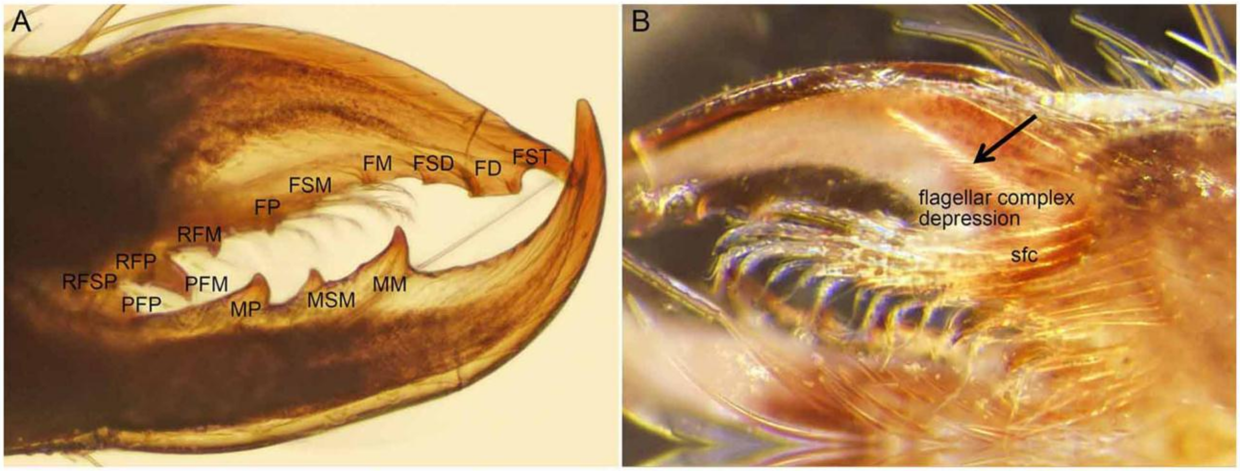

Fig. 21. Melanoblossiidae Roewer, 1933, Melanoblossiinae, *Melanoblossia braunsi* Purcell, 1903, ♂ (AMNH [LP 10737]), chelicerae, retrolateral (**A**) and prolateral (**B**) views, indicating hypothesized dentition (**A**) and position of flagellar complex. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial tooth; FST, fixed finger, subterminal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSP, movable finger, submedial tooth; *sfc*, setiform flagellar complex. Arrow indicates most prominent seta in setiform flagellar complex.

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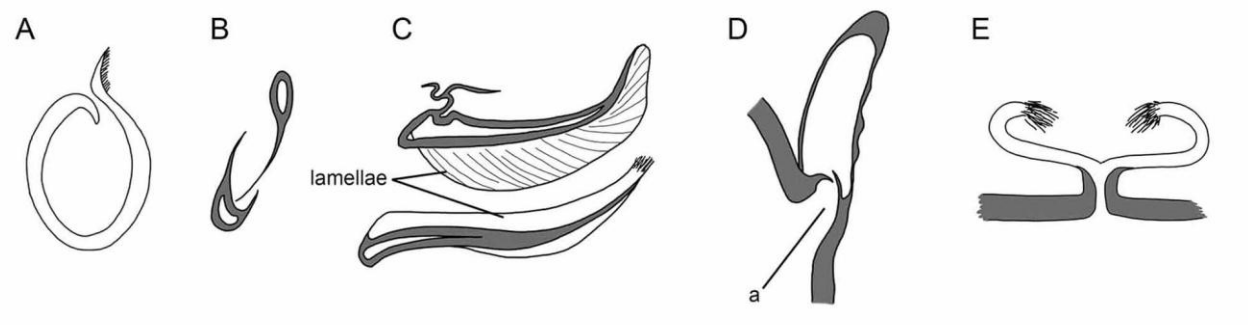

Fig. 22. Karschiidae Kraepelin, 1899 (**A**), Rhagodidae Pocock, 1897 (**B, C**), Solpugidae Leach, 1815 (**D**), Ammotrechidae Roewer, 1934 (**E**), male flagella, schematic cross sections (**A, B, D, E**) and longitudinal section (**C**) of shaft (**A**), flagellum (**B, C**), bulbous base (**D**) and attachment point (**E**), after Roewer (1934: 138–154, figs. 133c, 137, 143A$_1$, 156). **A.** *Karschia* (*K.*) *tibetana* Hirst, 1907. **B, C.** *Rhagodima nigrocincta* (Bernard, 1893). **D.** *Zeria sericea* (Pocock, 1897). **E.** *Oltacola gomezi* Roewer, 1932. Abbreviations: a, atrium.

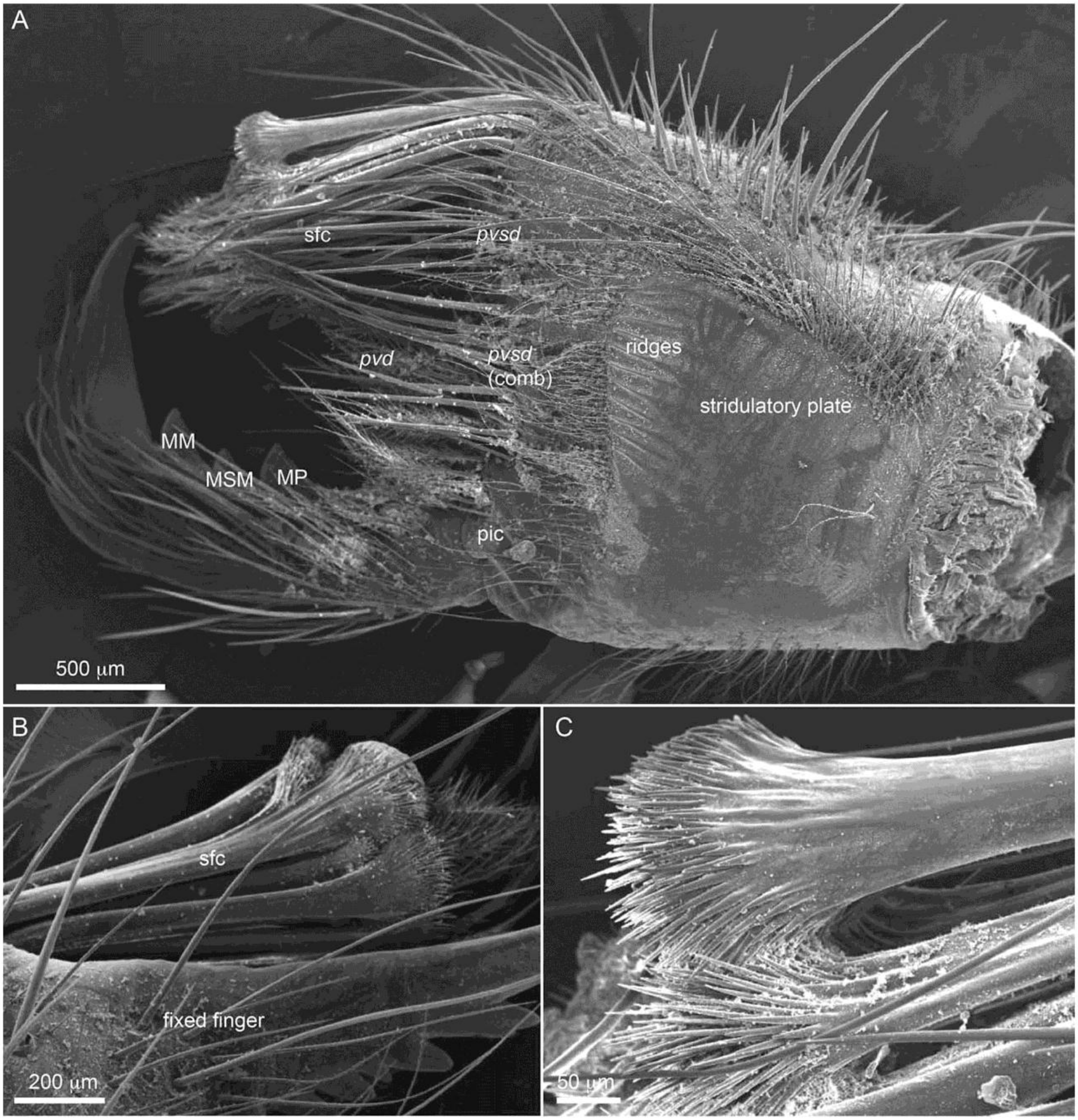

Fig. 23. Gylippidae Roewer, 1933, Lipophaginae Wharton, 1981, *Bdellophaga angulata* Wharton, 1981, ♂ (NMNW 11601), chelicera, prolateral view (**A**) and flagellar complex setae, retrolateral (**B**) and prolateral (**C**) views, indicating stridulatory apparatus and setiform flagellar complex. Abbreviations: MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; *pvsd*, proventral subdistal setae; *pvd*, proventral distal setae (plumose); pic, prolateral interdigital condyle, *sfc*, setiform flagellar complex.

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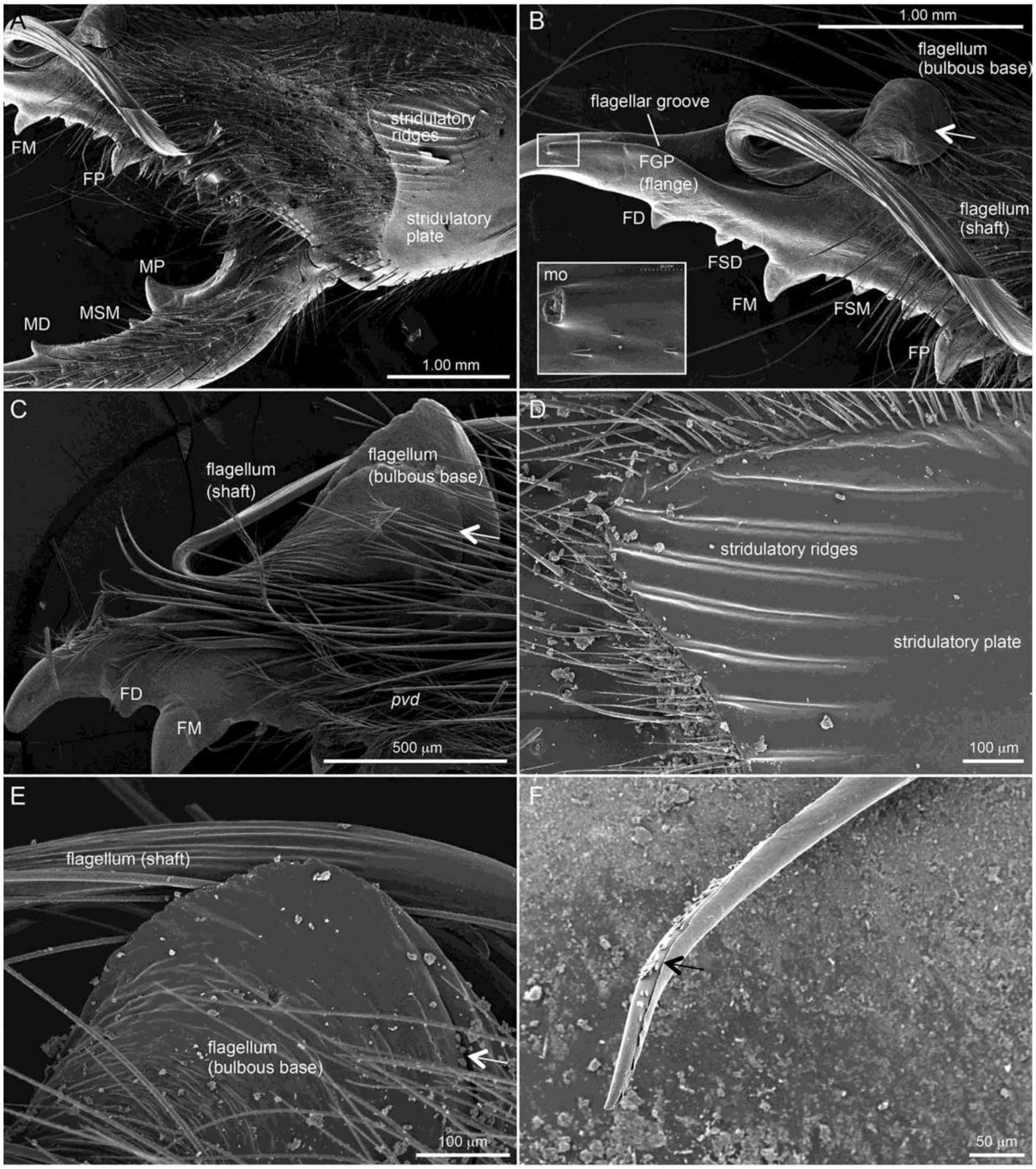


Fig. 24. Solpugidae Leach, 1815, chelicerae and cheliceral fixed (dorsal) fingers, prolateral views (**A, B, D, E**), manus, prolateral view (**C**), and apex of flagellum, prolateral view (**D**), indicating stridulatory organs (**A, D**) and flagellum (**B, C, E, F**). **A, B.** *Solpugiba lineata* (C.L. Koch, 1842), ♂ (NMNW 13814), shaft distorted during processing for scanning electron microscopy. Insert: closeup of mucron organ (mo). **C.** *Zeriassa cuneicornis* (Purcell, 1899), ♂ (NMNW 13883). **D, E.** *Zeria sericea* (Pocock, 1897), ♂ (NMNW 13800), bulbous base. **F.** *Metasolpuga picta* (Kraepelin, 1899), ♂, Namibia: Gobabeb, apex of flagellar shaft. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial teeth; MM, movable finger, distal tooth; MSM, movable finger, submedial tooth; *pvd*, proventral distal setae; mo, mucron organ. Arrows indicate suture in bulbous base (**B, C, E**) and shaft (**F**).

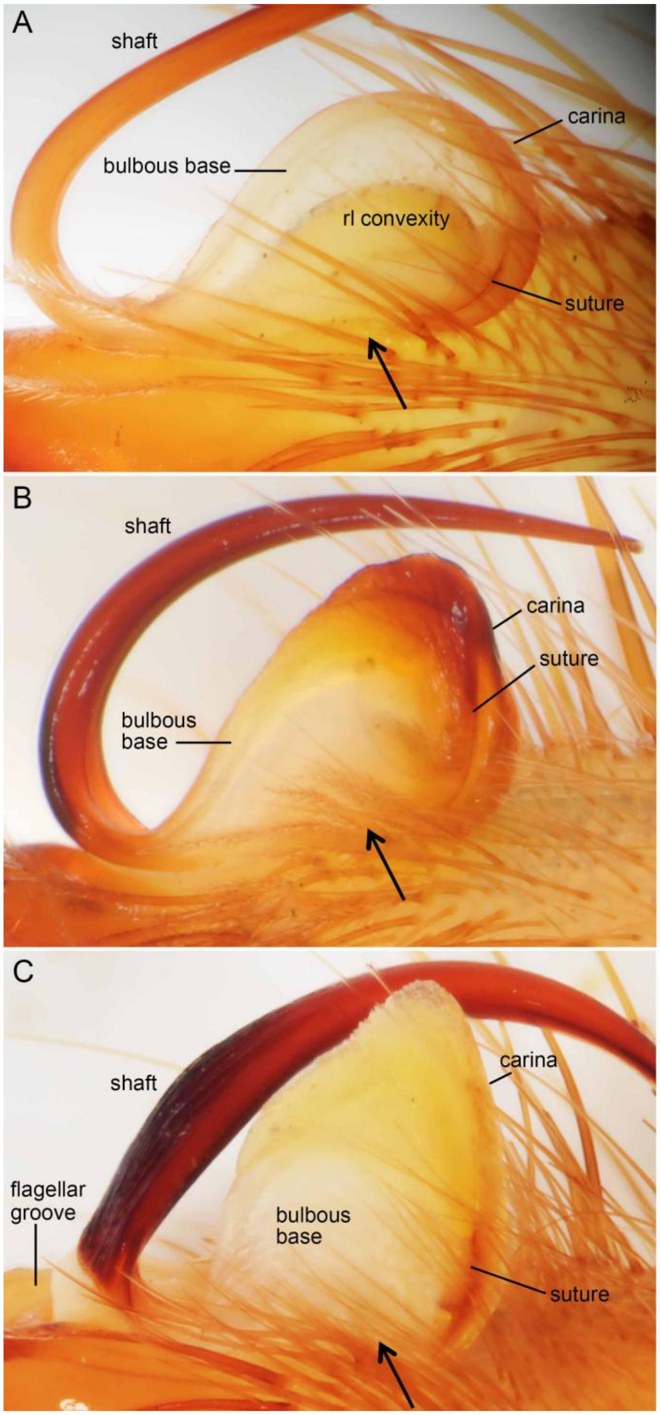


Fig 25. Solpugidae Leach, 1815, cheliceral flagella, prolateral views, indicating detail of bulbous base with smooth (**A, B**) and jagged (**C**) bulbous base carinae. **A.** *Zeria glabricornis* (Lawrence, 1928), ♂ (AMNH [LP 3614]), with retrolateral (rl) convexity visible through transparent bulb. **B.** *Solpugyla* sp., ♂ (AMNH [LP 10764]). **C.** *Solpugema brachyceras* (Lawrence, 1931), ♂ (AMNH [LP 1960B]). Abbreviations: FGP, flagellar groove process; mo, mucron organ. Arrows indicate external opening of alembic canal.

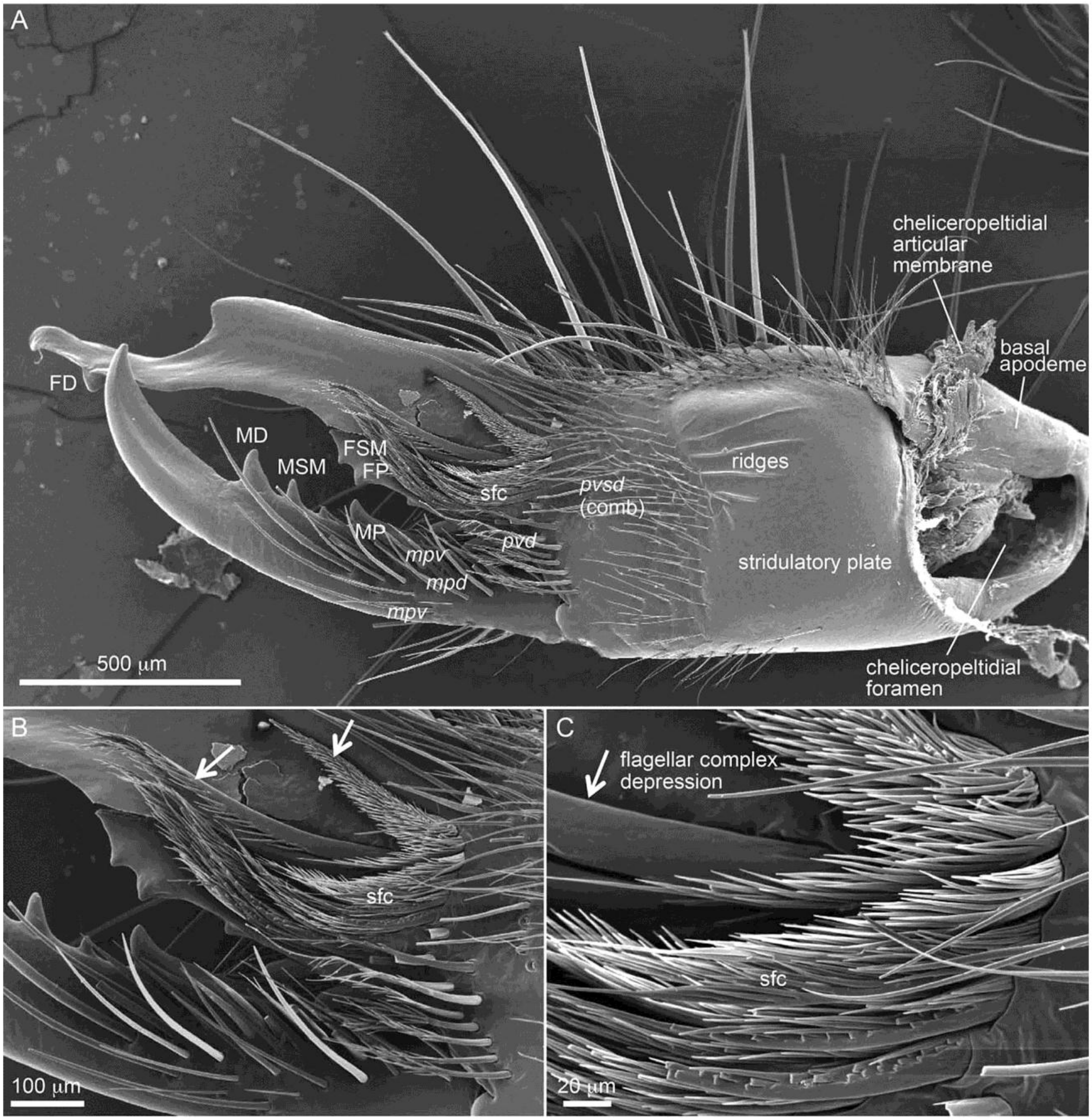


Fig. 26. Melanoblossiidae Roewer, 1933, Melanoblossiinae, *Melanoblossia* sp., ♂ (NMNW 13396), chelicera (**A**) and setiform flagellar complex (**B–C**), prolateral views. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MSM, movable finger, submedial tooth; *mpd*, movable finger prodorsal setae; *mpm*, movable finger promedial setae; *mpv*, movable finger proventral setae; pic, prolateral interdigital condyle; *pvsd*, proventral subdistal setae; *pvd*, proventral distal setae; *sfc*, setiform flagellar complex. Arrows indicate potential setiform flagella.

Plate 1. Galeodidae Sundevall, 1833 (**A**), Solpugidae Leach, 1815 (**B**), Daesiidae Kraepelin, 1899 (**C**), Mummuciidae Roewer, 1934 (**D**), Hexisopodidae Pocock, 1897 (**E**), Rhagodidae Pocock, 1897 (**F**), habitus in life. **A.** *Galeodes* sp., ♀, Turkey: Antalya. **B.** *Zeria sericea* (Pocock, 1897), ♂, Namibia. **C.** *Hemiblossia* sp., ♀, Namibia: Sperrgebiet. **D.** *Gaucha fasciata* Mello-Leitão, 1924, ♂. **E.** *Hexisopus* sp., ♂, Namibia: Gondwana Cañon Park. **F.** *Rhagodopa* sp., ♂, India.

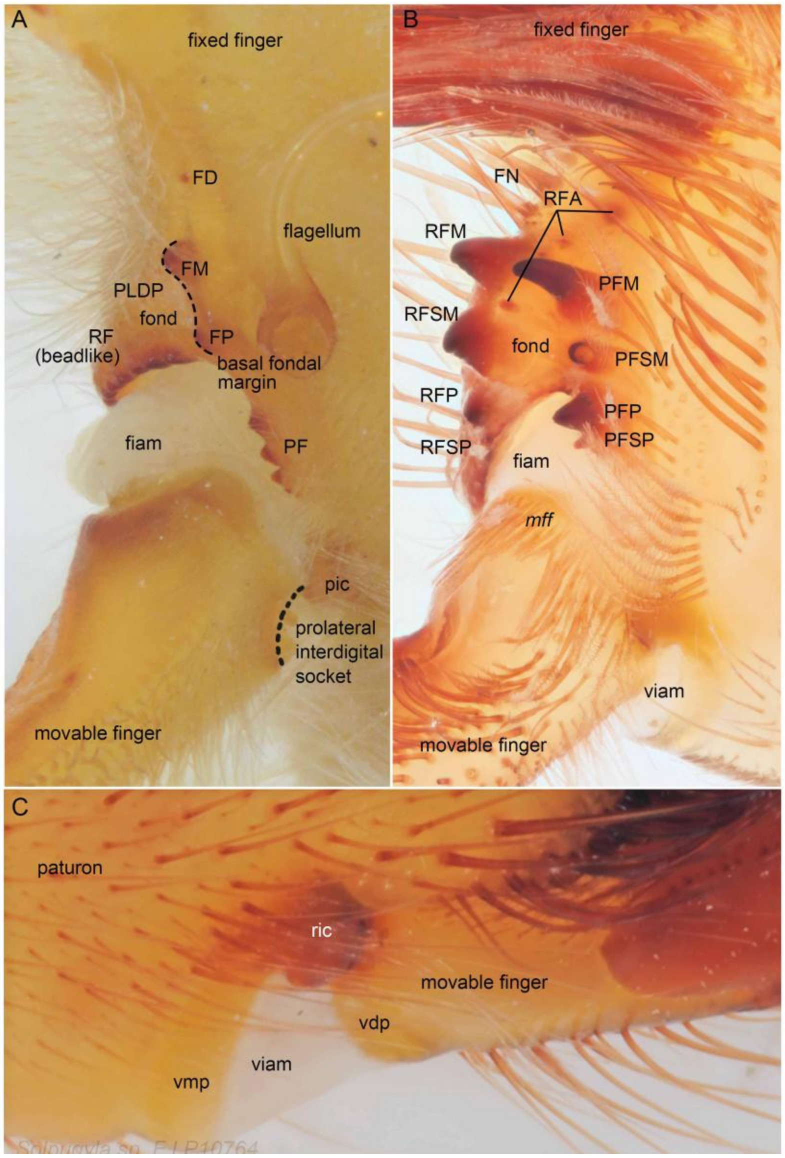


Plate 2. Hexisopodidae Pocock, 1897 (**A**), Eremobatidae Kraepelin, 1899 (**B**), and Solpugidae Leach, 1815 (**C**), cheliceral fond and interdigital articulation site. **A.** *Hexisopus lanatus* (C.L. Koch, 1942), ♂ (NMNW 10795), modified fondal area, prodistal view. **B.** *Eremobates palpisetulosus* Fichter, 1941, ♂ (DMNS ZA.15683), modified fondal area, prodistal view. **C.** *Solpugyla* sp., ♀ (AMNH [LP 10764]), movable finger attachment to paturon, retrolateral view, illustrating ventral interdigital articulation. Stippled line indicates movable finger, prolateral interdigital socket. Abbreviations. FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; PF, profondal teeth; PLDP, prolateral dental process; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFSM, retrofondal submedial tooth; RFP, retrofondal proximal tooth; RFA, retrofondal apical teeth; RFSP, retrofondal subproximal tooth; *mff*, movable finger fondal setae; fiam, fondal interdigital articular membrane; pic, prolateral interdigital condyle; ric, retrolateral interdigital condyle; viam, ventral interdigital articular membrane; vdp, ventral digital plagula; vmp; ventral manus plagula.

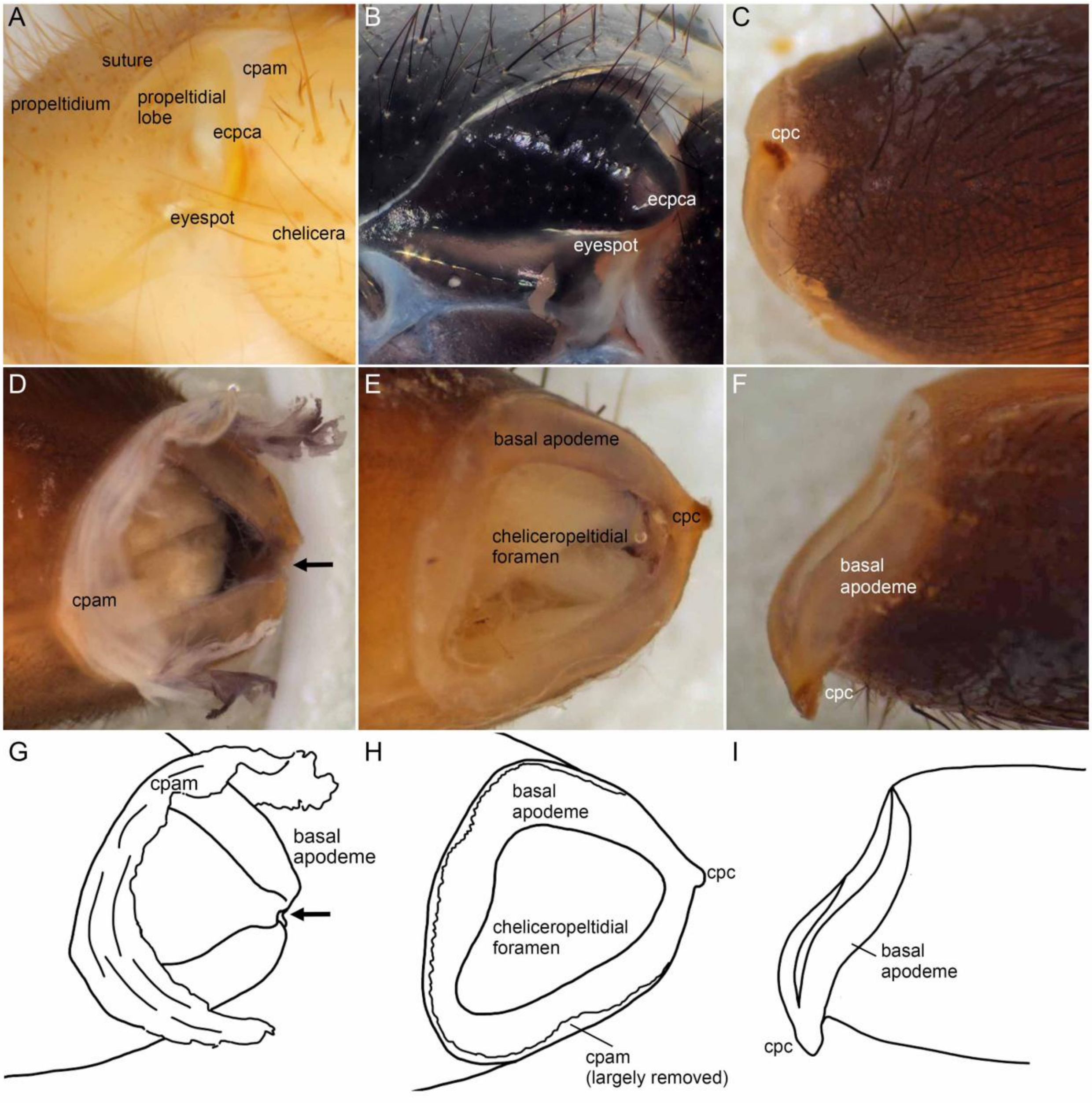


Plate 3. Solpugidae Leach, 1815 (**A**) and Rhagodidae Pocock, 1897 (**B–F**), cheliceropeltidial articulation. **A.** *Zeria lawrencei* (Roewer, 1933), ♀ (NMNW 13820), cheliceral attachment to propeltidium, lateral view. **B–F.** *Rhagodes melanus* (Olivier, 1807), ♂ (NMNW), Israel: Agur Sands, cheliceral attachment to propeltidium, lateral view (**B**) and chelicera removed from propeltidium, retrolateral view, illustrating basal area of articulation (**C**); prolateral view, membrane that connects chelicera to prosoma attached (**D, G**); prolateral proximal view, articular membrane removed, illustrating condyle, cheliceral foramen and basal apodeme (**E, H**); dorsal view, illustrating condyle projecting retrolaterally (**F, I**). Abbreviations: ecpca, external cheliceropeltidial condylar attachment; cpam, cheliceropeltidial articular membrane; cpc, cheliceropeltidial condyle. Arrows indicate position of cpc.

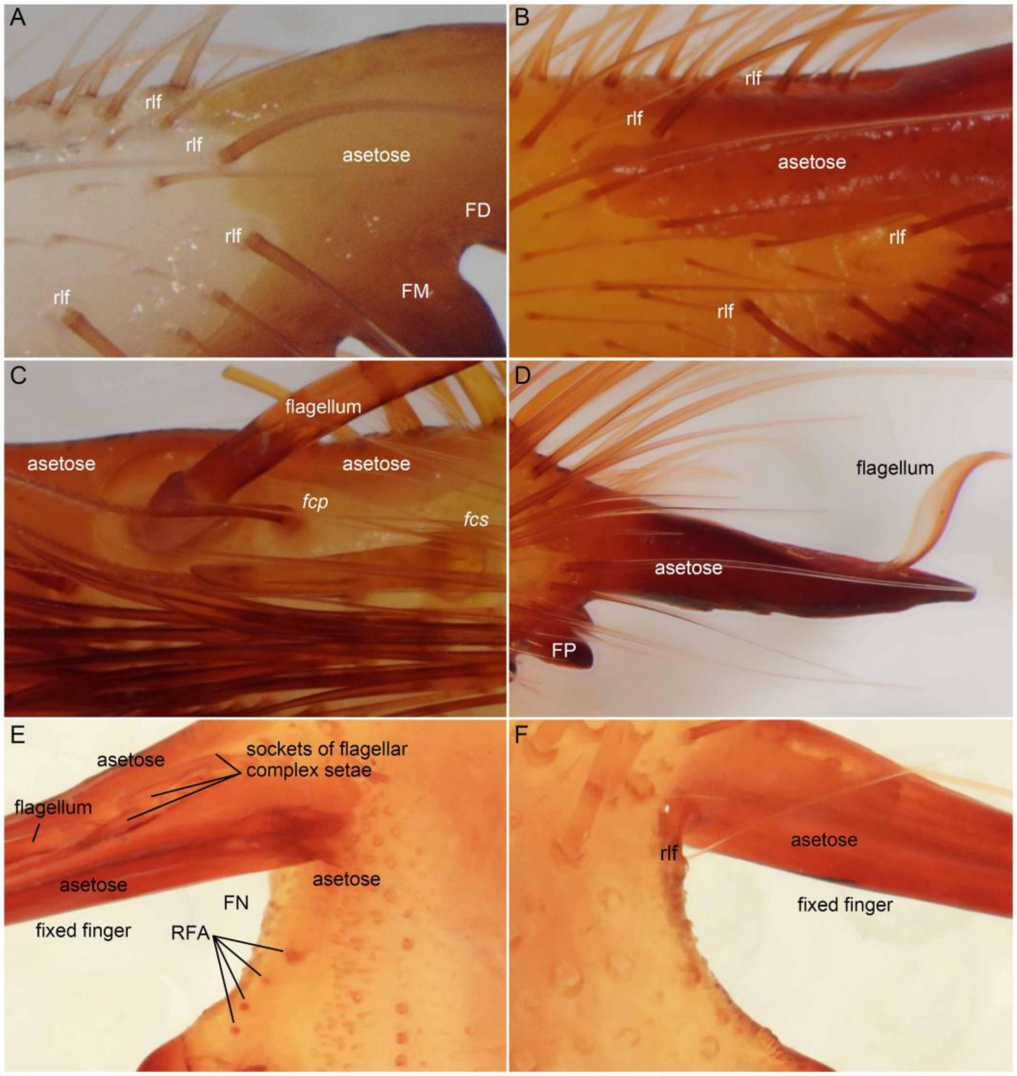


Plate 4. Ceromidae Roewer, 1933 (**A**), Galeodidae Sundevall, 1833 (**B, C**), Gylippidae Roewer, 1933, Gylippinae (**D**), and Eremobatidae Kraepelin, 1899 (**E, F**), cheliceral fixed (dorsal) finger, retrolateral (**A, B, D, F**) and prolateral (**C, E**) views, illustrating asetose area curving around bases of retrolateral finger setae (*rlf*) (**A, B**) or around base of flagellum (**C**), apparent origin of flagellum on asetose area (**D**), and setose area reduced to narrow strip with flagellar complex setae situated therein, and asetose area reduced to narrow strip, situated slightly prolateral in fondal notch (**E**), and with setae situated in fondal notch but not on asetose area (**F**). **A.** *Ceroma inerme* Purcell, 1899, ♀ (AMNH [LP 8425]). **B.** *Galeodes araneoides* (Pallas, 1772), ♀ (AMNH), Turkey: Gurgen. **C.** *Galeodes olivieri* Simon 1879, ♂ (AMNH [LP 4630]). **D.** *Gyllipus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). **E, F.** *Eremobates chihuaensis* Brookhart & Cushing, 2002, holotype ♂ (DMNS ZA.10002). Abbreviations: FD, fixed finger, distal tooth; FN, fondal notch; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; *fcp*, flagellar complex plumose seta(e); *fcs*, flagellar complex spiniform setae; *rlf*, retrolateral finger setae.

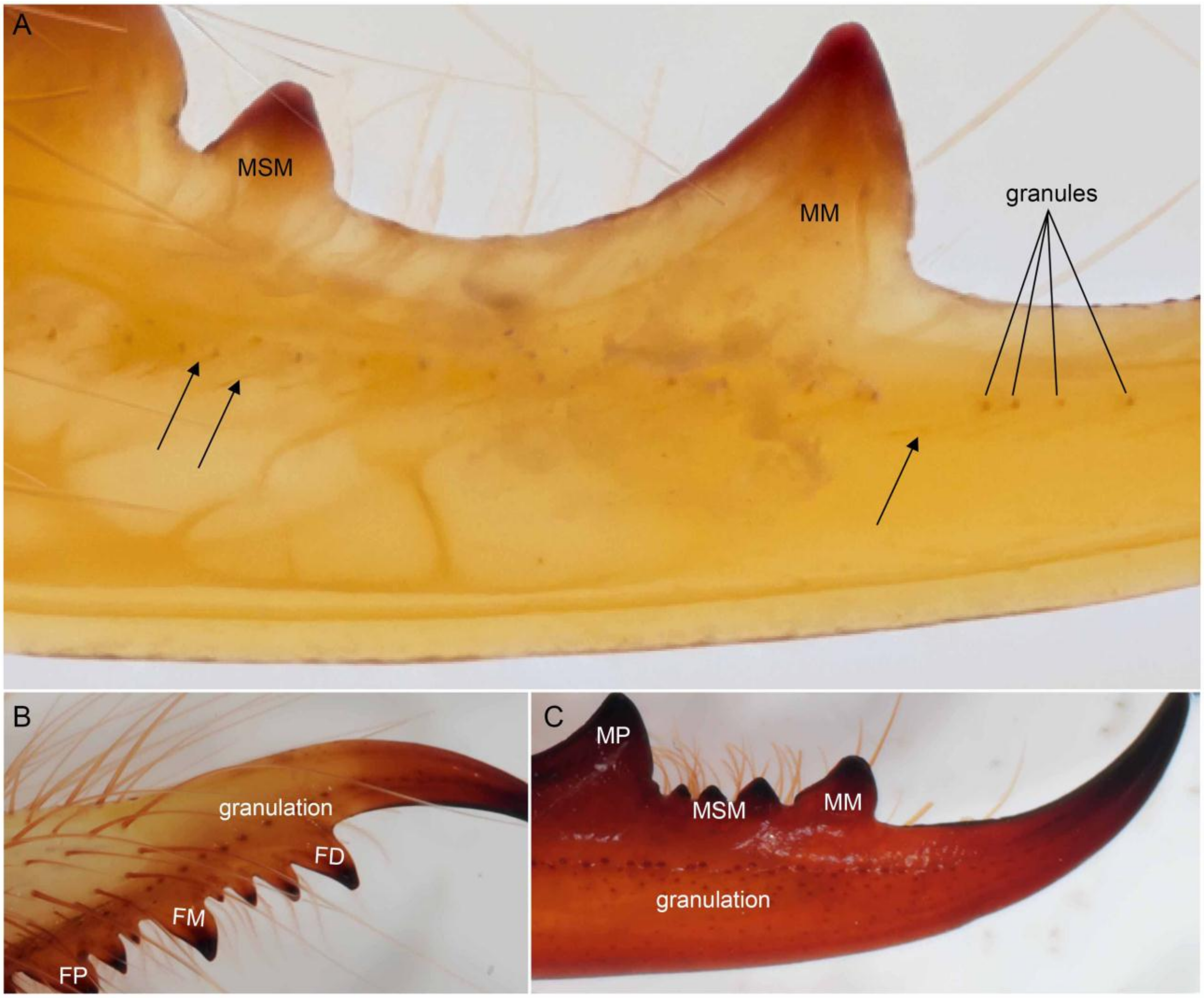


Plate 5. Solpugidae Leach, 1815 (**A**), Daesiidae Kraepelin, 1899 (**B**), and Galeodidae Sundevall, 1833 (**C**), cheliceral fingers, retrolateral views, illustrating asetose areas. **A.** *Metasolpuga picta* (Kraepelin, 1899), subad. ♂, (AMNH), movable (ventral) finger, illustrating fine canals (arrows) terminating in "granules". **B.** *Namibesia pallida* Lawrence, 1962, ♀ (AMNH [LP 4017]), fixed (dorsal) finger, illustrating prominent granular row. **C.** *Galeodes araneoides* (Pallas, 1772), ♀ (AMNH), Turkey: Gurgen, movable finger, illustrating sparse, scattered "granules" in addition to prominent granular row. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth.

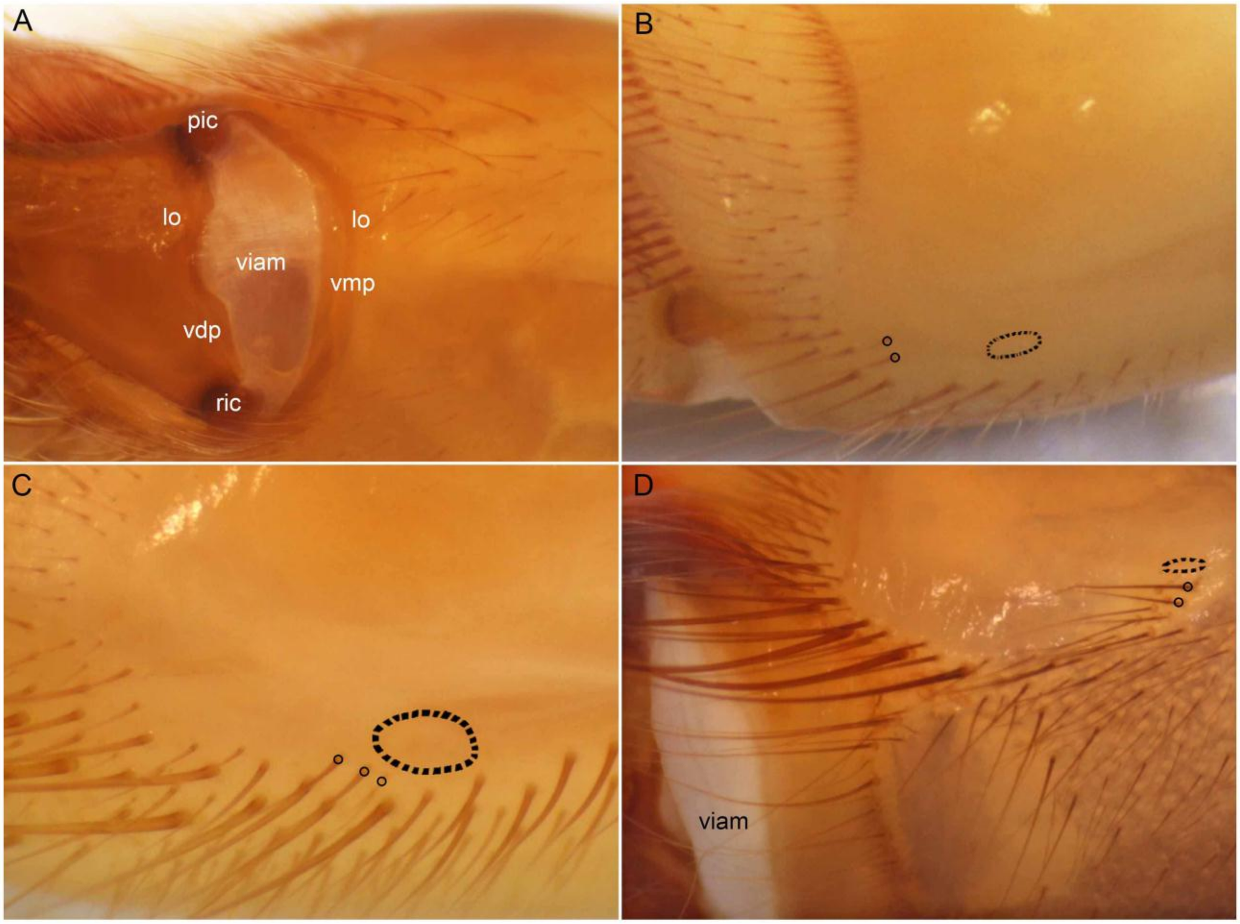


Plate 6. Solpugidae Leach, 1815 (**A, B**), Galeodidae Sundevall, 1833 (**C**), and Rhagodidae Pocock, 1897 (**D**), chelicerae, interdigital articulation, ventral view (**A**), and manus, prolateral views (**B–D**), illustrating putative sensory organs. **A.** *Solpuga chelicornis* Lichtenstein, 1796, ♂ (AMNH [LP 10285]). **B.** *Oparbella* sp., ♂ (MRAC 230.211). **C.** *Galeodes toelgi* Werner, 1922, ♂ (AMNH [LP 7536]). **D.** *Rhagodes melanus* (Olivier, 1807), ♂ (NMNW), Israel: Agur Sands. Dotted lines indicate medioventral organ. Circles indicate sockets of setae probably associated with medioventral organ. Abbreviations: lo, lyriform organ; pic, prolateral interdigital condyle; ric, retrolateral interdigital condyle; viam, ventral interdigital articular membrane; vdp, ventral digital plagula; vmp; ventral manus plagula.

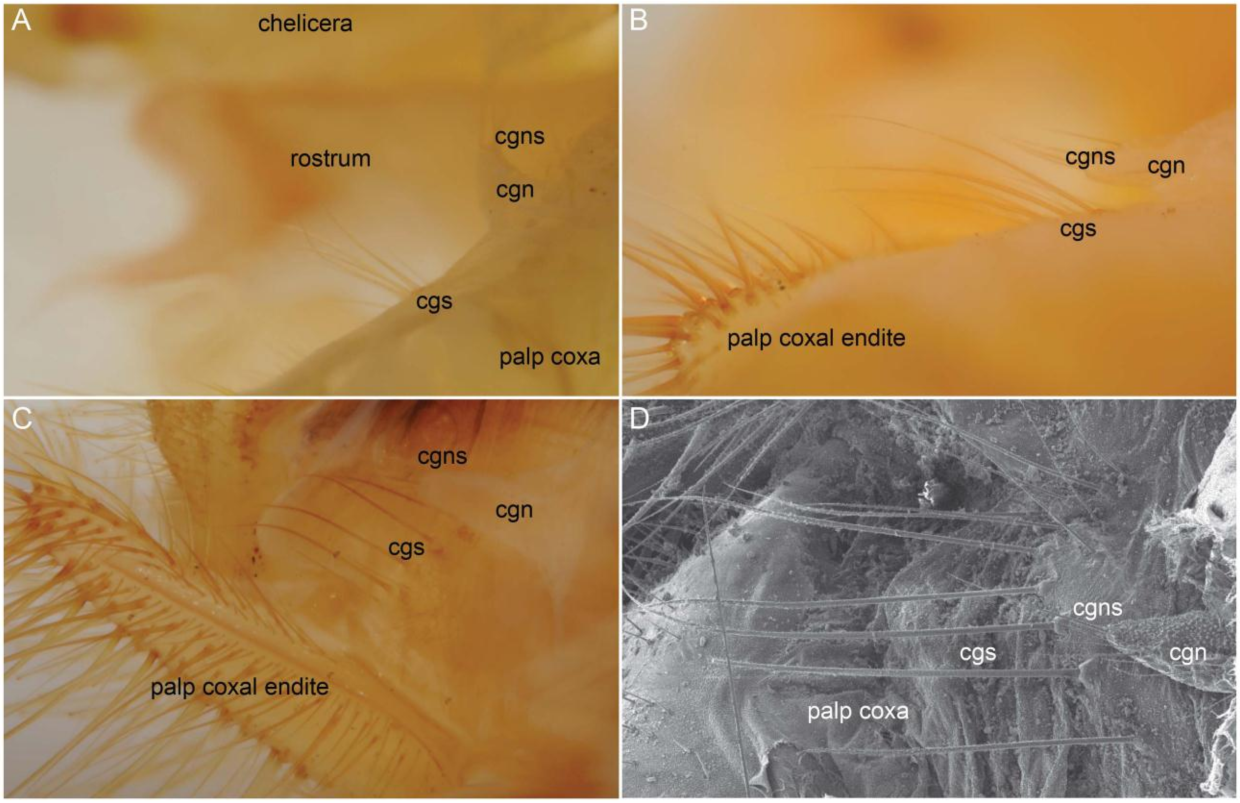


Plate 7. Galeodidae Sundevall, 1833 (**A**), Ceromidae Roewer, 1933 (**B**), Solpugidae Leach, 1815 (**C**), and Gylippidae Roewer, 1933, Lipophaginae Wharton, 1981 (**D**), pedipalpal coxae, dorsal surfaces, lateral (**A, B**) and dorsal (**C, D**) views (anterior at left), illustrating anterodorsal projection of coxal gland papillae and setae, bringing structure in contact with ventral chelicera. **A.** *Paragaleodes pallidus* (Birula, 1890), ♂ (AMNH [LP 3922]). **B.** *Ceroma ornatum* Karsch, 1885, ♂ (MRAC 213.106). **C.** *Solpugema brachyceras* (Lawrence, 1931), ♂ (AMNH [LP 1960B]). **D**. *Bdellophaga angulata* Wharton, 1981, ♂ (NMNW 11601). Abbreviations: cgp, coxal gland nozzle; *cgns*, coxal gland nozzle setae; *cgs*, coxal gland setae.

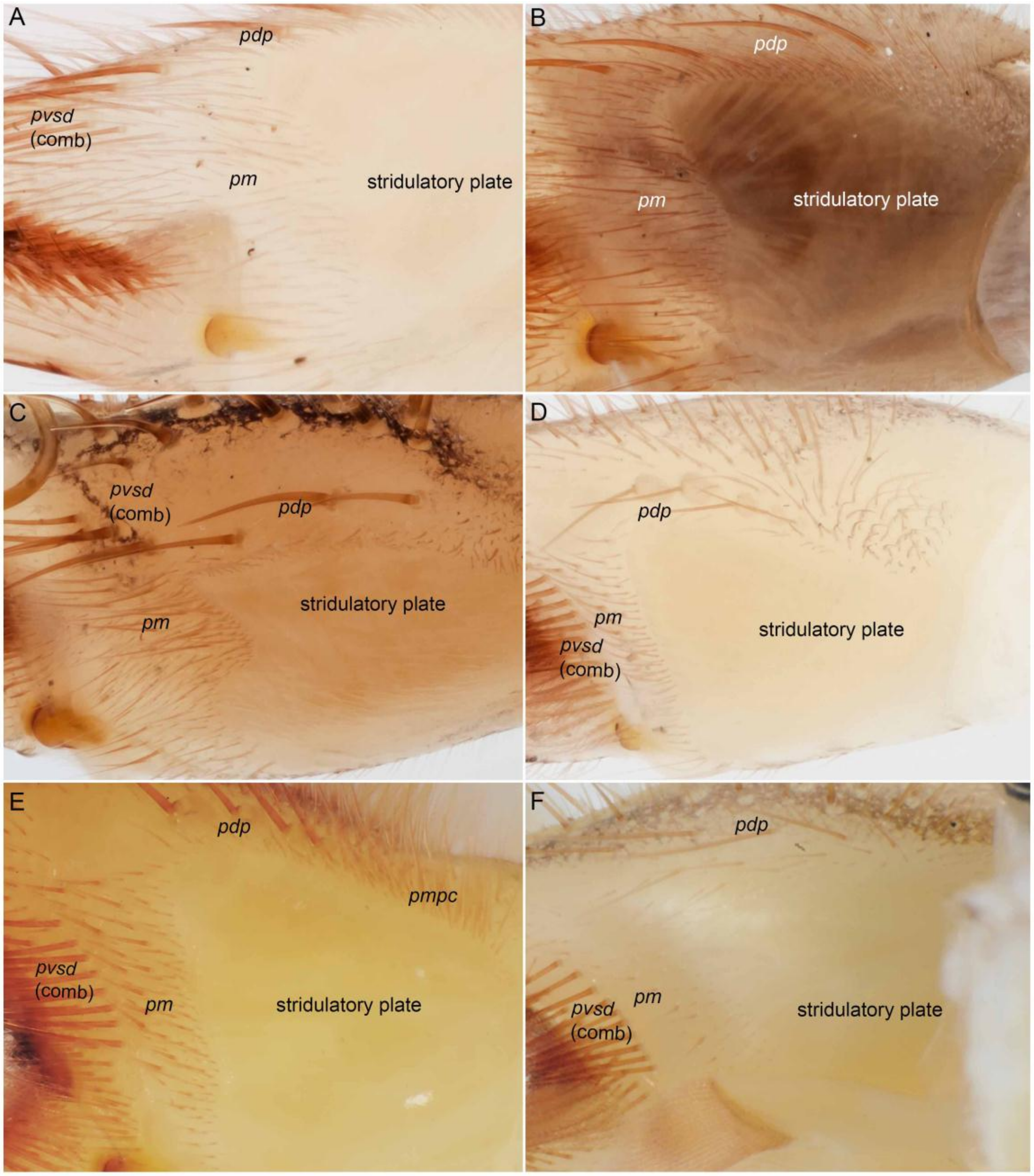


Plate 8. Karschiidae Kraepelin, 1899 (**A–C**), Gylippidae Roewer, 1933, Gylippinae (**D, E**), and Ceromidae Roewer, 1933 (**F**), chelicerae, prolateral views, illustrating differences in stridulatory apparatus with weak to absent ridges, field of promedial setae (*pm*) with unmodified to weakly modified stridulatory setae, prodorsal proximal setae (*pdp*), comb of proventral subdistal setae (*pvsd*) (situated dorsally in **A, C**), and setiform proximal cluster of promedial setae (*pmpc*). **A.** *Eusimonia turkestana* Kraepelin, 1899, ♀ (AMNH [LP 4097]). **B.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♀ (AMNH [LP 7476]). **C.** *Karschia* (*K.*) *tibetana* Hirst, 1907, ♂ (AMNH [LP 7719]). **D.** *Gylippus* (*Anoplogylippus*) *ferganensis* Birula, 1893, juv. (AMNH [LP 3921]). **E.** *Gyllipus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). **F.** *Ceroma inerme* Purcell, 1899, ♂ (AMNH [LP 9864]).

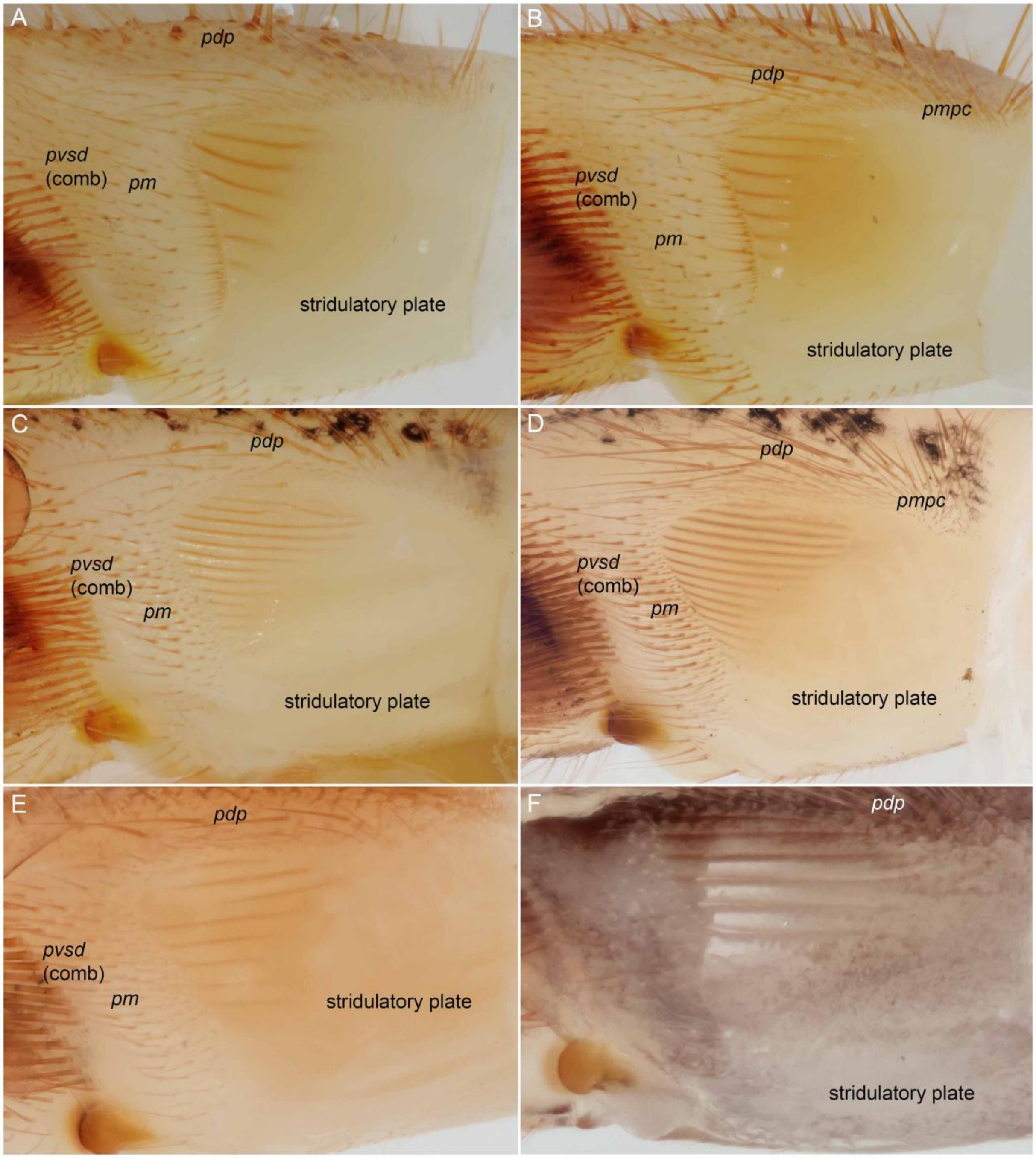


Plate 9. Solpugidae Leach, 1815 (**A, B**) and Daesiidae Kraepelin, 1899 (**C–F**), chelicerae, prolateral views, illustrating stridulatory apparatus with pronounced stridulatory ridges, field of promedial setae (*pm*) with unmodified to weakly modified stridulatory setae, prodorsal proximal setae (*pdp*), comb of proventral subdistal setae (*pvsd*), and setiform proximal cluster of promedial setae (*pmpc*). **A, B.** *Solpugassa furcifera* (Kraepelin, 1899). **A.** ♂ (AMNH [LP 3632]). **B.** ♀ (AMNH [LP 3632]). **C, D.** *Ammotrechelis goetschi* Roewer, 1934. **C.** ♂ (AMNH [LP 10673]). **D.** ♀ (AMNH [LP 10673]). **E.** *Gluviopsilla discolor* (Kraepelin, 1899), ♂ (AMNH [LP 7516]). **F.** *Hemiblossia australis* (Purcell, 1902), ♂ (AMNH [LP 9866]).

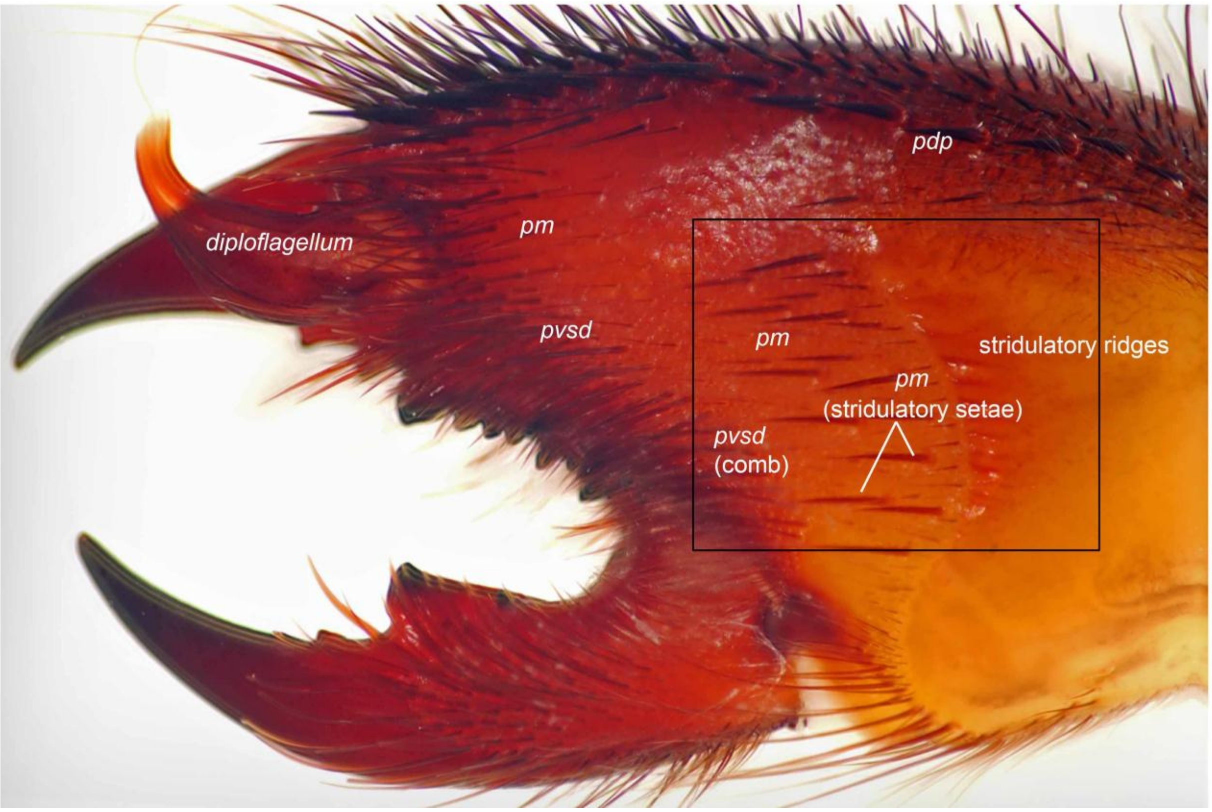


Plate 10. Rhagodidae Pocock, 1897, *Rhagoderma tricolor* Roewer, 1941, ♂ (AMNH [LP 5435]), chelicera, prolateral view, illustrating stridulatory apparatus, comprising stridulatory plate, ridges and stridulatory setae (modified promedial setae). Abbreviations: *pm*, promedial setae (including stridulatory setae); *pdp*, prodorsal proximal setae; *pvsd*, proventral subdistal setae, including comb. Box illustrates approximate area depicted in Pl. 11.

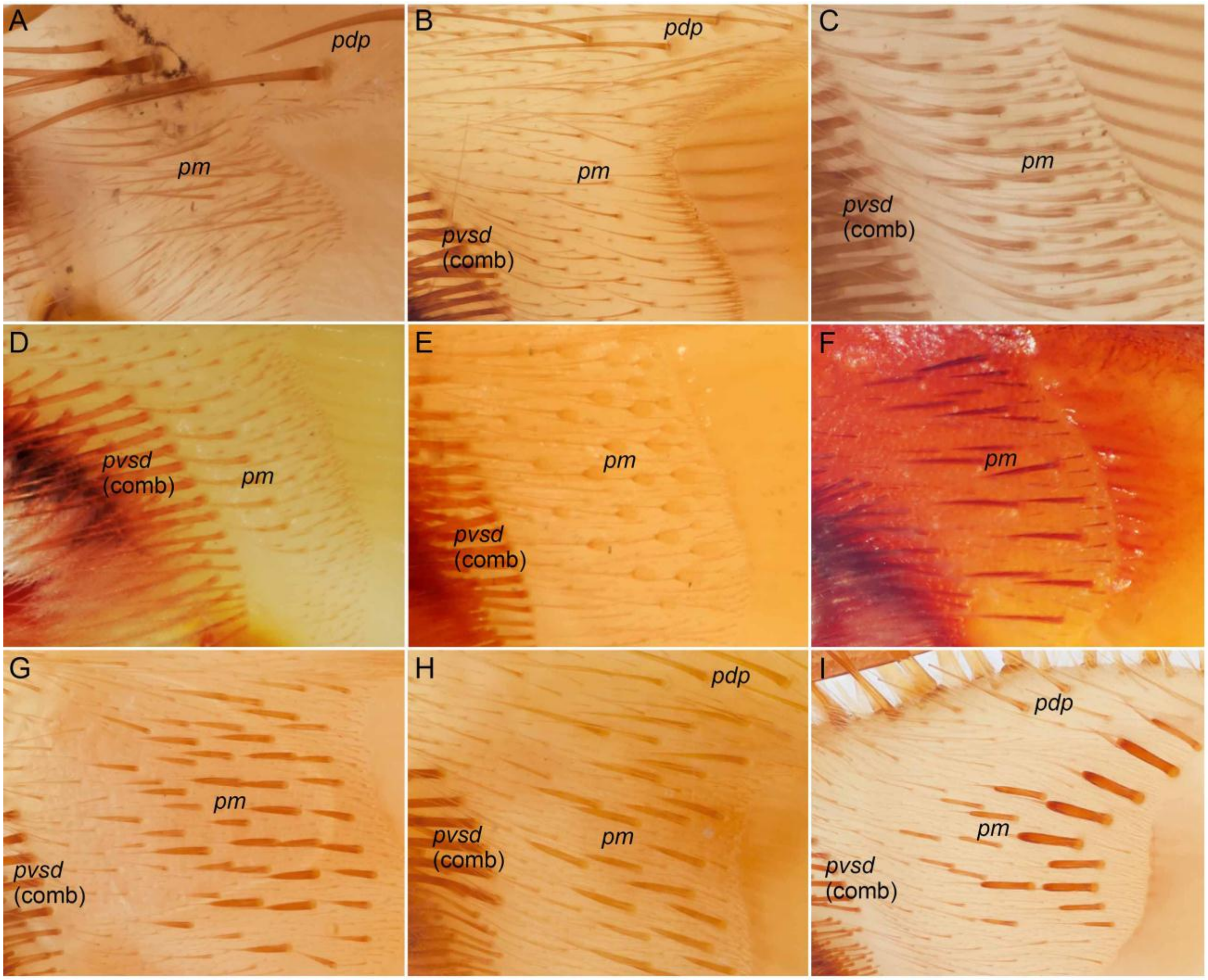


Plate 11. Karschiidae Kraepelin, 1899 (**A**), Solpugidae Leach, 1815 (**B**), Daesiidae Kraepelin, 1899 (**C**), Gylippidae Roewer, 1933, Lipophaginae Wharton, 1981 (**D**), Eremobatidae Kraepelin, 1899 (**E**), Rhagodidae Pocock, 1897 (**F**), and Galeodidae Sundevall, 1833 (**G–I**), chelicerae, prolateral views, illustrating differentiation in stridulatory setae (modified promedial setae). **A.** *Karschia* (*K.*) *tibetana* Hirst, 1907, ♂ (AMNH [LP 7719]). **B.** *Zeria lawrencei* (Roewer, 1933), ♂ (NMNW 13820). **C.** *Ammotrechelis goetschi* Roewer, 1934, ♀ (AMNH [LP 10673]). **D.** *Trichotoma michaelseni* (Kraepelin, 1914), ♂ (AMNH [LP 5724]). **E.** *Eremocosta titania* (Muma, 1951), ♂ (AMNH [LP 5035]). **F.** *Rhagoderma tricolor* Roewer, 1941, ♂ (AMNH [LP 5435]). **G.** *Galeodes toelgi* Werner, 1922, ♂ (AMNH [LP 7536]), type II (*araneoides* type) setae. **H.** *Paragaleodes* sp., ♀ (AMNH [LP 10550]). **I.** *Galeodes* sp., ♂ (AMNH [LP 11204]), type I (*arabs* type) setae. Abbreviations: *pm*, promedial setae (including stridulatory setae); *pdp*, prodorsal proximal setae; *pvsd*, proventral subdistal setae, including comb.

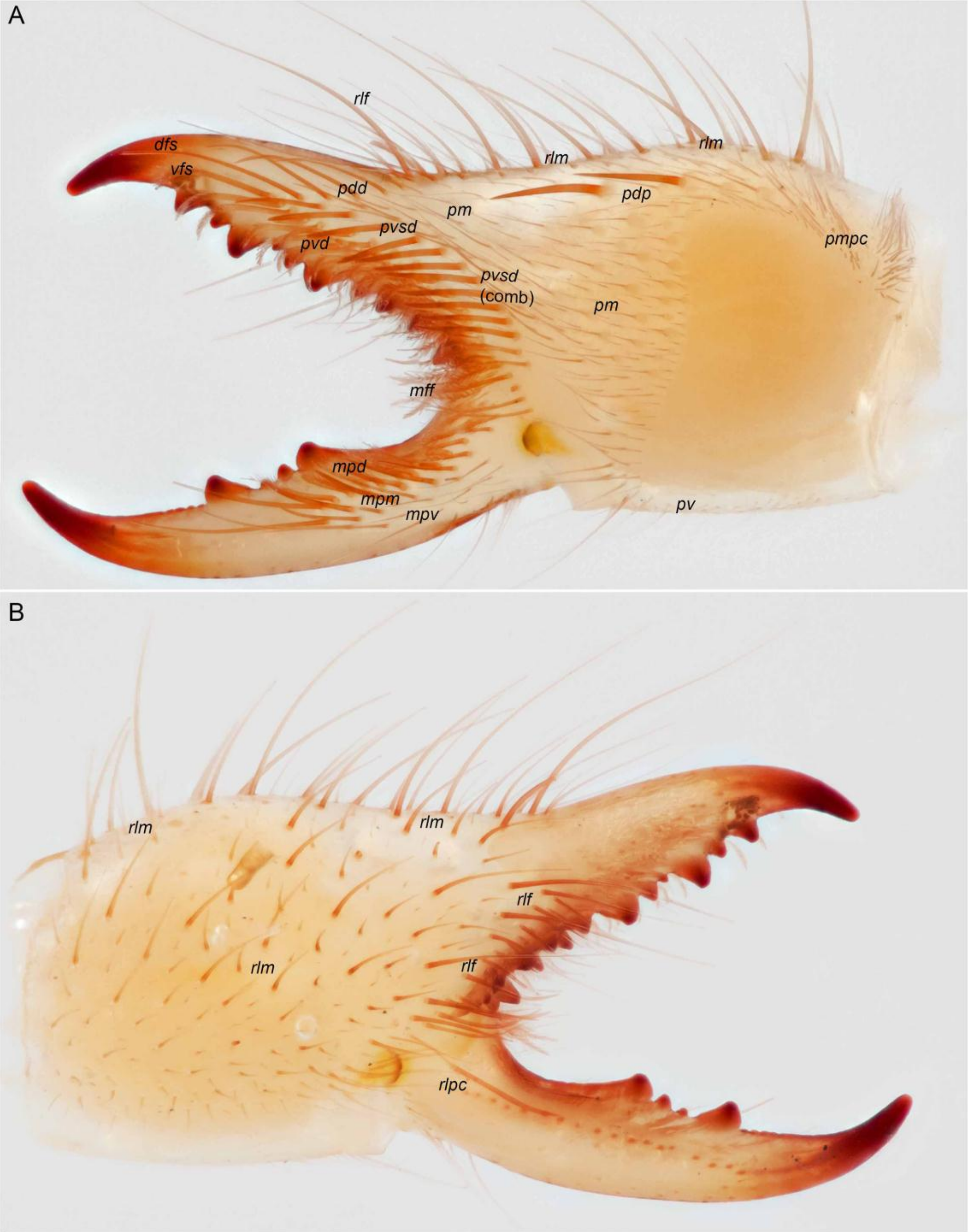


Plate 12. Eremobatidae Kraepelin, 1899, *Hemerotrecha branchi* Muma, 1951, ♀ (DMNS ZA.16786), chelicera, prolateral view, illustrating setal arrangements. Abbreviations: *dfs*, dorsal flagellar seta; *mff*, movable finger, fondal setae; *mpd*, movable finger, prodorsal setae; *mpm*, movable finger, promedial setae; *mpv*, movable finger, proventral setae; *pvd*, proventral distal setae; *pvsd*, proventral subdistal setae; *pdd*, prodorsal distal setae; *pdp*, prodorsal proximal setae; *pm*, promedial setae; *pmpc*, promedial proximal cluster of setae; *pv*, proventral setae; *rlf*, retrolateral finger setae; *rlm*, retrolateral manus setae; v*fs*, ventral flagellar seta..

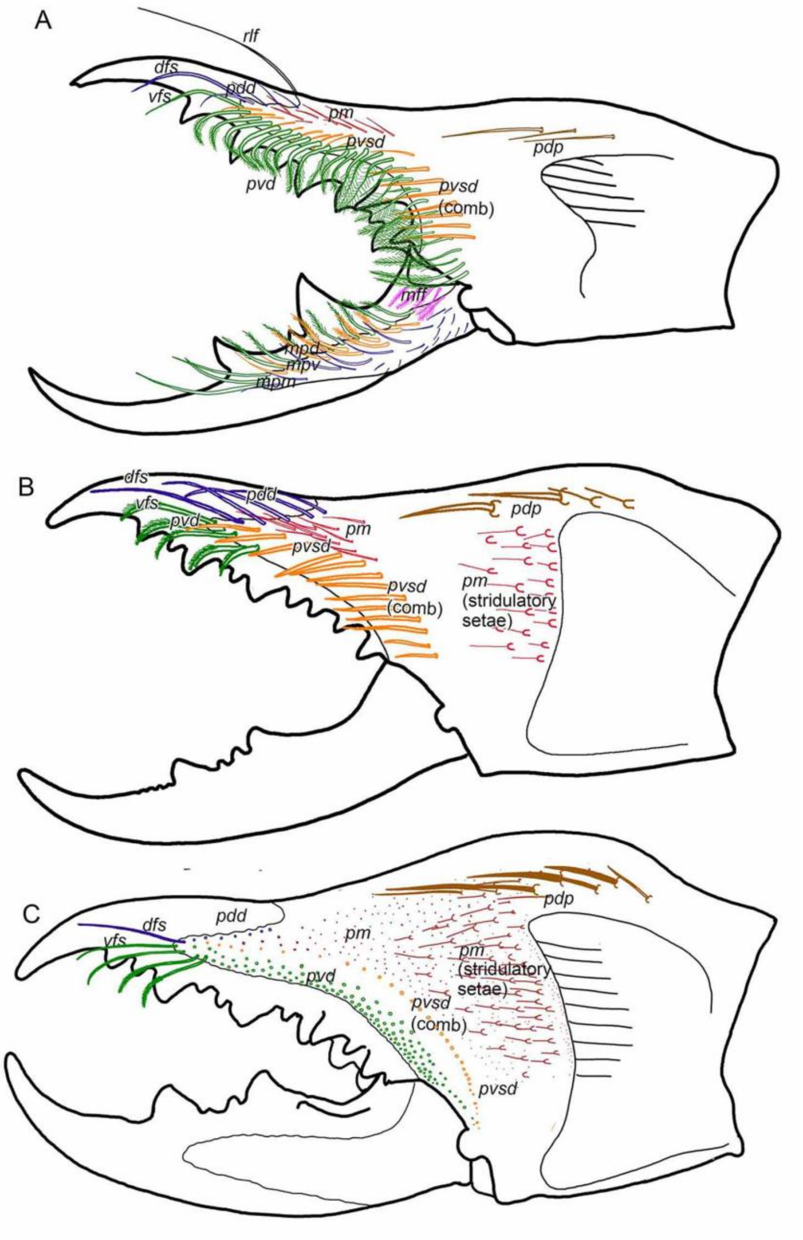


Plate 13. Solpugidae Leach, 1815 (**A**) and Eremobatidae Kraepelin, 1899 (**B, C**), chelicerae, prolateral views, illustrating setal arrangements. **A.** *Prosolpuga schultzei* (Kraepelin, 1908), ♀ (AMNH [LP 3605]). **B.** *Hemerotrecha branchi* Muma, 1951, ♂ (DMNS ZA.16786). **C.** *Eremocosta gigasella* (Muma, 1951), ♀ (DMNS ZA.17350). Selected setae indicated. Circles represent setal sockets. Abbreviations and color coding: *dfs*, dorsal flagellar seta; *mff*, movable finger, fondal setae (magenta); *mpd*, movable finger, prodorsal setae (green); *mpm*, movable finger, promedial setae (orange); *mpv*, movable finger, proventral setae (blue); *pdd*, prodorsal distal setae (blue); *pdp*, prodorsal proximal setae (brown); *plpc*, prolateral proximal cluster of setae; *pm*, promedial setae (maroon); *pv*, proventral setae; *pvd*, proventral distal setae (green); *pvsd*, proventral subdistal setae (orange); *rlf*, retrolateral finger setae; v*fs*, ventral flagellar seta.

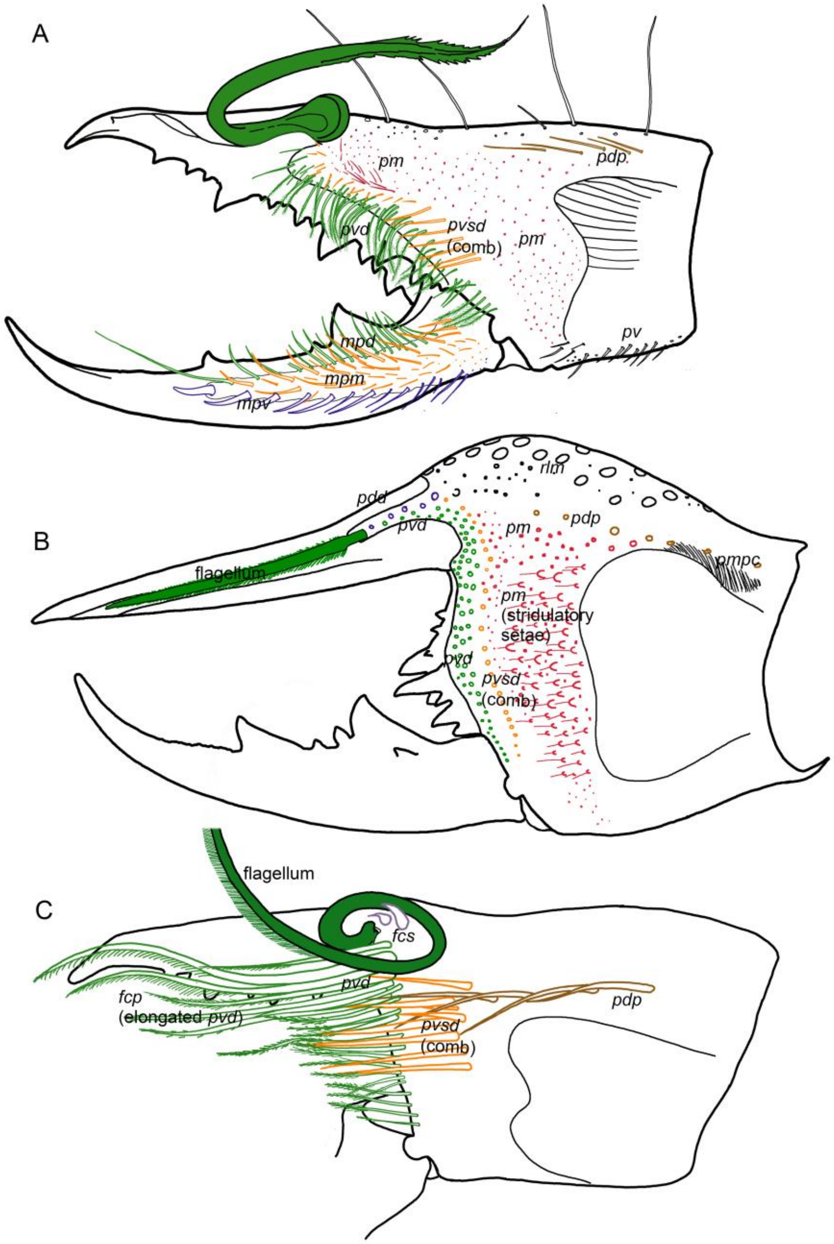


Plate 14. Solpugidae Leach, 1815 (**A**), Eremobatidae Kraepelin, 1899 (**B**), and Karschiidae Kraepelin, 1899 (**C**), chelicerae, prolateral views, illustrating setal arrangements. **A.** *Solpugiba lineata* (C.L. Koch, 1842), ♂ (AMNH [LP 5919]). **B.** *Eremobates gerbae* Brookhart & Cushing, 2002, holotype ♂ (DMNS ZA.10000)**. C.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♂ (AMNH [LP 7474]), illustrating elongated distal *pvsd* setae (= *fcp*). Selected setae indicated in **B** and **C**. Circles represent setal sockets. Abbreviations and color coding: *dfs*, dorsal flagellar seta; *mpd*, movable finger, prodorsal setae (green); *mpm*, movable finger, promedial setae (orange); *mpv*, movable finger, proventral setae (blue); *pdd*, prodorsal distal setae (blue); *pdp*, prodorsal proximal setae (brown); *plpc*, prolateral proximal cluster of setae; *pm*, promedial setae (maroon); *pv*, proventral setae; *pvd*, proventral distal setae (green); *pvsd*, proventral subdistal setae (orange); *rlm*, retrolateral manus setae..

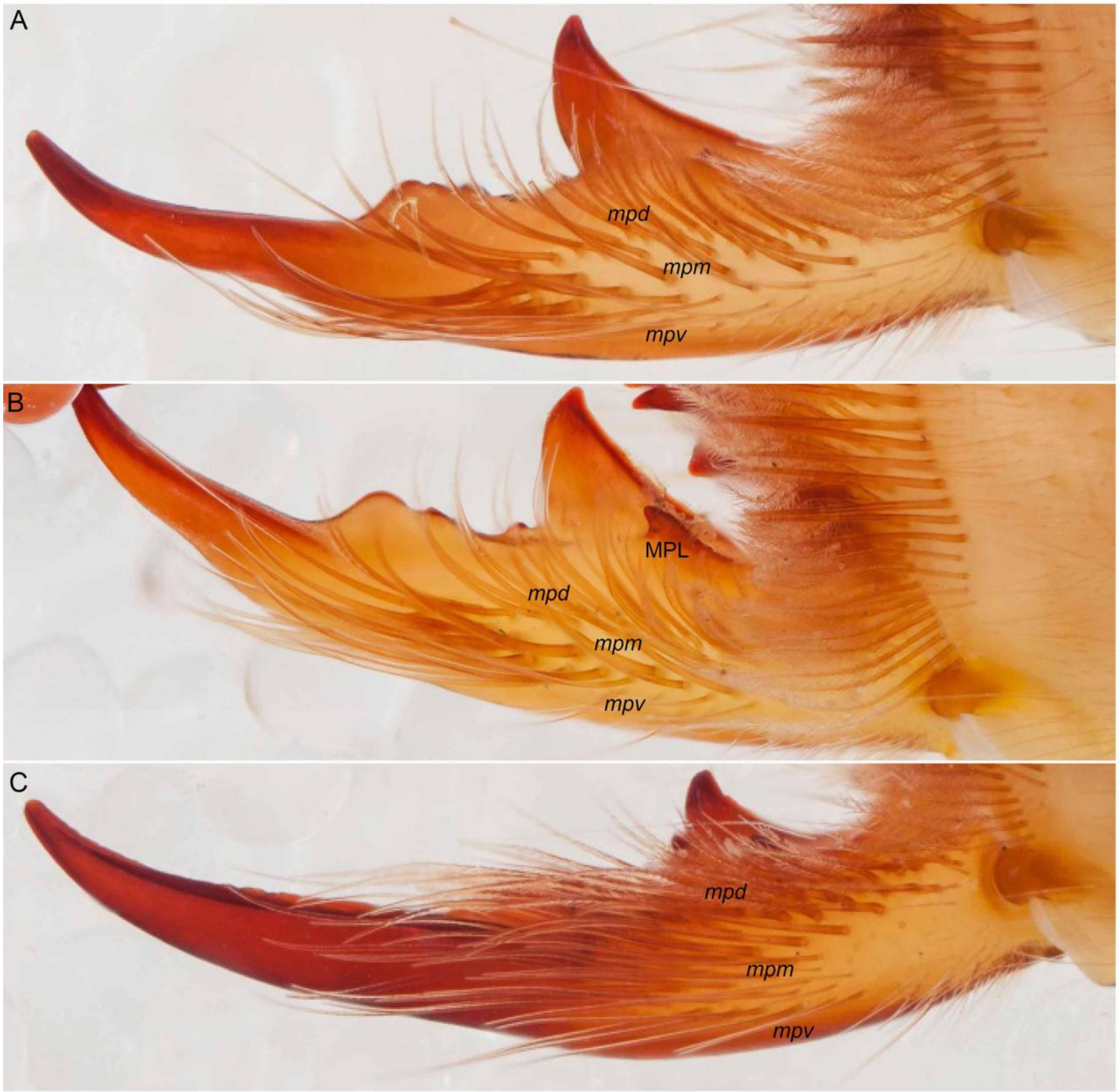


Plate 15. Eremobatidae Kraepelin, 1899, cheliceral movable fingers, prolateral views, illustrating arrangement and differentiation of setae. **A.** *Eremobates bixleri* Muma & Brookhart, 1988, paratype ♂ (DMNS ZA.17386). **B.** *Eremobates ajoanus* Muma & Brookhart, 1988, paratype ♂ (DMNS ZA.17311). **C.** *Eremobates angustus* Muma, 1951, paratype ♂ (DMNS ZA.16788). Abbreviations: *mpd*, movable finger, prodorsal setae; *mpm*, movable finger, promedial setae; *mpv*, movable finger, proventral setae.

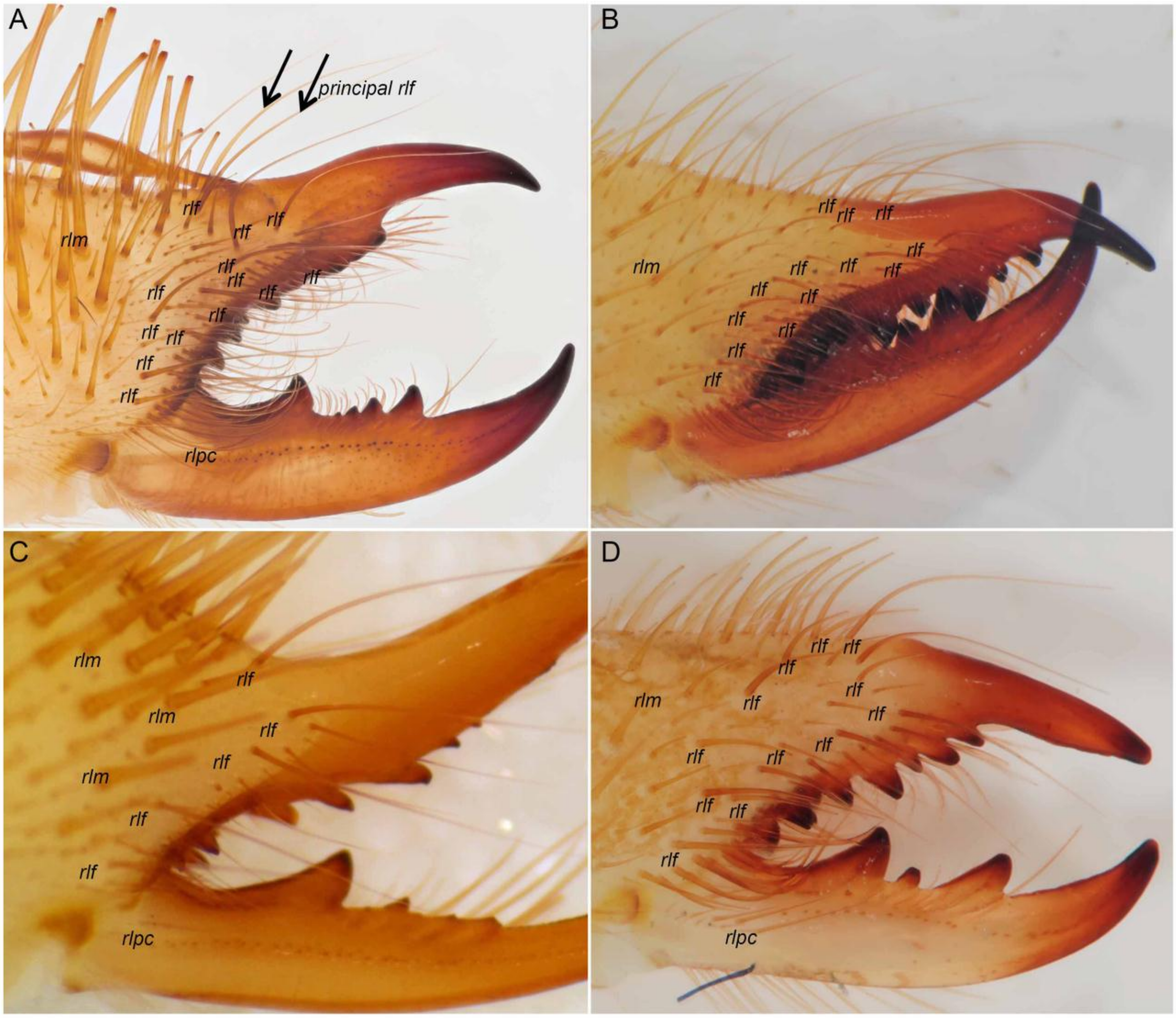


Plate 16. Galeodidae Sundevall, 1833 (**A, B**), Eremobatidae, Kraepelin, 1899 (**C**) and Ammotrechidae Roewer, 1934 (**D**), chelicerae, retrolateral views, illustrating setae. **A.** *Galeodes toelgi* Werner, 1922, ♂ (AMNH [LP 3536]). **B.** *Galeodes olivieri* Simon, 1879, ♀ (AMNH [LP 4628]). **C.** *Chanbria regalis* Muma, 1951, ♂ (AMNH [LP 10746]). **D.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). Abbreviations: *rlf*, retrolateral finger setae; *rlm*, retrolateral manus setae; *rlpc*, retrolateral proximal cluster of setae.

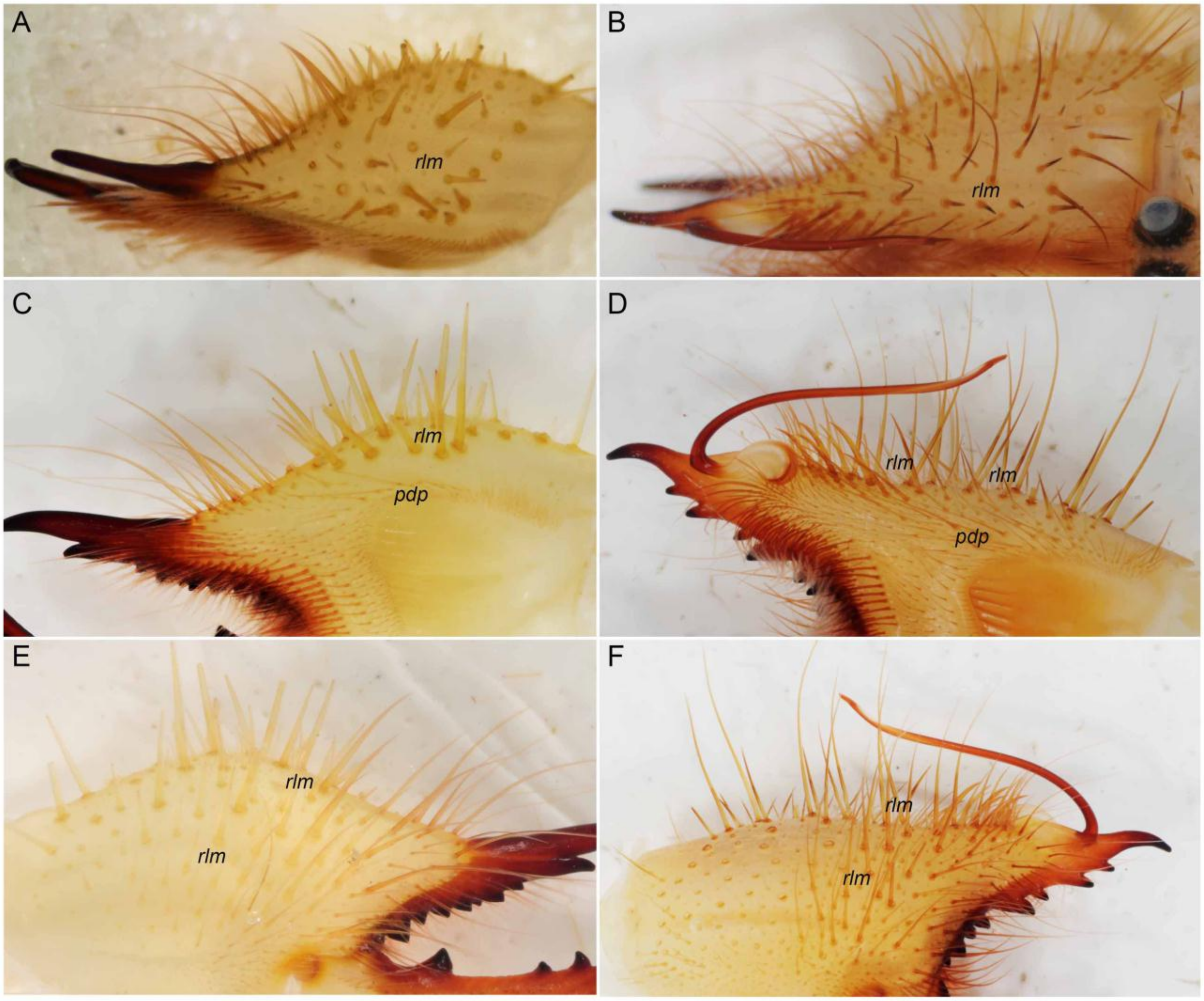


Plate 17. Gylippidae Roewer, 1933, Lipophaginae Wharton, 1981 (**A, C, E**) and Solpugidae Leach, 1815 (**B, D, F**), chelicera, dorsal (**A, B**), prolateral (**C, D**) and retrolateral (**E, F**) views, illustrating dorsal setae resembling retrolateral setae, arranged in row along prodorsal edge of chelicera, lining chelicera proximally. **A, C, E.** *Trichotoma michaelseni* (Kraepelin, 1914), ♂ (AMNH [LP 5724]), Namibia: Namib-Naukluft Park, Garub. **B, D, F.** *Zeria lawrencei* (Roewer, 1933), ♂ (AMNH [LP 9906]).

Plate 18. Rhagodidae Pocock, 1897 (**A, B**), Galeodidae Sundevall, 1833 (**C, D**), Eremobatidae Kraepelin, 1899 (**E, F**), Gylippidae Roewer 1933, Gylippinae (**G, H**), and Lipophaginae Wharton, 1981 (**I, J**), and Ceromidae Roewer, 1933 (**K, L**), cheliceral movable fingers, retrolateral views, illustrating retrolateral proximal cluster (*rlpc*) of setae and asetose area. **A, B.** *Rhagodes melanus* (Olivier, 1807), ♂ (AMNH [LP 2293]). **C, D.** *Galeodes toelgi* Werner, 1922, ♂ (AMNH [LP 7536]). **E, F.** *Eremobates corpink* Brookhart & Cushing, 2004, paratype ♀ (DMNS ZA.17379). **G, H.** *Gyllipus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). **I, J.** *Trichotoma michaelseni* (Kraepelin, 1914), ♂ (AMNH [LP 5724]). **K, L.** *Ceroma ornatum* Karsch, 1885, ♂ (MRAC 213.106).

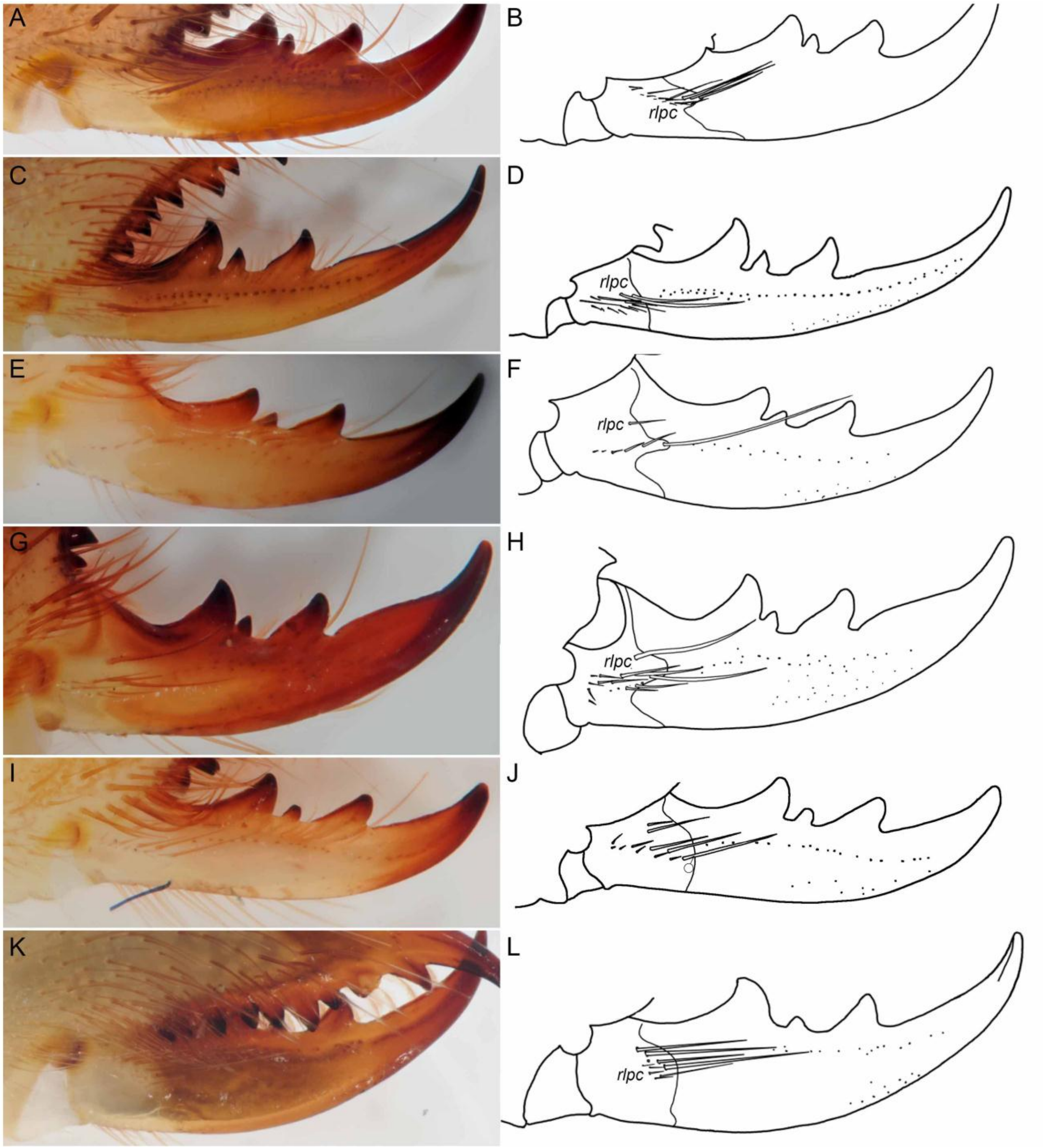


Plate 19. Solpugidae Leach, 1815 (**A, B**), Daesiidae Kraepelin, 1899. (**C–H**), Ammotrechidae Roewer, 1934 (**I, J**), and Mummuciidae Roewer, 1934 (**K, L**), cheliceral movable fingers, retrolateral views, illustrating retrolateral proximal cluster (*rlpc*) of setae and asetose area. **A, B.** *Solpugyla* sp., ♀ (AMNH [LP 10764]). **C, D.** *Namibesia pallida* Lawrence, 1962, ♀ (AMNH [LP 4017]). **E, F.** *Blossia grandicornis* Lawrence, 1929, ♂ (AMNH [LP 5905]). **G, H.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]). **I, J.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). **K, L.** *Gaucha fasciata* Mello-Leitão, 1924, ♂ (AMNH [LP 5858]).

Plate 20. Solpugidae Leach, 1815, cheliceral fixed (dorsal) finger mucra, prolateral views, indicating mucron organ (mo) and different manifestations of flagellar groove process (FGP). **A** *Metasolpuga picta* (Kraepelin, 1899), ♂ (AMNH [LP 10719]). **B.** *Zeria carli* (Roewer, 1933), ♂ (AMNH [LP 7915]). **C.** *Zeria venator* (Pocock, 1897), ♂ (AMNH [LP 5952]). **D.** *Solpuga chelicornis* Lichtenstein, 1796, ♂ (AMNH [LP 8158]). **E.** *Solpugista bicolor* (Lawrence, 1953), ♂ (AMNH [LP 7933]). **F.** *Solpugema genucornis* (Lawrence, 1935), ♂ (AMNH [LP 8167]). **G.** *Solpugema hamata* (Hewitt, 1914), ♂ (TM 6632). **H.** *Solpugema brachyceras* (Lawrence, 1931), ♂ (AMNH [LP 1960B]). Abbreviations: FD, fixed finger distal tooth; FGP, flagellar groove process; FST, fixed finger subterminal flange; mo, mucron organ.

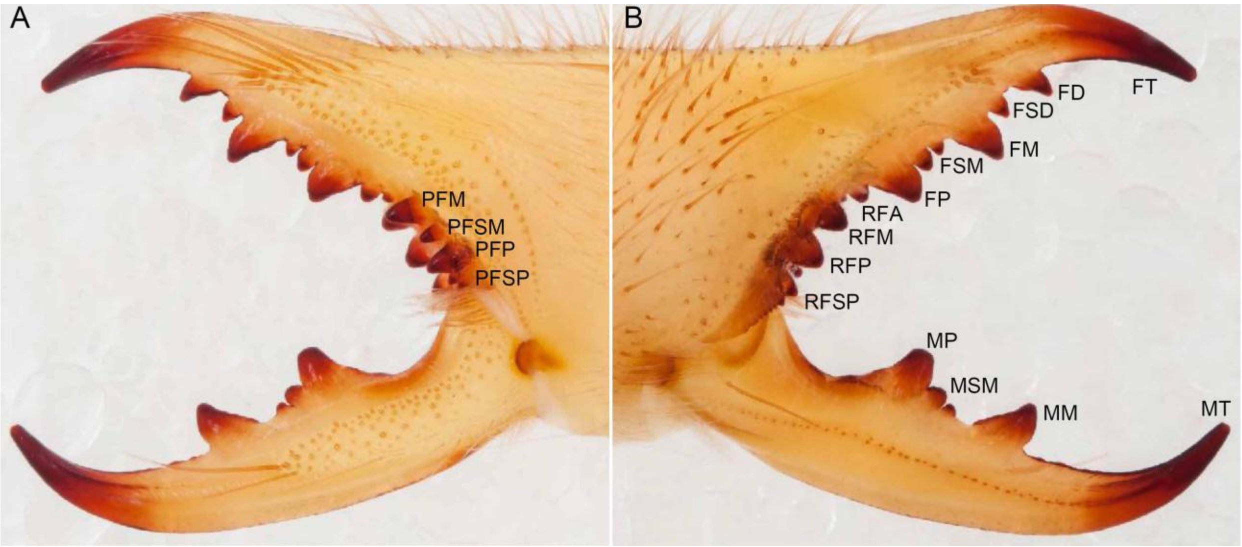


Plate 21. Eremobatidae Kraepelin, 1899, *Eremobates polhemusi* Muma & Brookhart, 1988, ♀ (DMNS ZA.10004), chelicera, prolateral (**A**) and retrolateral (**B**) views, indicating primary, secondary and fondal teeth. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial teeth; FT, fixed finger, terminal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MPL, movable finger, prolateral tooth; MSM, movable finger, submedial teeth; MT, movable finger, terminal tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal.

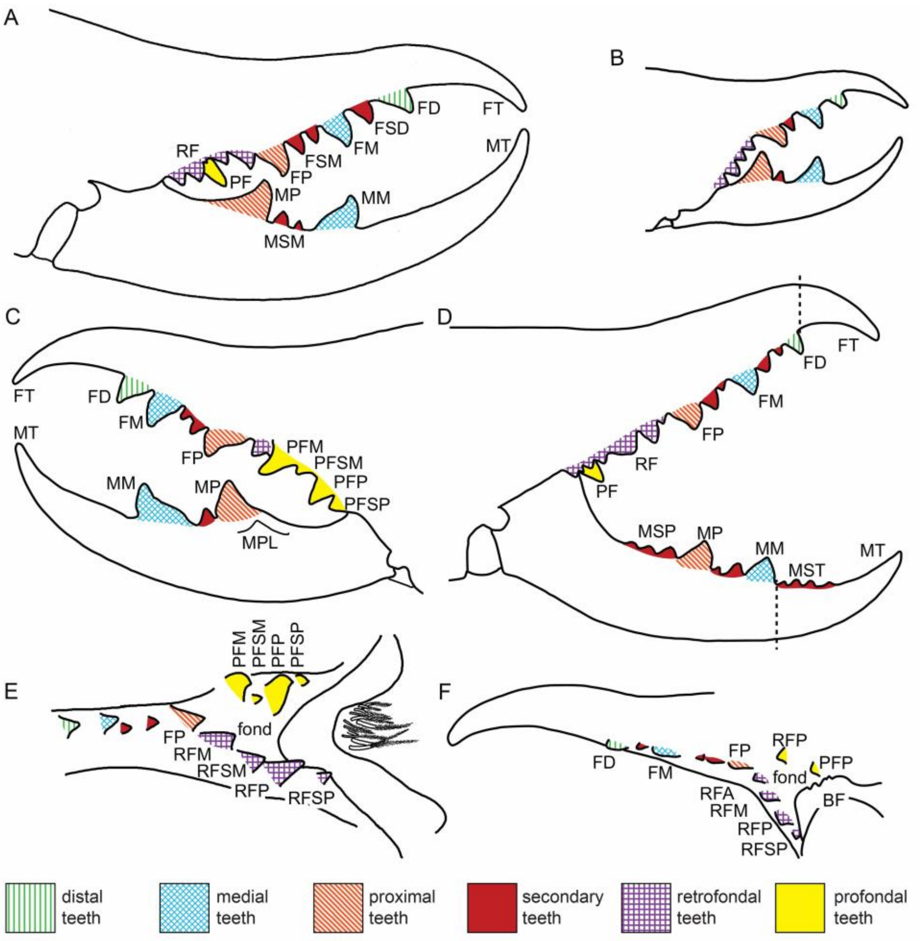


Plate 22. Ammotrechidae Roewer, 1934 (**A**), Solpugidae Leach, 1815 (**B, C, E**), Karschiidae Kraepelin, 1899 (**D**), and Galeodidae Sundevall, 1833 (**F**), chelicerae, prolateral views (**A–D**), and fixed (dorsal) finger, ventral views (**E, F**), indicating terminological abbreviations and color coding for dentition applied in text. **A.** *Sedna pirata* Muma, 1971, ♀ (AMNH [LP 2362]). **B.** *Zeria lawrencei* (Roewer, 1933), ♀ (NMNW 13820). **C.** *Solpugassa furcifera* (Kraepelin, 1899), ♀ (AMNH [LP 3632]). **D.** *Barrussus pentheri* (Werner, 1905), juv. (AMNH [LP 10693]). **E.** *Zeria sericea* (Pocock, 1897), ♂ (NMNW 13801). **F.** *Paragaleodes pallidus* (Birula, 1890), ♂ (AMNH [LP 3922]). Abbreviations: BF, basifondal teeth; FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth/ teeth; FSM, fixed finger, submedial tooth/teeth; FT, fixed finger, terminal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MPL, movable finger, prolateral tooth; MSM, movable finger, submedial tooth/teeth; MSP, movable finger, subproximal tooth/teeth; MST, movable finger, subterminal teeth; PF, profondal teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal. Mucra indicated distal to dotted horizontal lines in (**A**) and (**D**). Typical conserved or putatively plesiomorphic dentition pattern in **B**.

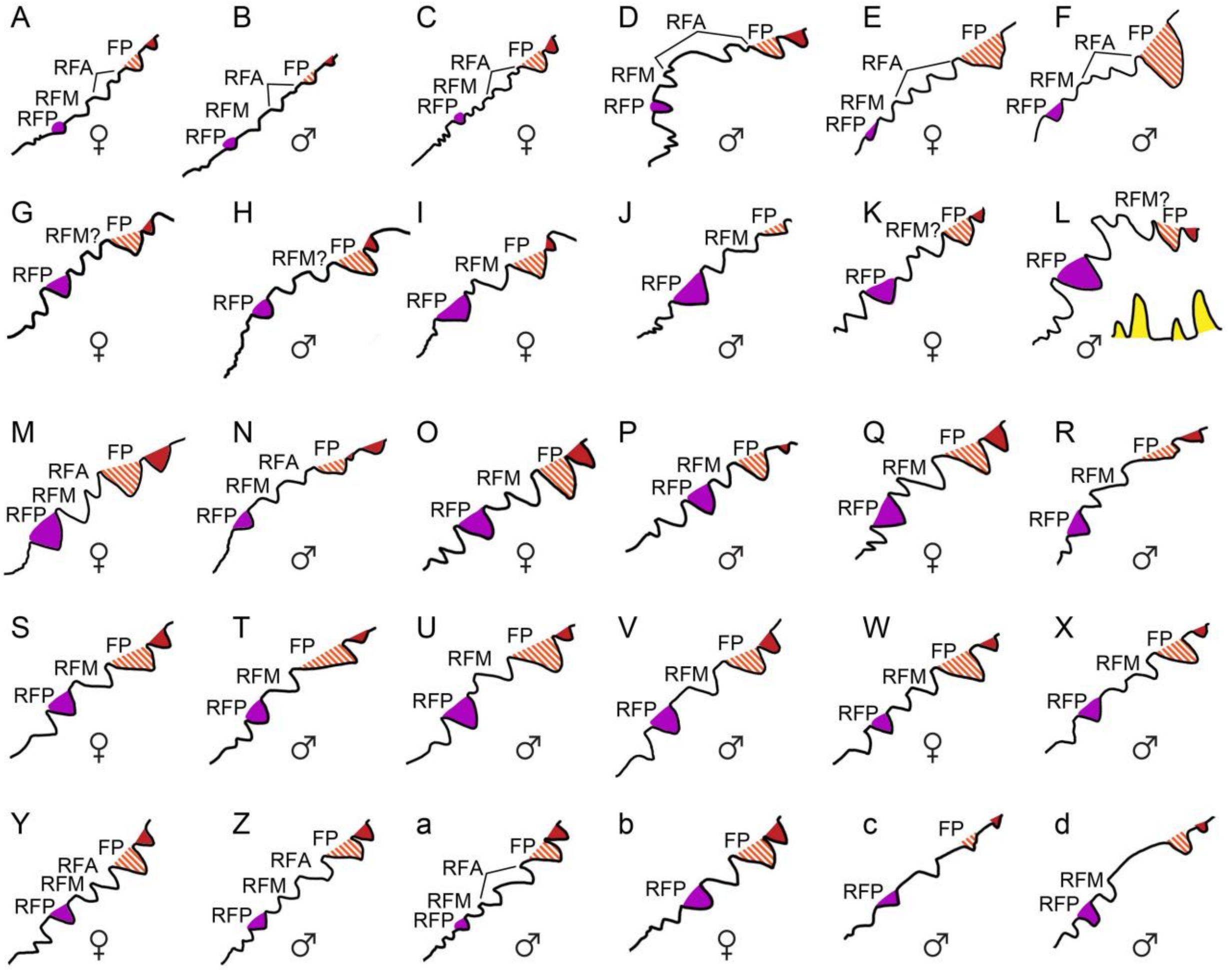
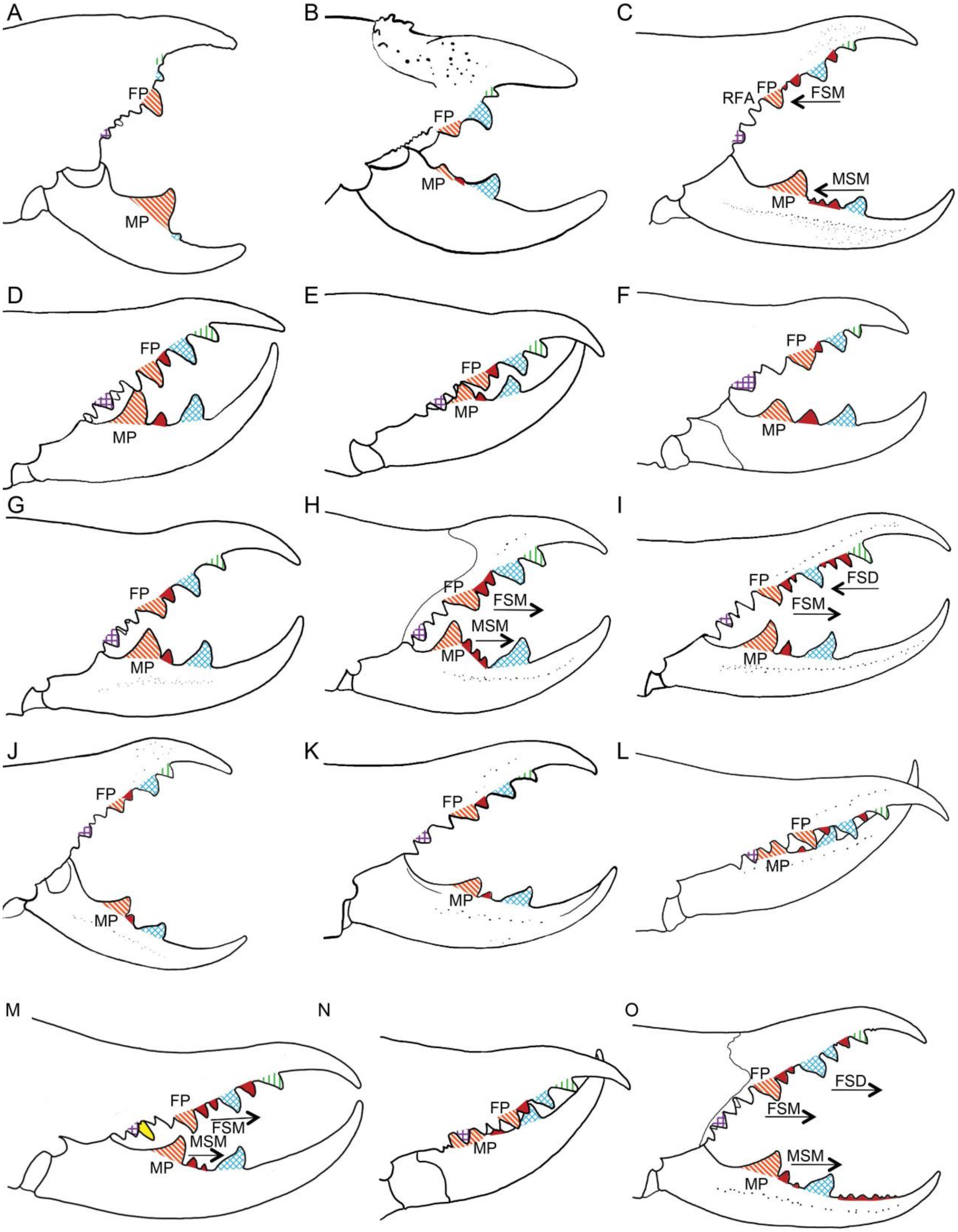


Plate 23. Karschiidae Kraepelin, 1899 (**A–D**), Rhagodidae, Pocock, 1897 (**E, F**), Gylippidae Roewer, 1933, Gylippinae (**G, H**), and Lipophaginae Wharton, 1981 (**I–L**), Galeodidae Sundevall, 1833 (**M, N**), Ceromidae Roewer, 1933 (**O, P**), Solpugidae Leach, 1815 (**Q, R**), Daesiidae Kraepelin, 1899 (**S–V**), Ammotrechidae Roewer, 1934 (**W, X**), Mummuciidae Roewer, 1934 (**Y–a)**, Melanoblossiidae Roewer, 1933, Melanoblossiinae (**b, c**), and Dinorhaxinae Roewer, 1933 (**d**), retrofondal teeth, retrolateral views. **A, B.** *Eusimonia divina* Birula, 1935, ♀ (AMNH [LP 4098]) (**A**), ♂ (AMNH [LP 4098]) (**B**). **C, D.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♀ (AMNH [LP 7476]) (**C**), ♂ (AMNH [LP 7474]) (**D**). **E, F.** *Rhagodes melanus* (Olivier, 1807), ♀ (AMNH [LP 10549]) (**E**), ♂ (AMNH [LP 2293]) (**F**). **G.** *Gylippus* (*Anoplogylippus*) *ferganensis* Birula, 1893, juv. (AMNH [LP 3921]). **H.** *Gylippus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). **I, J.** *Trichotoma michaelseni* (Kraepelin, 1914), ♀ (NMNW 12757) (**I**), ♂ (AMNH [LP 5724]) (**J**). **K, L.** *Bdellophaga angulata* Wharton, 1981, ♀ (NMNW 12240) (**K**), ♂ (NMNW 11601) (**L**). **M, N.** *Paragaleodes* Kraepelin, 1899, *Paragaleodes* sp., ♀ (AMNH [LP 10550]) (**M**), *Paragaleodes nesterovi* Birula, 1916, ♂ (AMNH [LP 7480]) (**N**). **O, P.** *Ceroma inerme* Purcell, 1899, ♀ (AMNH [LP 8425]) (**O**), ♂ (AMNH [LP 9864]) (**P**). **Q, R.** *Oparba asiatica* (Turk, 1948), ♀ (TAU 50313) (**Q**), ♂ (HUJI 360) (**R**). **S, T.** *Blossia grandicornis* Lawrence, 1929, ♀ (AMNH [LP 5905]) (**S**), ♂ (AMNH [LP 5905]) (**T**). **U.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]). **V.**

Hemiblossia etosha Lawrence, 1927, ♂ (AMNH [LP 9854]). **W, X.** *Pseudocleobis andinus* (Pocock, 1899), ♀ (AMNH [LP 2384]) (**W**), ♂ (AMNH [LP 2384]) (**X**). **Y, Z.** *Gaucha fasciata* Mello-Leitão, 1924, ♀ (AMNH [LP 5858]) (small RFSM tooth absent in sinistral chelicera) (**Y**), ♂ (AMNH [LP 10699]) (**Z**). **a.** *Uspallata pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]). **b, c.** *Melanoblossia braunsi*, Purcell, 1903, ♀ (AMNH [LP 10737]) (**b**), ♂ (AMNH [LP 10737]) (**c**). **d.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (AMNH [LP 7537]). Abbreviations: FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; PFM, profondal medial tooth; PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RFA, retrofondal apical tooth/teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth/teeth; RFSP, retrofondal subproximal tooth/teeth.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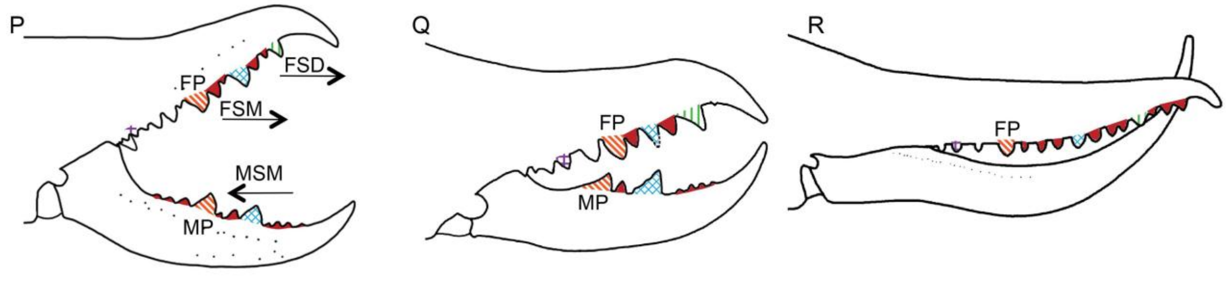
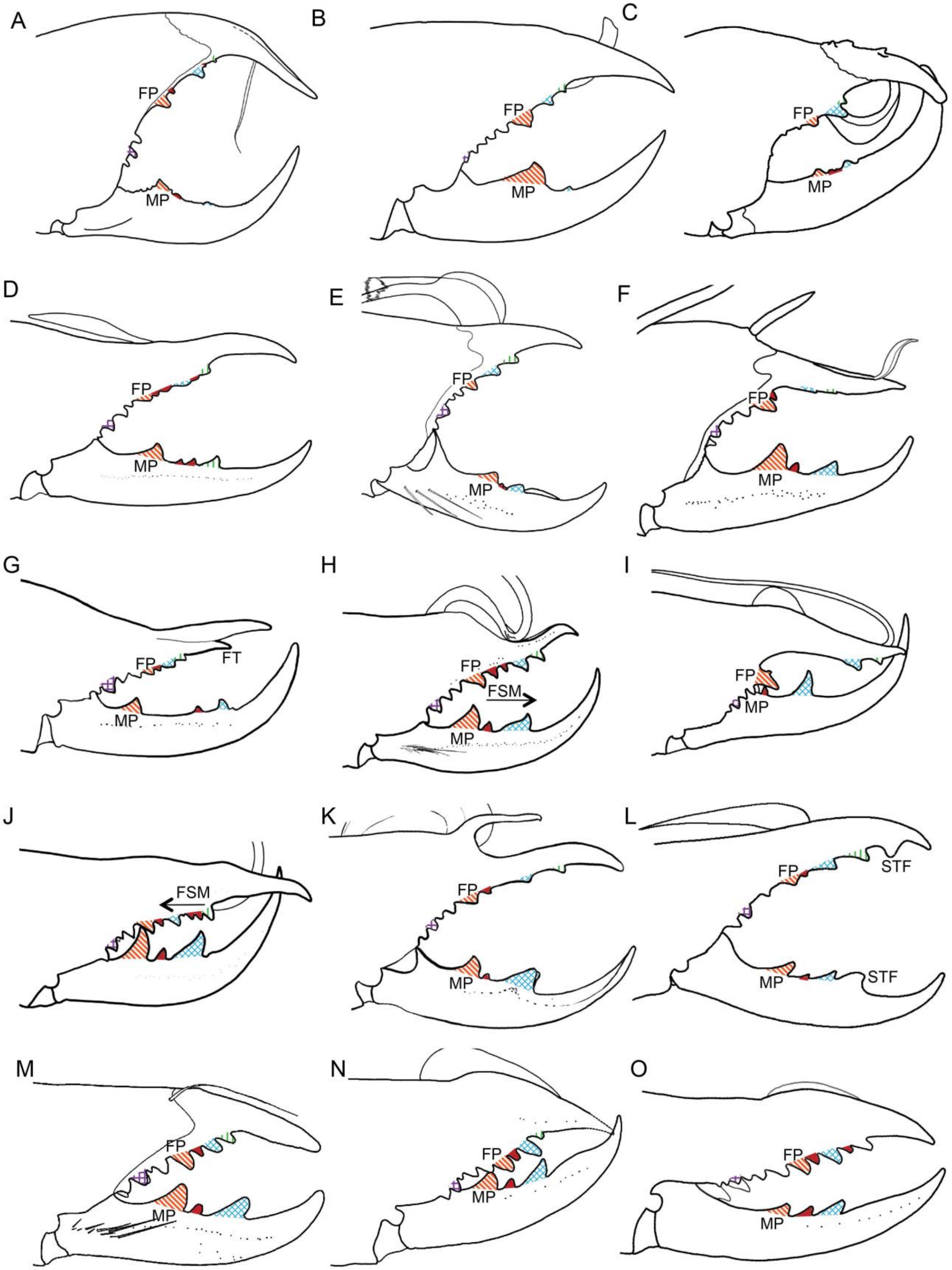


Plate 24. Rhagodidae, Pocock, 1897 (**A**), Hexisopodidae Pocock, 1897 (**B**), Galeodidae Sundevall, 1833 (**C**), Ceromidae Roewer, 1933 (**D**), Gylippidae Roewer, 1933, Gylippinae (**E**) and Lipophaginae Wharton, 1981 (**F**), Solpugidae Leach, 1815 (**G, H**), Daesiidae Kraepelin, 1899 (**I–K**), including Namibesiinae Wharton, 1981 (**I**), Ammotrechidae Roewer, 1934 (**L, M**), Mummuciidae Roewer, 1934 (**N**), Eremobatidae Kraepelin, 1899 (**O**), Karschiidae Kraepelin, 1899 (**P**), and Melanoblossiidae Roewer, 1933, Melanoblossiinae (**Q, R**), female chelicerae, retrolateral views, summarizing typical dentition patterns. **A.** *Barrussus pentheri* (Werner, 1905), juv. (AMNH [LP 10693]). **A.** *Rhagodes melanus* (Olivier, 1807), ♂ (AMNH [LP 2293]). **B.** *Hexisopus aureopilosus* Lawrence, 1968, ♀ (NMNW 11203). **C.** *Galeodes araneoides* (Pallas, 1772), ♀ (AMNH), Turkey: Gurgen. **D.** *Ceroma inerme* Purcell, 1899, ♀ (AMNH [LP 8425]). **E.** *Gyllipus* (*Paragylippus*) *monoceros* Werner, 1905, ♀ (KU), Turkey: Kayseri Province. **F.** *Trichotoma michaelseni* (Kraepelin, 1914), ♀ (NMNW 12757). **G.** *Solpuga chelicornis* Lichtenstein, 1796, ♀ (NCA 2008/3524). **H.** *Zeria fusca* (C.L. Koch, 1842), ♀ (AMNH [LP 1472]). **I.** *Namibesia pallida* Lawrence, 1962, ♀ (AMNH [LP 4017]). **J.** *Ammotrechelis goetschi* Roewer, 1934, ♀ (AMNH [LP 10673]). **K.** *Blossia grandicornis* Lawrence, 1929, ♀ (AMNH [LP 5905]). **L.** *Pseudocleobis andinus* (Pocock, 1899), ♀ (AMNH [LP 2384]). **M.** *Sedna pirata* Muma, 1971, ♀ (AMNH [LP 2362]). **N.** *Gaucha fasciata* Mello-Leitão, 1924, ♀ (AMNH [LP 10699]). **O.** *Horribates bantai* Muma, 1989, ♀ (DMNS ZA.17691). **P.** *Barrussus pentheri* (Werner, 1905), juv. (AMNH [LP 10693]). **Q.** *Melanoblossia braunsi* Purcell, 1903, ♂ (AMNH [LP 10737]). **R.** *Lawrencega minuta* Wharton, 1981, paratype ♂ (CAS 9033898). Abbreviations: FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal teeth; FSM, fixed finger, submedial teeth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth. Arrows indicate secondary teeth gradation patterns.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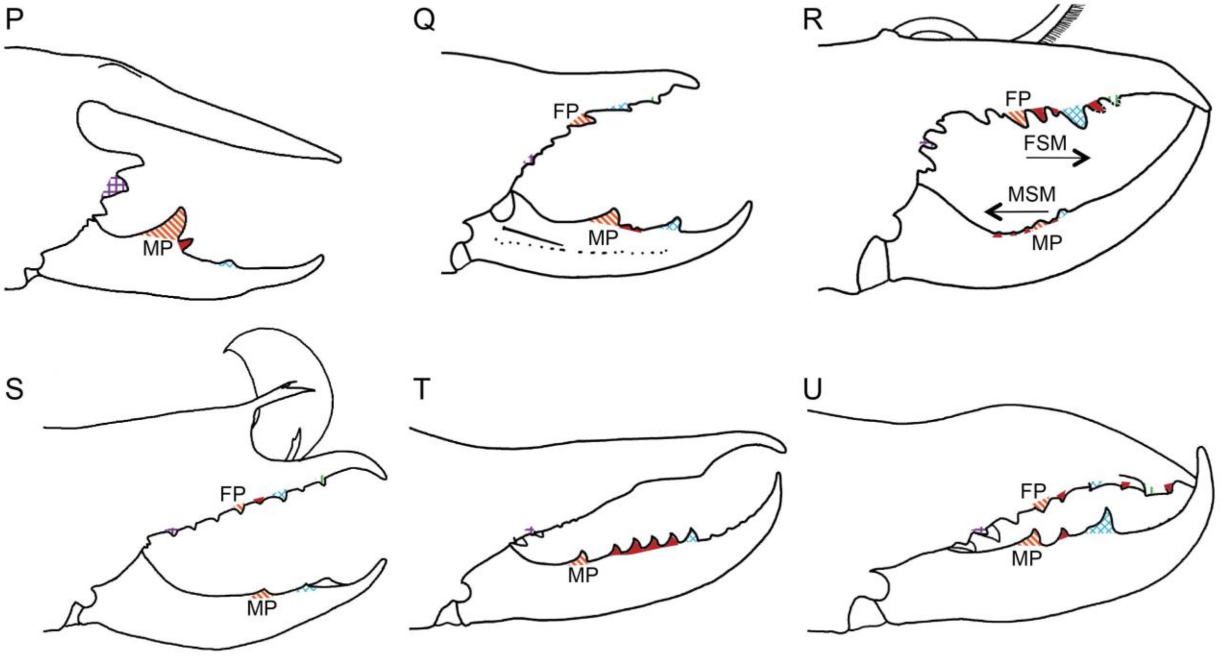

Plate 25. Melanoblossiidae Roewer, 1933, Dinorhaxinae Roewer, 1933 (**A**) and Melanoblossiinae (**T, U**), Rhagodidae Pocock, 1897 (**B**), Hexisopodidae Pocock, 1897 (**C**), Galeodidae Sundevall, 1833 (**D**), Ceromidae Roewer, 1933 (**E**), Gylippidae Roewer, 1933, Gylippinae (**F**) and Lipophaginae Wharton, 1981 (**G**), Solpugidae Leach, 1815 (**H, I**), Daesiidae Kraepelin, 1899 (**J–L**), including Namibesiinae Wharton, 1981 (**J**), Ammotrechidae Roewer, 1934 (**M**), Mummuciidae Roewer, 1934 (**N, O**), Eremobatidae Kraepelin, 1899 (**P, Q**), and Karschiidae Kraepelin, 1899 (**R, S**), male chelicerae, retrolateral views, summarizing typical dentition patterns. **A.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (AMNH [LP 7537]). **B.** *Rhagodes melanus* (Olivier, 1807), ♂ (AMNH [LP 2293]). **C.** *Chelypus hirsti* Hewitt, 1915, ♂ (NMNW 10804). **D.** *Galeodes araneoides* (Pallas, 1772), ♂ (AMNH), Turkey: Gurgen. **E.** *Ceromella* sp. n., ♂ (AMNH [LP 8527]). *Gyllipus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). **G.** *Trichotoma michaelseni* (Kraepelin, 1914), ♂ (NMNW 5724). **H.** *Solpugassa furcifera* (Kraepelin, 1899), ♂ (AMNH [LP 3632]). **I.** *Solpugema derbiana* (Pocock, 1895), ♂ (AMNH [LP 7709]). **J.** *Namibesia pallida* Lawrence, 1962, ♂ (AMNH [LP 10721]). **K.** *Ammotrechelis goetschi* Roewer, 1934, ♂ (AMNH [LP 10673]). **L.** *Blossia* cf. *rooica* (NMNW), Namibia: Gondwana Canõn Park. **M.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). **N.** *Gaucha fasciata* Mello-Leitão, 1924, ♂ (AMNH [LP 5858]). **O.** *Uspallata pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]). **P.** *Eremobates bajadae* Muma & Brookhart, 1988, ♂ (AMNH [LP 5740]). **Q.** *Hemerotrecha branchi* Muma, 1951, ♂ (DMNS ZA.16786). **R.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♂ (AMNH [LP 7474]). **S.** *Eusimonia divina* Birula, 1935, ♂ (AMNH [LP 4098]), **T.** *Lawrencega procera* Wharton, 1981, ♂ (AMNH [LP 9863]). **U.** *Melanoblossia braunsi* Purcell, 1903, ♂ (AMNH [LP 10737]). FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal teeth; FSM, fixed finger, submedial teeth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; STF, subterminal flange. Arrows indicate secondary teeth gradation patterns.

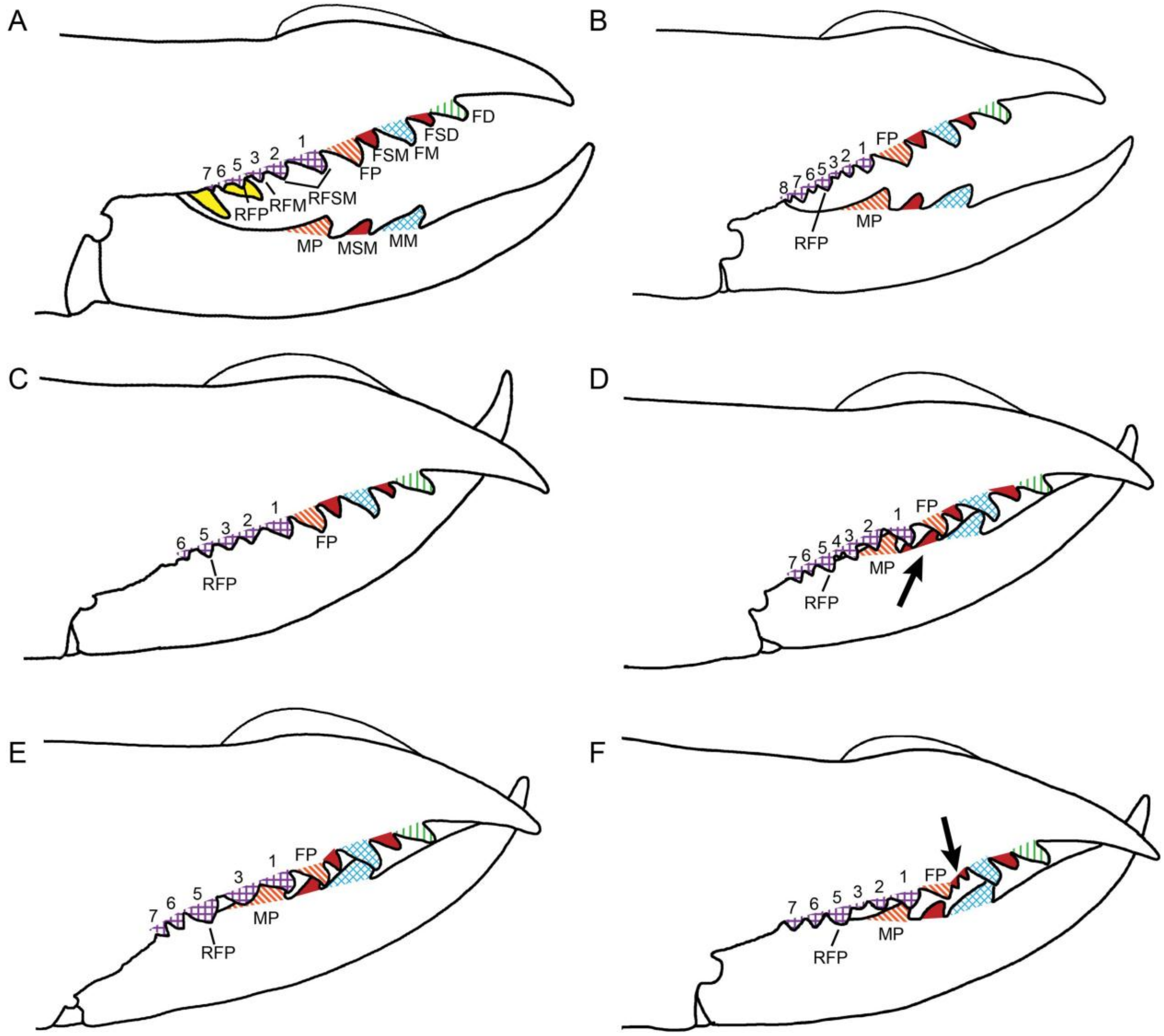

Plate 26 Mummuciidae Roewer, 1934, chelicerae, retrolateral views (**A–F**), illustrating variation in closure and dentition (arrows) among individuals from a single population. **A–F.** *Uspallata pulchra* Mello-Leitão, 1938, 5 ♂ (AMNH [LP 2403]). **A, B, E.** 3 ♂, dextral chelicerae. **C, D.** ♂, sinistral (**C**) and dextral (**D**) chelicerae. **F.** ♂, sinistral chelicera. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial tooth/teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth/teeth; RFA, retrofondal apical tooth/teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth/teeth. Numbers indicate possible homologs (RFA: 1, 2; RFM: 3; RFSM: 4; RFP: 5; RFSP: 6, 7, 8).

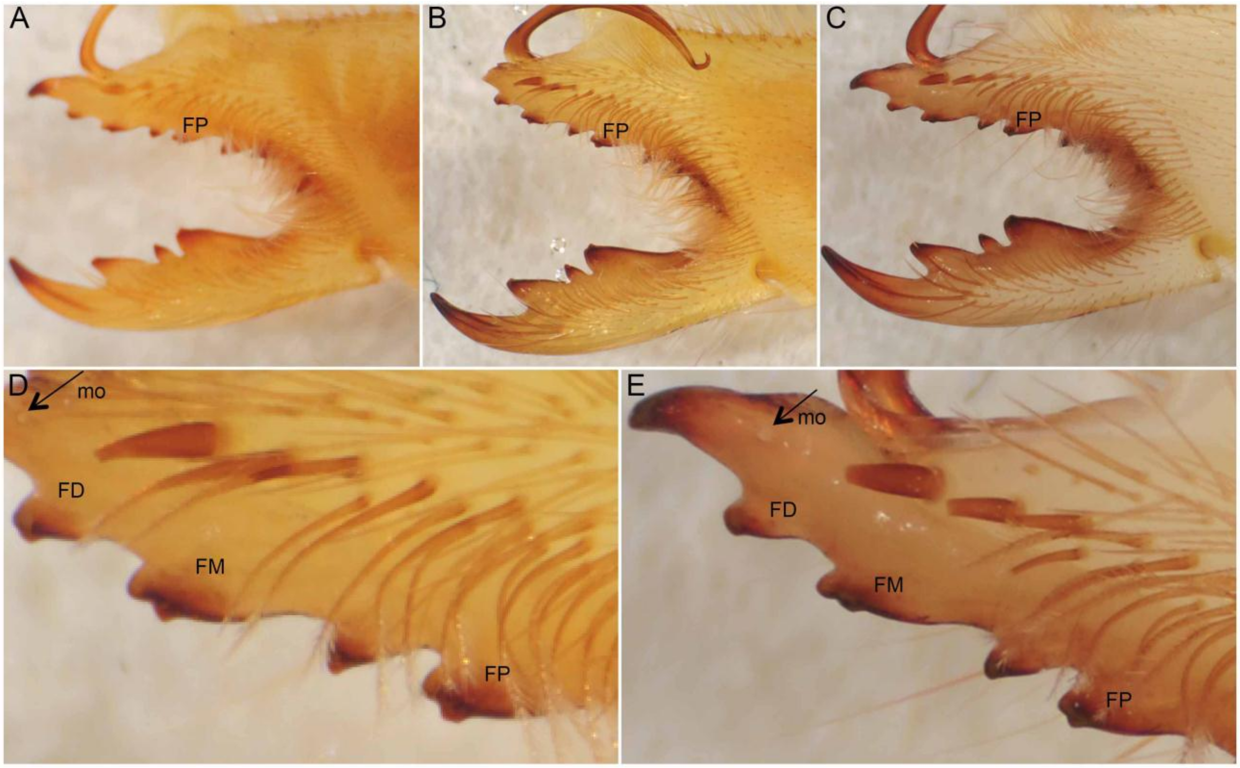

Plate 27. Solpugidae Leach, 1815, *Oparba asiatica* (Turk, 1948), chelicerae (**A–C**) and fixed (dorsal) fingers (**D, E**), prolateral views, indicating interpopulation similarity in pattern of dentition (**A–C**) and shape of primary teeth (**D, E**). **A.** Holotype ♂ (HUJI). **B, D.** ♂ (HUJI 360), distal half of fixed finger mucron broken. **C, E.** ♂ (HUJI 684). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth. *fcp*, flagellar complex plumose setae; *pvd*, proventral distal setae. Arrows indicate mucron organ (mo).

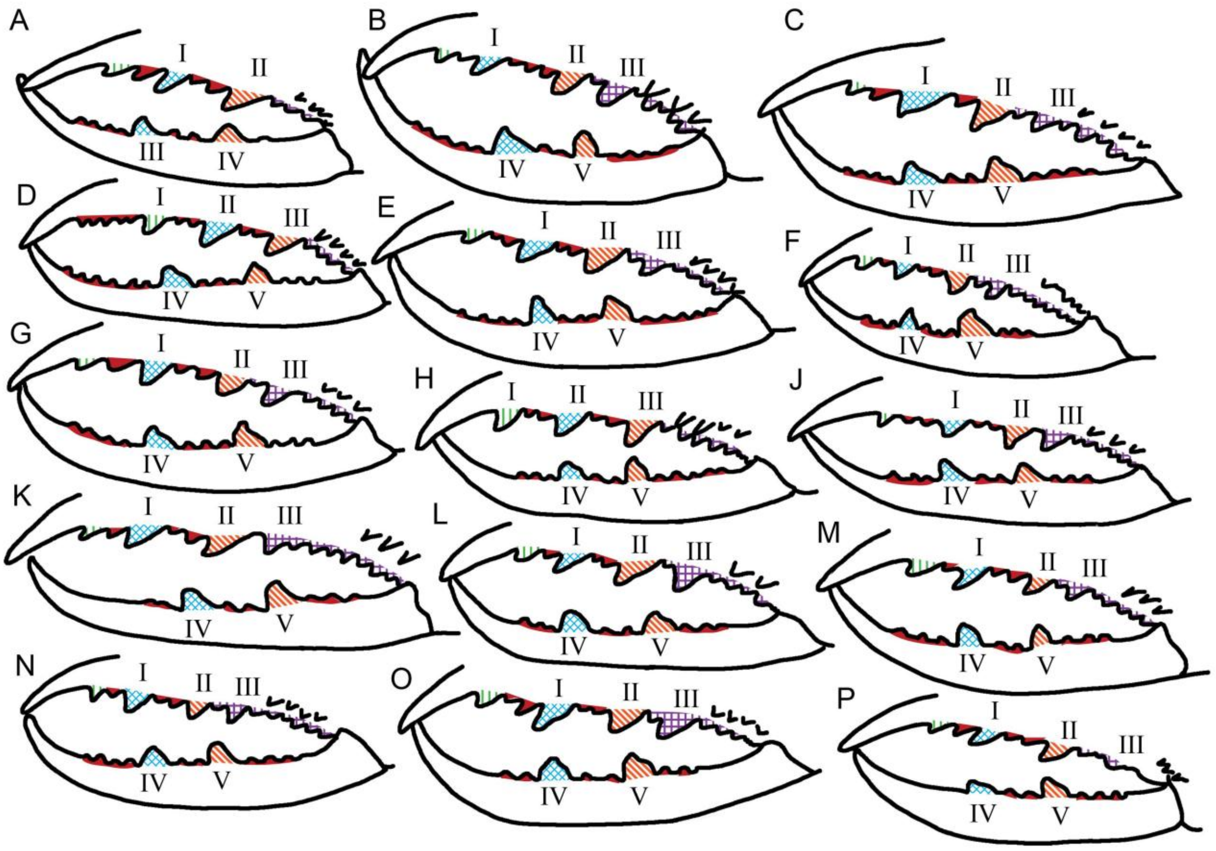

Plate 28. Karschiidae Kraepelin, 1899, *Karschia* Walter, 1889 (**A–F, K–M, O, P**) and *Eusimonia* Kraepelin, 1899 (**G–I, N**), reproduced and adapted from Roewer (1934: 296, fig. 223), indicating his interpretation of female dentition in Roman numerals and interpretation presented here, indicated with color coding. **A.** *Karschia* (*Rhinokarschia*) *pedaschenkoi* Birula, 1922, **B.** *K.* (*K.*) *tarimina* Roewer, 1933. **C.** *K.* (*K.*) *tienschanica* Roewer, 1933. **D.** *K.* (*K.*) *mongolica* Roewer, 1933. **E.** *E. arabica* Roewer, 1933. **F.** *E. furcillata* (Simon, 1872). **G.** *E. seistanica* Roewer, 1933. **H.** *E. nigrescens* Kraepelin, 1899. **I.** *E. kabiliana* (Simon, 1879). **K.** *K.* (*K.*) *mastigofera* Birula, 1890. **L.** *K.* (*K.*) *persica* Kraepelin, 1899. **M.** *K.* (*R.*) *rhinoceros* Birula, 1922. **N.** *Barella birulae* Roewer, 1933, currently in synonymy with *E. turkestana* Kraepelin, 1899. **O.** *K.* (*K.*) *tibetana* Hirst, 1907. **P.** *K.* (*R.*) *kaznakovi* Birula, 1922. Abbreviations, annotations and color coding: FD, fixed finger, distal tooth (indicated with I and green); FM, fixed finger, medial tooth (II, blue); FP, fixed finger, proximal tooth (III, patterned red); MM, movable finger, medial tooth (IV, blue); MP, movable finger, proximal tooth (V, patterned red); secondary teeth (solid red).

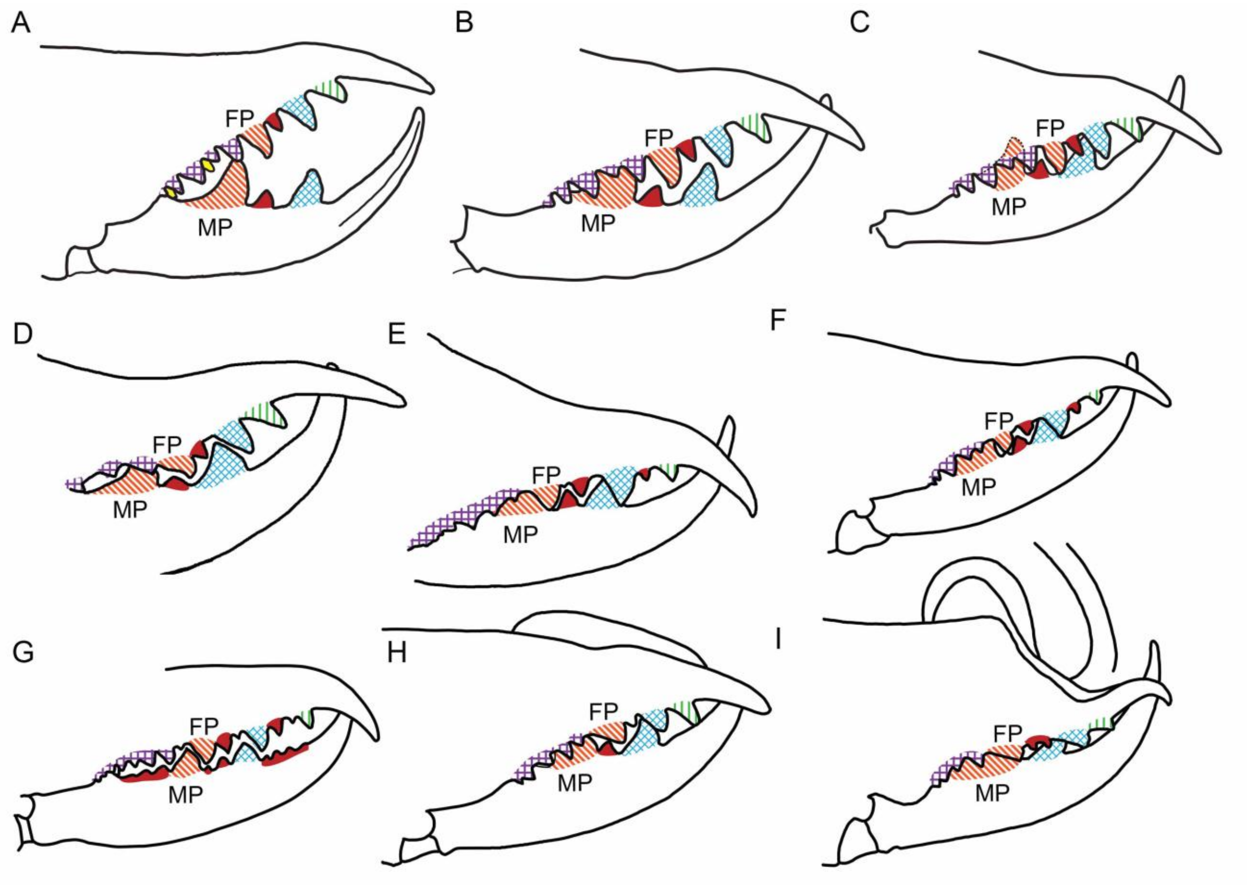

Plate 29. Ceromidae Roewer, 1933 (**A–C**), Galeodidae Sundevall, 1833 (**D–F**), Karschiidae Kraepelin, 1899 (**G**), Ammotrechidae Roewer, 1934 (**H**), and Solpugidae Leach, 1815 (**I**), chelicerae, retrolateral views, indicating manner of closure of fixed (dorsal) versus movable (ventral) finger dentition (homology criterion 3) from relatively conserved (**A–F, H**) to highly modified (**G, I**) dentition patterns. **A–C.** *Ceroma inerme* Purcell, 1899. ♀ (AMNH [LP 8425]). **D, E.** *Galeodes* sp. ♀ (MCZ), Mali. **F.** *Galeodes olivieri* Simon 1879, ♀ (AMNH [LP 4628]). **G.** *Barrussus pentheri* (Werner, 1905), juv. (AMNH [LP 10693]). **H.** *Ammotrecha stollii* (Pocock, 1895), ♂ (AMNH [LP 8605]). **I.** *Zeria fusca* (C.L. Koch, 1842), ♂ (AMNH [LP 1473]). Abbreviations: FP, fixed finger, proximal tooth; MP, movable finger, proximal tooth.

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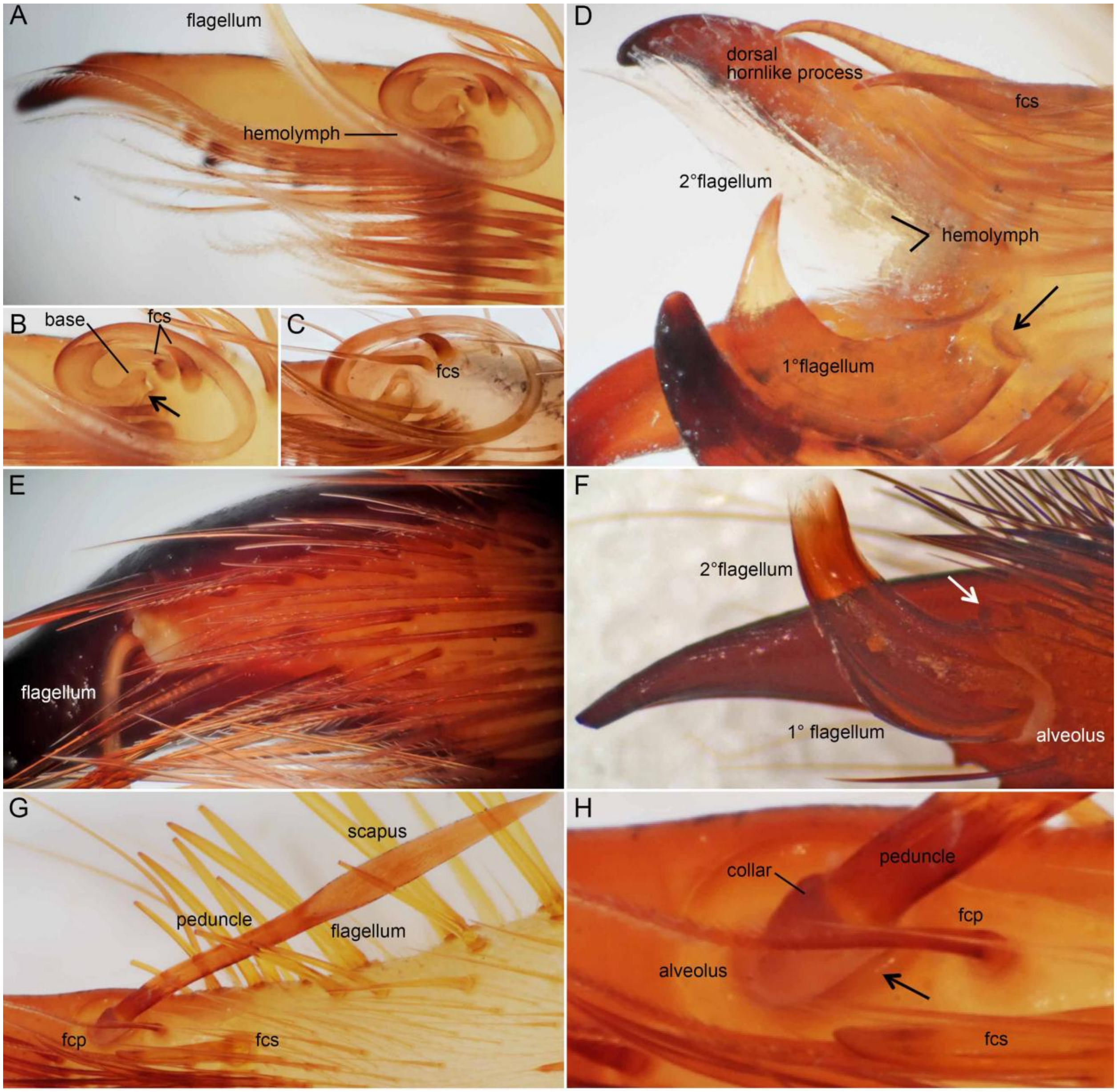

Plate 30. Karschiidae Kraepelin, 1899 (**A–D**), Melanoblossiidae Roewer, 1933, Dinorhaxinae Roewer, 1933 (**E**), Rhagodidae, Pocock, 1897 (**F**), and Galeodidae Sundevall, 1833 (**G, H**), male flagellar complex comprising sessile flagella and associated setae, prolateral views. **A, B.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♂ (AMNH [LP 7474]). **C.** *Karschia* (*K.*) *tibetana* Hirst, 1907, ♂ (AMNH [LP 7719]). **D.** *Eusimonia nigrescens* Kraepelin, 1899, ♂ (AMNH [LP 7473]). **E.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (AMNH [LP 7537]). **F.** *Rhagodes melanus* (Olivier, 1807), ♂ (NMNW), Israel: Agur Sands. **G, H.** *Galeodes olivieri* Simon 1879, ♂ (AMNH [LP 4630]). Abbreviations: *fcs*, flagellar complex subspiniform or spiniform setae; *fcp*, flagellar complex plumose setae; 1°, primary; 2°, secondary. Arrows (**B, D, F, H**) indicate excrescence at base of socket.

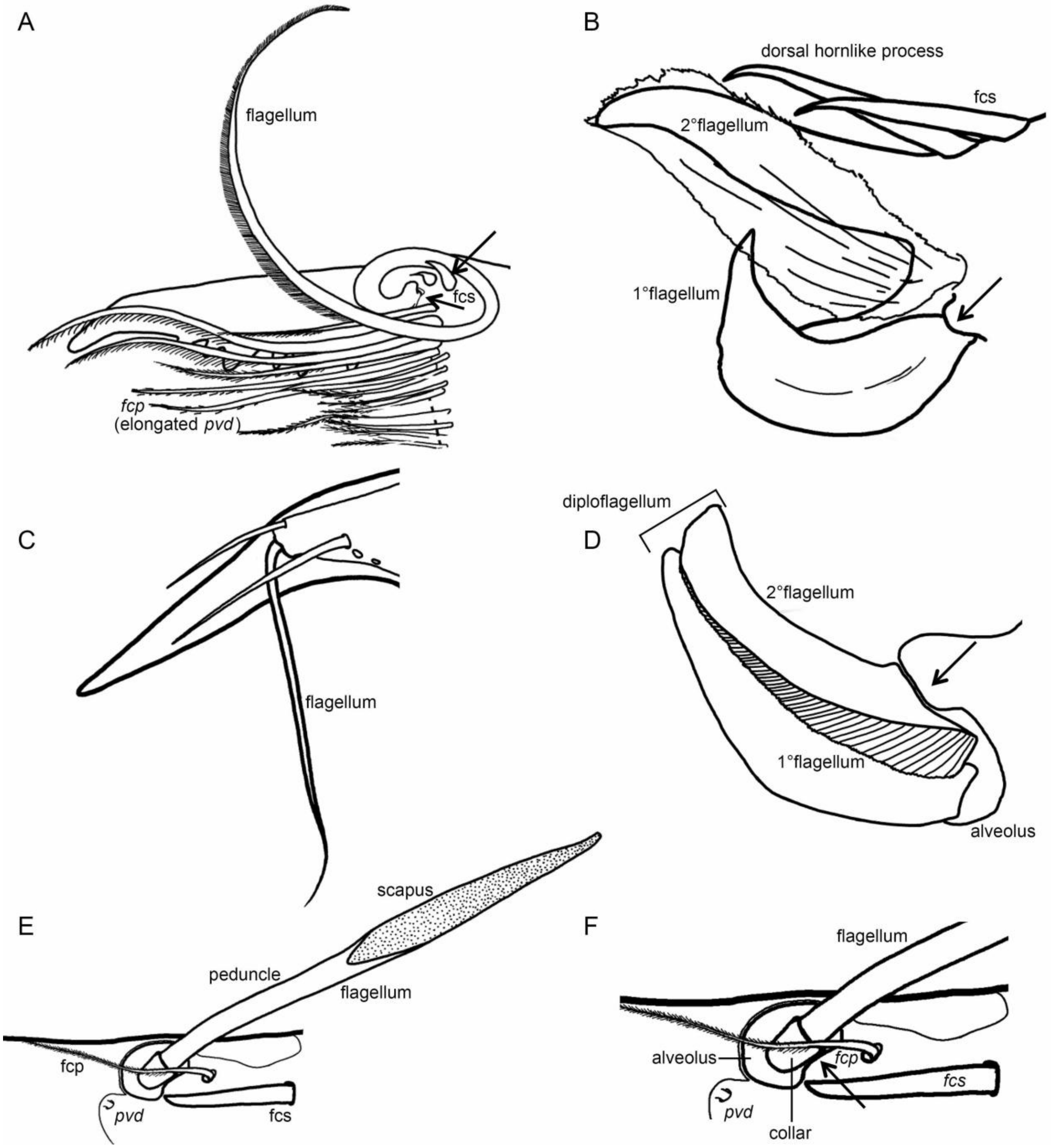

Plate 31. Karschiidae Kraepelin, 1899 (**A, B**), Melanoblossiidae Roewer, 1933, Dinorhaxinae Roewer, 1933 (**C**), Rhagodidae, Pocock, 1897 (**D**), and Galeodidae Sundevall, 1833 (**E, F**), male flagellar complex comprising sessile flagella and associated setae, prolateral views. **A.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♂ (AMNH [LP 7474]). **B.** *Eusimonia nigrescens* Kraepelin, 1899, ♂ (AMNH [LP 7473]). **C.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (AMNH [LP 7537]). **D.** *Rhagodes melanus* (Olivier, 1807), ♂ (NMNW), Israel: Agur Sands. **E, F.** *Galeodes olivieri* Simon 1879, ♂ (AMNH [LP 4630]). Abbreviations: *fcs*, flagellar complex subspiniform or spiniform setae; *fcp*, flagellar complex plumose setae; 1°, primary; 2°, secondary. Arrows (**A, B, D, F**) indicate excrescence at base of socket.

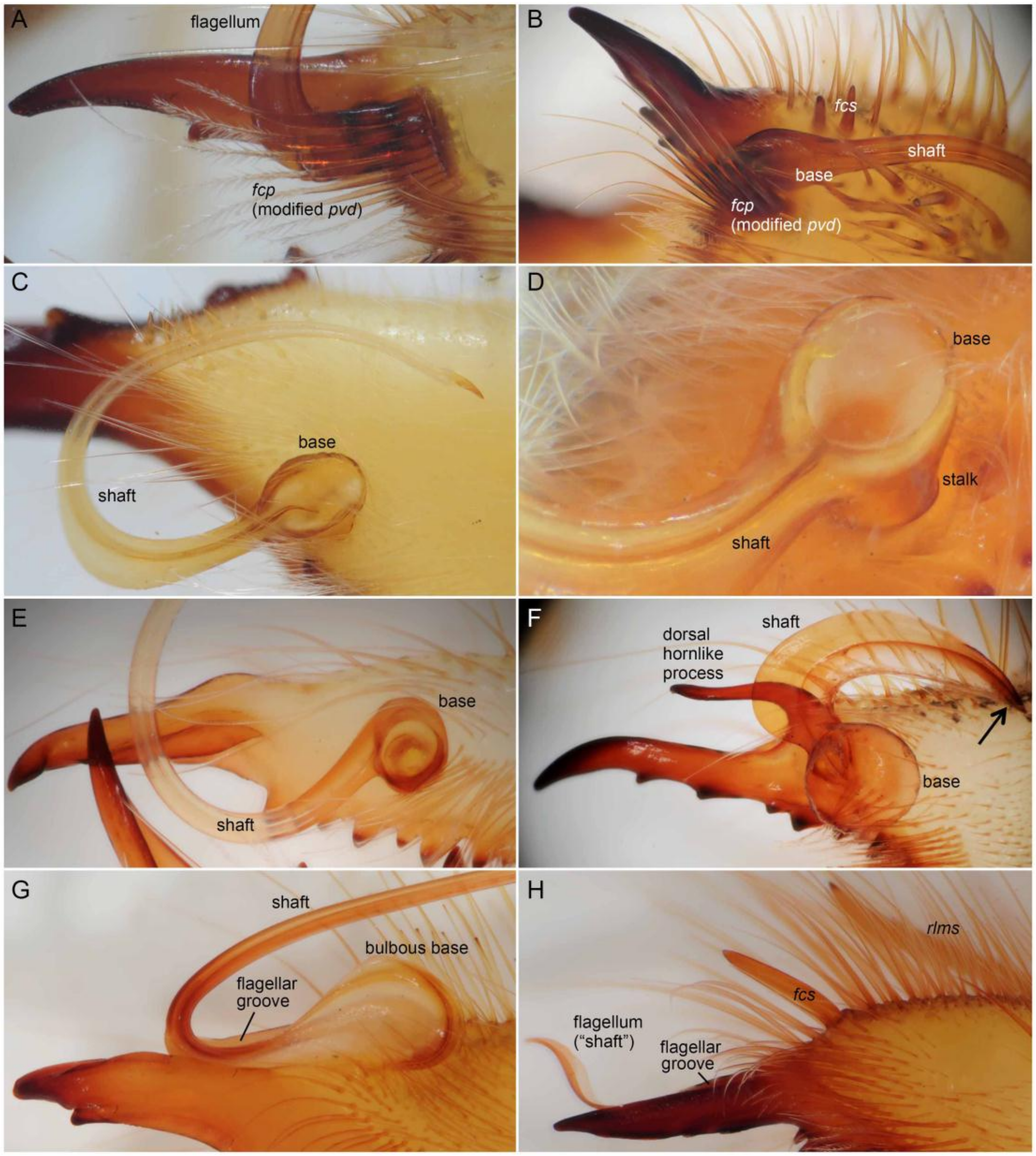

Plate 32. Ceromidae Roewer, 1933 (**A, B**), Hexisopodidae Pocock, 1897 (**C, D**), Daesiidae Kraepelin, 1899 (**E, F**), including Namibesiinae Wharton, 1981 (**E**), Solpugidae Leach, 1815 (**G**), and Gylippidae Roewer, 1933, Gylippinae (**H**), male flagellar complex comprising compound flagella and associated setae, prolateral (**A, C–H**) and prodorsal (**B**) views. **A.** *Ceroma swierstrae* Lawrence, 1935, ♂ (NCA 2009/4355). **B.** *Ceroma ornatum* Karsch, 1885, ♂ (MRAC 213.106). **C.** *Chelypus shortridgei* Hewitt, 1931, ♂ (NMNW 12632). **D.** *Chelypus hirsti* Hewitt, 1915, ♂ (NMNW 10804). **E.** *Namibesia pallida* Lawrence, 1962, ♂ (AMNH [LP 10721]). **F.** *Ammotrechelis goetschi* Roewer, 1934, ♂ (AMNH [LP 10673]). Arrow indicates exterior opening of putative alembic canal. **G.** *Solpuga chelicornis* Lichtenstein, 1796, ♂ (AMNH [LP 8158]). **H.** *Gylippus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). Abbreviations: *fcs*, flagellar complex subspiniform or spiniform setae; *fcp*, flagellar complex plumose setae; *pvd*, proventral distal setae; *rlms*, retrolateral manus setae.

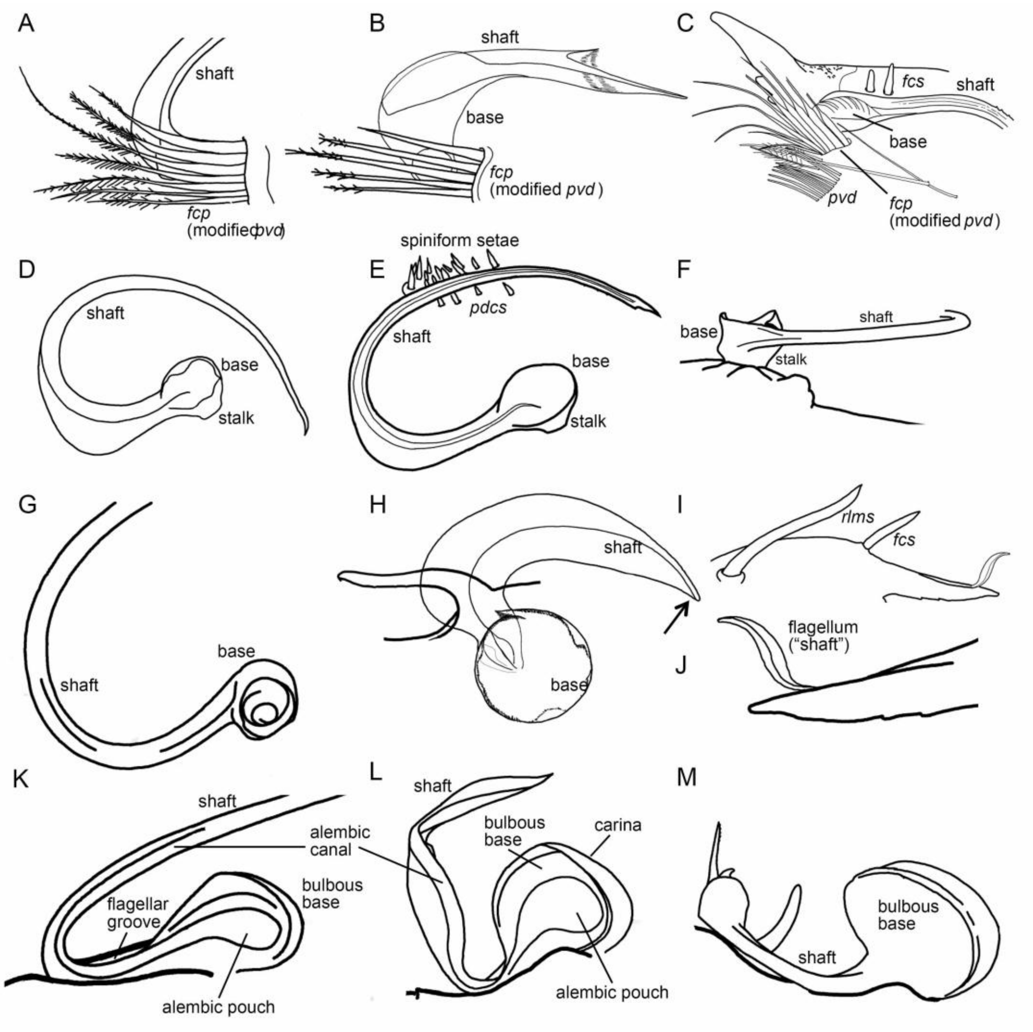

Plate 33. Ceromidae Roewer, 1933 (**A–C**), Hexisopodidae Pocock, 1897 (**D–F**), Daesiidae Kraepelin, 1899 (**G, H**), including Namibesiinae Wharton, 1981 (**G**), Gylippidae Roewer, 1933, Gylippinae (**I, J**), and Solpugidae Leach, 1815 (**K–M**), male flagellar complex comprising compound flagella and associated setae, prolateral (**A, B, D, E, G, H, J–M**), prodorsal (**C**), ventral (**F**), and retrolateral (**I**) views. **A.** *Ceroma swierstrae* Lawrence, 1935, ♂ (NCA 2009/4355). **B.** *Ceromella* sp. n., ♂ (AMNH [LP 8527]). **C.** *Ceroma ornatum* Karsch, 1885, ♂ (MRAC 213.106). **D.** *Chelypus hirsti* Hewitt, 1915, ♂ (NMNW 10804). **E.** *Chelypus shortridgei* Hewitt, 1931, ♂ (NMNW 12632). **F.** *Hexisopus pusillus* Lawrence, 1962, ♂ (NMNW 11426). **G.** *Namibesia pallida* Lawrence, 1962, ♂ (AMNH [LP 10721]). **H.** *Ammotrechelis goetschi* Roewer, 1934, ♂ (AMNH [LP 10673]). Arrow indicates exterior opening of putative alembic canal. **I, J.** *Gylippus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). **K.** *Solpuga chelicornis* Lichtenstein, 1796, ♂ (AMNH [LP 8158]). **L.** *Solpugema genucornis* (Lawrence, 1935), ♂ (AMNH [LP 8167]). **M.** *Solpuguna* cf. *orangica*, ♂ (AMNH [LP 5969]). Abbreviations: *fcs*, flagellar complex subspiniform or spiniform setae; *fcp*, flagellar complex plumose setae; *pvd*, proventral distal setae; *rlms*, retrolateral manus setae; *pdcs*, prodorsal cluster of setae.

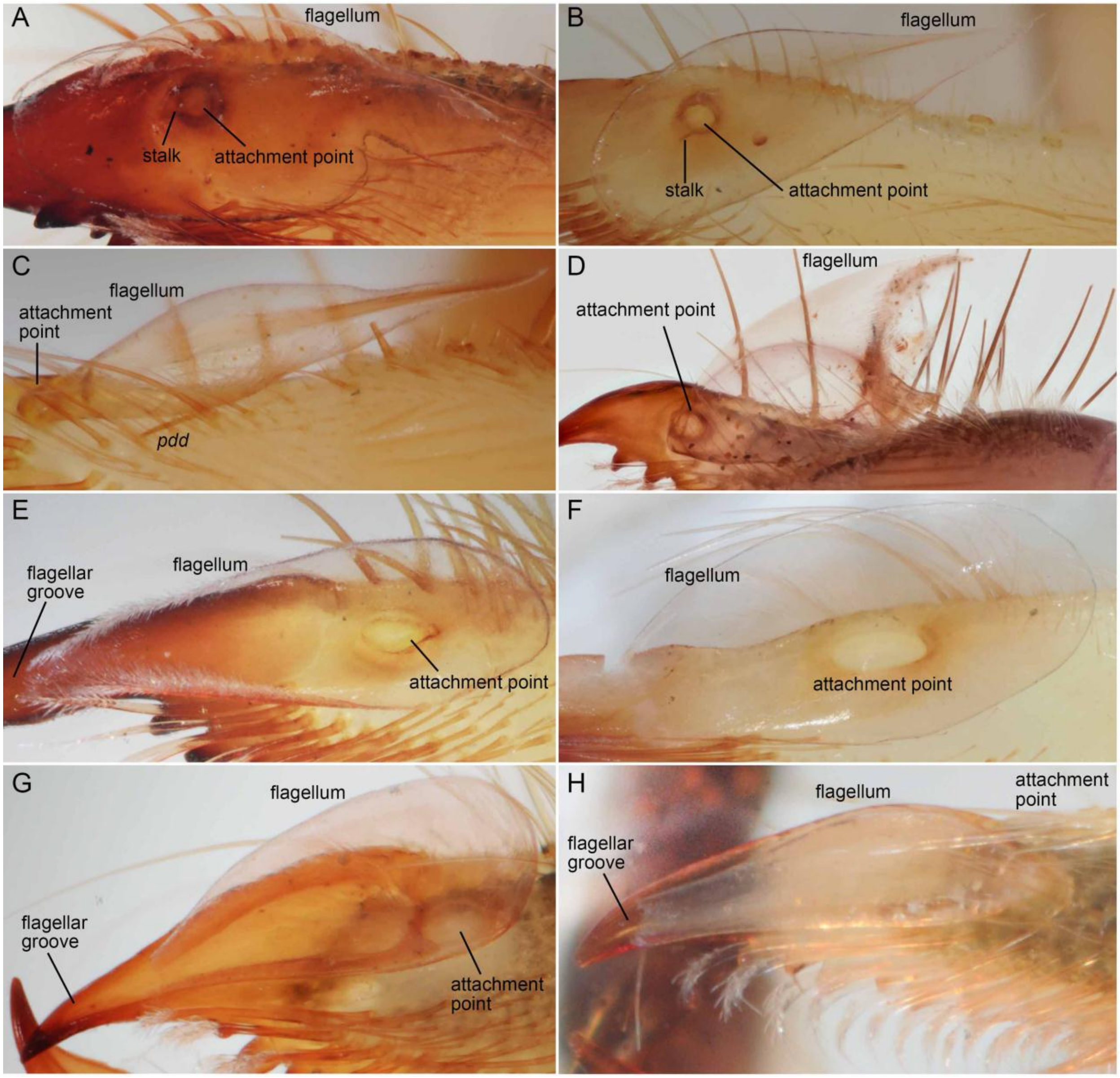

Plate 34. Daesiidae Kraepelin, 1899 (**A–D**), Ammotrechidae Roewer, 1934 (**E, F**) and Mummuciidae Roewer, 1934 (**G, H**), compound flagella, prolateral views, indicating membranous husk (**A**), bowl (**B–C**), and vesicular (**D, E**) shapes. **A.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]). **B.** *Biton* (*B.*) *rossicus* (Birula, 1905), ♂ (AMNH [LP 3959]). **C.** *Blossia grandicornis* Lawrence, 1929, ♂ (AMNH [LP 5905]). **D.** *Hemiblossia etosha* Lawrence, 1927, ♂ (AMNH [LP 9854]). **E.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). **F.** *Nothopuga cuyana* Maury, 1976, ♂ (AMNH [LP 2263]). **G.** *Gaucha fasciata* Mello-Leitão, 1924, ♂ (AMNH [LP 5858]). **H.** *Uspallata pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]). Abbreviations: *pdd*, prodorsal distal setae..

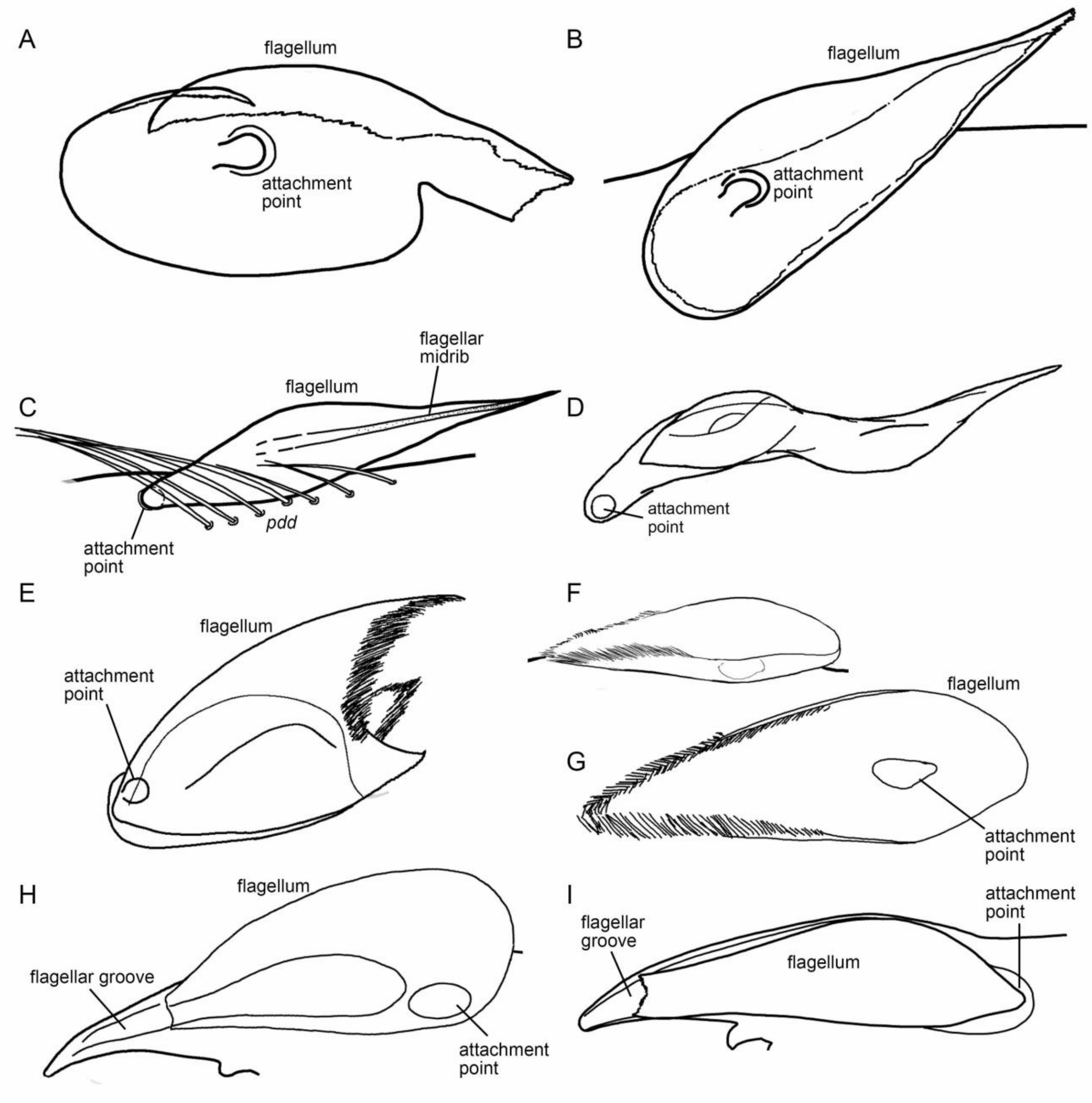

Plate 35. Daesiidae Kraepelin, 1899 (**A–E**), Ammotrechidae Roewer, 1934 (**F, G**) and Mummuciidae Roewer, 1934 (**H, I**), compound flagella, prolateral (**A–E, G–I**) and ventral (**F**) views, indicating membranous husk (**A–E**), bowl (**F, G**), and vesicular (**H, I**) shapes. **A.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]). **B.** *Biton* (*B.*) *rossicus* (Birula, 1905), ♂ (AMNH [LP 3959]). **C.** *Blossia grandicornis* Lawrence, 1929, ♂ (AMNH [LP 5905]). **D.** *Hemiblossia australis* (Purcell, 1902), ♂ (AMNH [LP 9866]). **E.** *Hemiblossia etosha* Lawrence, 1927, ♂ (AMNH [LP 9854]). **F, G.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). **H.** *Gaucha fasciata* Mello-Leitão, 1924, ♂ (AMNH [LP 5858]). **I.** *Uspallata pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]). Abbreviations: *pdd*, prodorsal distal setae.

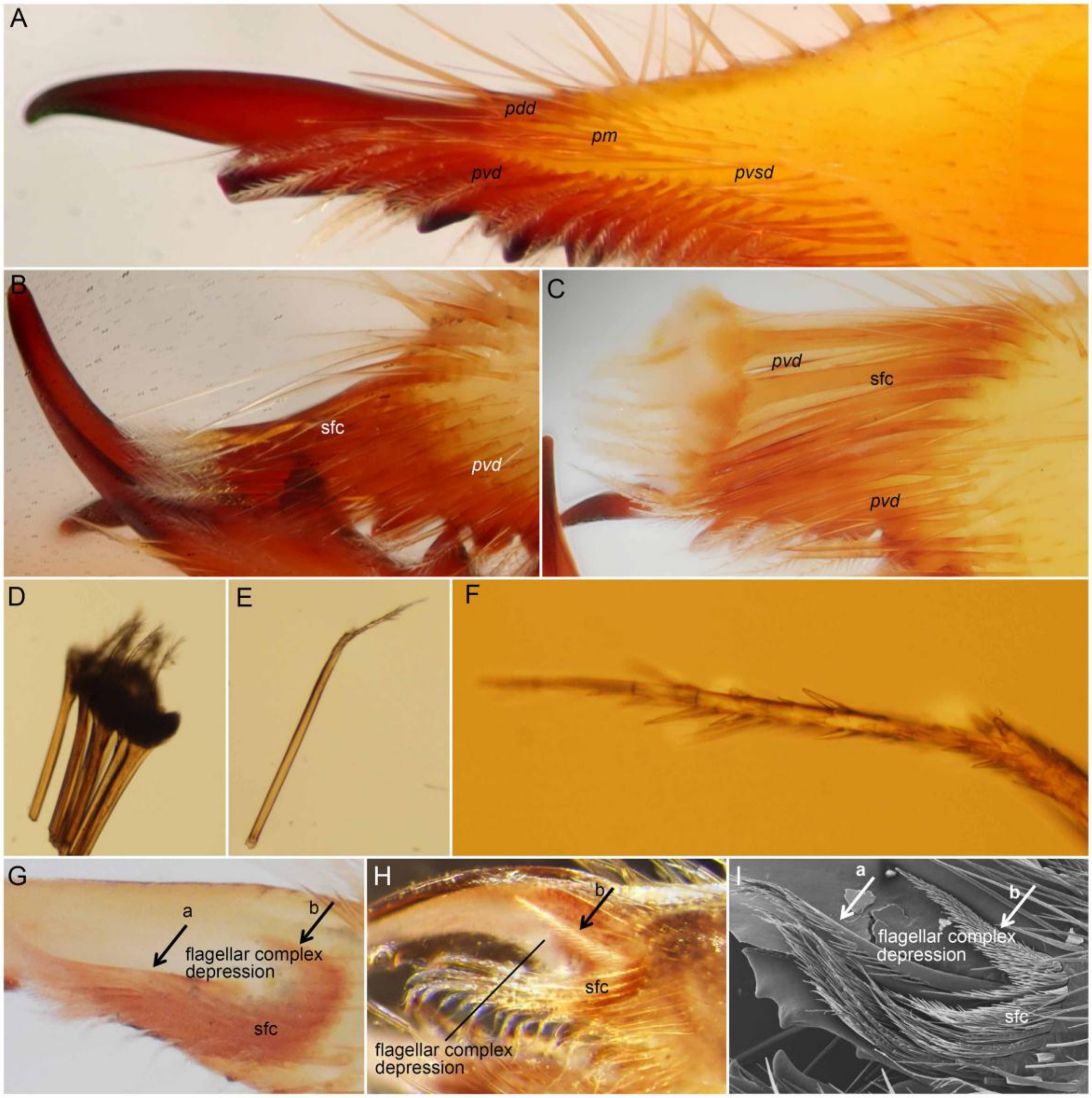

Plate 36. Gylippidae Roewer, 1933, Lipophaginae Wharton, 1981 (**A–F**) and Melanoblossiidae Roewer, 1933, Melanoblossiinae (**G, H**), fixed (dorsal) fingers, prolateral views, indicating weak to absent (**A**) and highly modified (**B, C**) type B setiform flagellar complex without a flagellum, comprising modified *pvd* setae (**D–F**), and type C setiform flagellar complex comprising modified proventral distal (*pvd*) setae, prolateral views indicating two (a, b) distinctly differentiated setae, with setae "a" interpreted as homologous to the primary flagella of other solifuge families. **A.** *Trichotoma michaelseni* (Kraepelin, 1914), ♂ (NMNW 12757). **B.** *Lipophaga trispinosa* Purcell, 1903, ♂ (NMNW 12503). **C–F.** *Bdellophaga angulata* Wharton, 1981, ♂ (NMNW 11601), with modified dorsal *pvd* setae fused apically (**D**), ventral, angular modified *pvd* setae, whole mount (**E**) and close-up (**F**). **G.** *Lawrencega procera* Wharton, 1981, ♂ (AMNH [LP 9863]). **H.** *Melanoblossia braunsi* Purcell, 1903, ♂ (AMNH [LP 10737]). **I.** *Melanoblossia* sp., ♂ (NMNW 13396). Abbreviations: *pdd*, prodorsal distal setae; *pm*, promedial setae; *pvd*, proventral distal setae; *pvsd*, proventral subdistal setae; *sfc*, setiform flagellar complex..

Plate 37. Eremobatidae Kraepelin, 1899, fixed (dorsal) fingers, prolateral views, indicating type A setiform flagellar complex comprising modified *pdd* and *pvd* setae, without a flagellum. **A.** *Chanbria regalis* Muma, 1951, ♂ (AMNH [LP10746]). **B.** *Eremothera sculpturata* Muma, 1951, ♂ (DMNS ZA.16475). **C.** *Eremocosta titania* (Muma, 1951), ♂ (AMNH [LP 5035]). **D.** *Hemerotrecha hanfordana* Brookhart & Cushing, 2008, holotype ♂ (DMNS ZA.21371). Abbreviations: *pdd*, prodorsal distal setae; *pvd*, proventral distal setae; *sfc*, setiform flagellar complex.

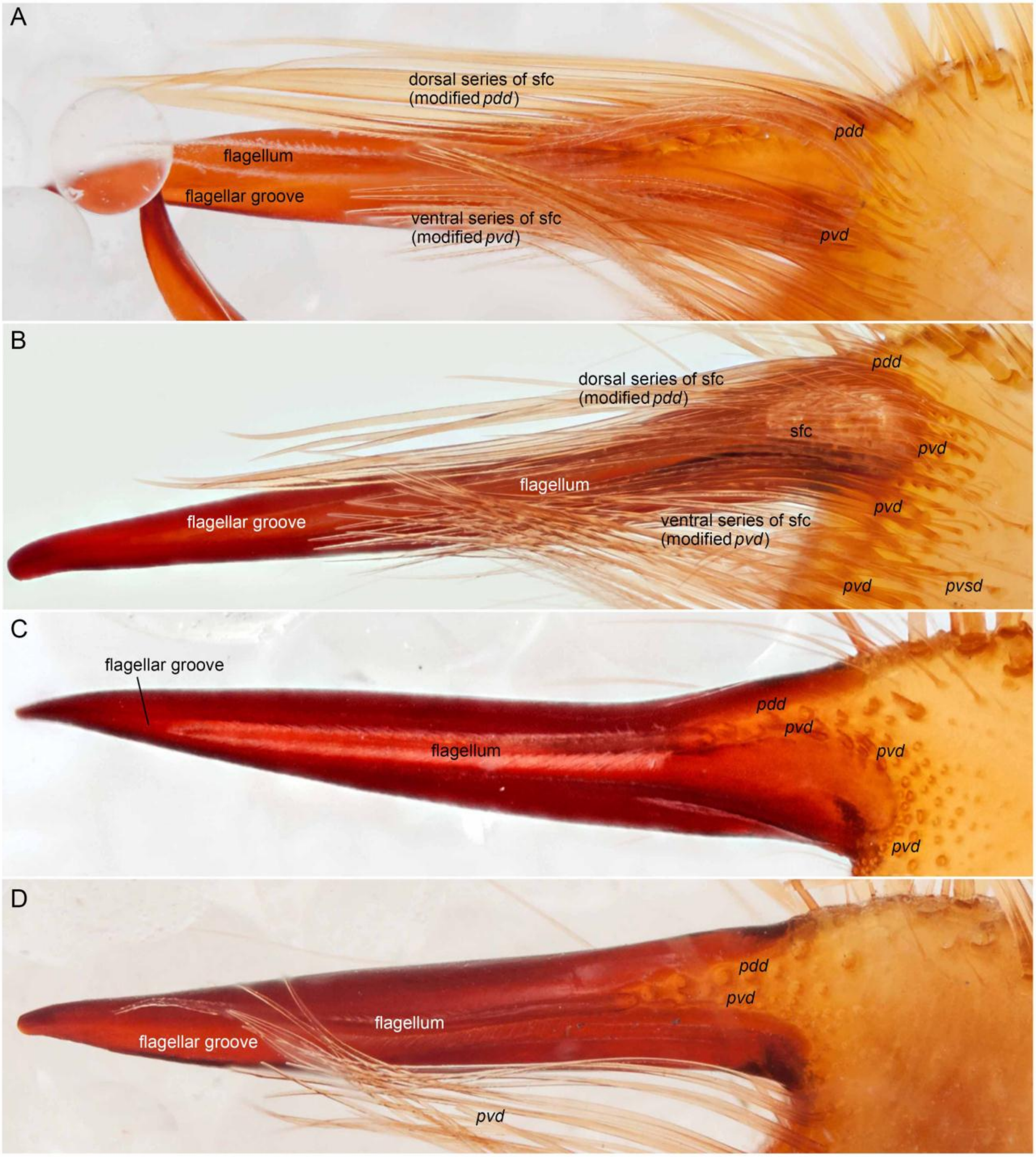

Plate 38. Eremobatidae Kraepelin, 1899, fixed (dorsal) fingers, prolateral views, indicating type A setiform flagellar complex comprising modified *pdd* and *pvd* setae, with a flagellum. **A.** *Eremobates ajoanus* Muma & Brookhart, 1988, paratype ♂ (DMNS ZA.17384). **B.** *Eremobates pallipes* (Say, 1823), ♂ (DMNS ZA.16258). **C.** *Eremobates gerbae* Brookhart & Cushing, 2002, holotype ♂ (DMNS ZA.10000). **D**. *Eremobates angustus* Muma, 1951, paratype ♂ (DMNS ZA.16789). Abbreviations: *pdd*, prodorsal distal setae; *pvd*, proventral distal setae; *pvsd*, proventral subdistal setae; *sfc*, setiform flagellar complex.

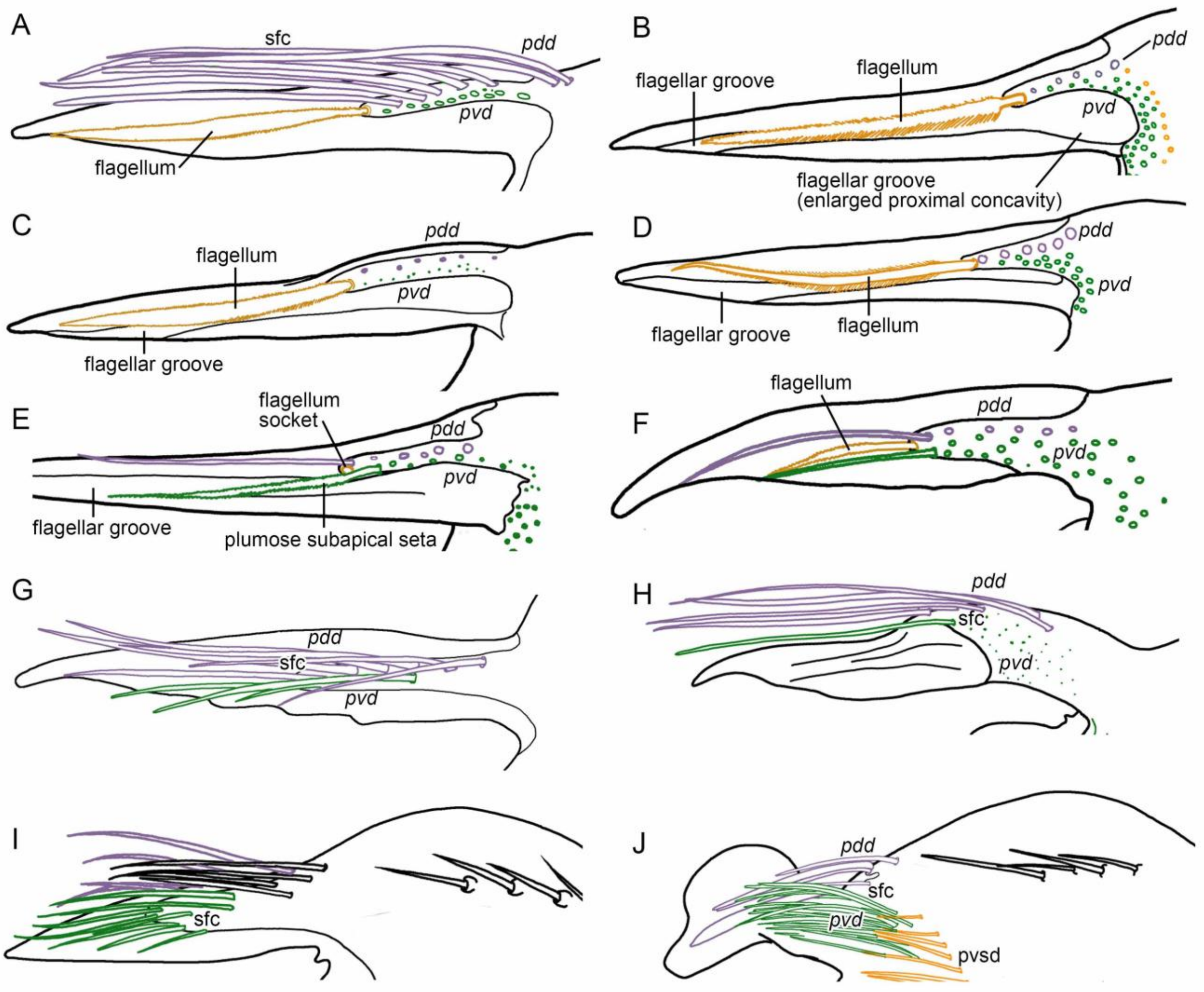

Plate 39. Eremobatidae Kraepelin, 1899, fixed (dorsal) fingers, prolateral views, indicating type A setiform flagellar complex comprising modified *pdd* and *pvd* setae, with (**A–F**) and without (**G–J**) a flagellum (modified apical setae). **A.** *Eremobates bajadae* Muma & Brookhart, 1988, ♂ (AMNH [LP 5740]). **B.** *Eremobates gerbae* Brookhart & Cushing, 2002, holotype ♂ (DMNS ZA.10000). **C.** *Eremobates* cf. *palpisetulosus*, ♂ (AMNH), Mexico: Coahuila. **D.** *Eremobates angustus* Muma, 1951, paratype ♂ (DMNS ZA.16789). **E.** *Eremobates chihuaensis* Brookhart & Cushing, 2002, holotype ♂ (DMNS ZA.10002). **F.** *Eremochelis oregonensis* Brookhart & Cushing, 2002, holotype ♂ (DMNS ZA.10008). **G.** *Eremochelis andreasana* (Muma, 1962), holotype ♂ (AMNH). **H.** *Eremochelis bilobatus* (Muma, 1951), ♂ (DMNS ZA.16039). **I.** *Eremocosta titania* (Muma, 1951), ♂ (AMNH [LP 5035]). **J.** *Eremothera sculpturata* Muma, 1951, ♂ (DMNS ZA.16475). Abbreviations: *pdd*, prodorsal distal setae (indicated in blue); *pdp*, prodorsal proximal setae (indicated in brown); *pvd*, proventral distal setae (indicated in green); *pvsd*, proventral subdistal setae (indicated in orange); *sfc*, setiform flagellar complex. Flagellum indicated in green (solid).

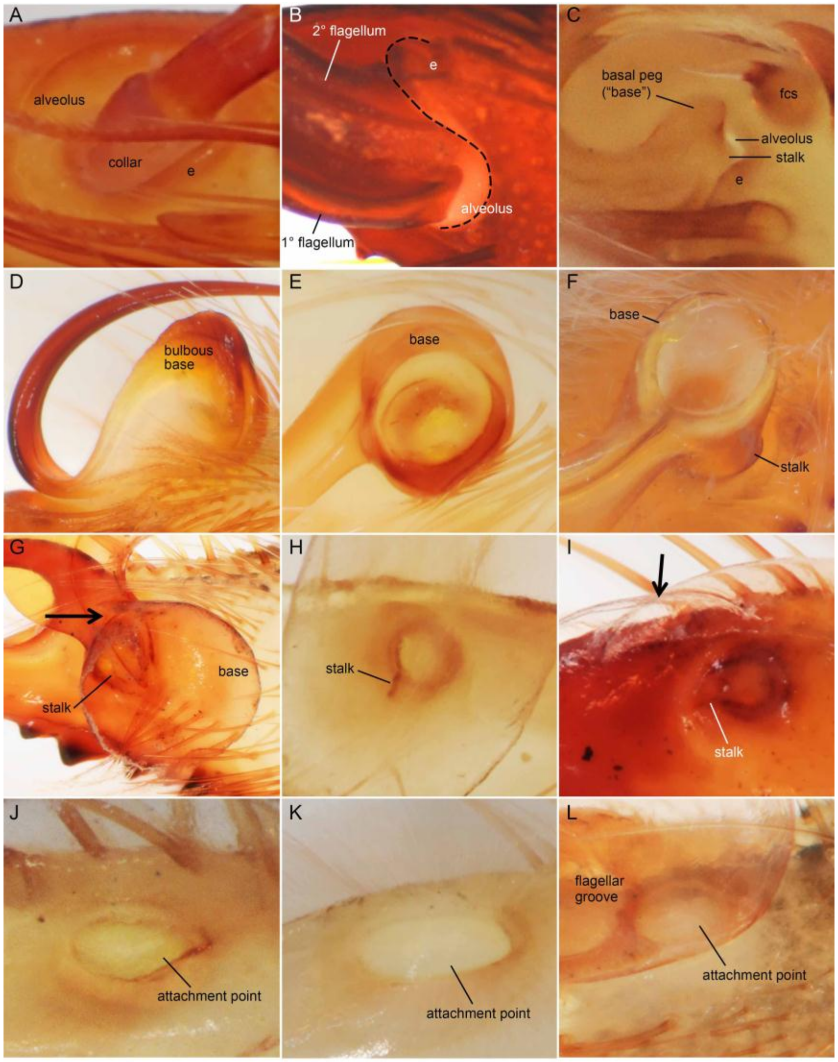

Plate 40. Galeodidae Sundevall, 1833 (**A**), Rhagodidae Pocock, 1897 (**B**), Karschiidae Kraepelin, 1899 (**C**), Solpugidae Leach, 1815 (**D**), Daesiidae Kraepelin, 1899 (**E, G–I**), including Namibesiinae Wharton, 1981 (**E**), Hexisopodidae Pocock, 1897 (**F**), Ammotrechidae Roewer, 1934 (**J, K**), and Mummuciidae Roewer, 1934 (**L**), flagellar attachment points, prolateral views, indicating flagella movably (**A, E–I**) and immovably (**B–D, J–L**) fixed to cheliceral finger. **A.** *Galeodes olivieri* Simon 1879, ♂ (AMNH [LP 4630]). **B.** *Rhagodes melanus* (Olivier, 1807), ♂ (NMNW), Israel: Agur Sands. **C.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♂ (AMNH [LP 7474]). **D.** *Solpugyla* sp., ♂ (AMNH [LP 10764]). **E.** *Namibesia pallida* Lawrence, 1962, ♂ (AMNH [LP 10721]). **F.** *Chelypus shortridgei* Hewitt, 1931, ♂ (NMNW 12632). **G.** *Ammotrechelis goetschi* Roewer, 1934, ♂ (AMNH [LP 10673]). **H.** *Biton* (*B.*) *rossicus* (Birula, 1905), ♂ (AMNH [LP 3959]). **I.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]). **J.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). **K.** *Nothopuga cuyana* Maury, 1976, ♂ (AMNH [LP 2263]). **L.** *Uspallata pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]). Abbreviations: e, elevation of flagellar socket. Arrows (**G, I**) indicate crossover of margins of membranous base.

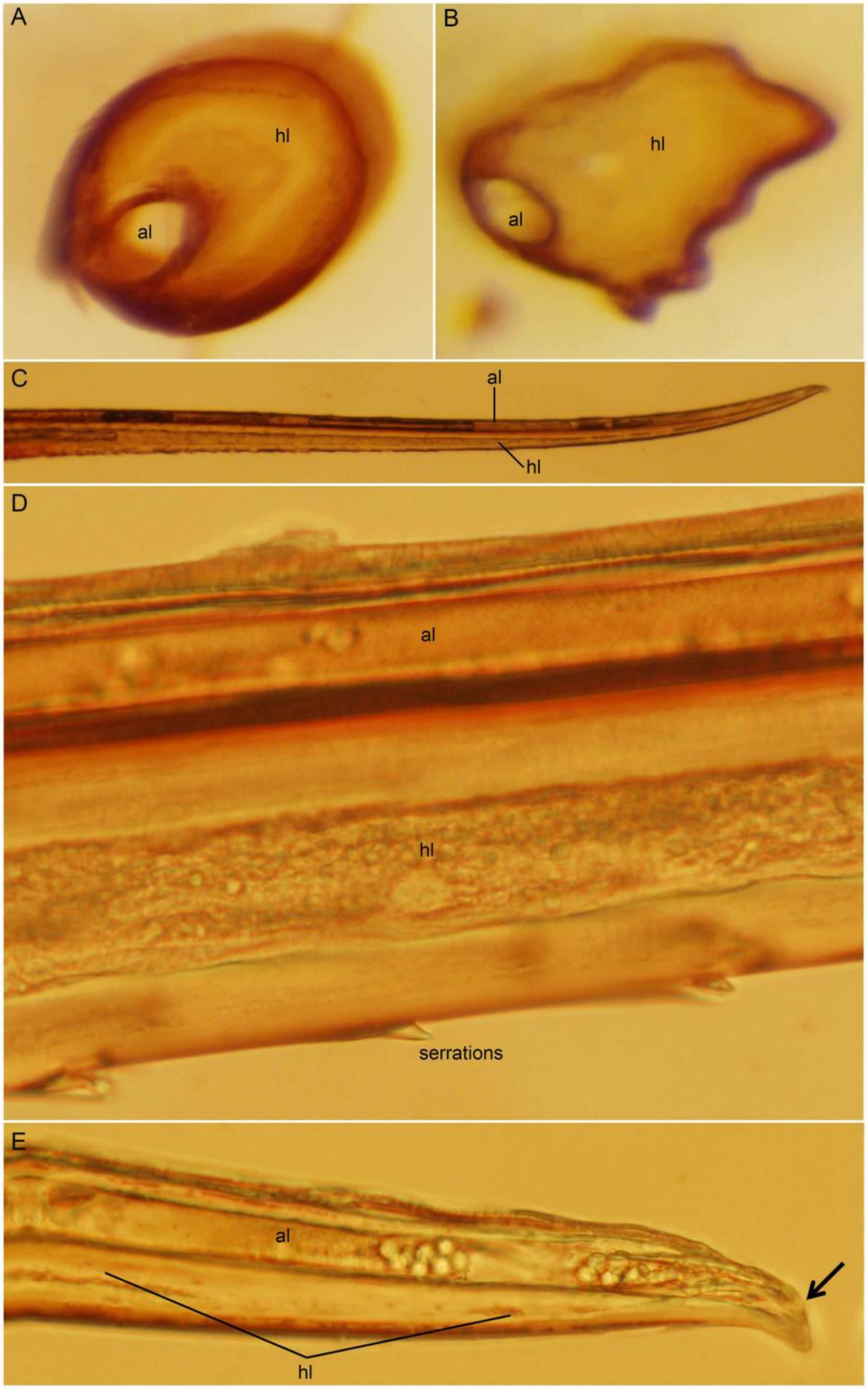

Plate 41. Solpugidae Leach, 1815 (**A**) and Ceromidae Roewer, 1933 (**B–E**), male flagella, cross sections (**A, B**) and whole mount (**C–E**), indicating alembic lumen (=alembic canal) apparently opening externally at the apex (**E**) and broad hemolymph canal near base (**C, D**), narrowing and eventually disappearing towards apex (**C, E**). **A.** *Zeria venator* (Pocock, 1897), ♂ (AMNH [LP 5952]). **B–E.** *Ceroma inerme* Purcell, 1899, ♂ (NMNW 13632). Abbreviations: al, alembic canal; hl, hemolymph canal.

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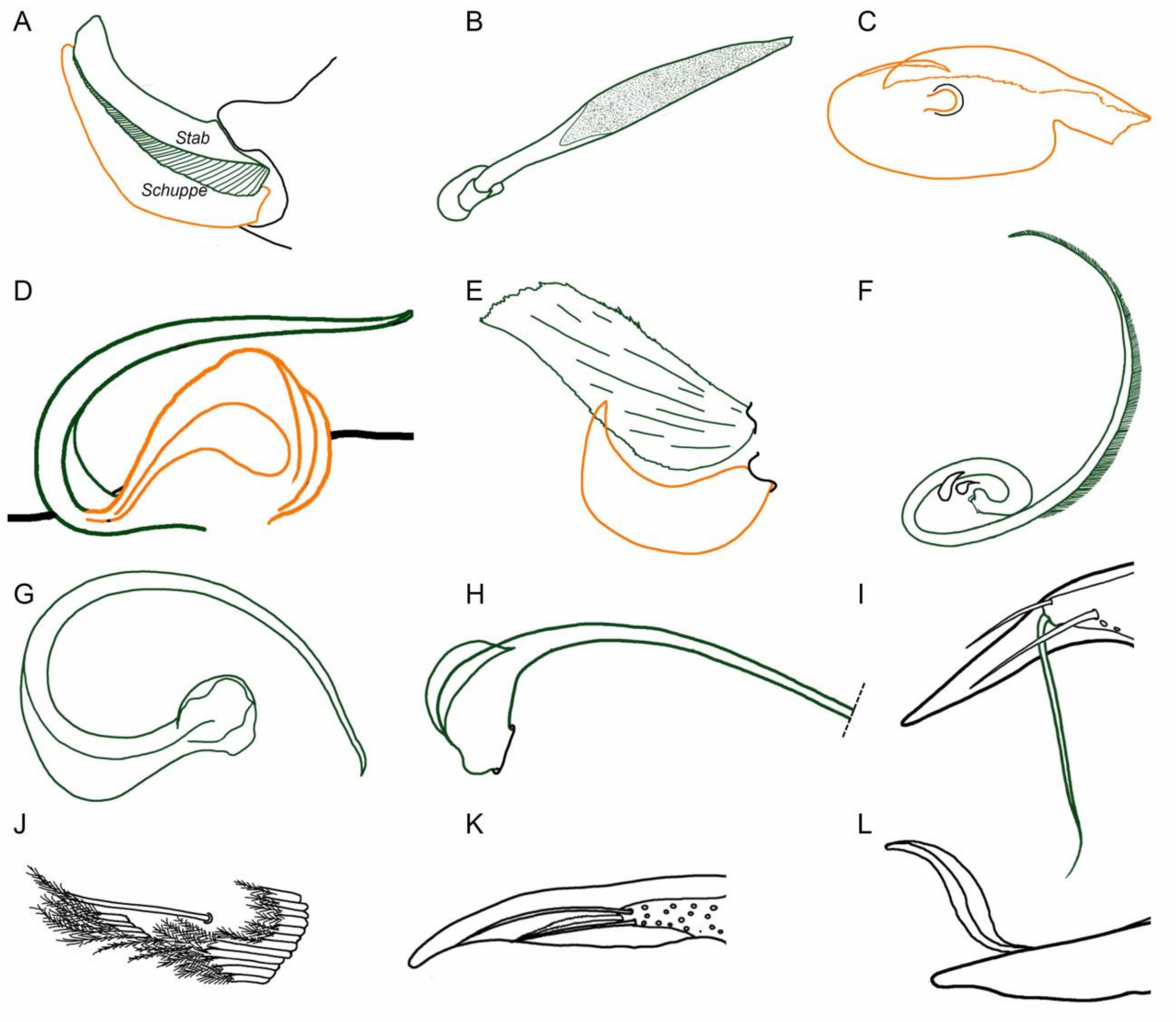

Plate 42. Rhagodidae Pocock, 1897 (**A**), Galeodidae Sundevall, 1833 (**B**), Daesiidae Kraepelin, 1899, (**C**), Solpugidae Leach, 1815 (**D**), Karschiidae Kraepelin, 1899 (**E, F**), *Eusimonia* Kraepelin, 1899 (**E**) and *Karschia* Walter, 1889 (**F**), Hexisopodidae Pocock, 1897 (**G**), Ceromidae Roewer, 1933 (**H**), Melanoblossiidae Roewer, 1933, Dinorhaxinae Roewer, 1933 (**I**) and Melanoblossiinae (**J**), Eremobatidae Kraepelin, 1899 (**K**), and Gylippidae Roewer, 1933, Gylippinae (**L**), schematic representation of Kraepelin's (1908a) hypotheses of flagellar origin based on the two rhagodid flagella, termed the *Stab* (indicated in green) and *Schuppe* (indicated in orange). Uncertain affinities indicated in black.

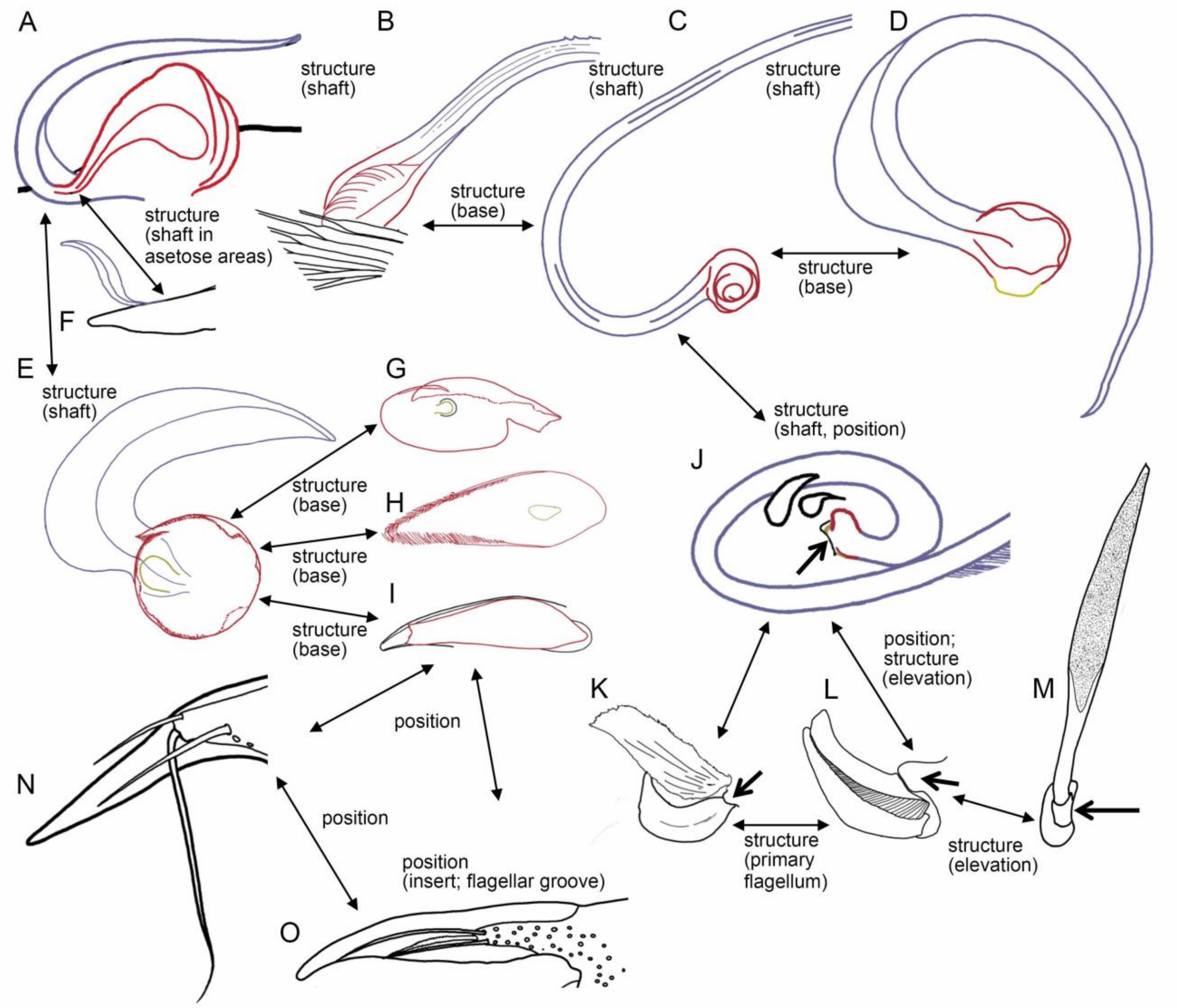

Plate 43. Solpugidae Leach, 1815 (**A**), Ceromidae Roewer, 1933 (**B**), Daesiidae Kraepelin, 1899 (**C, E, G**), including Namibesiinae Wharton, 1981 (**C**) and *Ammotrechelis goetschi* Roewer, 1934 (**E**), Hexisopodidae Pocock, 1897 (**D**), Gylippidae Roewer, 1933, Gylippinae (**F**), Ammotrechidae Roewer, 1934 (**H**), Mummuciidae Roewer, 1934 (**I**), Karschiidae Kraepelin, 1899, *Karschia* Walter, 1889 (**J**), Karschiidae, *Eusimonia* Kraepelin, 1899 (**K**), Rhagodidae Pocock, 1897 (**L**), Galeodidae Sundevall, 1833 (**M**), Melanoblossiidae Roewer, 1933, Dinorhaxinae Roewer, 1933 (**N**), and Eremobatidae Kraepelin, 1899 (**O**), schematic representations of hypothesized single origin of primary flagellum based on structural and positional hypotheses of primary homology. Abbreviations: 1°, primary; 2°, secondary. Short arrows indicate flagellar socket elevation.

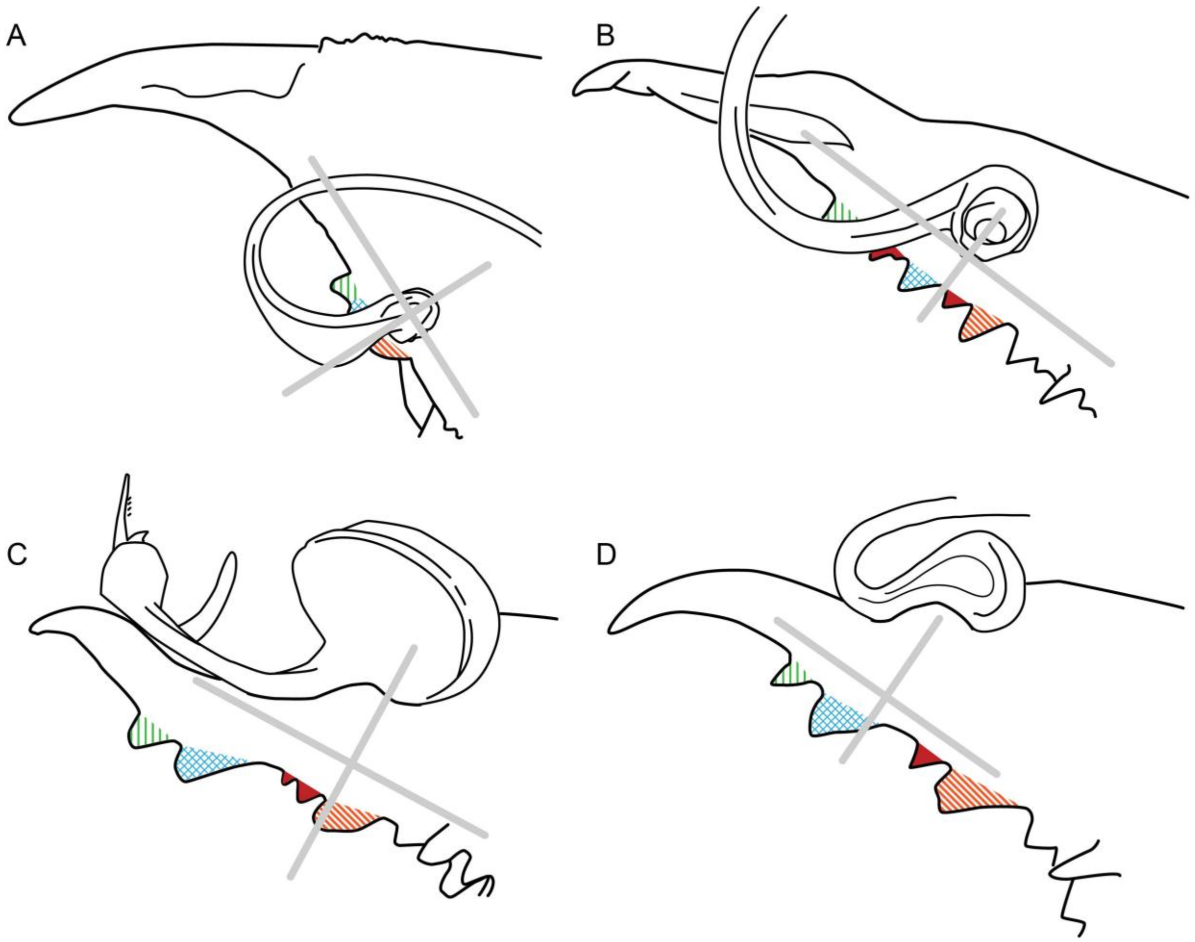

Plate 44. Hexisopodidae Pocock, 1897 (**A**), Daesiidae Kraepelin, 1899, Namibesiinae Wharton, 1981 (**B**), and Solpugidae Leach, 1815 (**C, D**), fixed (dorsal) fingers, prolateral views, indicating point of attachment of the flagellum relative to individual teeth. **A.** *Hexisopus pusillus* Lawrence, 1962, ♂ (NMNW 11426). **B.** *Namibesia pallida* Lawrence, 1962, ♂ (AMNH [LP 10721]), **C.** *Solpuguna* cf. *orangica*, ♂ (AMNH [LP 5969]). **D.** *Zeria keyserlingi* (Pocock, 1895), ♂ (AMNH [LP 4632]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth/teeth.

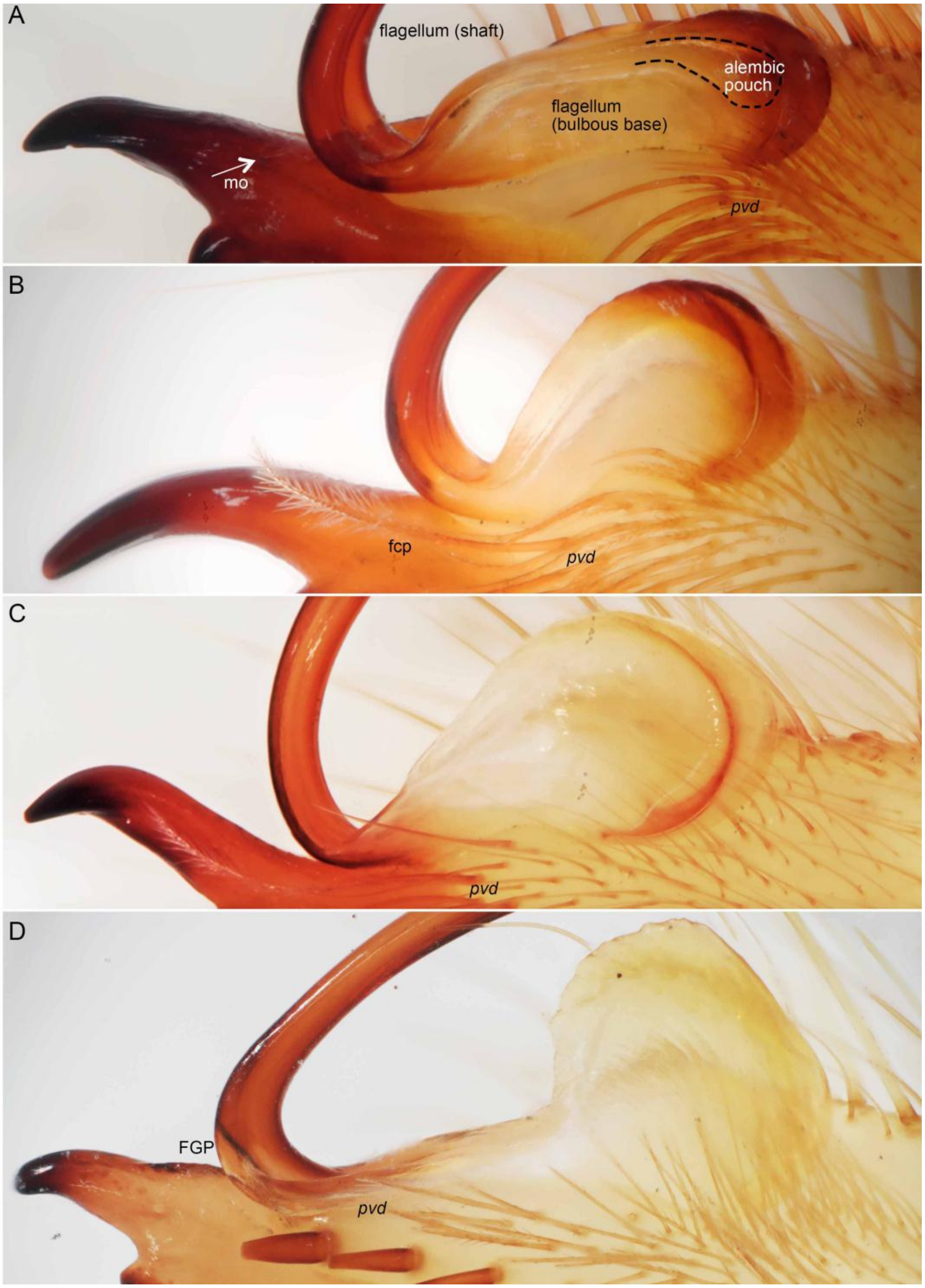

Plate 45. Solpugidae Leach, 1815, fixed (dorsal) finger, prolateral views, indicating proventral distal (*pvd*) setae at base of flagellum, and flagellar attachment point relative to *pvd* setae. **A.** *Zeria carli* (Roewer, 1933), ♂ (AMNH [LP 7915]). **B.** *Zeria adunca* (Roewer, 1933), ♂ (MRAC 216.105). **C.** *Solpugassa furcifera* (Kraepelin, 1899), ♂ (AMNH [LP 3632]). **D.** *Oparba asiatica* (Turk, 1948), ♂ (HUJI 360). Abbreviations: FGP, flagellar groove process; *fcp*, flagellar complex plumose seta; *pvd*, proventral distal setae.

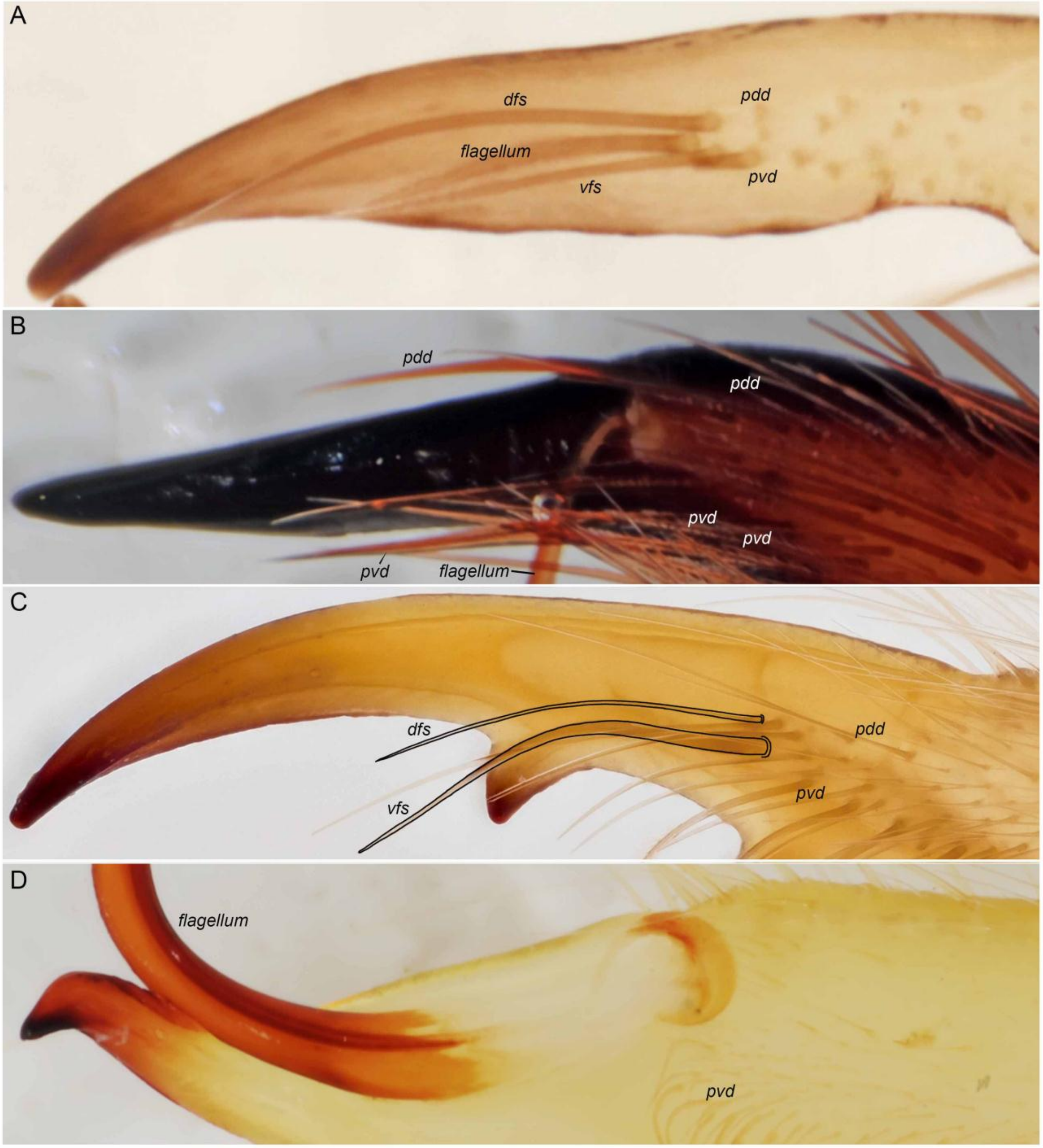

Plate 46. Eremobatidae Kraepelin, 1899 (**A**), Melanoblossiidae Roewer, 1933, Dinorhaxinae Roewer, 1933 (**B**), and Solpugidae Leach, 1815 (**C, D**), cheliceral fixed (dorsal) finger, prolateral views, indicating distal setae. **A.** *Eremochelis oregonensis* Brookhart & Cushing, 2002, holotype ♂ (DMNS ZA.10008). **B.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (AMNH [LP 7537]). **C, D.** *Metasolpuga picta* (Kraepelin, 1899), subad. ♂ (AMNH), Namibia: Gobabeb (**C**), and ♂ (AMNH [LP 10719]) (**D**). Abbreviations: *dfs*, dorsal flagellar seta; *pdd*, prodorsal distal setae; *pvd*, proventral distal setae; v*fs*, ventral flagellar seta.

Plate 47. Eremobatidae Kraepelin, 1899 (**A, B**), Solpugidae Leach, 1815 (**C**), and Daesiidae Kraepelin, 1899 (**E, F**), cheliceral fixed (dorsal) finger, prolateral views, indicating apicalmost setae. **A.** *Hemerotrecha sevilleta* Brookhart & Cushing, 2002, allotype ♀ (DMNS ZA.10007). **B.** *Eremochelis insignatus* Roewer, 1934, ♀ (DMNS ZA.16136). **C.** *Prosolpuga schultzei* (Kraepelin, 1908), ♀ (AMNH [LP 3605]). **D.** *Blossia grandicornis* Lawrence, 1929, ♀ (AMNH [LP 5905]), indicating two setae as potential *dfs*. **E.** *Biton* (*B.*) *rossicus* (Birula, 1905), ♀ (AMNH [LP 3959]). Abbreviations: *dfs*, dorsal flagellar seta; *pdd*, prodorsal distal setae; *pvd*, proventral distal setae; *vfs*, ventral flagellar seta.

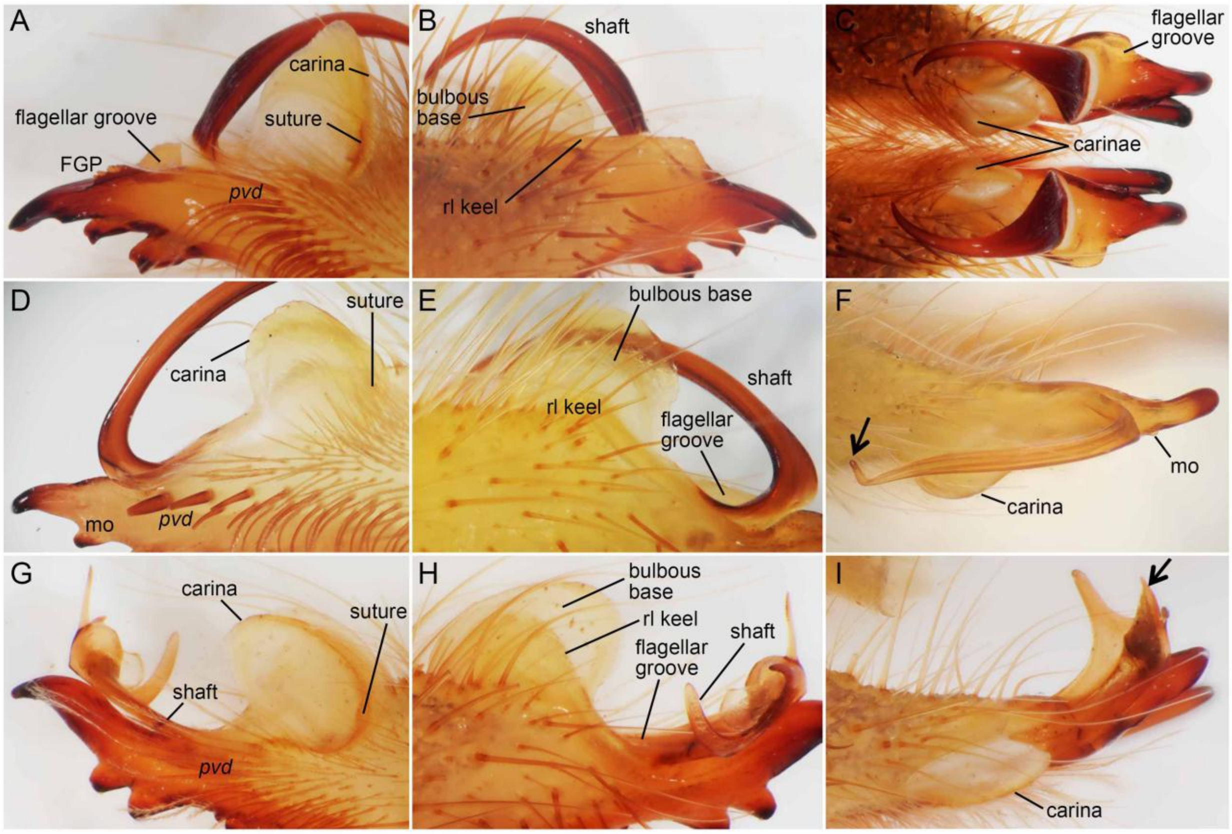

Plate 48. Solpugidae Leach, 1815, cheliceral fixed (dorsal) finger, prolateral (**A, D, G**), retrolateral (**B, E, H**) and dorsal (**C, F, I**) views, indicating different aspects of bulbous base. **A–C.** *Solpugema brachyceras* (Lawrence, 1931), ♂ (AMNH [LP 1960B]). **D–F.** *Oparba asiatica* (Turk, 1948). **D, F.** Holotype ♂ (HUJI). **E.** ♂ (HUJI 360). **G–I.** *Solpuguna* cf. *orangica*, ♂ (AMNH [LP 5969]). Abbreviations: FGP, flagellar groove process; *pvd*, proventral distal setae. Arrows indicate external opening of alembic canal.

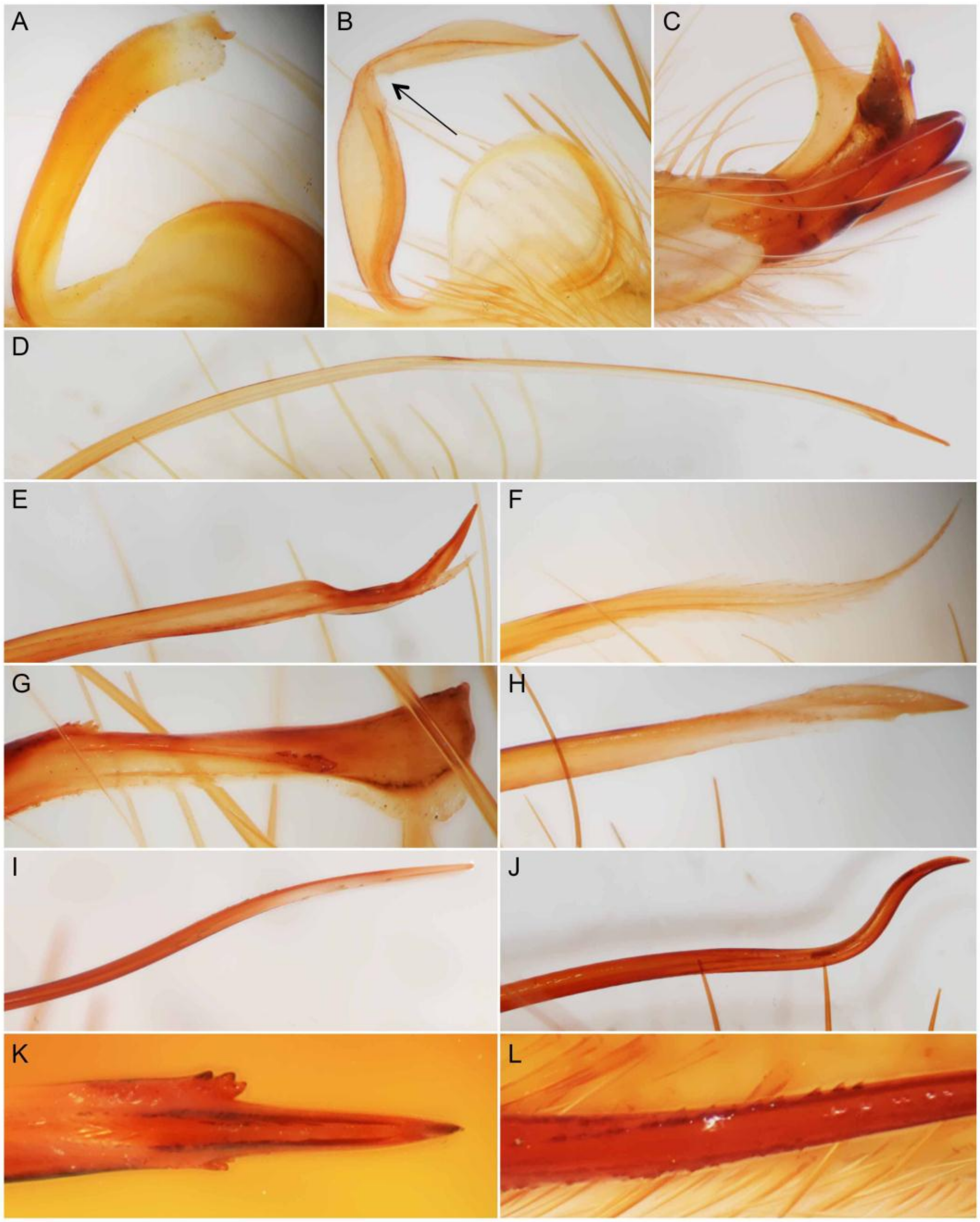

Plate 49. Solpugidae Leach, 1815, cheliceral flagella and flagellar shafts, prolateral (**A, B, D–J**) and dorsal (**C, K, L**) views, indicating structural diversity. **A.** *Solpugella* sp., ♂ (NMNW 11097). **B.** *Solpugema genucornis* (Lawrence, 1935), ♂ (AMNH [LP 8167]). **C.** *Solpuguna* cf. *orangica*, ♂ (AMNH [LP 5969]). **D.** *Solpugista bicolor* (Lawrence, 1953), ♂ (AMNH [LP 7933]). **E.** *Solpugassa furcifera* (Kraepelin, 1899), ♂ (AMNH [LP 3632]). **F.** *Solpugiba lineata* (C.L. Koch, 1842), ♂ (AMNH [LP 5919]). **G.** *Zeria fordi* (Hirst, 1907), ♂ (AMNH [LP 9090]). **H.** *Zeria fusca* (C.L. Koch, 1842), ♂ (AMNH [LP 1473]). **I.** *Zeria carli* (Roewer, 1933), ♂ (AMNH [LP 7915]). **J.** *Zeria venator* (Pocock, 1897), ♂ (AMNH [LP 5952]). **K.** *Zeria lawrencei* (Roewer, 1933), ♂ (AMNH [LP 9906]). **L.** *Zeria keyserlingi* (Pocock, 1895), ♂ (AMNH [LP 4632]). Arrows indicate weakened area of shaft (possible point of articulation).

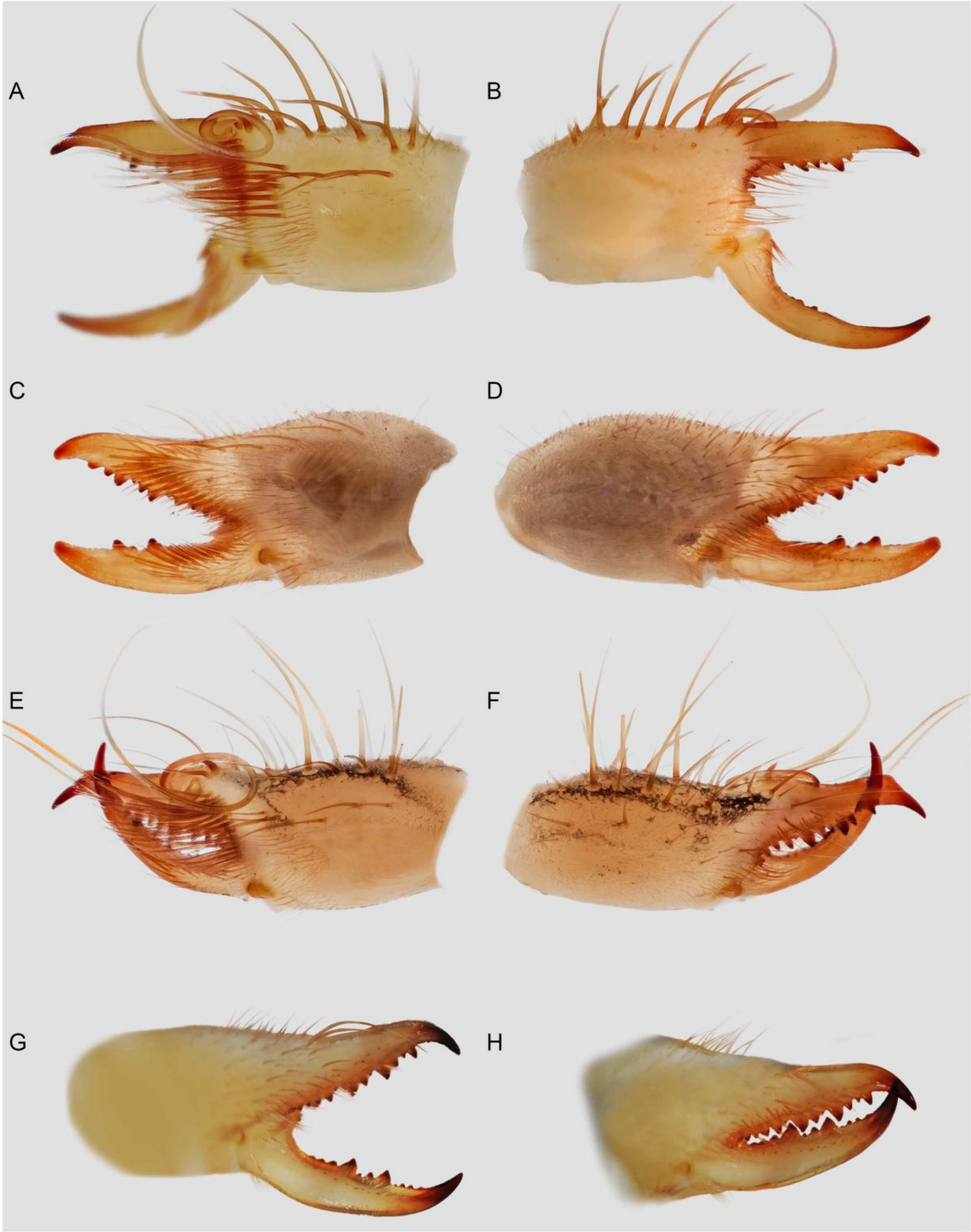

Plate 50. Karschiidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E**) and retrolateral (**B, D, E–H**) views. **A–D.** *Karschia* (*K.*) *mastigofera* Birula, 1890. **A, B.** ♂ (AMNH [LP 7474]). **C, D.** ♀ (AMNH [LP 7476]). **E, F**. *Karschia* (*K.*) *tibetana* Hirst, 1907, ♂ (AMNH [LP 7719]). **G, H.** *Barrussus pentheri* (Werner, 1905), juv. (AMNH [LP 10693]), with cheliceral fingers open (**G**) and closed (**H**).

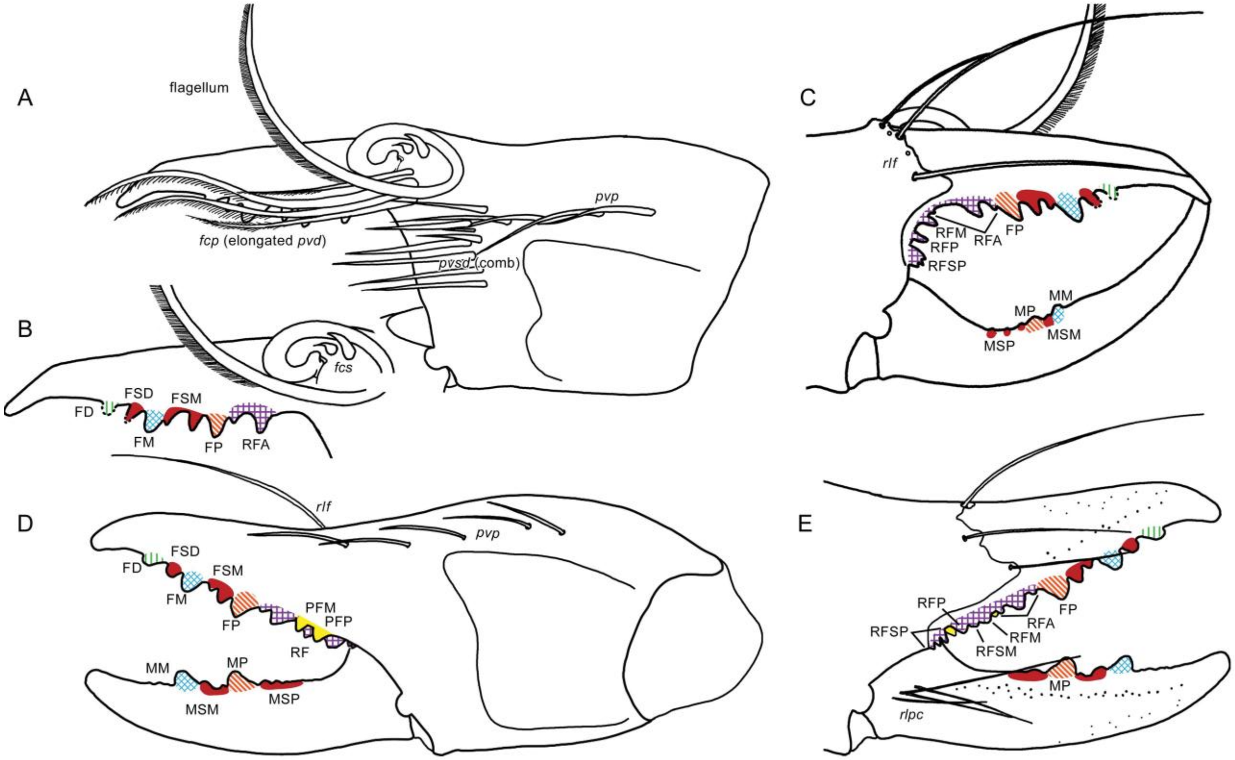

Plate 51. Karschiidae Kraepelin, 1899, *Karschia* (*K.*) *mastigofera* Birula, 1890, chelicerae, prolateral (**A, B, D**) and retrolateral (**C, E**) views illustrating dentition, setae, and flagellar complex. **A–C.** ♂ (AMNH [LP 7474]). **B.** Fixed finger with *pvd* setae not shown to expose dentition. **D, E.** ♀ (AMNH [LP 7476]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; MSP, movable finger, subproximal teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; RFA, retrofondal apical teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal teeth; RFSM, retrofondal submedial tooth; *fcp*, flagellar complex plumose setae; *fcs*, flagellar complex subspiniform setae; *pdp*, prodorsal proximal setae; *pvd*, proventral distal setae; *pvsd*, proventral subdistal setae (setal comb only); *rlf*, retrolateral finger setae; *rlpc*, retrolateral proximal cluster of setae.

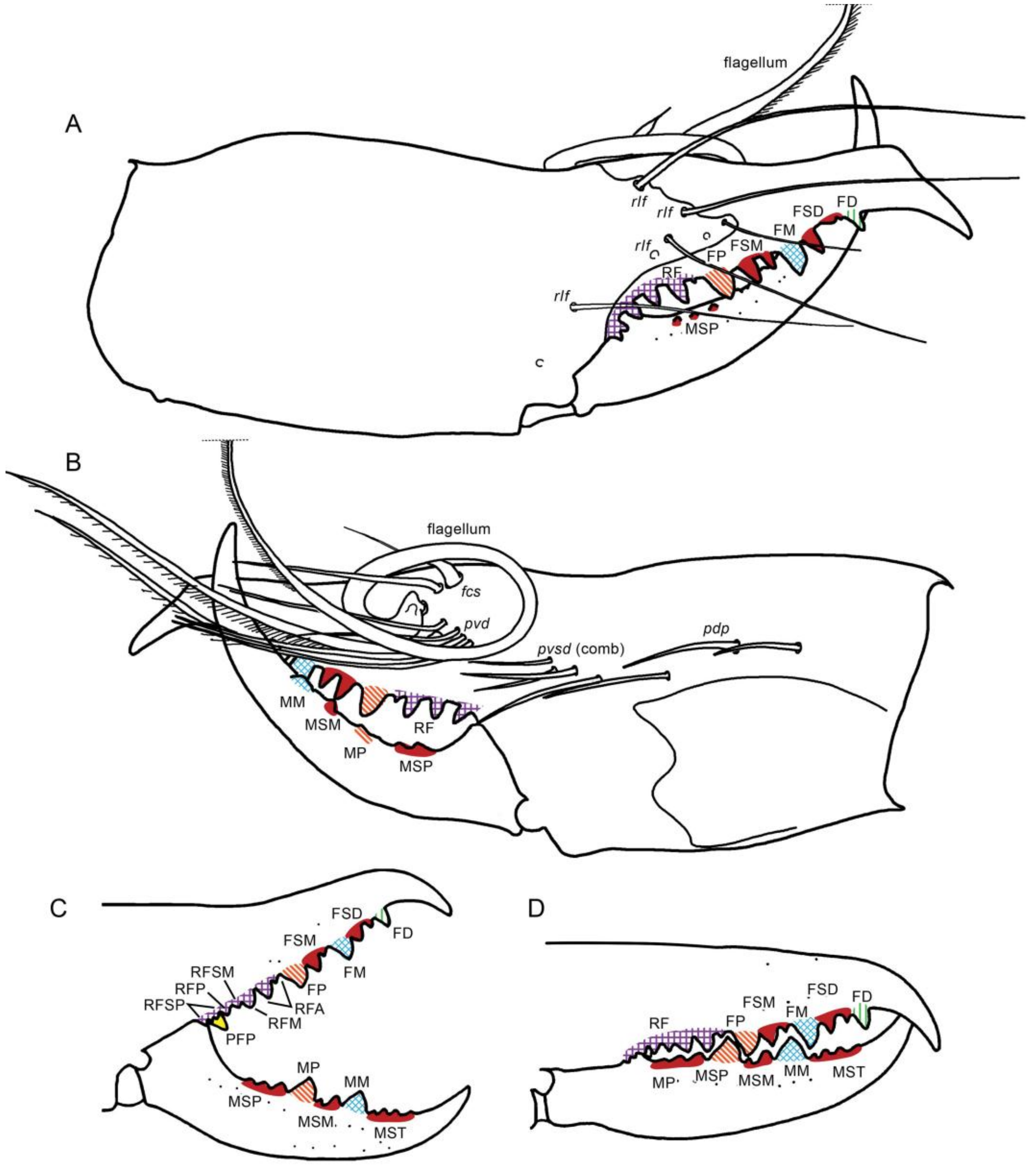

Plate 52. Karschiidae Kraepelin, 1899, chelicerae, prolateral (**B**) and retrolateral (**A, C, D**) views, illustrating dentition, setae, and flagellar complex. **A, B.** *Karschia* (*K.*) *tibetana* Hirst, 1907, ♂ (AMNH [LP 7719]). **C, D.** *Barrussus pentheri* (Werner, 1905), juv. (AMNH [LP 10693]), with cheliceral fingers open (**D**), and closed (**E**). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal teeth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; MSP, movable finger, subproximal teeth; MST, movable finger, subterminal teeth; PFP, profondal proximal teeth; RFA, retrofondal apical teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal teeth; *fcp*, flagellar complex plumose setae; *fcs*, flagellar complex subspiniform setae; *pdp*, prodorsal proximal setae; *pvd*, proventral distal setae’; *pvsd*, proventral subdistal setae (setal comb only); *rlf*, retrolateral finger setae.

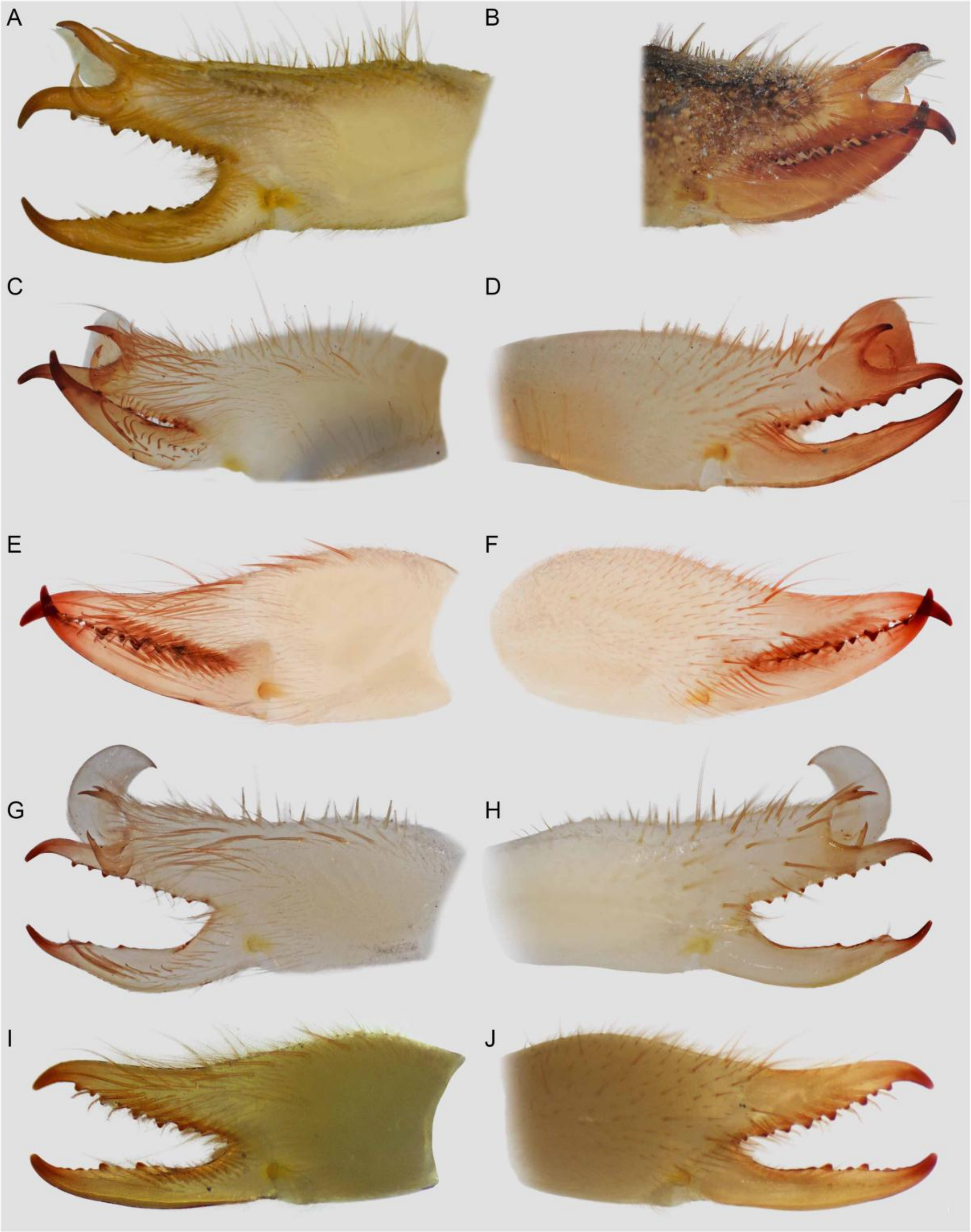

Plate 53. Karschiidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Eusimonia nigrescens* Kraepelin, 1899, ♂ (AMNH [LP 7473]). **C–F.** *Eusimonia turkestana* Kraepelin, 1899. **C, D.** ♂ (AMNH [LP 4096]). **E, F.** ♀ (AMNH [LP 4097]). **G–J.** *Eusimonia divina* Birula, 1935. **G, H.** ♂ (AMNH [LP 4098]). **I, J.** ♀ (AMNH [LP 4098]).

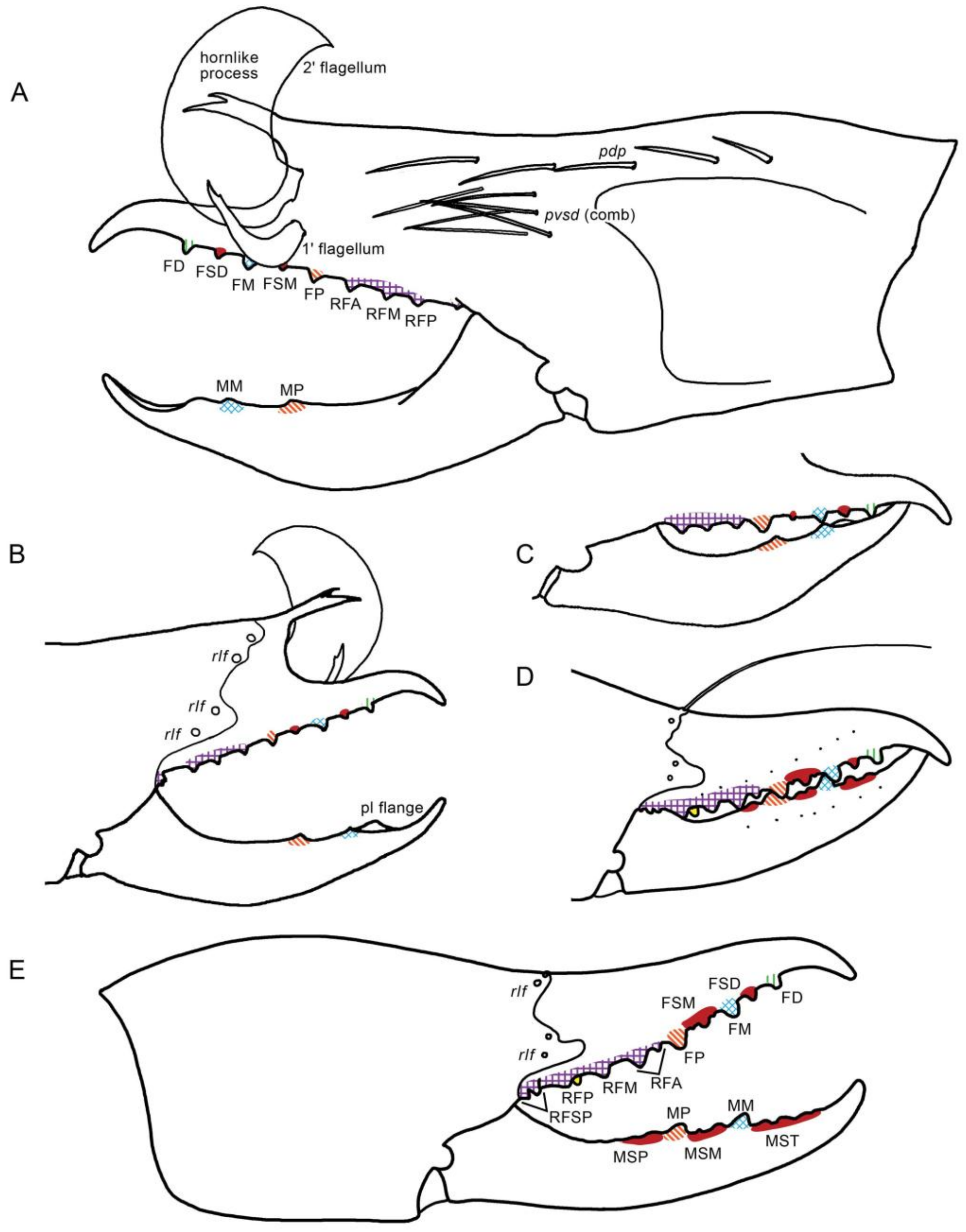

Plate 54. Karschiidae Kraepelin, 1899, *Eusimonia divina* Birula, 1935, chelicerae, prolateral (**A**) and retrolateral (**B–E**) views, illustrating dentition, setae, and flagellar complex. **A–C.** ♂ (AMNH [LP 4098]). **D, E.** ♀ (AMNH [LP 4098]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; MSP, movable finger, subproximal teeth; MST, movable finger, subterminal teeth; RFA, retrofondal apical teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal teeth; *pdp*, prodorsal proximal setae; *pvsd*, proventral subdistal setae (setal comb only); *rlf*, retrolateral finger setae; 1°, primary; 2°, secondary.

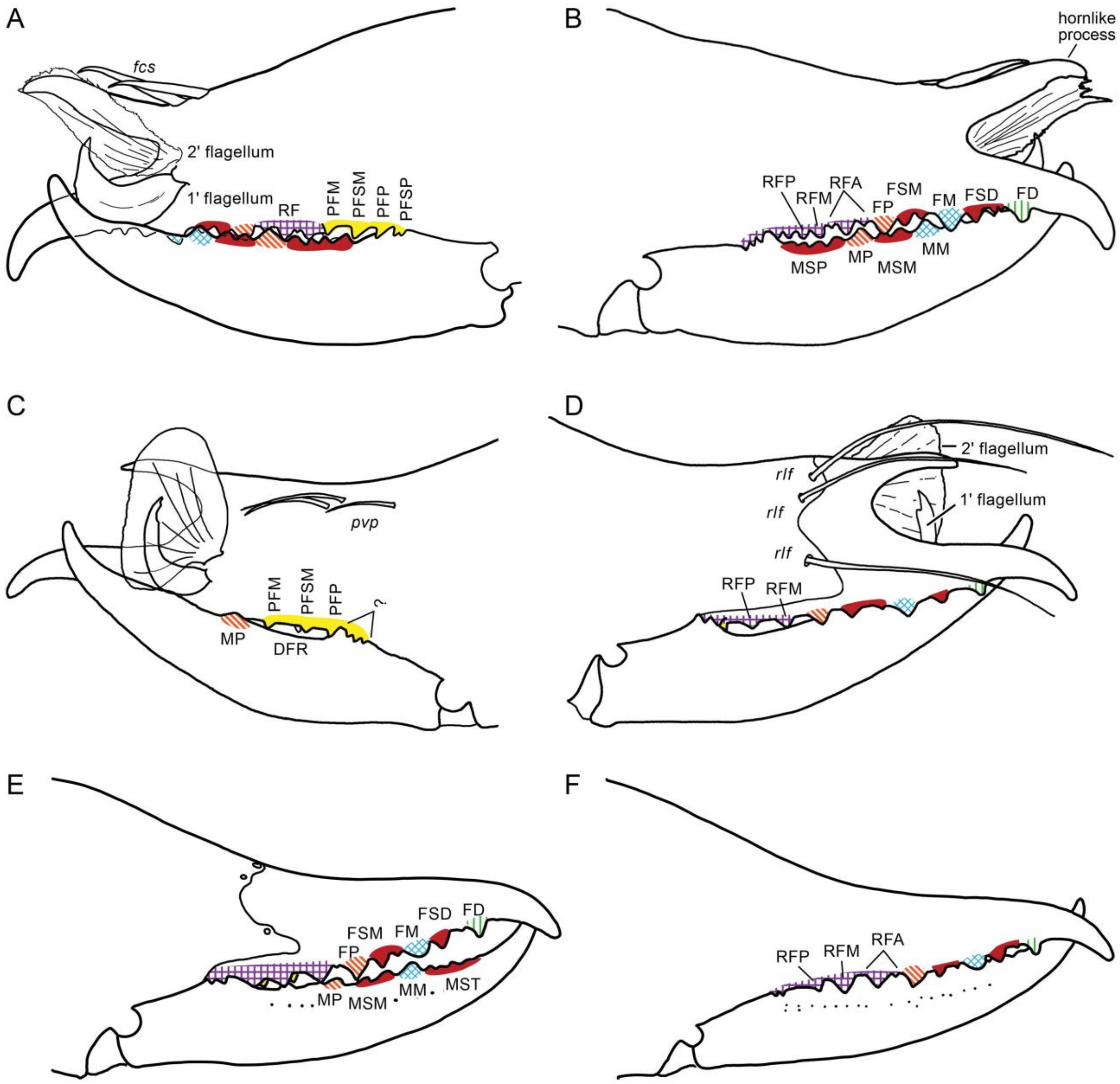

Plate 55. Karschiidae Kraepelin, 1899, chelicerae, prolateral (**A, C**) and retrolateral (**B, D–F**) views, illustrating dentition, setae, and flagellar complex. **A, B.** *Eusimonia nigrescens* Kraepelin, 1899, ♂ (AMNH [LP 7473]). **C–F.** *Eusimonia turkestana* Kraepelin, 1899. **C, D.** ♂ (AMNH [LP 4096]). **E, F.** ♀ (AMNH [LP 4097]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal teeth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; MST, movable finger, subterminal teeth; PFM, profondal medial tooth; PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFA, retrofondal apical teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; *fcs*, flagellar complex subspiniform setae; *pvp*, proventral proximal setae; *rlf*, retrolateral finger setae; 1°, primary; 2°, secondary.

Plate 56. Melanoblossiidae Roewer, 1933, Dinorhaxinae Roewer, 1933 (**A, B**) and Rhagodidae, Pocock, 1897 (**C–H**), chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A, B.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (AMNH [LP 7537]). **C, D.** *Rhagoderma tricolor* Roewer, 1941, ♂ (AMNH [LP 5435]). **E–H.** *Rhagodes melanus* (Olivier, 1807). **E, F.** ♂ (AMNH [LP 2293]). **G, H.** ♀ (AMNH [LP 10549]).

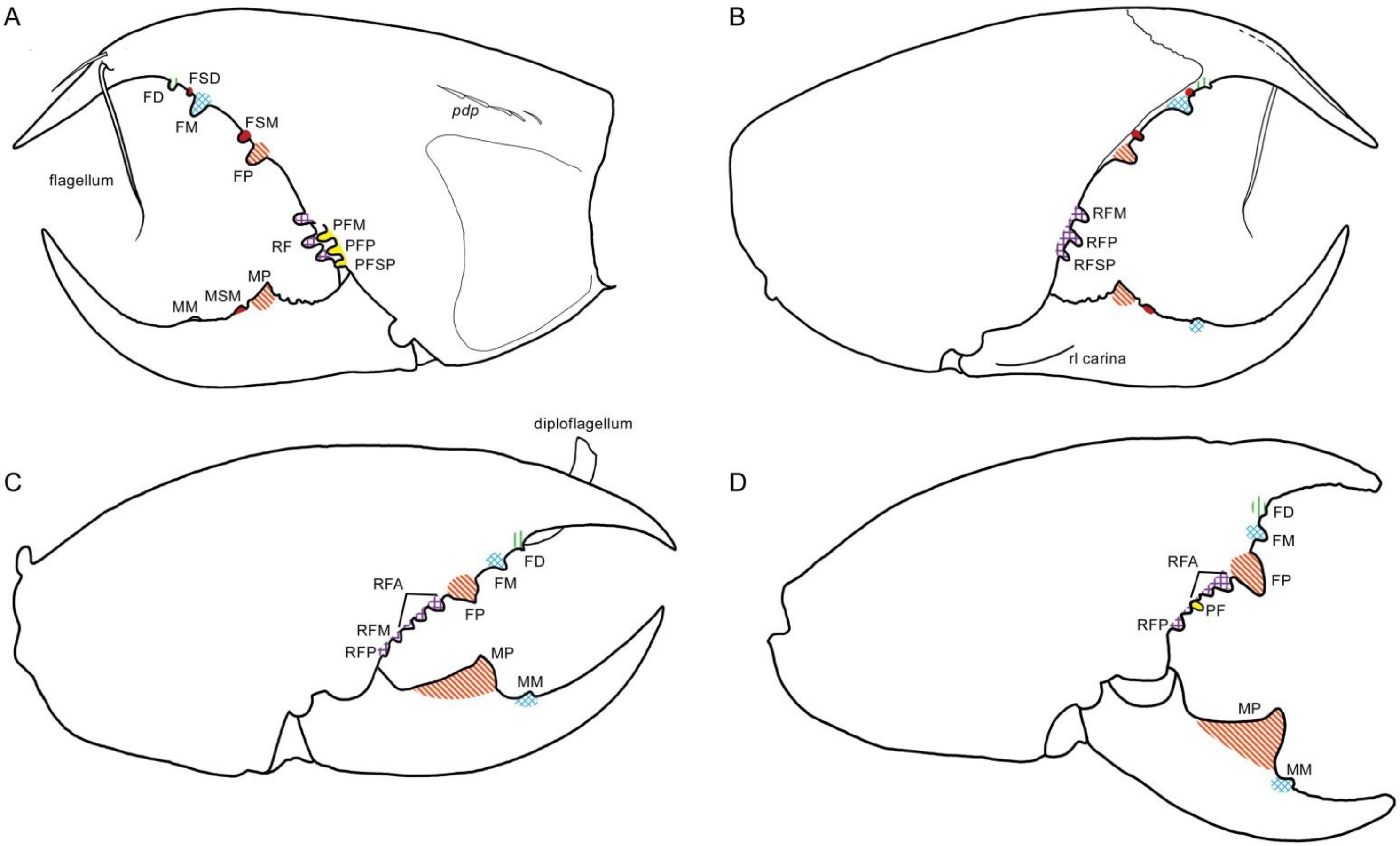

Plate 57. Melanoblossiidae Roewer, 1933, Dinorhaxinae Roewer, 1933 (**A, B**) and Rhagodidae Pocock, 1897 (**C, D**), chelicerae, prolateral (**A**) and retrolateral (**B–D**) views, illustrating dentition, setae, and flagellar complex. **A, B.** *Dinorhax rostrumpsittaci* (Simon, 1877), ♂ (AMNH [LP 7537]). **C, D.** *Rhagodes melanus* (Olivier, 1807). **C.** ♂ (AMNH [LP 2293]). **D.** ♀ (AMNH [LP 10549]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth; PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RFA, retrofondal apical teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal teeth; *pdp*, prodorsal proximal setae; rl, retrolateral.

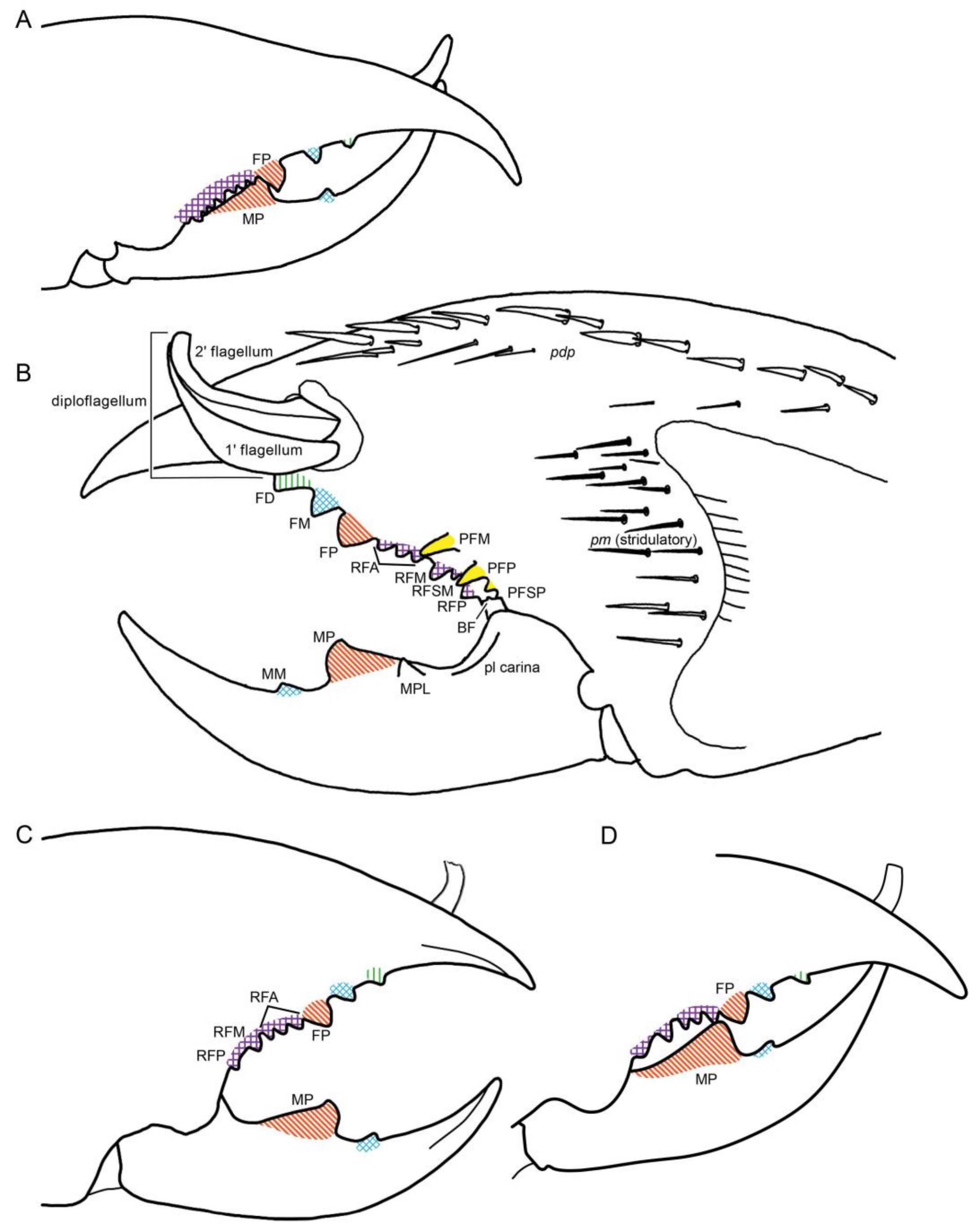

Plate 58. Rhagodidae, Pocock, 1897, chelicerae, prolateral (**B**) and retrolateral (**A, C, D**) views, illustrating dentition, setae, and flagellar complex. **A.** Undetermined ♂ (MCZ 126321). **B–D.** *Rhagoderma tricolor* Roewer, 1941, ♂ (AMNH [LP 5435]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MPL, movable finger, prolateral tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RFA, retrofondal apical teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial teeth; *pdp*, prodorsal proximal setae; *pm*, promedial setae; 1°, primary; 2°, secondary; pl, prolateral.

Plate 59. Galeodidae Sundevall, 1833, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Paragaleodes nesterovi* Birula, 1916, ♂ (AMNH [LP 7480]). **C, D.** *Paragaleodes pallidus* (Birula, 1890), ♂ (AMNH [LP 3922]). **E, F.** *Paragaleodes* sp., ♀ (AMNH [LP 10550]). **G–J.** *Galeodes araneoides* (Pallas, 1772). **G, H.** ♂ (AMNH), Turkey: Gurgen. **I–J.** ♀ (AMNH), Turkey: Gurgen

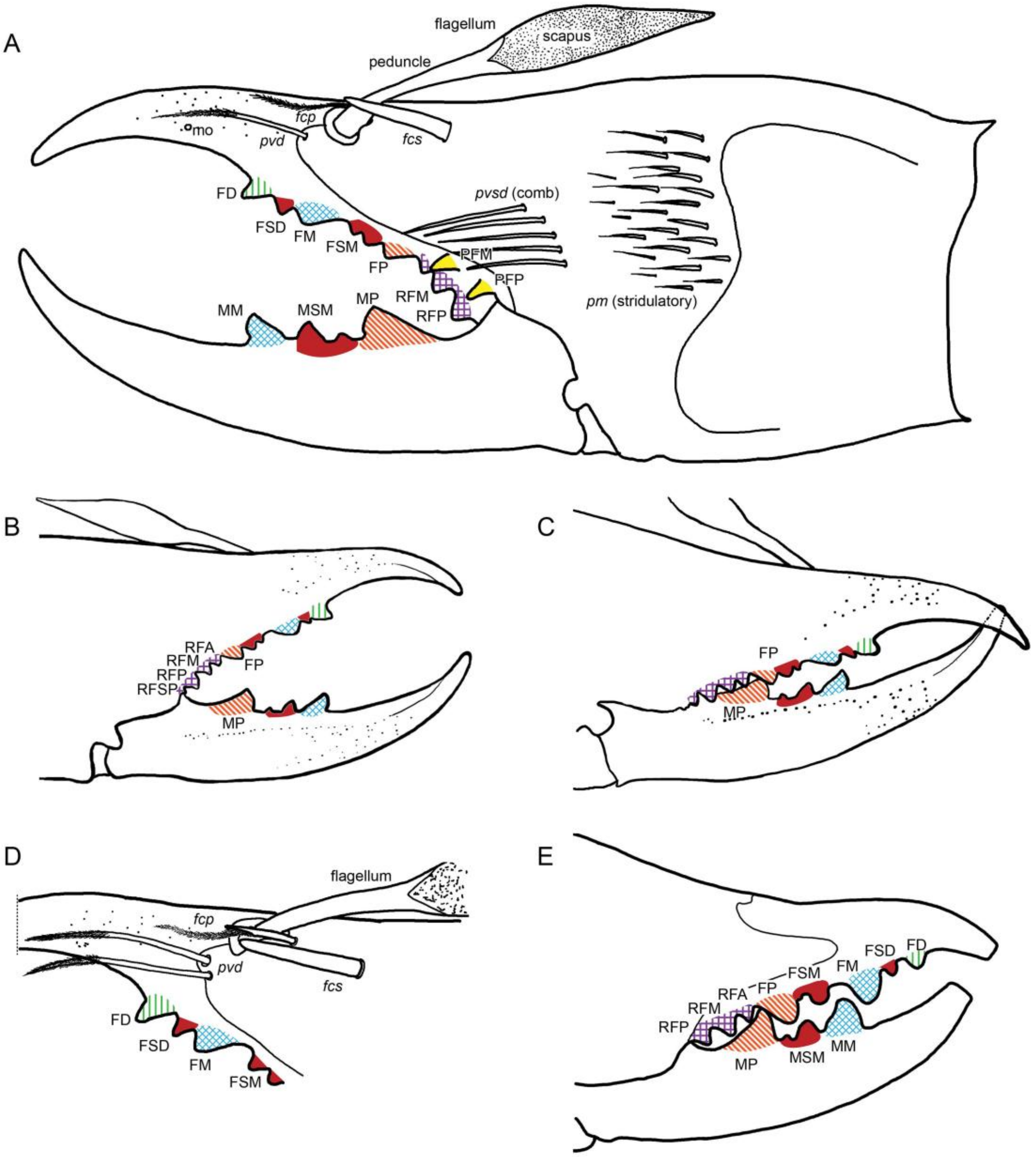

Plate 60. Galeodidae Sundevall, 1833, chelicerae, prolateral (**A, D**) and retrolateral (**B, C, E**) views, illustrating dentition, setae, and flagellar complex. **A–D.** *Paragaleodes pallidus* (Birula, 1890), ♂ (AMNH [LP 3922]) with *fcp* apparent aberrant (spinose proximally and plumose distally). **E.** *Galeodes* sp., ♀ (MCZ), Niger, 120 km W of Birri N'kare. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; RFA, retrofondal apical; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal teeth; *fcp*, flagellar complex plumose setae; *fcs*, flagellar complex spiniform seta; *pm*, promedial setae (only stridulatory setae shown); *pvd*, proventral distal setae (only one or two apicalmost setae shown); *pvsd*, proventral subdistal setae (setal comb only); mo, mucron organ.

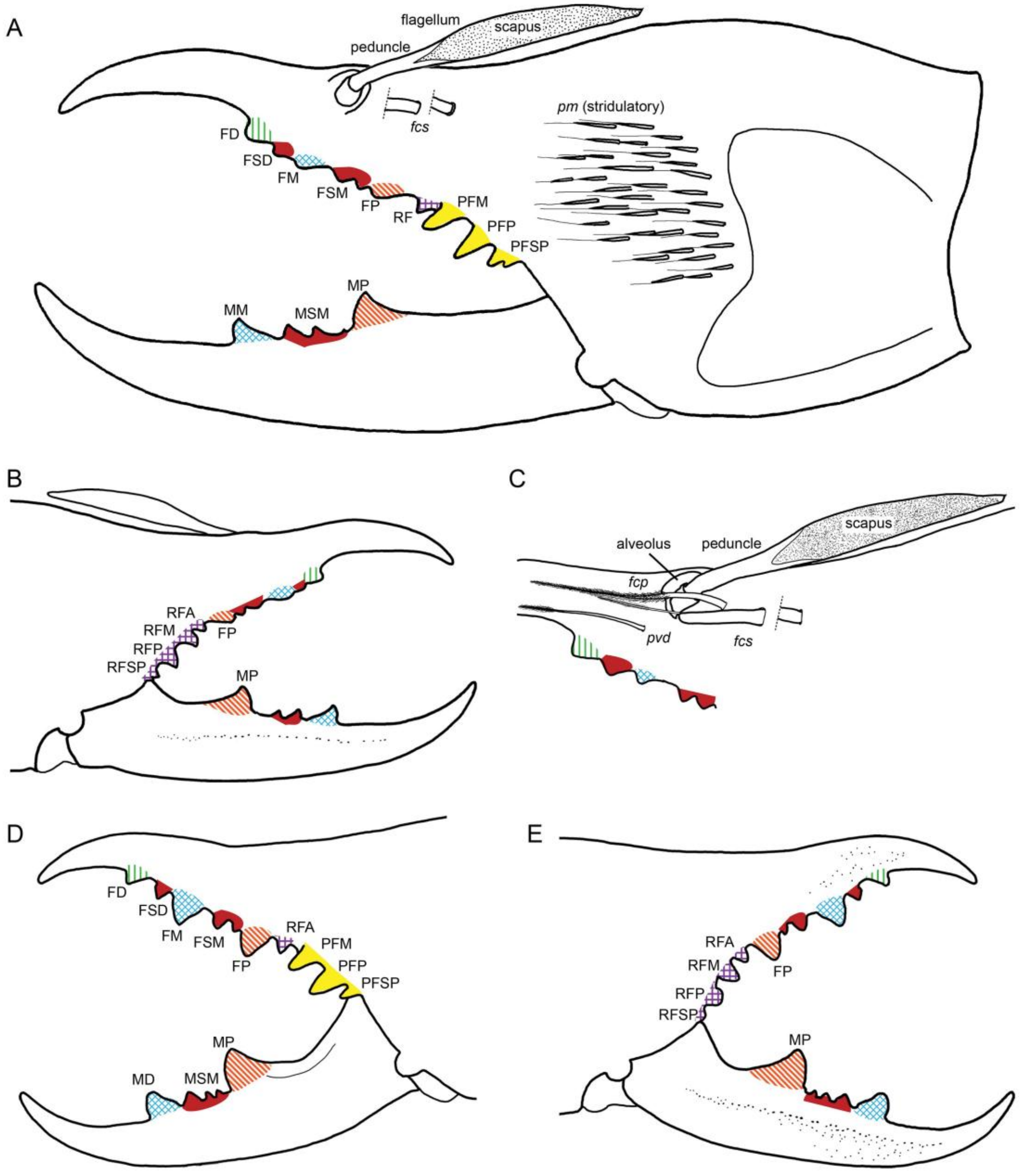

Plate 61. Galeodidae Sundevall, 1833, *Galeodes araneoides* (Pallas, 1772), chelicerae, prolateral (**A, C**) and retrolateral (**B, D, E**) views, illustrating dentition, setae, and flagellar complex. **A–C.** ♂ (AMNH), Turkey: Gurgen. **D, E.** ♀ (AMNH), Turkey: Gurgen. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RFA, retrofondal apical tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal tooth; *fcp*, flagellar complex plumose seta; *fcs*, flagellar complex spiniform setae; *pm*, promedial setae (only stridulatory setae shown); *pvd*, proventral distal setae (only apicalmost seta shown).

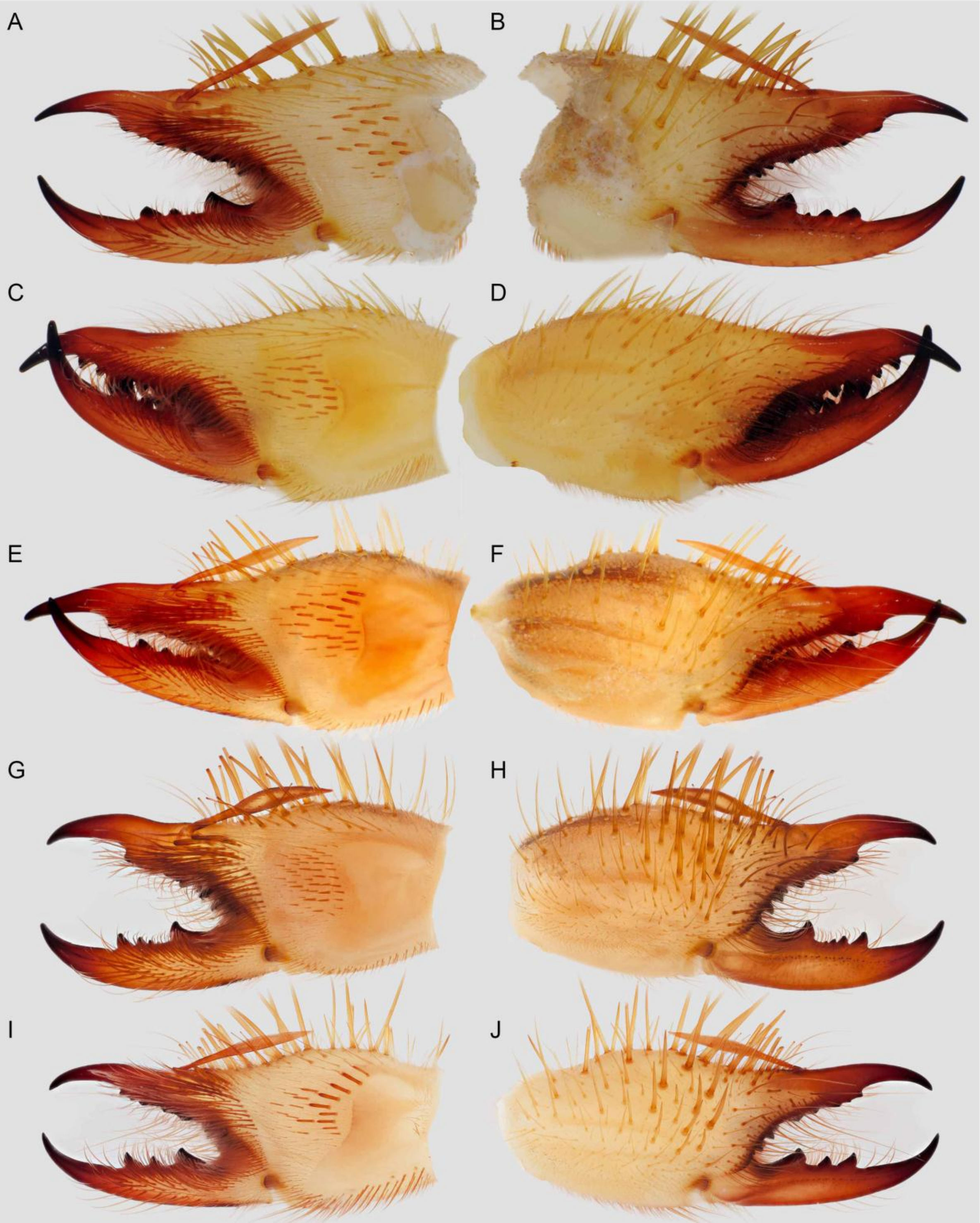

Plate 62. Galeodidae Sundevall, 1833, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A–D.** *Galeodes olivieri* Simon 1879. **A, B.** ♂ (AMNH [LP 4630]). **C, D.** ♀ (AMNH [LP 4628]). **E, F.** *Galeodes arabs* C.L. Koch, 1842, ♂ (AMNH [LP 9123]). **G, H.** *Galeodes toelgi* Werner, 1922, ♂ (AMNH [LP 7536]). **I, J.** *Galeodes* sp., ♂ (AMNH [LP 11204]).

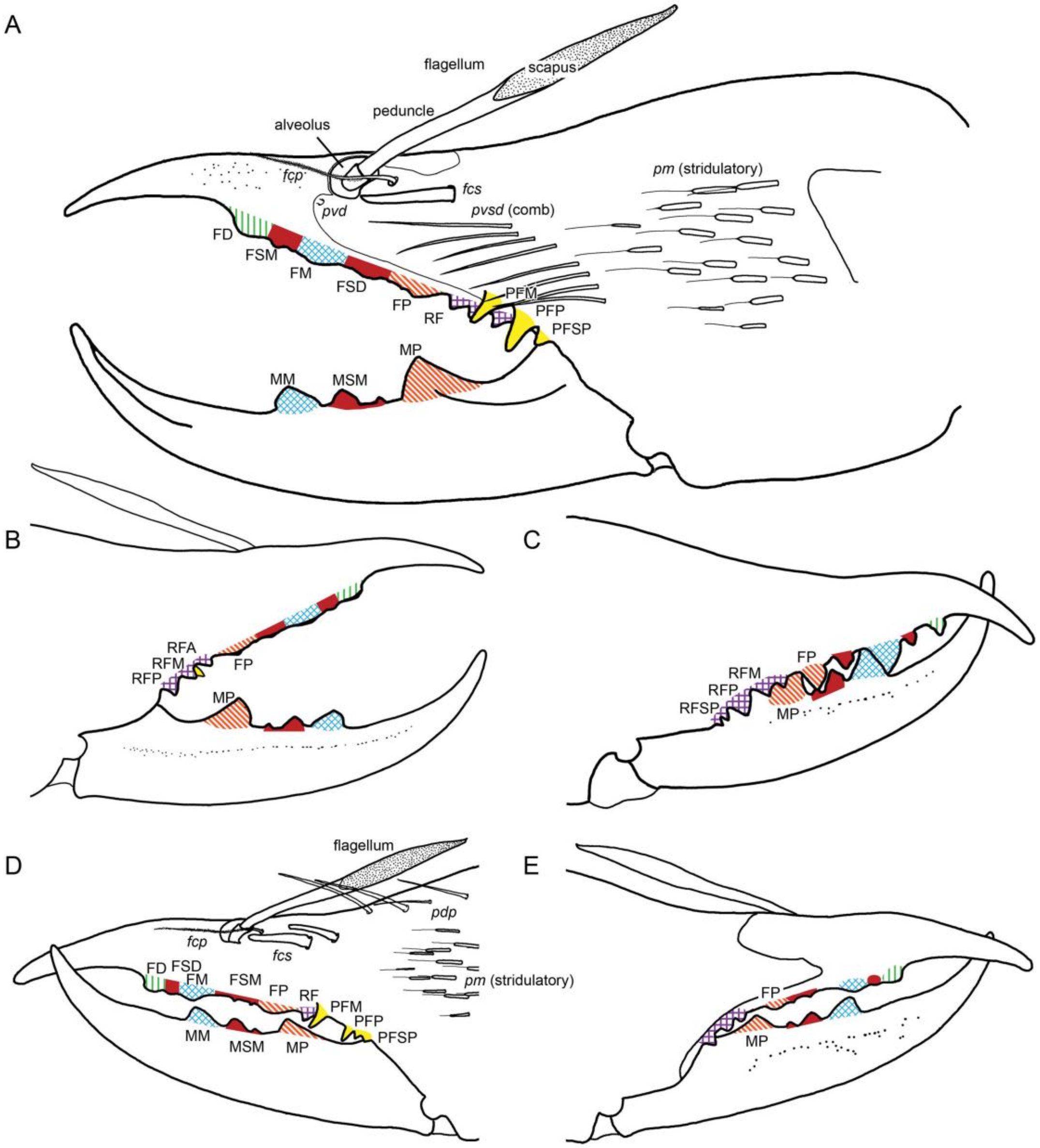

Plate 63. Galeodidae Sundevall, 1833, chelicerae, prolateral (**A, D**) and retrolateral (**B, C, E**) views, illustrating dentition, setae, and flagellar complex. **A–C.** *Galeodes olivieri* Simon 1879*.* **A, B***.* ♂ (AMNH [LP 4630]). **C.** ♀ (AMNH [LP 4628]). **D, E.** *Galeodes arabs* C.L. Koch, 1842, ♂ (AMNH [LP 9123]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal teeth; *fcp*, flagellar complex plumose seta; *fcs*, flagellar complex spiniform setae; *pdp*, prodorsal proximal setae; *pm*, promedial setae (only stridulatory setae shown); *pvd*, proventral distal seta (socket only); *pvsd*, profondal subdistal (setal comb only).

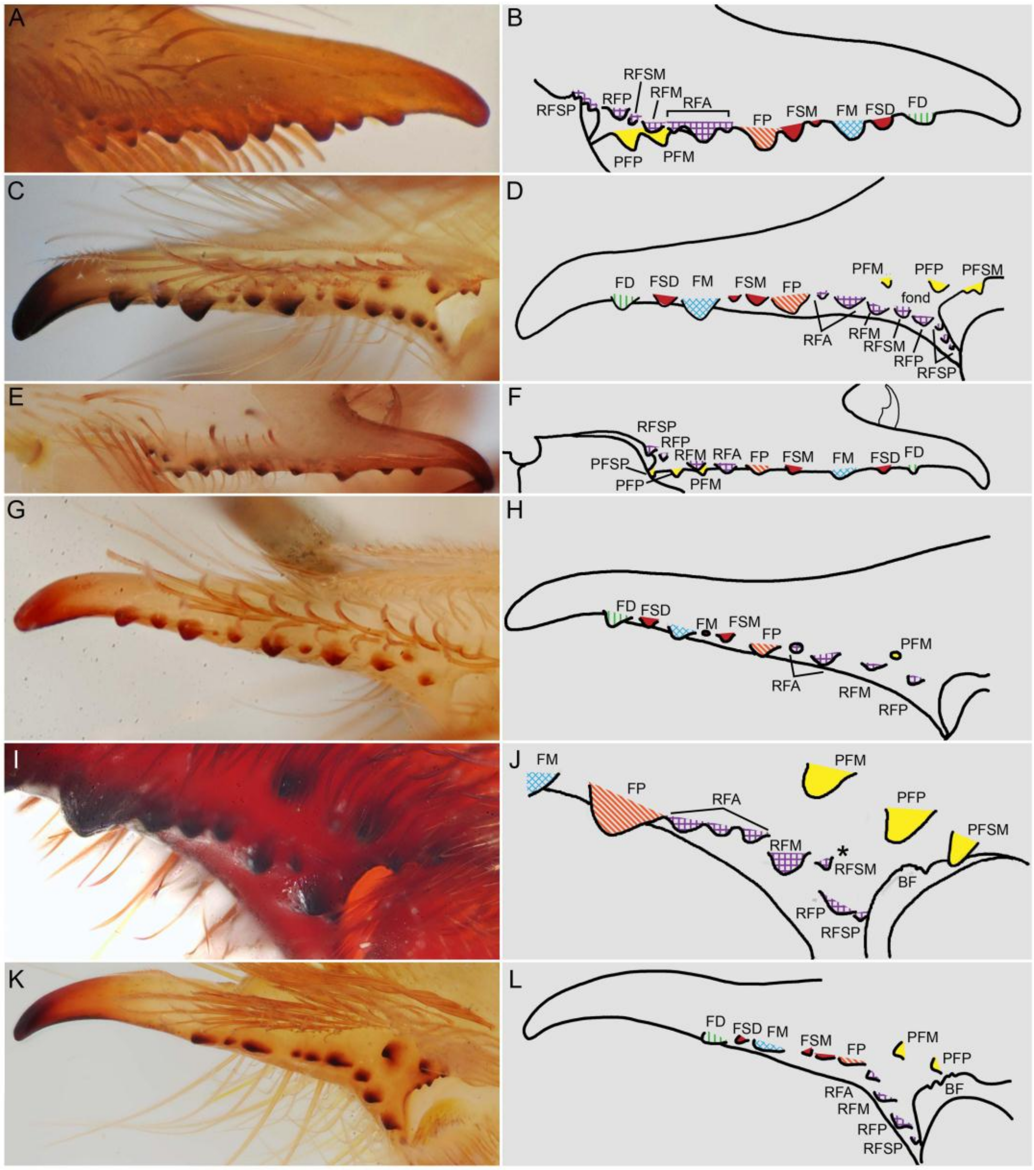

Plate 64. Karschiidae Kraepelin, 1899 (**A–H**), Rhagodidae Pocock, 1897 (**I, J**) and Galeodidae Sundevall, 1833 (**K, L**), cheliceral fixed fingers, proventral (**C, D, G–L**) and retroventral (**A, B, E, F**) views illustrating fondal area and basal fondal teeth (**I, J, K, L**). **A, B.** *Karschia* (*K.*) *mastigofera* Birula, 1890, ♀ (AMNH [LP 7476]). **C, D** *Barrussus pentheri* (Werner, 1905), juv. (AMNH [LP 10693]). **E, F.** *Eusimonia turkestana* Kraepelin, 1899, ♂ (AMNH [LP 4096]). **G, H.** *Eusimonia divina* Birula, 1935, ♀ (AMNH [LP 4098]). **I, J.** *Rhagoderma tricolor* Roewer, 1941, ♂ (AMNH [LP 5435]). **K, L.** *Paragaleodes pallidus* (Birula, 1890), ♂ (AMNH [LP 3922]). Abbreviations: BF, basifondal teeth; FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RFA, retrofondal apical teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP; retrofondal subproximal teeth. Asterisk indicates tooth not visible in retrolateral view.

Plate 65. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A–D.** *Eremobates ajoanus* Muma & Brookhart, 1988. **A, B.** Paratype ♂ (DMNS ZA.17384). **C, D.** Paratype ♀ (DMNS ZA.17311). **E, F.** *Eremobates angustus* Muma, 1951, paratype ♂ (DMNS ZA.16789). **G, H.** *Eremobates bajadae* Muma & Brookhart, 1988, ♂ (AMNH [LP 5740]). **I, J.** *Eremobates bixleri* Muma & Brookhart, 1988, paratype ♂ (DMNS ZA.17386).

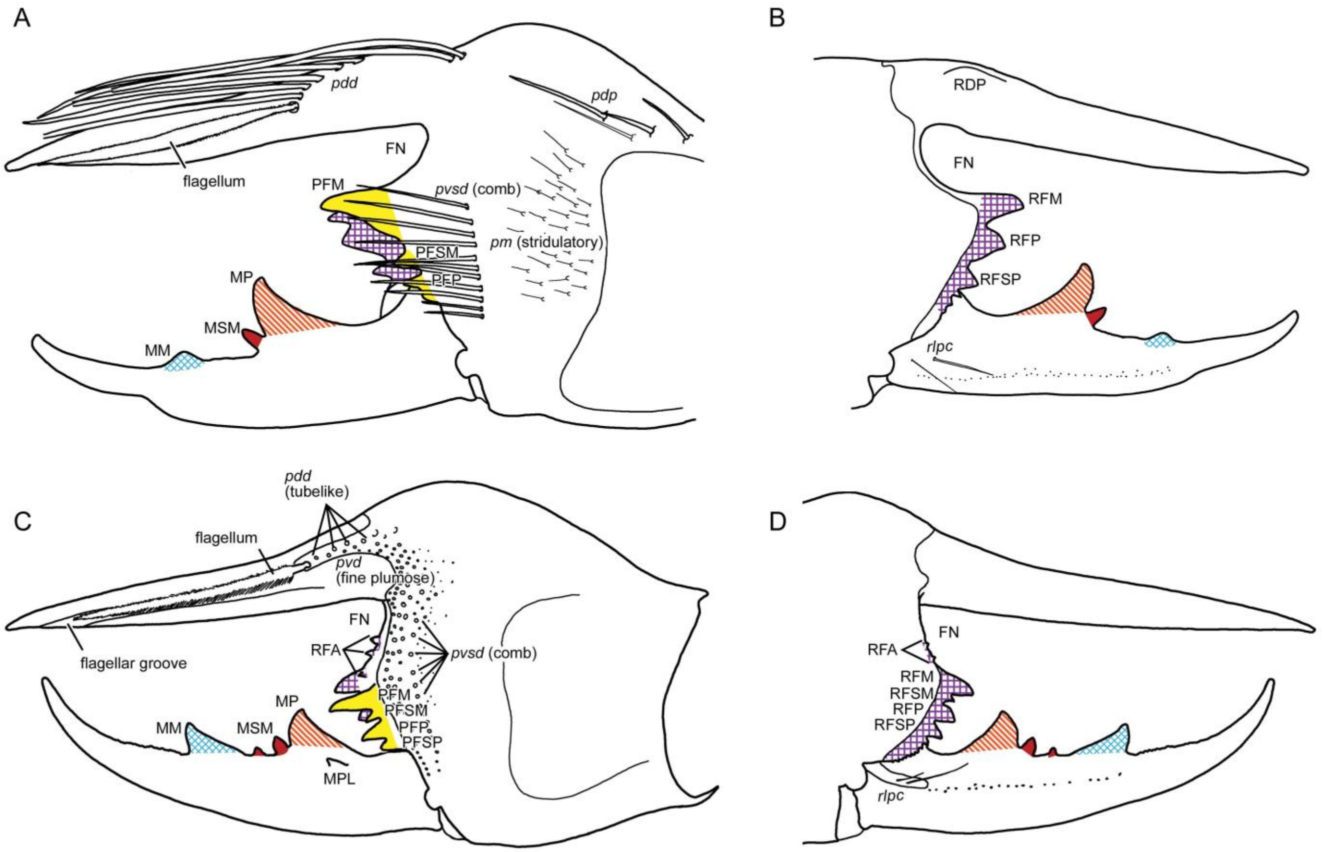

Plate 66. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellar complex. **A, B.** *Eremobates bajadae* Muma & Brookhart, 1988, ♂ (AMNH [LP 5740]). **C, D.** *Eremobates gerbae* Brookhart & Cushing, 2002, holotype ♂ (DMNS ZA.10000). Abbreviations: FN, fondal notch; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MPL, movable finger, prolateral tooth; MSM, movable finger, submedial teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RFA, retrofondal apical teeth (denticles); RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; RDP, retrodorsal process; *pdd*, prodorsal distal setae; *pdp*, prodorsal proximal setae; *pm*, promedial setae (stridulatory setae only); *pvsd*, proventral subdistal setae (including setal comb); *rlpc*, retrolateral proximal cluster of setae.

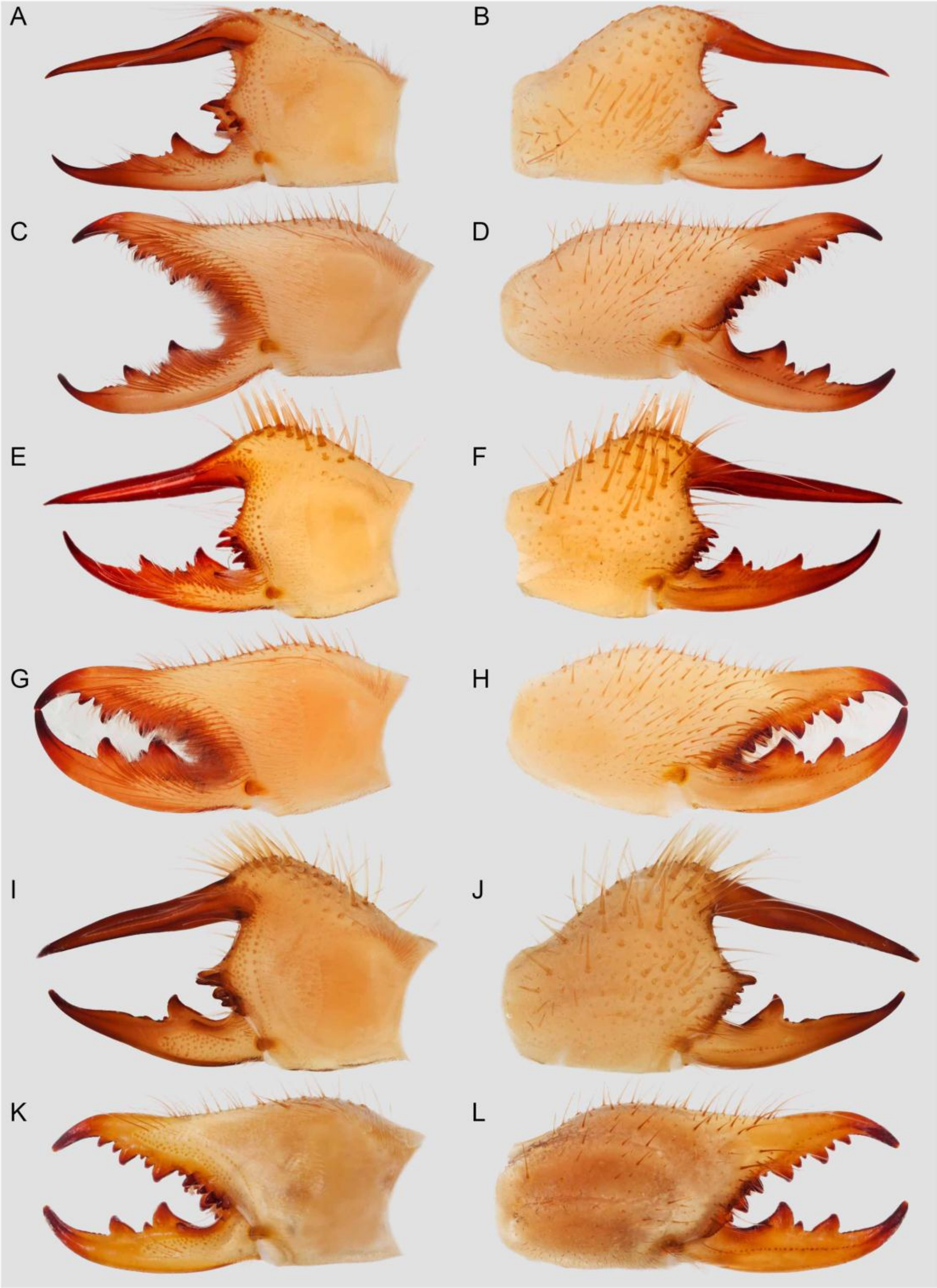

Plate 67. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I, K**) and retrolateral (**B, D, F, H, J, L**) views. **A–D.** *Eremobates corpink* Brookhart & Cushing, 2004. **A, B.** Holotype ♂ (DMNS ZA.17380). **C, D.** Paratype ♀ (DMNS ZA.17379). **E–H.** *Eremobates gerbae* Brookhart & Cushing, 2002. **E, F.** Holotype ♂ (DMNS ZA.10000). **G, H.** Paratype ♀ (DMNS ZA.10001). **I–L.** *Eremobates icenoglei* Brookhart & Cushing, 2004. **I, J.** Holotype ♂ (DMNS ZA.17376). **K, L.** Paratype ♀ (DMNS ZA.17377).

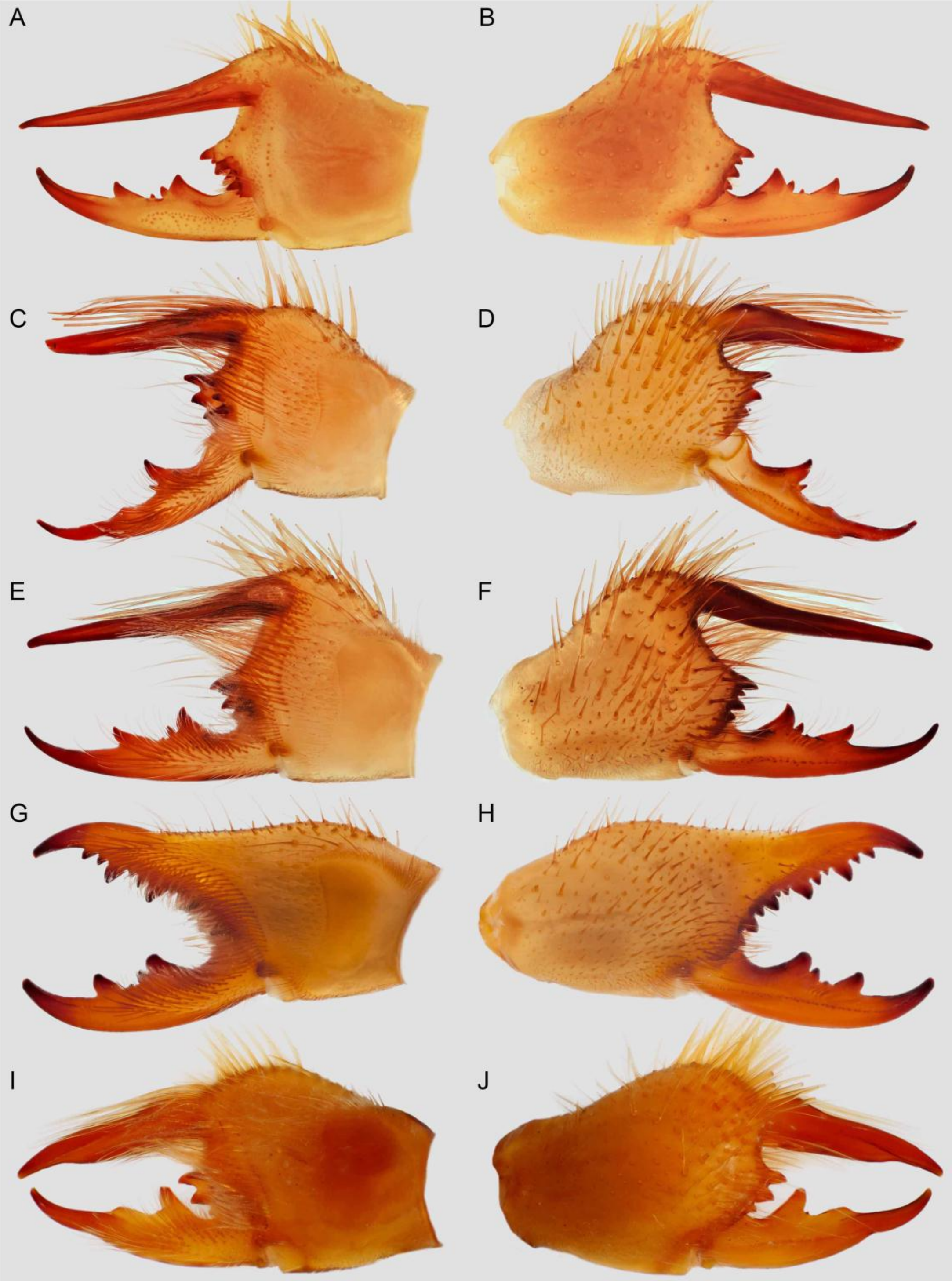

Plate 68. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Eremobates chihuaensis* Brookhart & Cushing, 2002, holotype ♂ (DMNS ZA.10002). **C, D.** *Eremobates palpisetulosus* Fichter, 1941, ♂ (DMNS ZA.15683). **E–H.** *Eremobates pallipes* (Say, 1823). **E, F.** ♂ (DMNS ZA.16258). **G, H.** ♀ (DMNS ZA.15662). **I, J.** *Eremobatus tuberculatus* (Kraepelin, 1899), ♂ (AMNH), Mokelumne Hill.

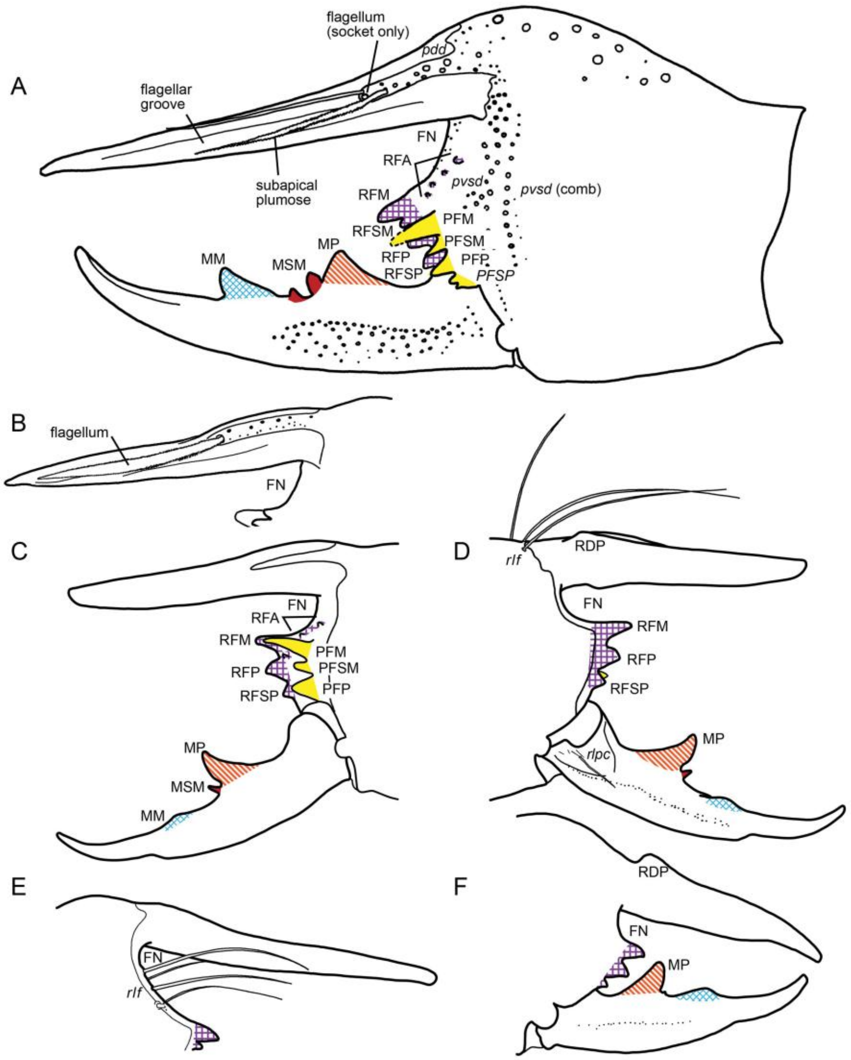

Plate 69. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A–C**) and retrolateral (**D–F**) views, illustrating dentition, setae, and flagellar complex. **A.** *Eremobates chihuaensis* Brookhart & Cushing, 2002, holotype ♂ (DMNS ZA.10002). **B.** *Eremobates* cf. *palpisetulosus*, ♂ (AMNH), Mexico: Coahuila, dorsal finger showing male flagellum (apical setae) and setal sockets. **C, D.** *Eremobates palpisetulosus* Fichter, 1941, ♂ (DMNS ZA.15683). **E.** *Eremobates pallipes* (Say, 1823), ♂ (DMNS ZA.16258), dorsal finger showing setae situated distal in fondal notch. **F.** *Eremobatus tuberculatus* (Kraepelin, 1899), ♂ (AMNH), Mokelumne Hill. Abbreviations: FN, fondal notch; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal teeth; RDP, retrodorsal process; RFA, retrofondal apical teeth (denticles); RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal tooth; *pdd*, prodorsal distal setae; *pvd*, proventral distal setae; *pvsd*, proventral subdistal setae (including setal comb); *rlf*, retrolateral finger setae; *rlpc*, retrolateral proximal cluster of setae; *rlms*, retrolateral manus setae.

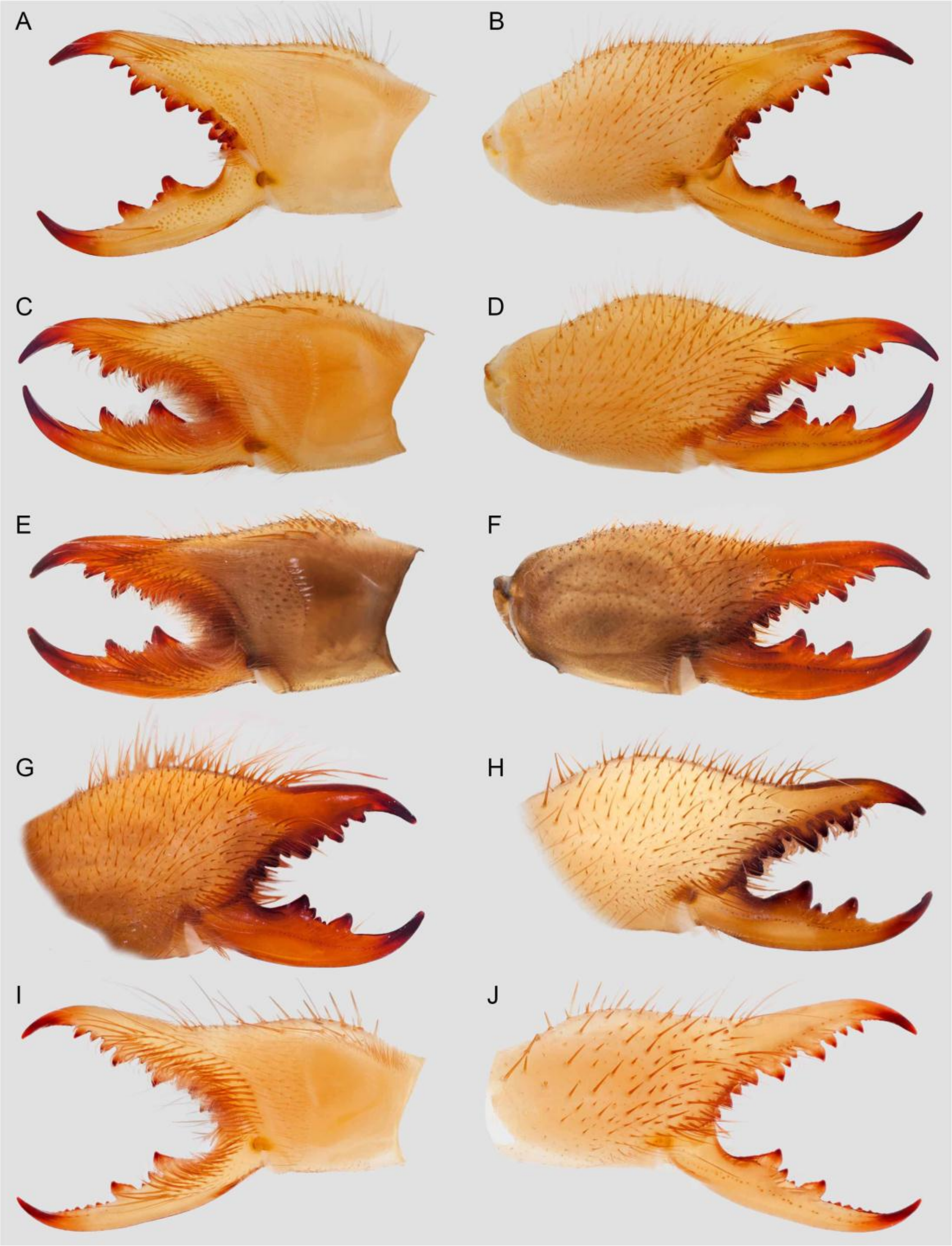

Plate 70. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, I**) and retrolateral (**B, D, F–H, J**) views. **A, B.** *Eremobates polhemusi* Muma & Brookhart, 1988, ♀ (DMNS ZA.10004). **C, D.** *Eremobates inkopaensis* Brookhart & Cushing, 2005, paratype ♀ (DMNS ZA.17310). **E, F.** *Eremobates kiseri* Muma & Brookhart, 1988, paratype ♀ (DMNS ZA.17385). **G.** *Eremobates norrisi* Muma & Brookhart, 1988, paratype ♀ (DMNS ZA.17383). **H.** *Eremobates socal* Brookhart & Cushing, 2004, paratype ♀ (DMNS ZA.17378). **I, J.** *Horribates bantai* Muma, 1989, ♀ (DMNS ZA.17691).

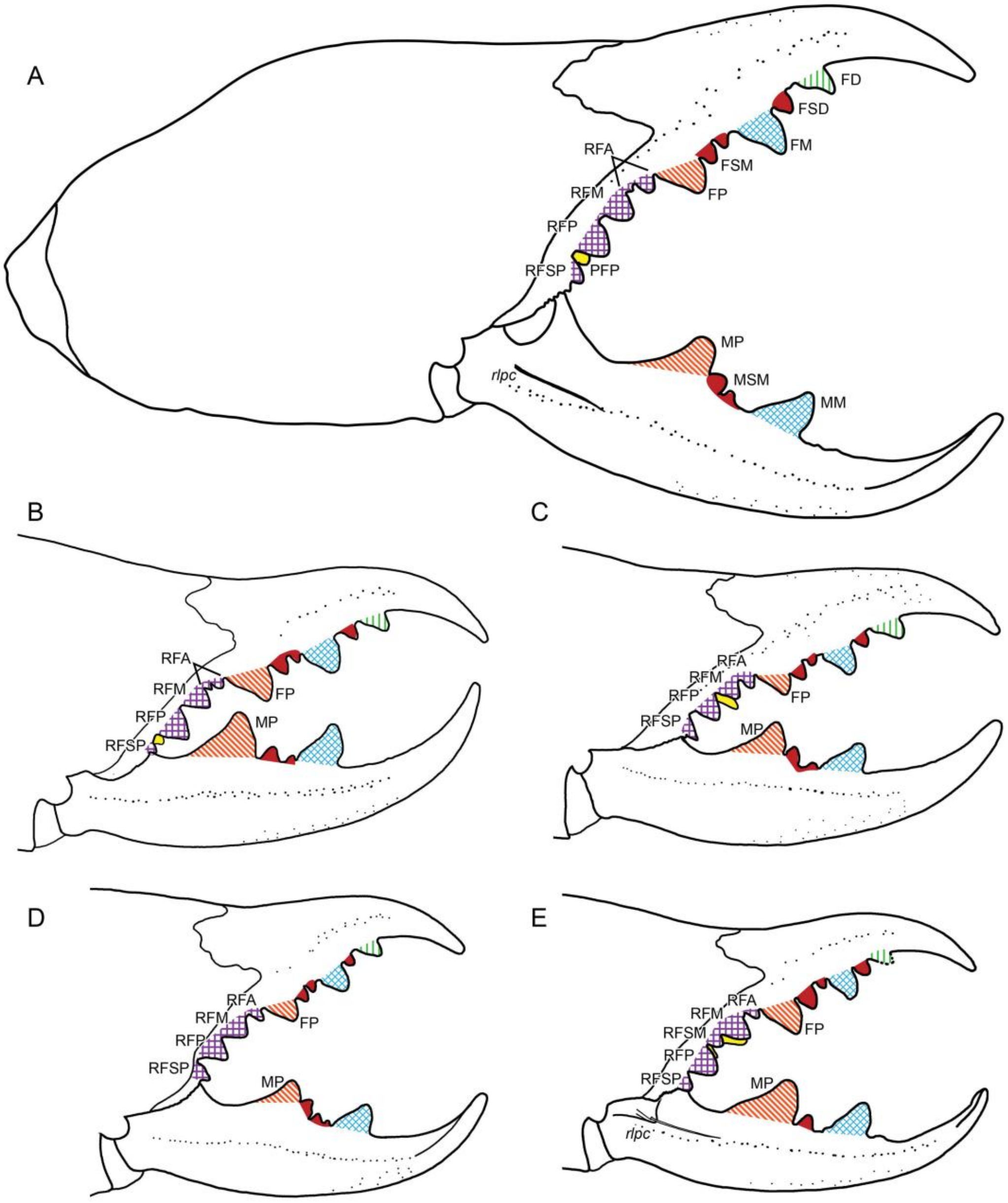

Plate 71. Eremobatidae Kraepelin, 1899, chelicerae, retrolateral views, illustrating dentition and setae. **A.** *Eremobates polhemusi* Muma & Brookhart, 1984, ♀ (DMNS ZA.10004). **B.** *Eremobates inkopaensis* Brookhart & Cushing, 2005, paratype ♀ (DMNS ZA.17310). **C.** *Eremobates kiseri* Muma & Brookhart, 1988, paratype ♀ (DMNS ZA.17385). **D.** *Eremobates norrisi* Muma & Brookhart, 1988, paratype ♀ (DMNS ZA.17383). **E.** *Eremobates socal* Brookhart & Cushing, 2004, paratype ♀ (DMNS ZA.17378). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; PFP, profondal proximal tooth; RFA, retrofonal apical teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal tooth; *rlpc*, retrolateral proximal cluster of setae.

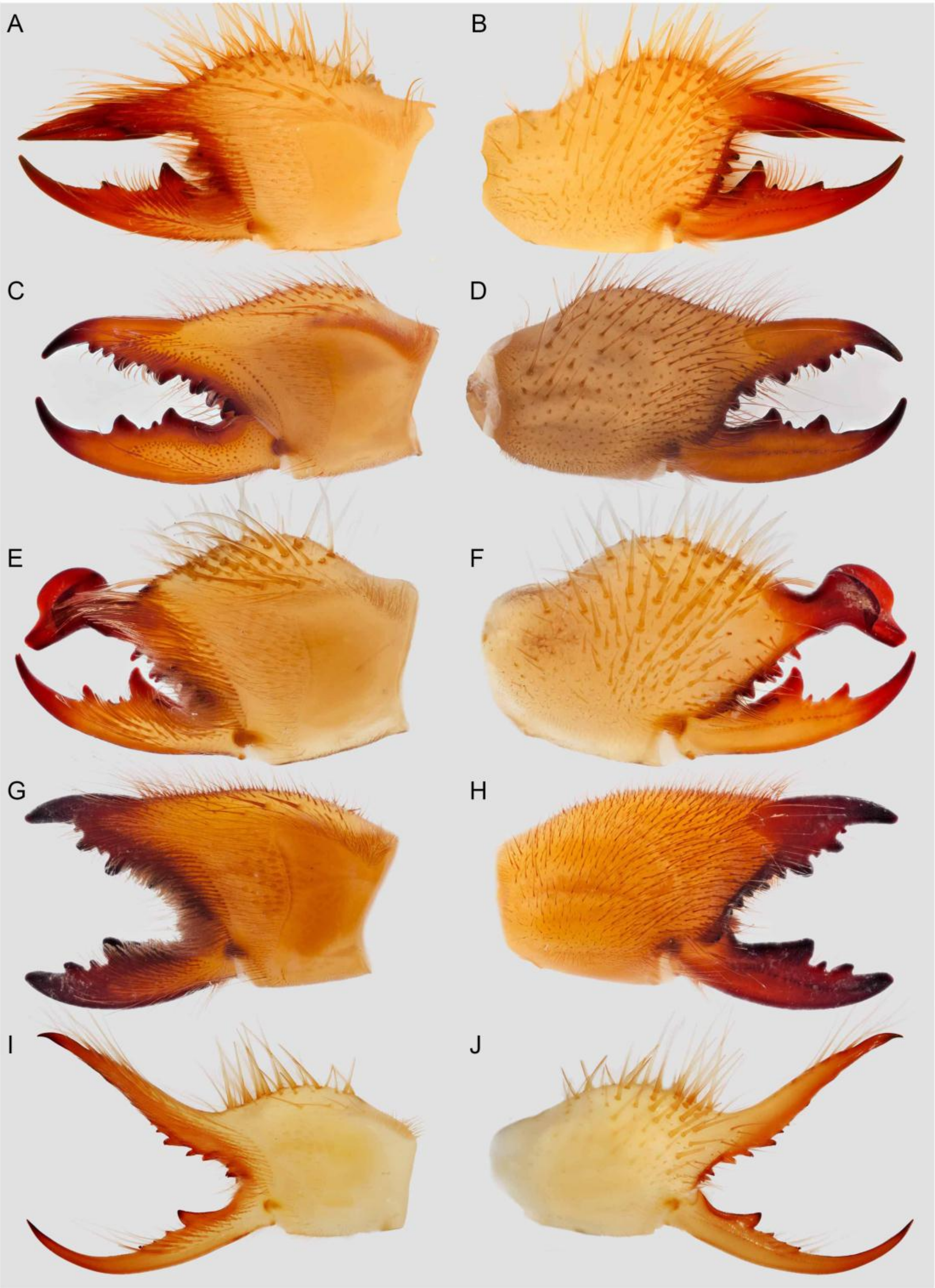

Plate 72. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Eremocosta titania* (Muma, 1951), ♂ (AMNH [LP 5035]). **C, D.** *Eremocosta gigasella* (Muma, 1970), ♀ (DMNS ZA.17350). **E, F**. *Eremothera sculpturata* Muma, 1951, ♂ (DMNS ZA.16475). **G, H.** *Eremorhax joshui* (Brookhart & Muma, 1987), ♀ (DMNS ZA.16415). **I, J.** *Chanbria regalis* Muma, 1951, ♂ (AMNH [LP 10746]).

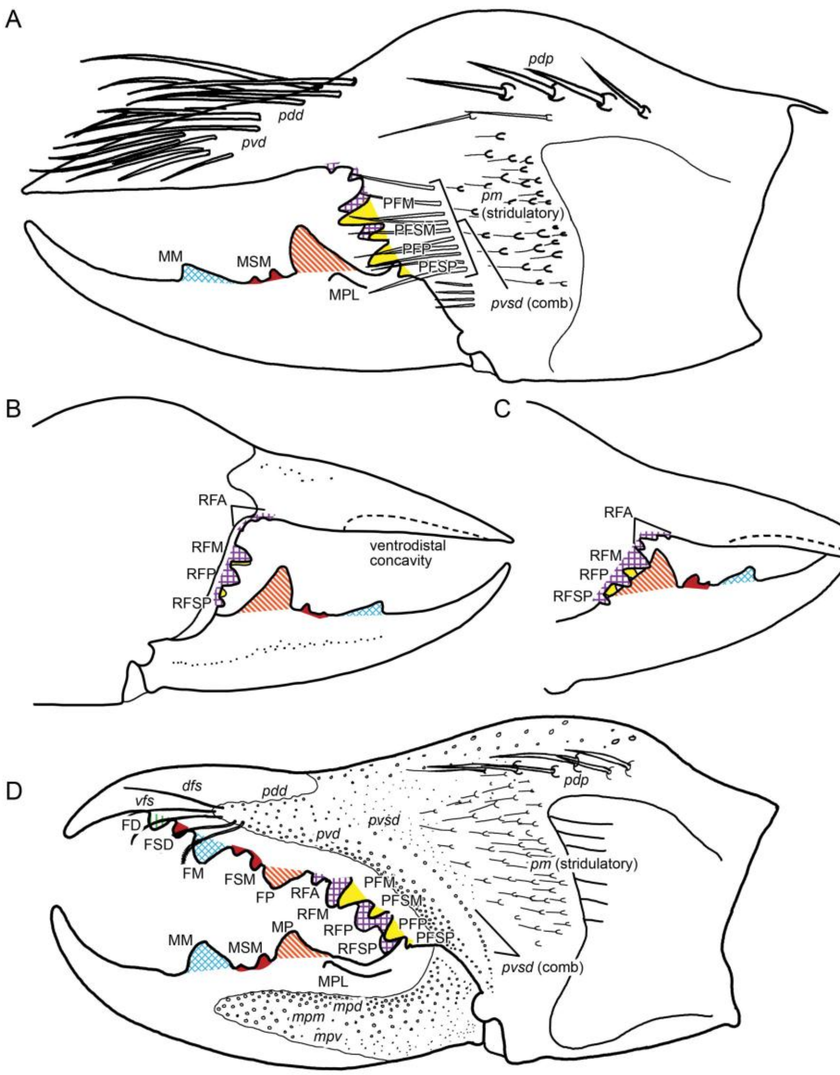

Plate 73. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, D**) and retrolateral (**B, C**) views, illustrating dentition, setae, and flagellar complex. **A–C.** *Eremocosta titania* (Muma, 1951). **A, B.** ♂ (AMNH [LP 5035]). **C.** ♂ (MNHN). **D.** *Eremocosta gigasella* (Muma, 1970), ♀ (DMNS ZA.17350). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MPL, movable finger, prolateral tooth; MSM, movable finger, submedial teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFA, retrofondal apical teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *dfs*, dorsal flagellar seta; *mpd*, movable finger, prodorsal setae; *mpm*, movable finger, promedial setae; *mpv*, movable finger, proventral setae; *pdd*, prodorsal distal setae; *pdp*, prodorsal proximal setae; *pm*, promedial setae (including stridulatory setae); *pdd*, prodorsal distal setae; *pdd*, prodorsal proximal setae; *pvd*, proventral distal setae; *pvsd*, proventral subdistal setae (including setal comb); *vfs*, ventral flagellar seta.

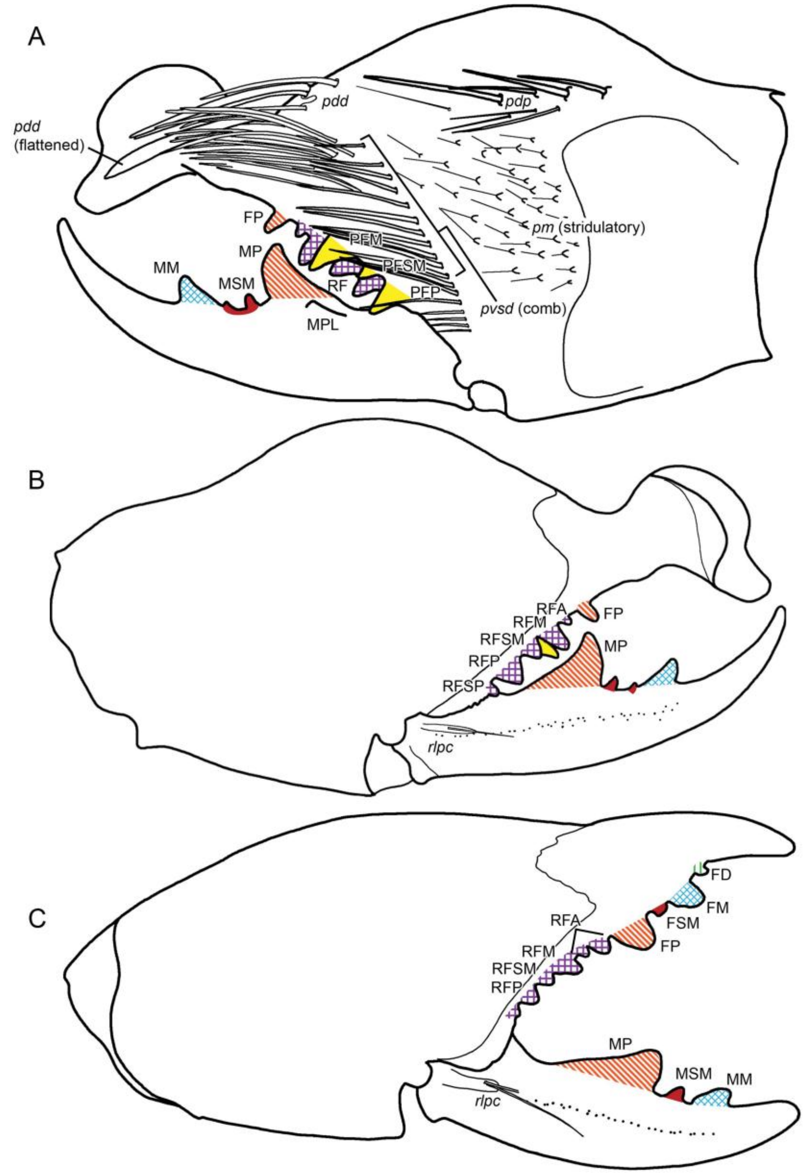

Plate 74. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A**) and retrolateral (**B, C**) views, illustrating dentition, setae, and flagellar complex. **A, B.** *Eremothera sculpturata* Muma, 1951, ♂ (DMNS ZA.16475). **C.** *Eremorhax joshui* (Brookhart & Muma, 1987), ♀ (DMNS ZA.16415). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MPL, movable finger, prolateral tooth; MSM, movable finger, submedial teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; RFA, retrofondal apical tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pdd*, prodorsal distal setae; *pdp*, prodorsal proximal setae; *pm*, promedial setae (stridulatory setae only); *pvsd*, proventral subdistal (including setal comb); *rlpc*, retrolateral proximal cluster of setae.

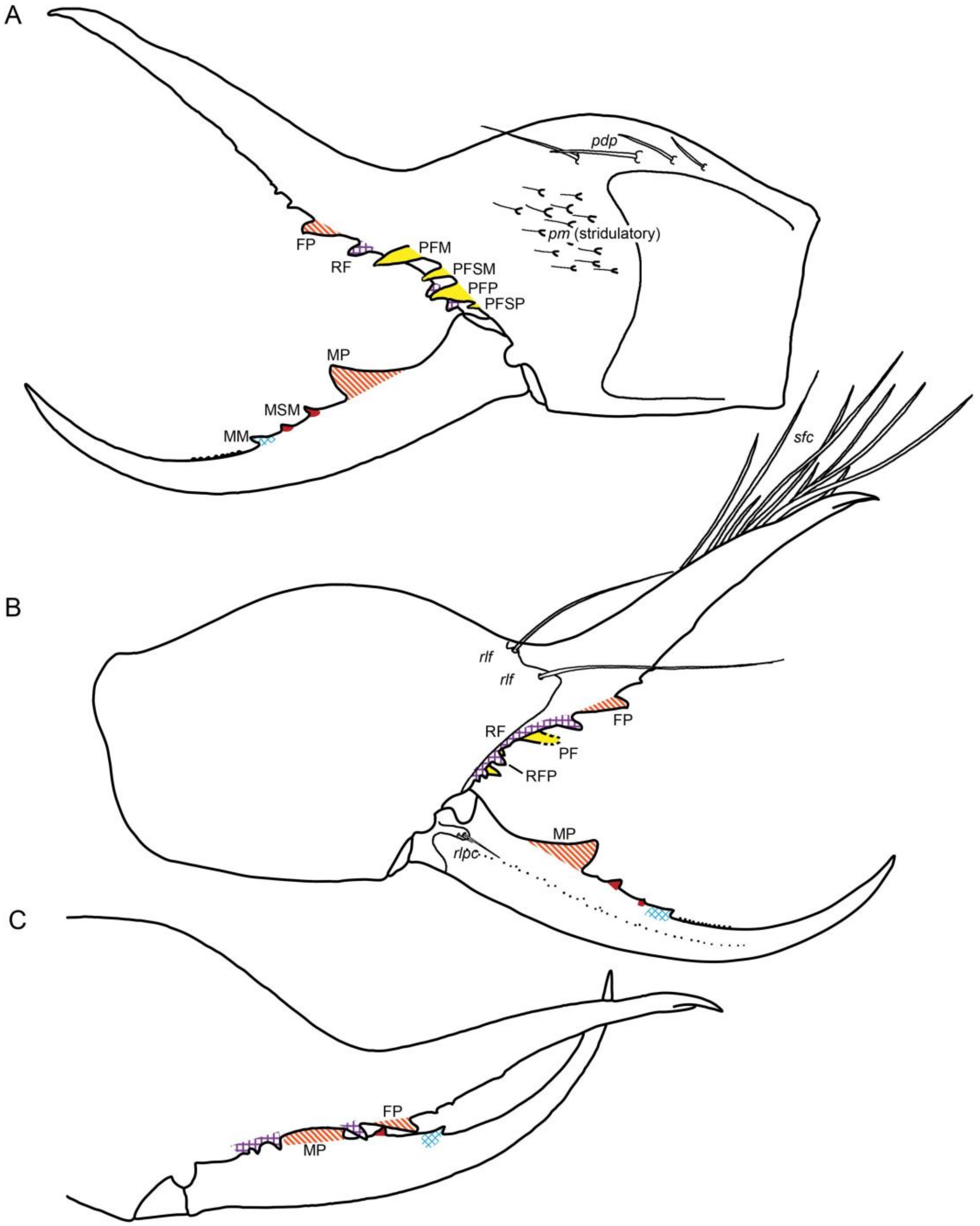

Plate 75. Chelicerae of Eremobatidae Kraepelin, 1899, *Chanbria regalis* Muma, 1951, ♂ (AMNH [LP 10746]), chelicerae, prolateral (**A**) and retrolateral (**B, C**) views, illustrating dentition, setae, and flagellar complex. Abbreviations: FP, fixed finger, proximal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; PF, profondal teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFP, retrofondal proximal tooth; *pm*, promedial setae (stridulatory setae only); *pdp*, prodorsal proximal setae; *rlf*, retrolateral finger setae; *rlpc*, retrolateral proximal cluster of setae; *sfc*, setiform flagellar complex.

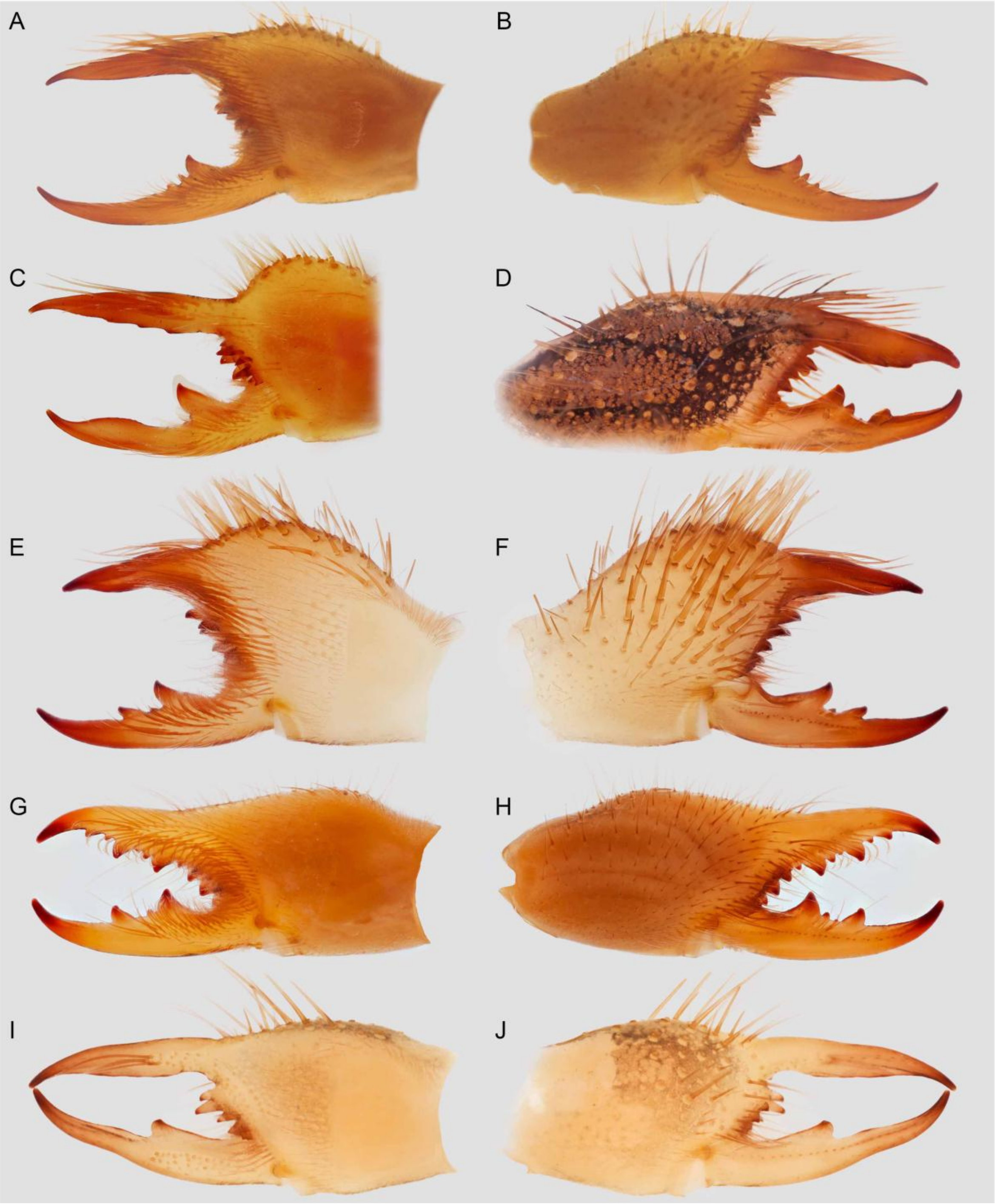

Plate 76. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Eremochelis acrilobatus* (Muma, 1962), ♂ (DMNS ZA.16067). **C.** *Eremochelis andreasana* (Muma, 1962), holotype ♂ (AMNH). **D.** *Eremochelis albaventralis* Brookhart & Cushing, 2005, paratype ♂ (DMNS ZA.17382). **E–H.** *Eremochelis insignatus* Roewer, 1934. **E, F.** ♂ (DMNS ZA.25434). **G, H.** ♀ (DMNS ZA.16136). **I, J.** *Eremochelis oregonensis* Brookhart & Cushing, 2002, holotype ♂ (DMNS ZA.10008).

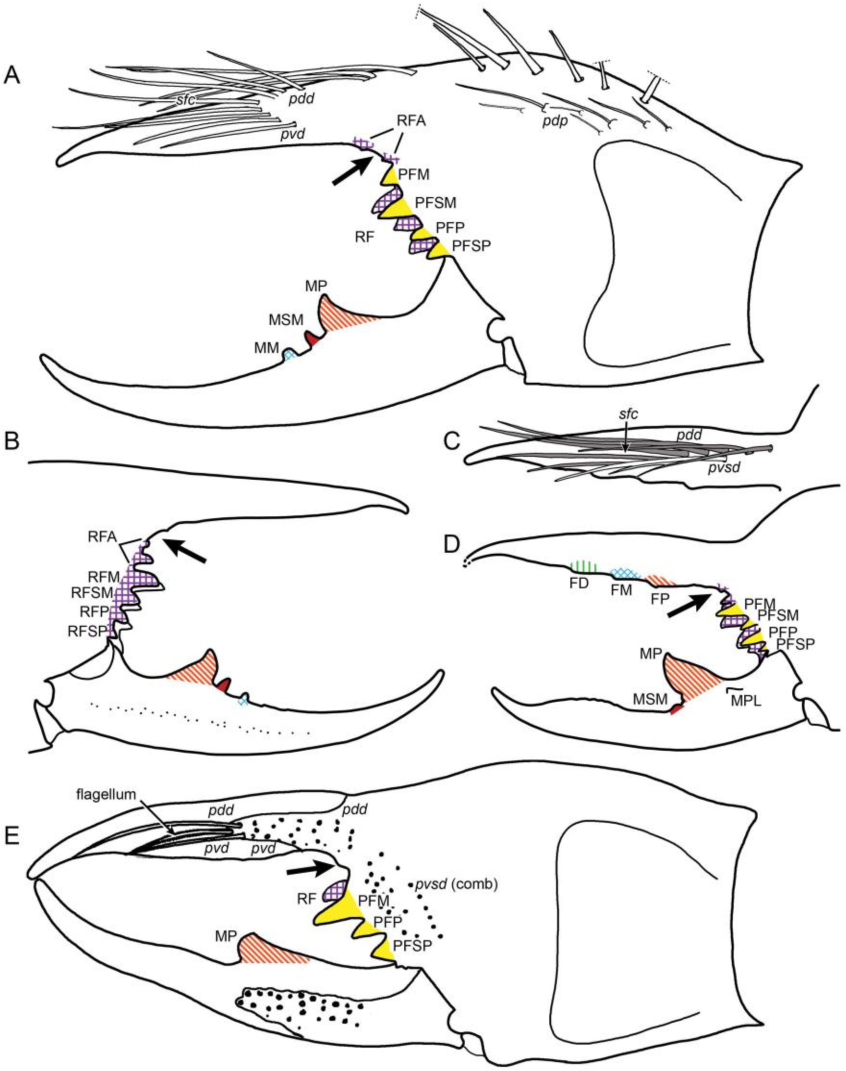

Plate 77. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C–E**) and retrolateral (**B**) views, and fixed (dorsal) finger, prolateral view (**B**), illustrating dentition, setae, and flagellar complex. **A.** *Eremochelis acrilobatus* (Muma, 1962), ♂ (DMNS ZA.16067). **B–D.** *Eremochelis andreasana* (Muma, 1962), holotype ♂ (AMNH), with closeup of dorsal finger to show arrangement of apical setae (**B**). **E.** *Eremochelis oregonensis* Brookhart & Cushing, 2002, holotype ♂ (DMNS ZA.10008). Arrows indicate weakly developed fondal notch. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MPL, movable finger, prolateral tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFA, retrofondal apical teeth (denticles); RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pdd*, prodorsal distal setae; *pdp*, prodorsal proximal setae; *pvd*, proventral distal setae; *pvsd*, proventral subdistal setae (including setal comb); *rlpc*, retrolateral proximal cluster of setae; *sfc*, setal flagellar complex.

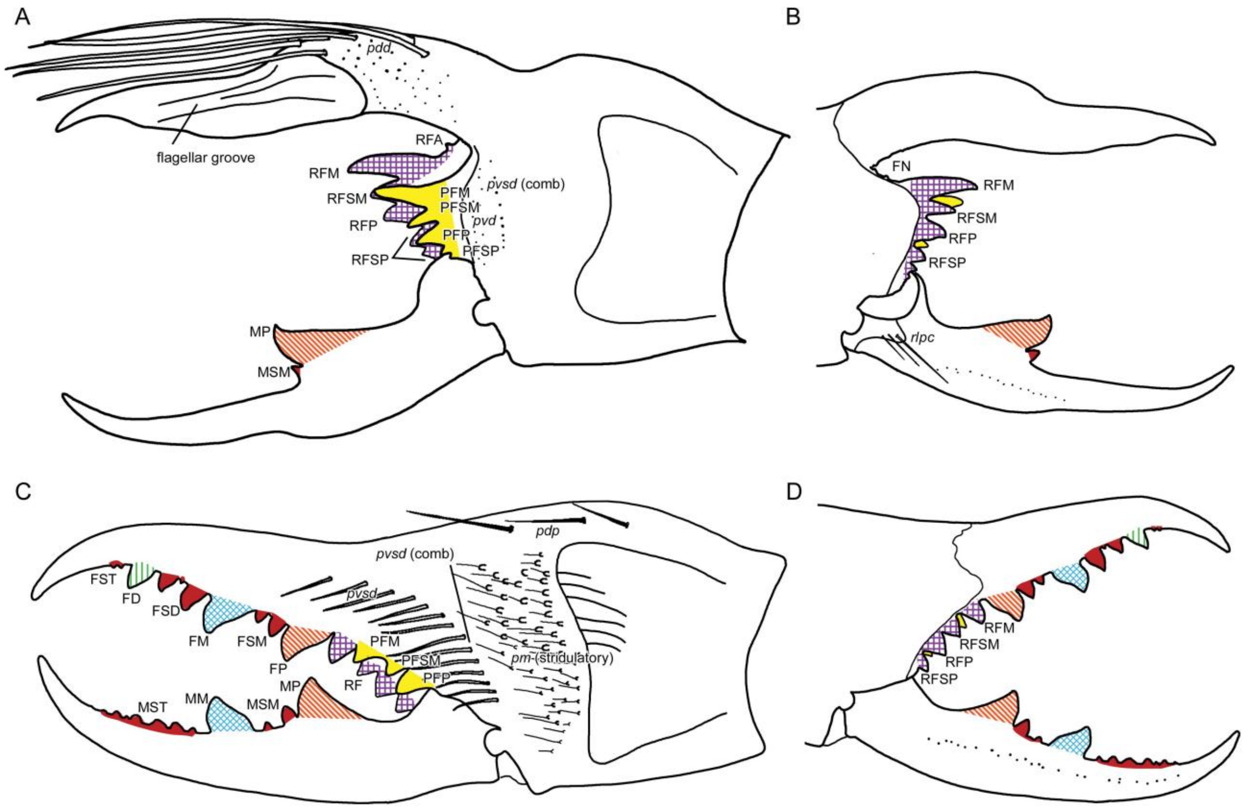

Plate 78. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellar complex. **A, B.** *Eremochelis bilobatus* (Muma, 1951), ♂ (DMNS ZA.16039). **C, D.** *Horribates bantai* Muma, 1989, ♀ (DMNS ZA.17691). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FN, fondal notch; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal teeth; FSM, fixed finger, submedial teeth; FST, fixed finger, subterminal tooth (denticle); MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; MST, movable finger, subterminal teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFA, retrofondal apical teeth (denticles); RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pdd*, prodorsal distal setae; *pm*, promedial setae (stridulatory setae only); *pvd*, proventral distal setae; *pvsd*, proventral subdistal setae (including setal comb); *rlpc*, retrolateral proximal cluster of setae.

Plate 79. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I, K**) and retrolateral (**B, D, F, H, J, L**) views. **A–D.** *Hemerotrecha fruitana* Muma, 1951. **A, B.** ♂ (DMNS ZA.17312). **C, D.** ♀ (DMNS ZA.17313). **E–H.** *Hemerotrecha branchi* Muma, 1951. **E, F.** ♂ (DMNS ZA.16786). **G, H.** ♀ (DMNS ZA.16786). **I, J.** *Hemerotrecha cornuta* Brookhart & Cushing, 2002, holotype ♂ (DMNS ZA.10005). **K, L.** *Hemerotrecha prenticei* Brookhart & Cushing, 2008, holotype ♂ (DMNS ZA.21376).

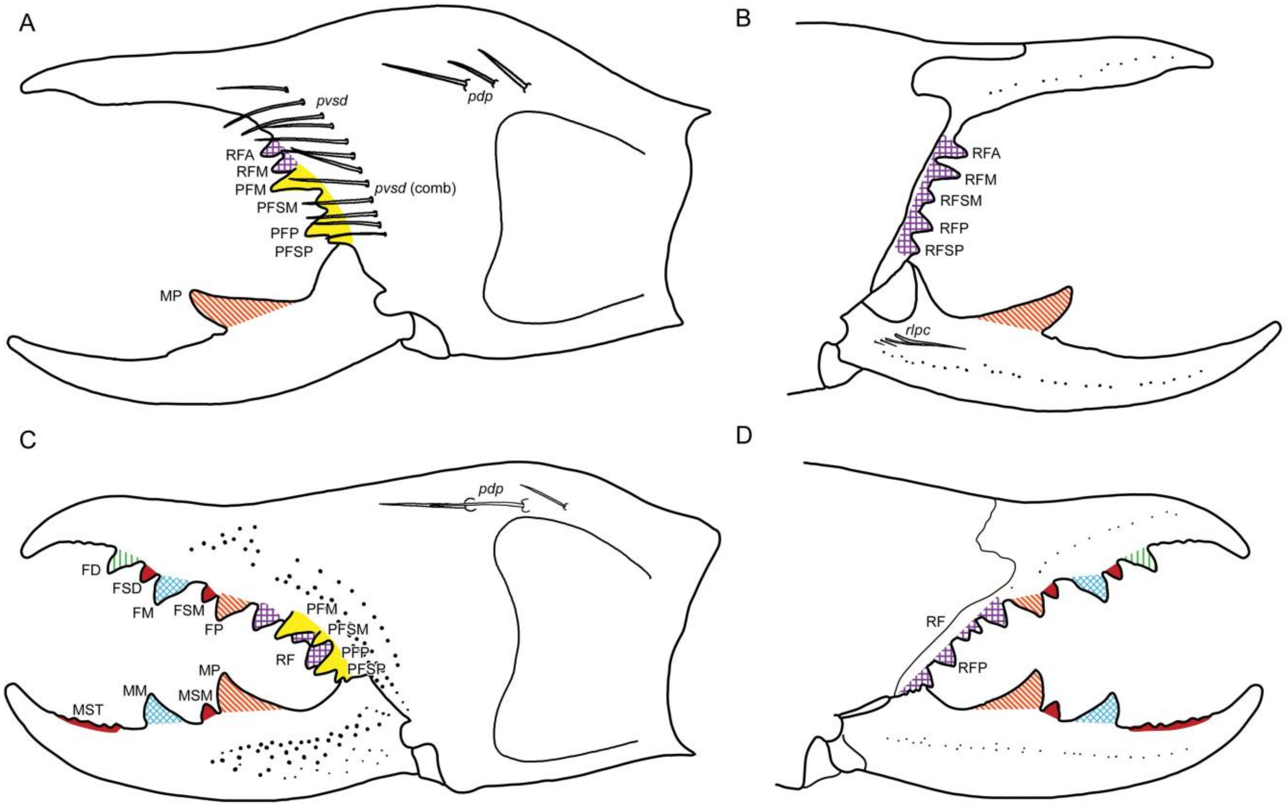

Plate 80. Eremobatidae Kraepelin, 1899, *Hemerotrecha fruitana* Muma, 1951, chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellar complex. **A, B.** ♂ (DMNS ZA.17312). **C, D.** ♀ (DMNS ZA.17313). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; MST, movable finger, subterminal teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *mpd*, movable finger, prodorsal setae; *mfm*, movable finger, promedial setae; *mpv*, movable finger, proventral setae; pdp, prodorsal proximal setae; *pvsd*, proventral subdistal setae (including setal comb); *rlpc*, retrolateral proximal cluster of setae.

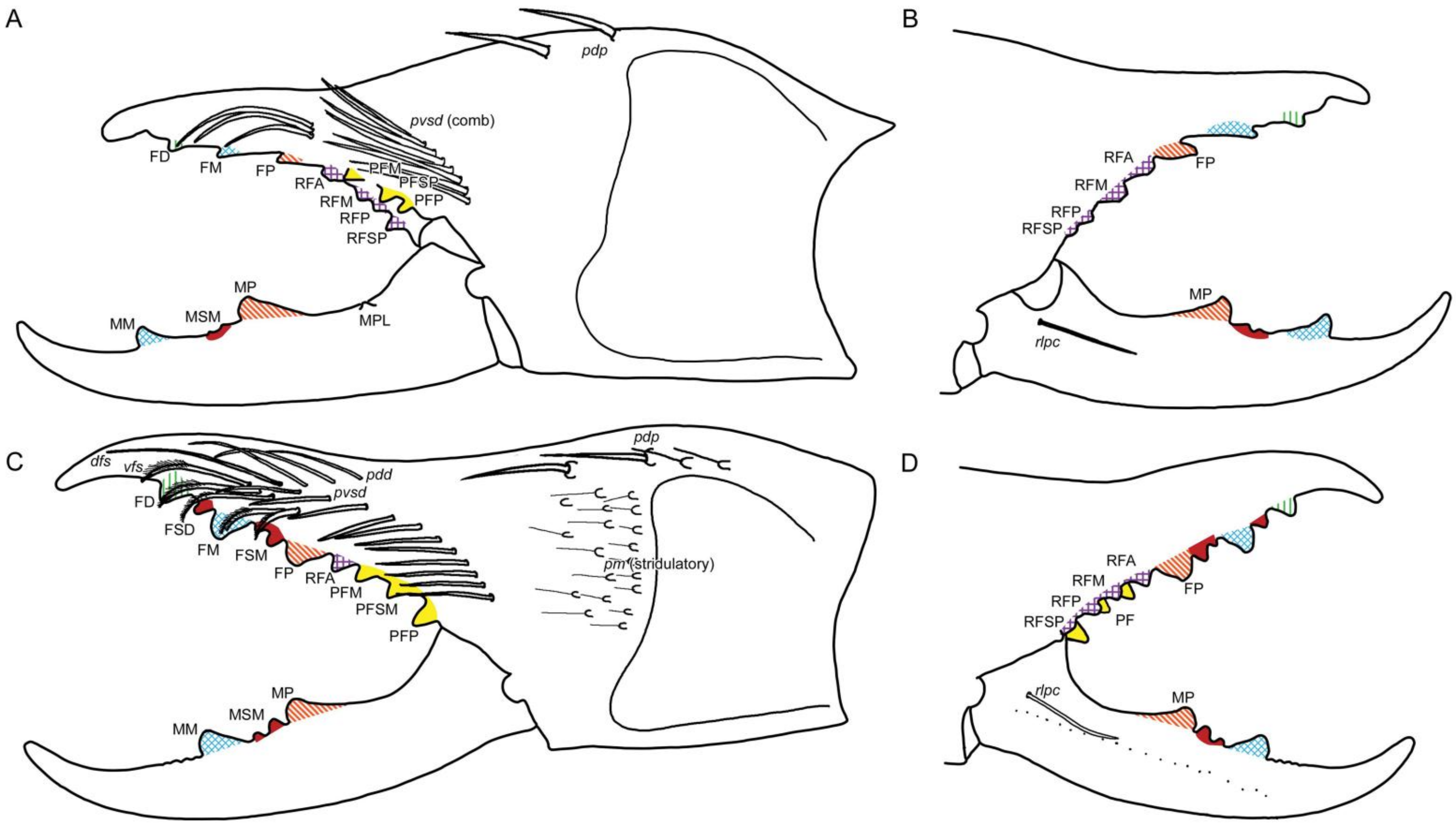

Plate 81. Eremobatidae Kraepelin, 1899, *Hemerotrecha branchi* Muma, 1951, chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellar complex. **A, B.** ♂ (DMNS ZA.16786). **C, D.** ♀ (DMNS ZA.16786). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; RF, retrofondal teeth; RFA, retrofondal apical tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *dfs*, dorsal flagellar seta; *pdp*, prodorsal proximal setae; *pm*, promedial setae (stridulatory setae only); *pvd*, proventral distal setae; *pvsd*, proventral subdistal setae (including setal comb); *rlpc*, retrolateral proximal cluster of setae; *vfs*, ventral flagellar seta.

Plate 82. Eremobatidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I, K**) and retrolateral (**B, D, F, H, J, L**) views. **A–D.** *Hemerotrecha hanfordana* Brookhart & Cushing, 2008. **A, B.** Holotype ♂ (DMNS ZA.21371). **C, D.** Paratype ♀ (DMNS ZA.19402). **E, F.** *Hemerotrecha marginata* (Kraepelin, 1911). **E.** Syntype ♂ (ZMUH). **F.** Syntype ♀ (ZMUH). **G–J** *Hemerotrecha sevilleta* Brookhart & Cushing, 2002. **G, H.** Holotype ♂ (DMNS ZA.10006). **I, J.** Paratype ♀ (DMNS ZA.10007). **K, L.** *Hemerotrecha vetteri* Brookhart & Cushing, 2008, holotype ♂ (DMNS ZA.21377).

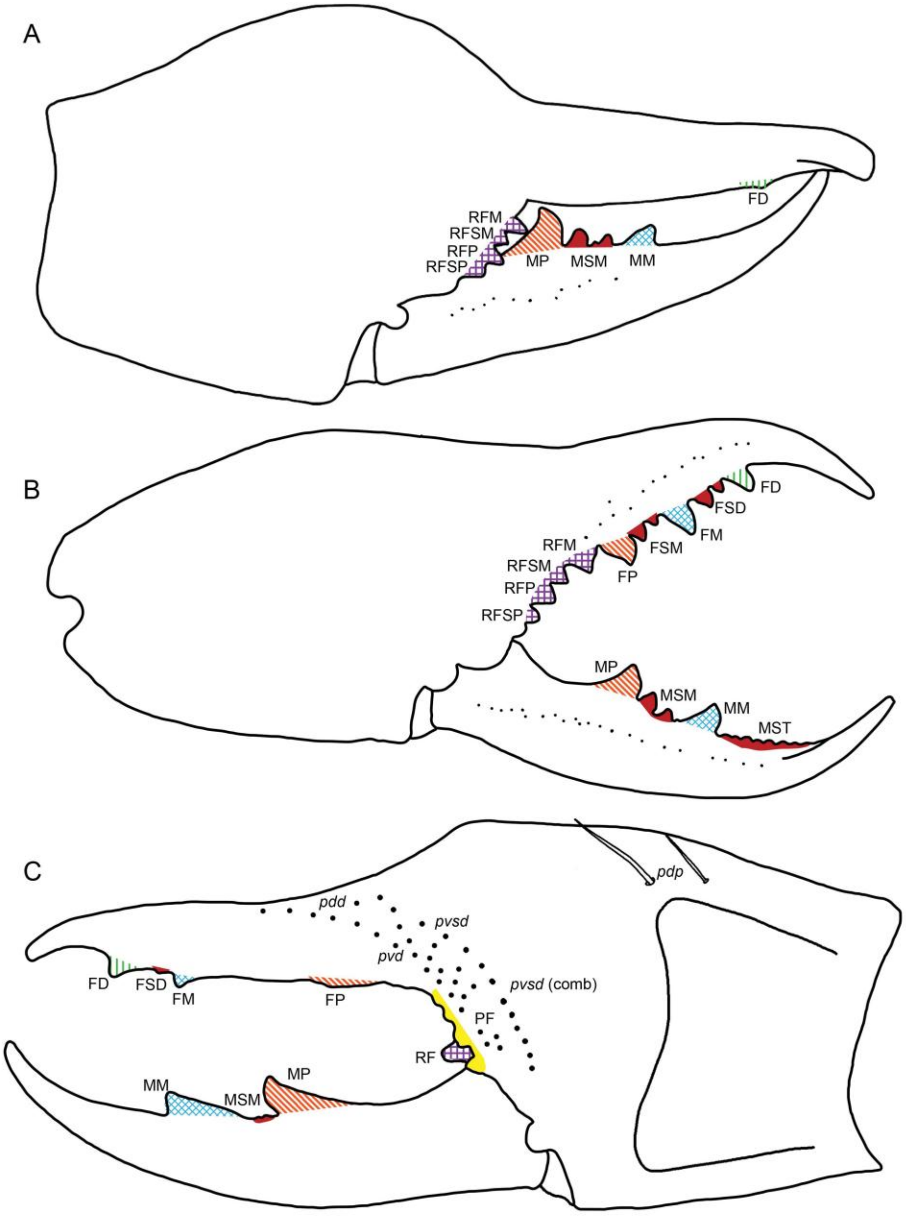

Plate 83. Eremobatidae Kraepelin, 1899, chelicerae, retrolateral (**A, B**) and prolateral (**C**) views, illustrating dentition and setae. **A, B.** *Hemerotrecha marginata* (Kraepelin, 1911). **A.** Syntype ♂ (ZMUH). **B.** Syntype ♀ (ZMUH). **C.** *Hemerotrecha sevilleta* Brookhart and Cushing, 2002, holotype ♂ (DMNS ZA.10006). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal teeth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; MST, movable finger, subterminal teeth; PF, profondal teeth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pdd*, prodorsal distal setae; *pdp*, prodorsal proximal setae; *pvd*, proventral distal setae; *pvsd*, proventral subdistal setae (including setal comb).

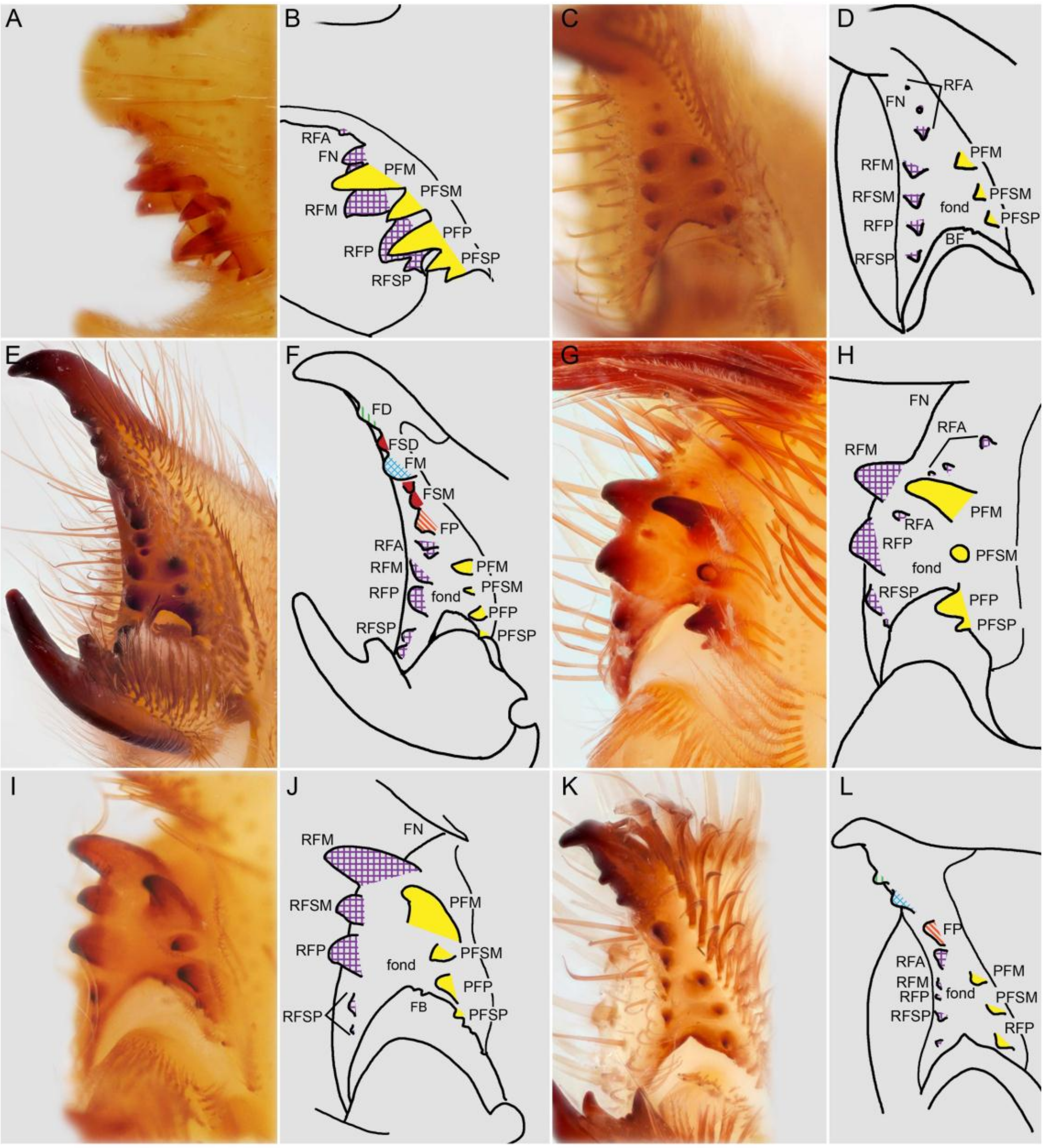

Plate 84. Eremobatidae Kraepelin, 1899, cheliceral fixed fingers, proventral views illustrating fondal area and basal fondal teeth (**E, F**). **A, B.** *Eremochelis andreasana* (Muma, 1962), holotype ♂ (AMNH). **C, D.** *Eremochelis acrilobatus* (Muma, 1962), ♂ (DMNS ZA.16067). **E–H.** *Eremobates palpisetulosus* Fichter, 1941. **E, F.** ♀ (DMNS ZA.15686). **G, H.** ♂ (DMNS ZA.15683). **I, J.** *Eremochelis bilobatus* (Muma, 1951), ♂ (DMNS ZA.16039). **K, L.** *Hemerotrecha branchi* Muma, 1951, ♂ (DMNS ZA.16786). Abbreviations: BF, basifondal teeth; FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FN, fondal notch; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RFA, retrofondal apical teeth or denticles; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth.

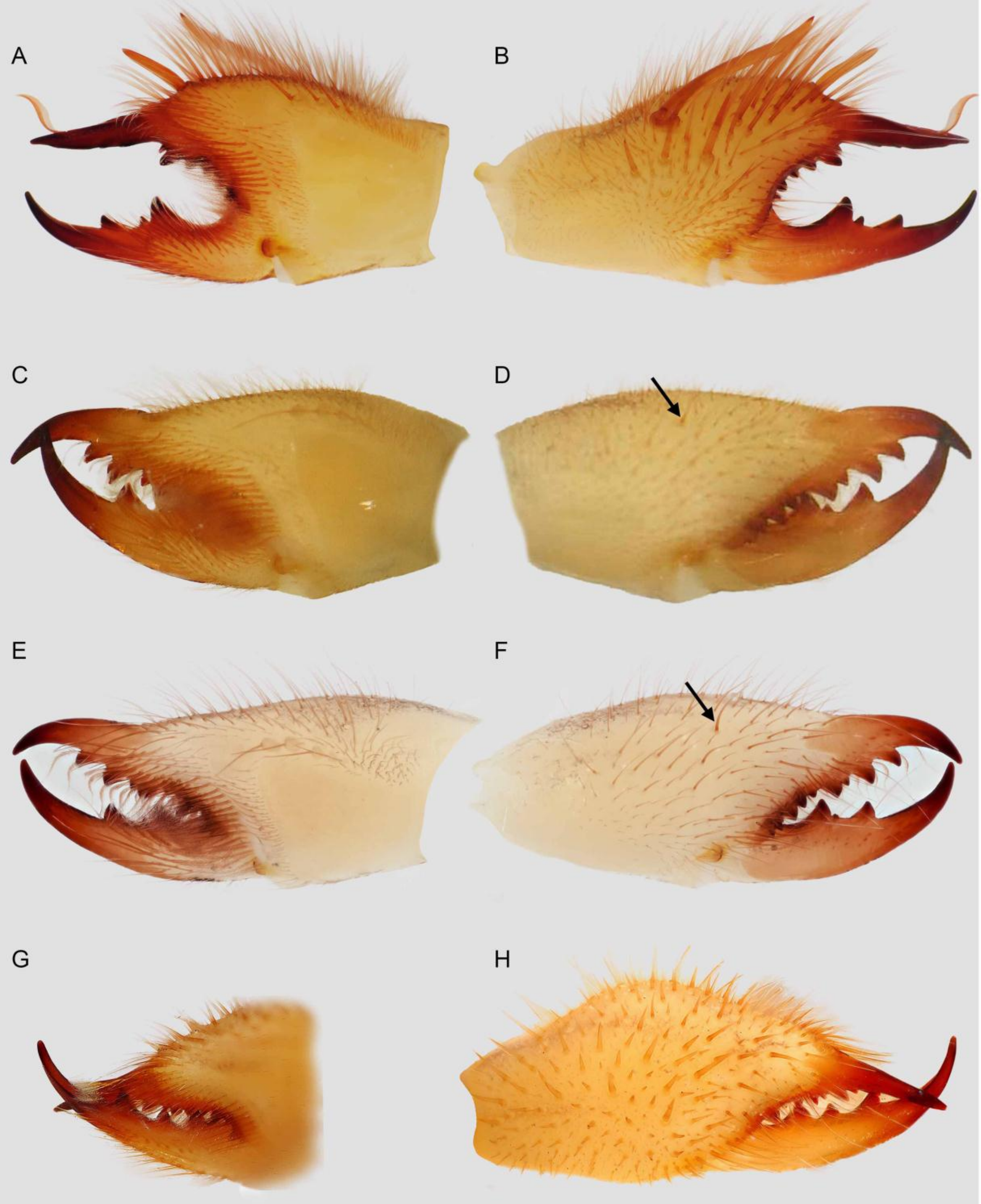

Plate 85. Gylippidae Roewer, 1933, Gylippinae (**A–F)** and Lipophaginae Wharton, 1981. (**G, H**), chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A–D.** *Gylippus* (*Paragylippus*) *monoceros* Werner, 1905. **A, B.** ♂ (AMNH [LP 5437]). **C, D.** ♀ (KU) [topotype], Turkey: Kayseri Province. **E, F.** *Gylippus* (*Anoplogylippus*) *ferganensis* Birula, 1893, juv. (AMNH [LP 3921]). **G, H.** *Lipophaga trispinosa* Purcell, 1903, ♂ (NMNW 12503). Arrows indicate seta in ♀ homologous to retrolateral manus spiniform (*rlms*) seta in ♂.

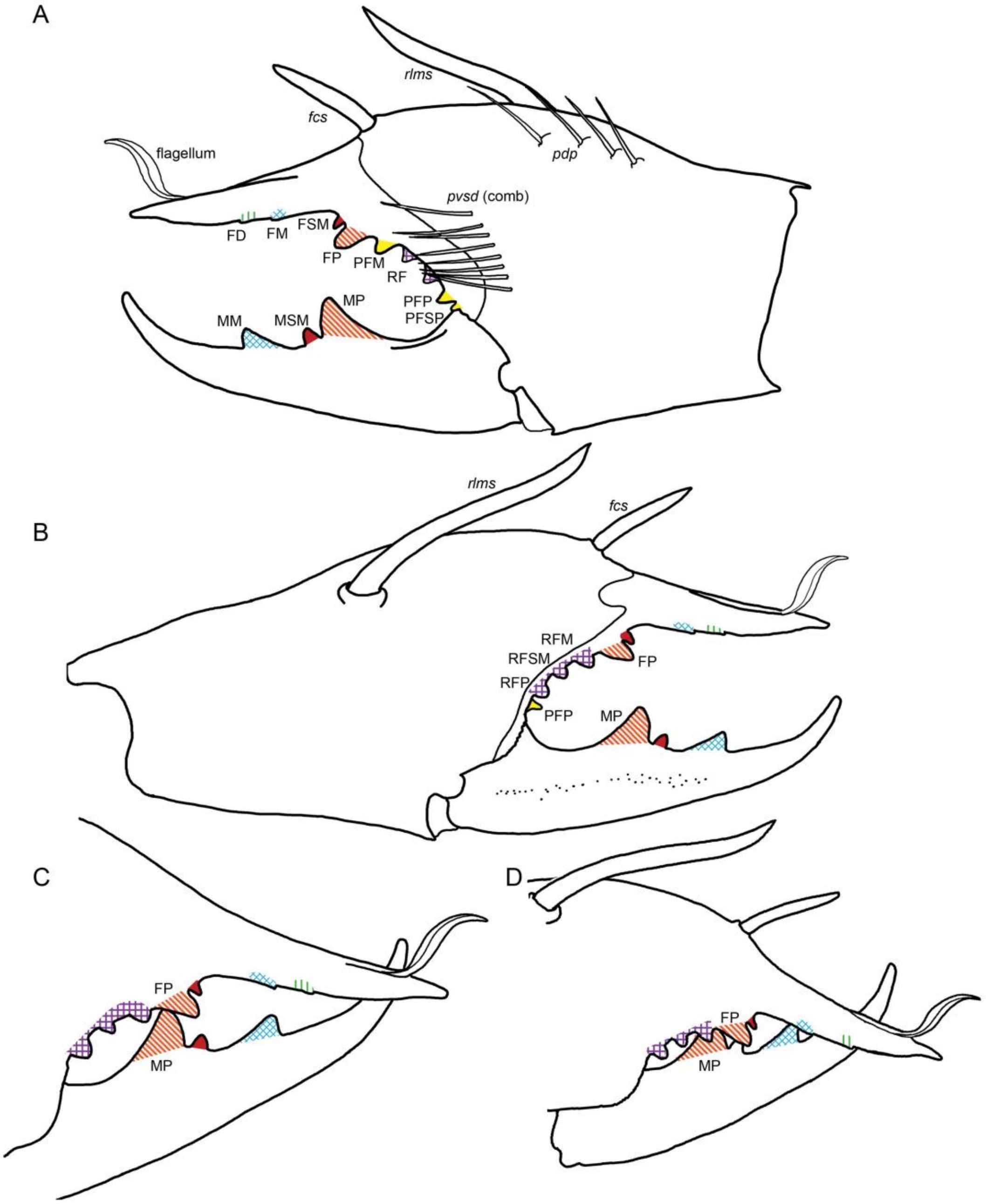

Plate 86. Gylippidae Roewer, 1933, Gylippinae, *Gyllipus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]), chelicerae, prolateral (**A**) and retrolateral (**B–D**) views, illustrating dentition, setae, and flagellar complex. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth; PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; *fcs*, flagellar complex spiniform seta; *pvsd*, proventral subdistal setae (setal comb only); *rlms*, retrolateral manus spiniform seta.

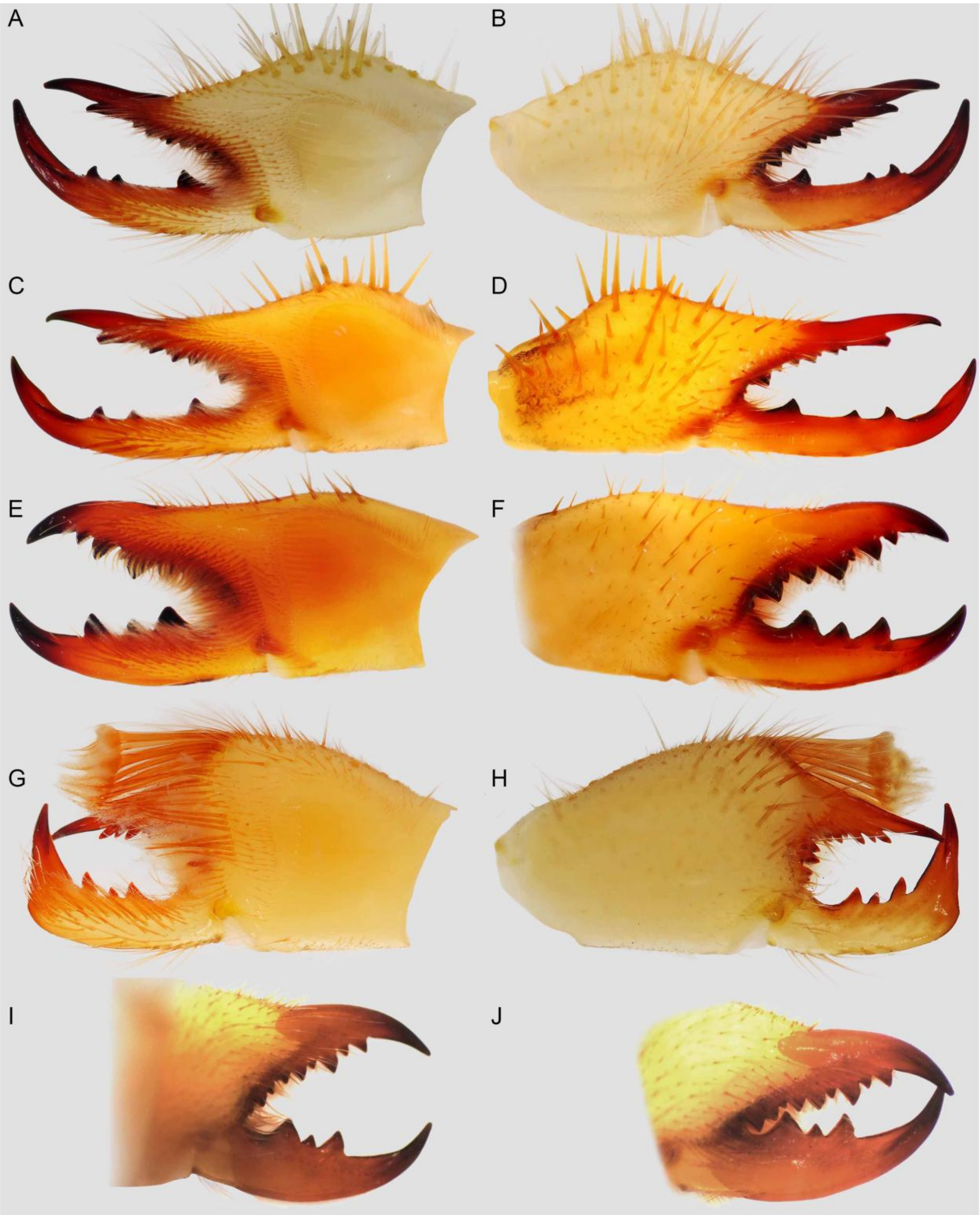

Plate 87. Gylippidae Roewer, 1933, Lipophaginae Wharton, 1981, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H–J**) views. **A–F.** *Trichotoma michaelseni* (Kraepelin, 1914). **A, B.** ♂ (AMNH [LP 5724]). **C, D.** ♂ (NMNW 12757). **E, F.** ♀ (NMNW 12757). **G–J.** *Bdellophaga angulata* Wharton, 1981. **G, H.** ♂ (NMNW 11601). **I, J.** ♀ (NMNW 12240), with cheliceral fingers open (**I**) and closed (**J**).

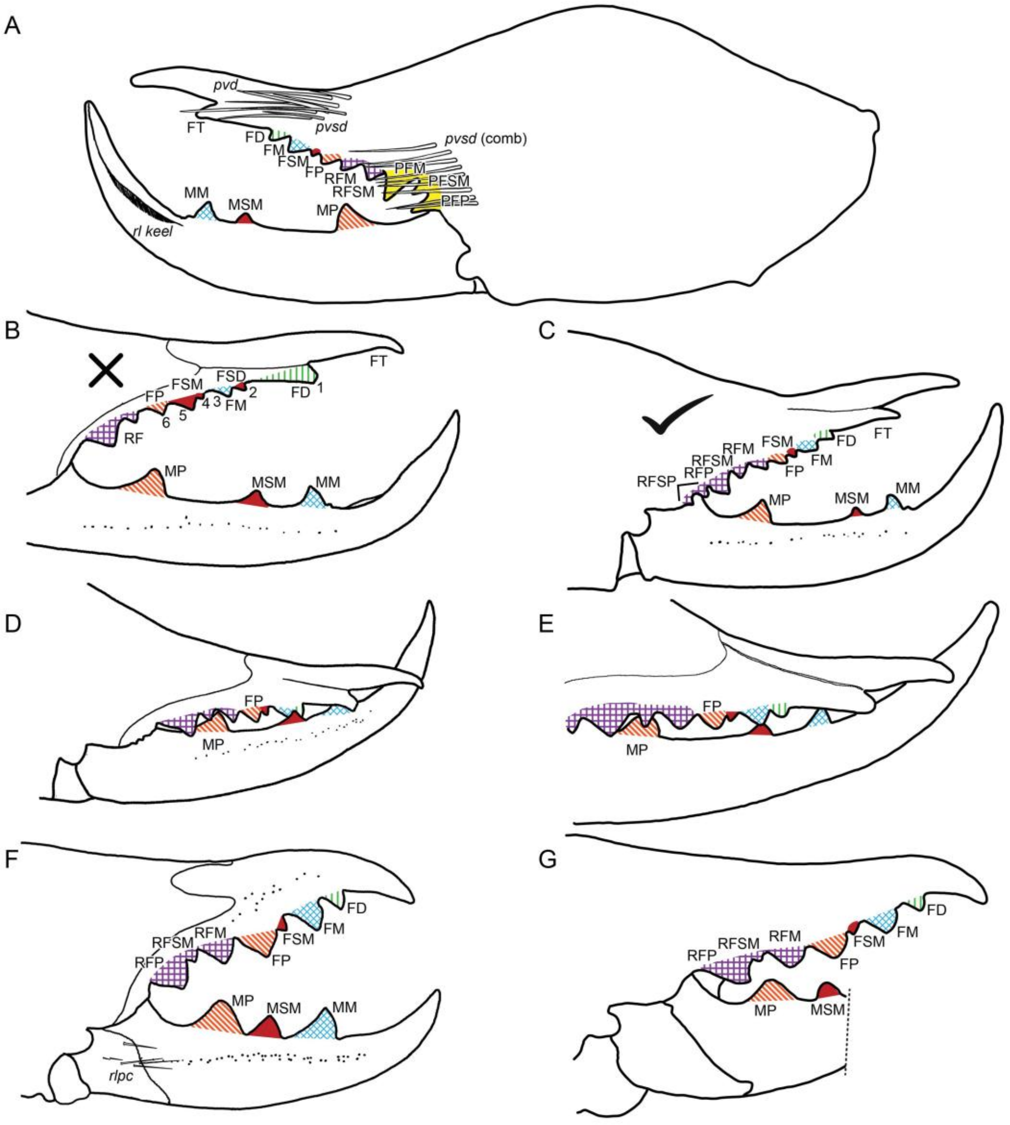

Plate 88. Gylippidae Roewer, 1933, Lipophaginae Wharton, 1981, *Trichotoma michaelseni* (Kraepelin, 1914), chelicerae, prolateral (**A**) and retrolateral (**B–G**) views, illustrating dentition, setae, and flagellar complex. **A, C, E.** ♂ (AMNH [LP 5724]), **B, D.** ♂ NMNW (12757), illustrating fixed (dorsal) finger interpretations of dentition by previous authors (1 = FD, 6 = FP; Roewer, 1941; Wharton, 1981), insicated with a X (**B**), and proposed here (1 = FT, 2 = FD, 5 = FP), indicated with a check mark (**C**). **F.** ♀ (NMNW 12757). **G.** *Trichotoma brunnea* Lawrence, 1968, ♂ (LP 9870), Namibia: Swakopmund. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; FT, fixed finger, terminal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth; PFP, profondal proximal tooth; PFSM, profondal submedial tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvd*, proventral distal setae; *pvsd*, proventral subdistal setae (setal comb only); *rlpc*, retrolateral proximal cluster of setae; rl, retrolateral.

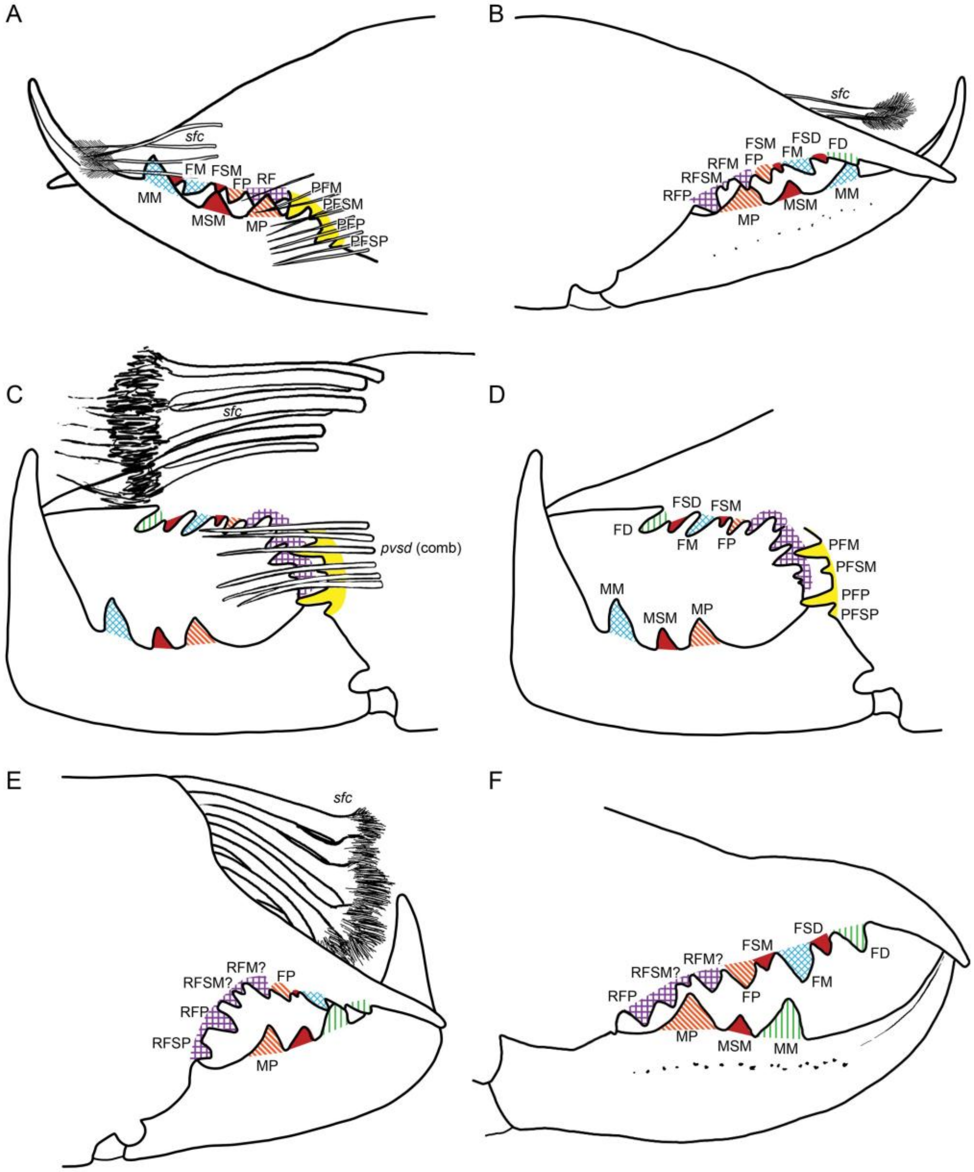

Plate 89. Gylippidae Roewer, 1933, Lipophaginae Wharton, 1981, chelicerae, prolateral (**A, C, D**) and retrolateral (**B, E, F**) views, illustrating dentition, setae, and flagellar complex. **A, B.** *Lipophaga trispinosa* Purcell, 1903, ♂ (NMNW 12503). **C–F.** *Bdellophaga angulata* Wharton, 1981. **C–E.** ♂ (NMNW 11601). **F.** ♀ (NMNW 12240). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only); *sfc*, setiform flagellar complex.

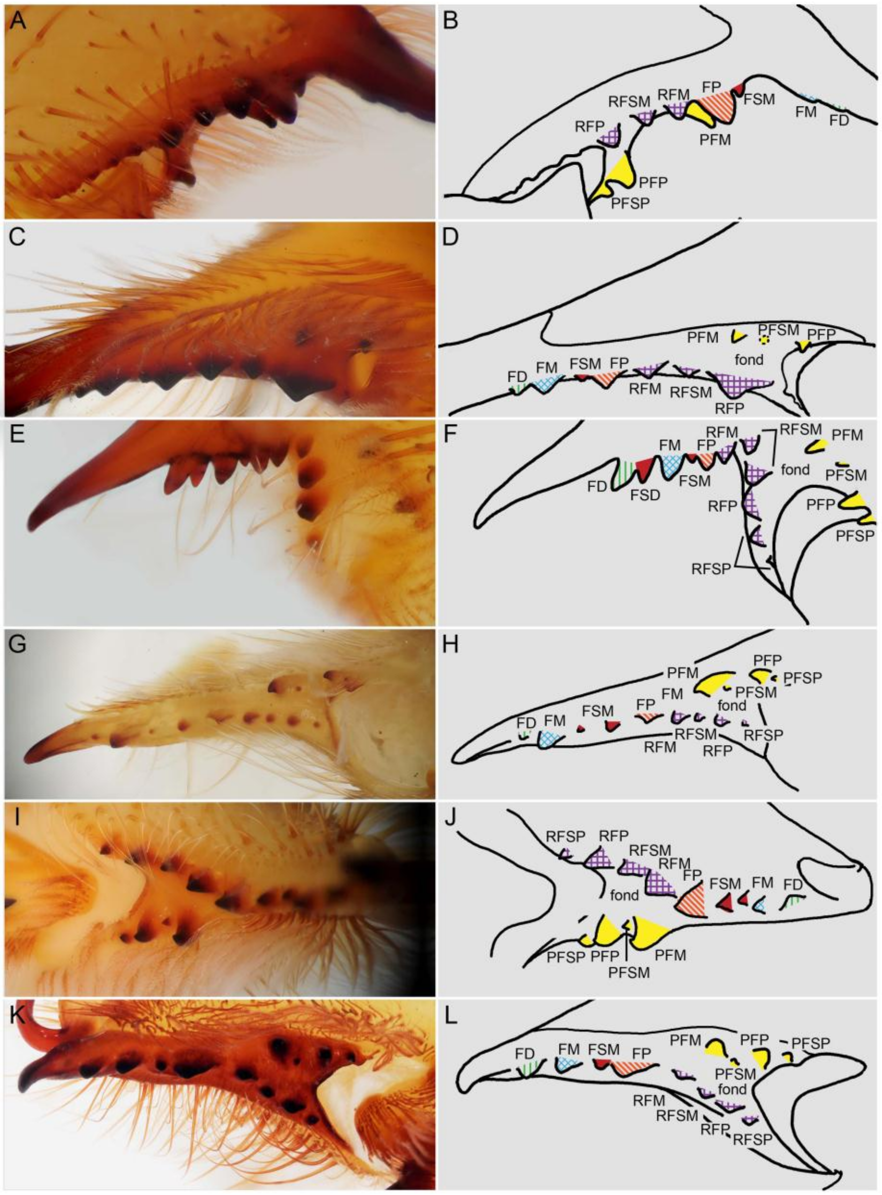

Plate 90. Gylippidae Roewer, 1933, Gylippinae (**A, B**), and Lipophaginae Wharton, 1981 (**C–F**) and Solpugidae Leach, 1815 (**G–L**), cheliceral fixed fingers, proventral (**C–H, K, L**) and retroventral (**A, B, I, J**) views illustrating fondal area. **A, B.** *Gyllipus* (*Paragylippus*) *monoceros* Werner, 1905, ♂ (AMNH [LP 5437]). **C, D.** *Trichotoma michaelseni* (Kraepelin, 1914), ♂ (AMNH [LP 5724]). **E, F.** *Bdellophaga angulata* Wharton, 1981, ♂ (NMNW 11601). **G, H.** *Solpugisticella kenyae* Turk, 1960, holotype ♂ (HUJI). **I, J.** *Zeria sericea* (Pocock, 1897), ♂ (NMNW 13801). **K, L.** *Zeria venator* (Pocock, 1897), ♂ (AMNH [LP 5952]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial teeth; RFSP, retrofondal subproximal teeth.

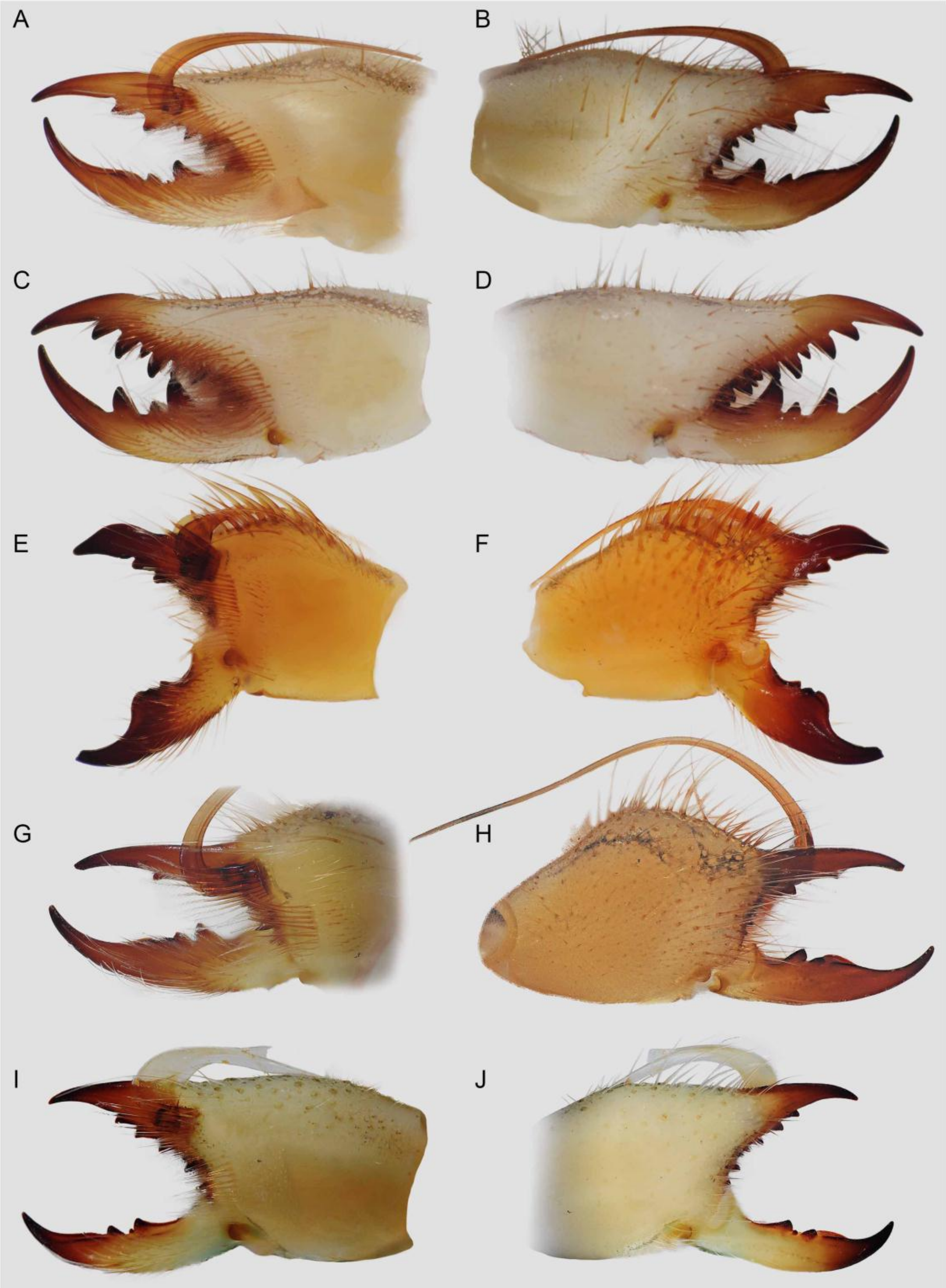

Plate 91. Ceromidae Roewer, 1933, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A–D.** *Ceroma inerme* Purcell, 1899. **A, B.** ♂ (AMNH [LP 9864]). **C, D.** ♀ (AMNH [LP 8425]). **E, F.** *Ceroma ornatum* Karsch, 1885, ♂ (MRAC 213.106). **G, H.** *Ceroma swierstrae* Lawrence, 1935, ♂ (NCA 2009/4355). **I, J.** *Ceromella* sp. n., ♂ (AMNH [LP 8527]).

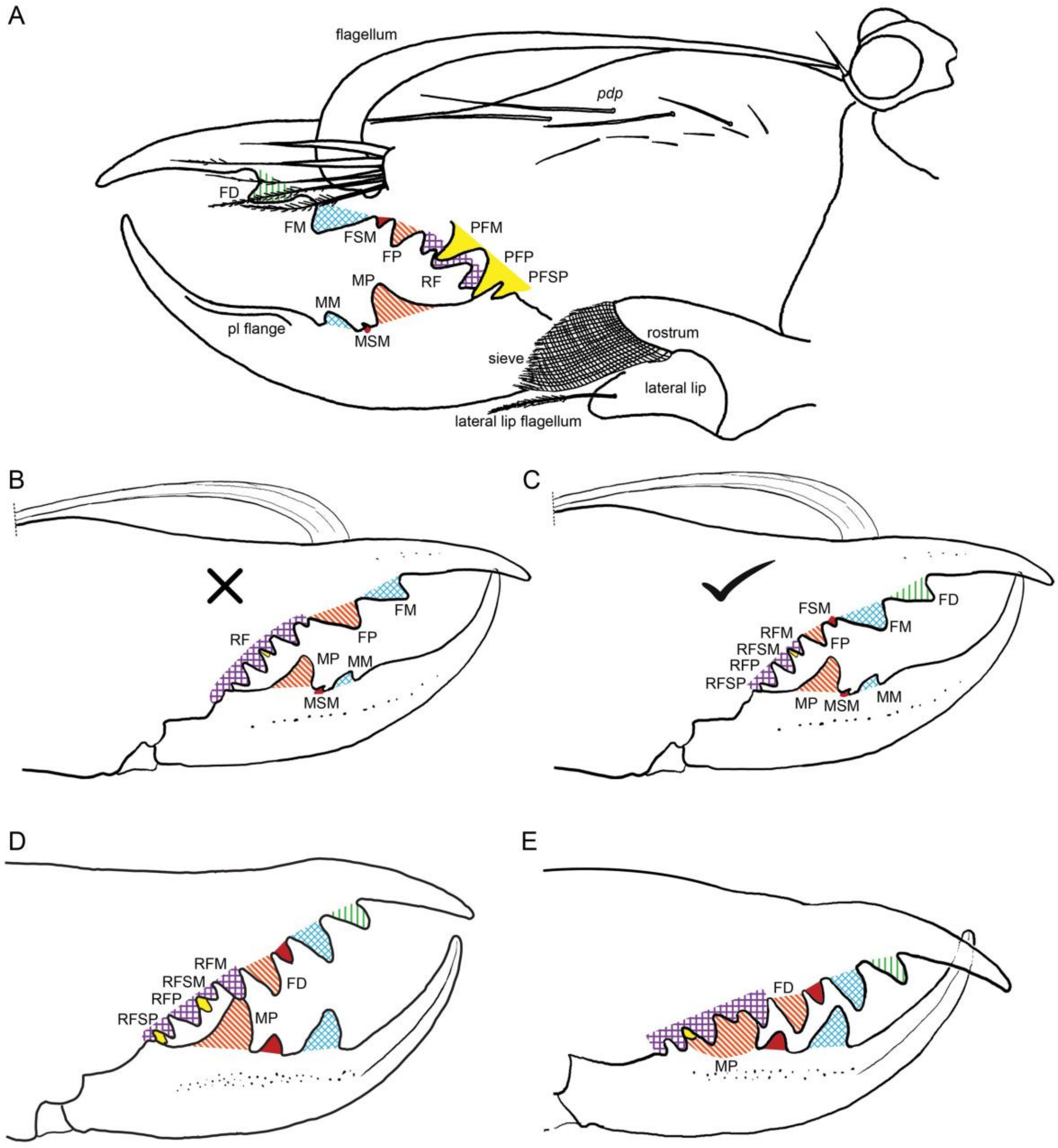

Plate 92. Ceromidae Roewer, 1933, *Ceroma inerme* Purcell, 1899, chelicerae, prolateral (**A**) and retrolateral (**B–E**) views, illustrating interpretations of fixed (dorsal) finger dentition by previous authors (Purcell, 1899; Roewer, 1934: 323; Wharton, 1981) (**B**) and proposed here (**C**), setae, and flagellar complex. **A–C.** ♂ (AMNH [LP 9864]). **D, E.** ♀ (AMNH [LP 8425]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *fcp*, flagellum complex plumose setae (modified proventral distal, *pvd,* setae); *pdp*, prodorsal proximal setae; pl, prolateral.

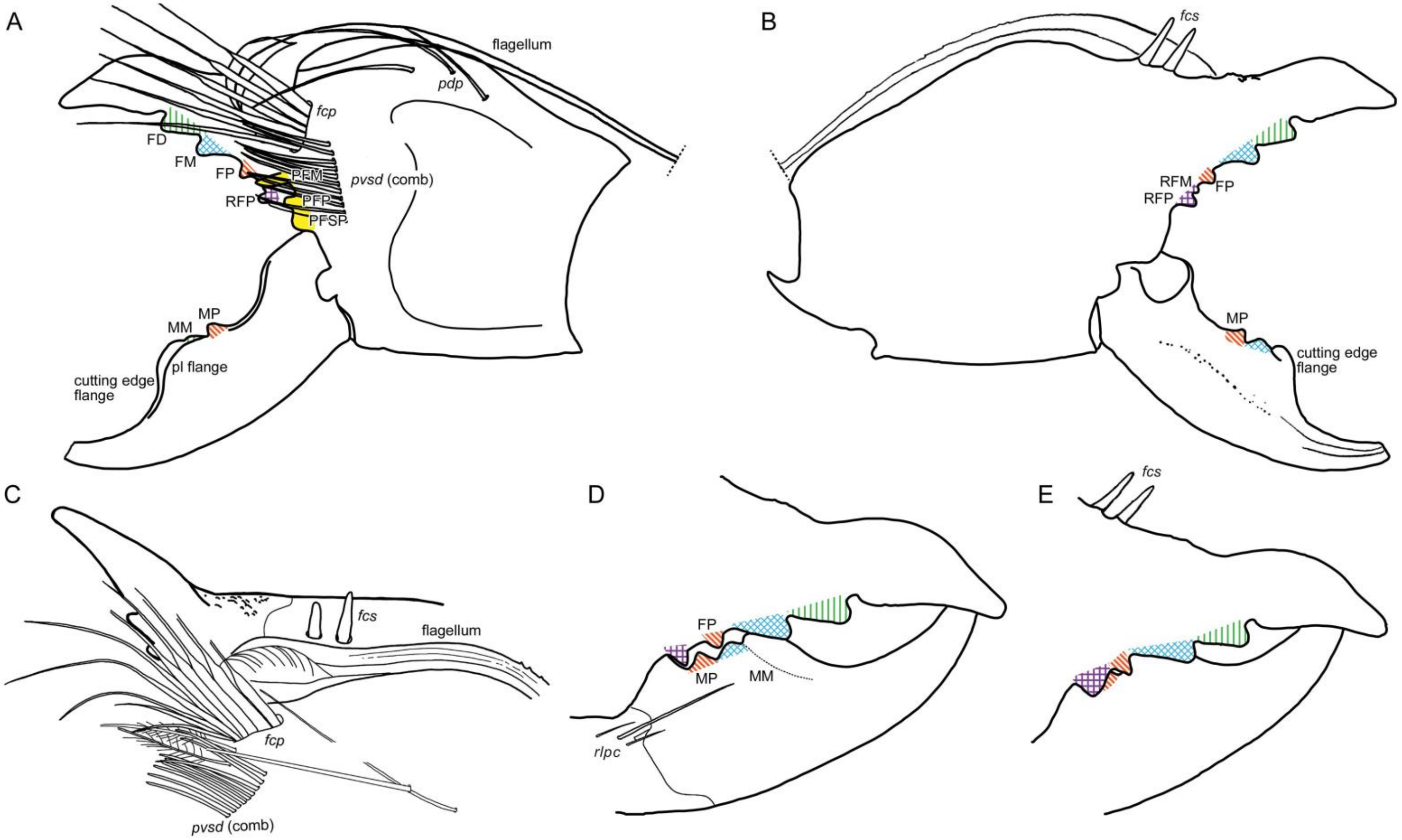

Plate 93. Ceromidae Roewer, 1933, *Ceroma ornatum* Karsch, 1885, ♂ (MRAC 213.106), chelicerae, prolateral (**A**) and retrolateral (**B, D, E**) views, fixed finger prodorsal view (**C**), illustrating setae, and flagellar complex. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; PFM, profondal medial tooth; PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; *fcp*, flagellum complex plumose setae (modified proventral distal, *pvd*, setae); *fcs*, flagellar complex spiniform setae (modified prodorsal distal, *pdd*, setae); *pdp*, prodorsal proximal setae; *pvsd*, proventral subdistal setae (setal comb only); *rlpc*, retrolateral proximal cluster of setae; pl, prolateral.

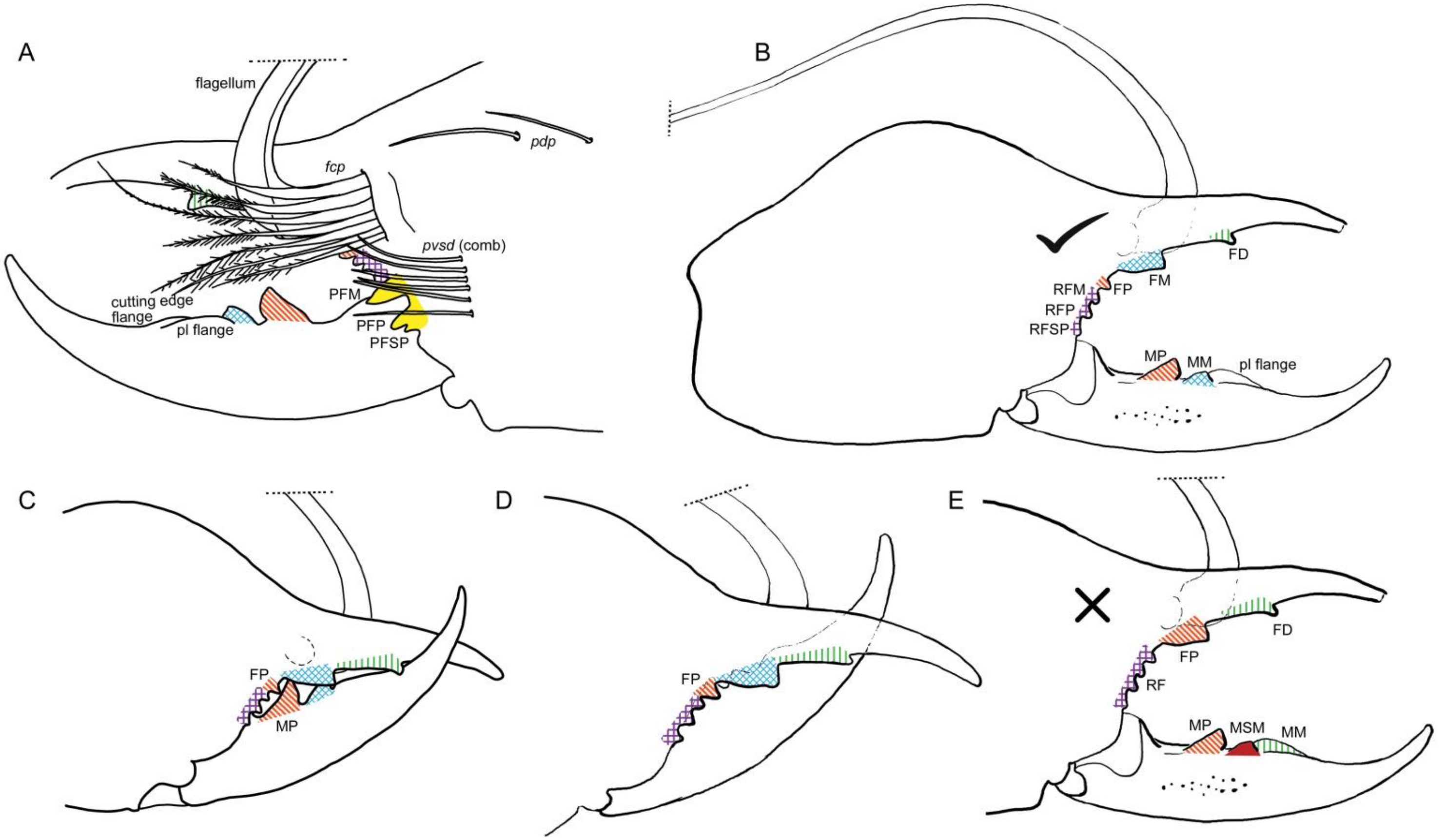

Plate 94. Ceromidae Roewer, 1933, *Ceroma swierstrae* Lawrence, 1935, ♂ (NCA 2009/4355), chelicerae, prolateral (**A**) and retrolateral (**B–E**) views, illustrating movable (ventral) finger interpretations of dentition by previous authors (Lawrence, 1935b; Roewer, 1941), indicated with a X (**B**) and proposed here, indicated with a check mark (**E**), setae, and flagellar complex. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth; PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal tooth; *fcp*, flagellum complex plumose setae (modified proventral distal, *pvd*, setae); *pdp*, prodorsal proximal setae; *pvsd*, proventral subdistal setae (setal comb only); pl, prolateral..

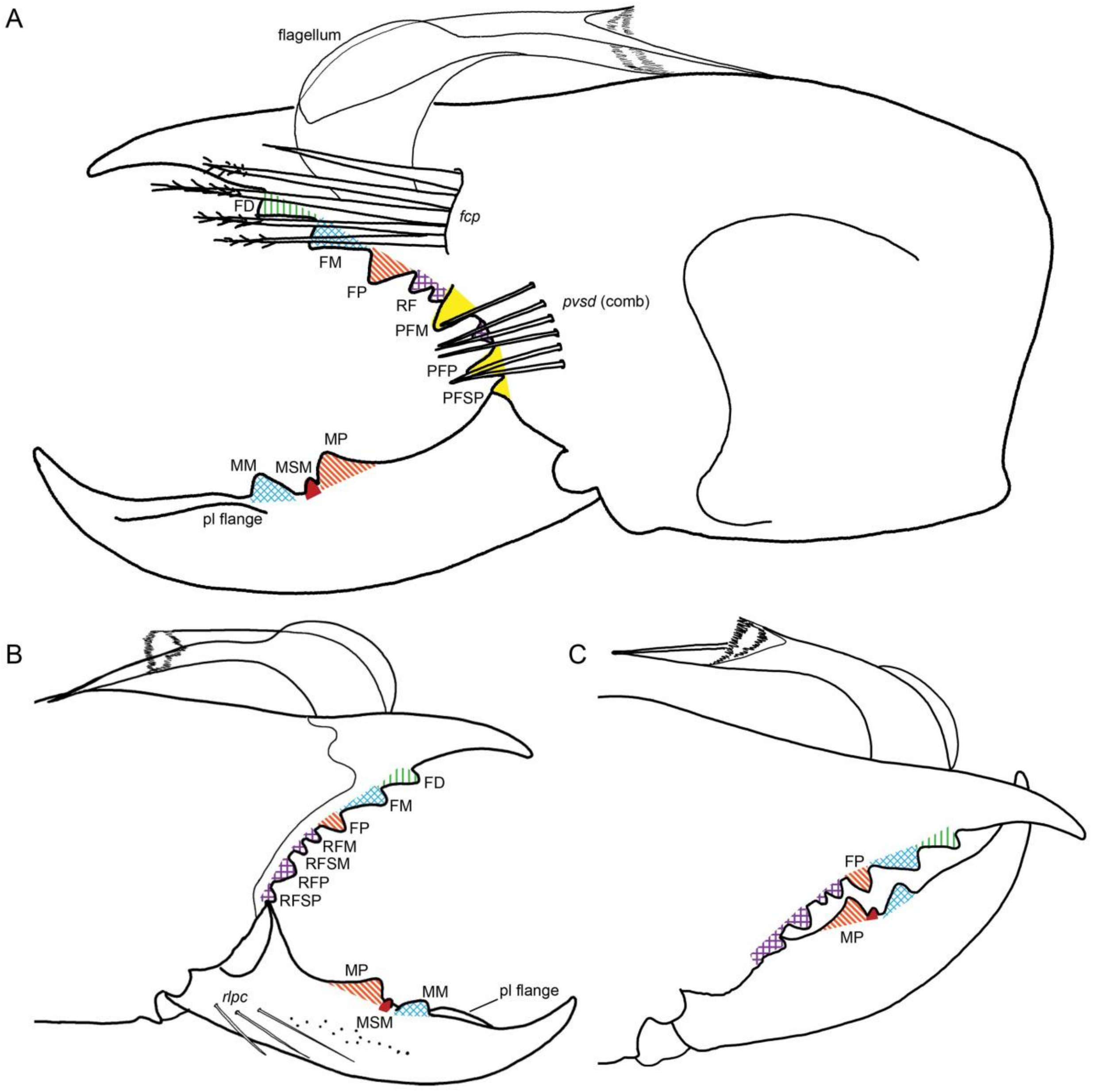

Plate 95. Ceromidae Roewer, 1933, *Ceromella* sp. n., ♂ (AMNH [LP 8527]), chelicerae, prolateral (**A**) and retrolateral (**B, C**) views, illustrating dentition, setae, and flagellar complex. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RF retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *fcp*, flagellum complex plumose setae (modified proventral distal, *pvd*, setae); *pvsd*, proventral subdistal setae (setal comb only); *rlpc*, retrolateral proximal cluster of setae; pl, prolateral.

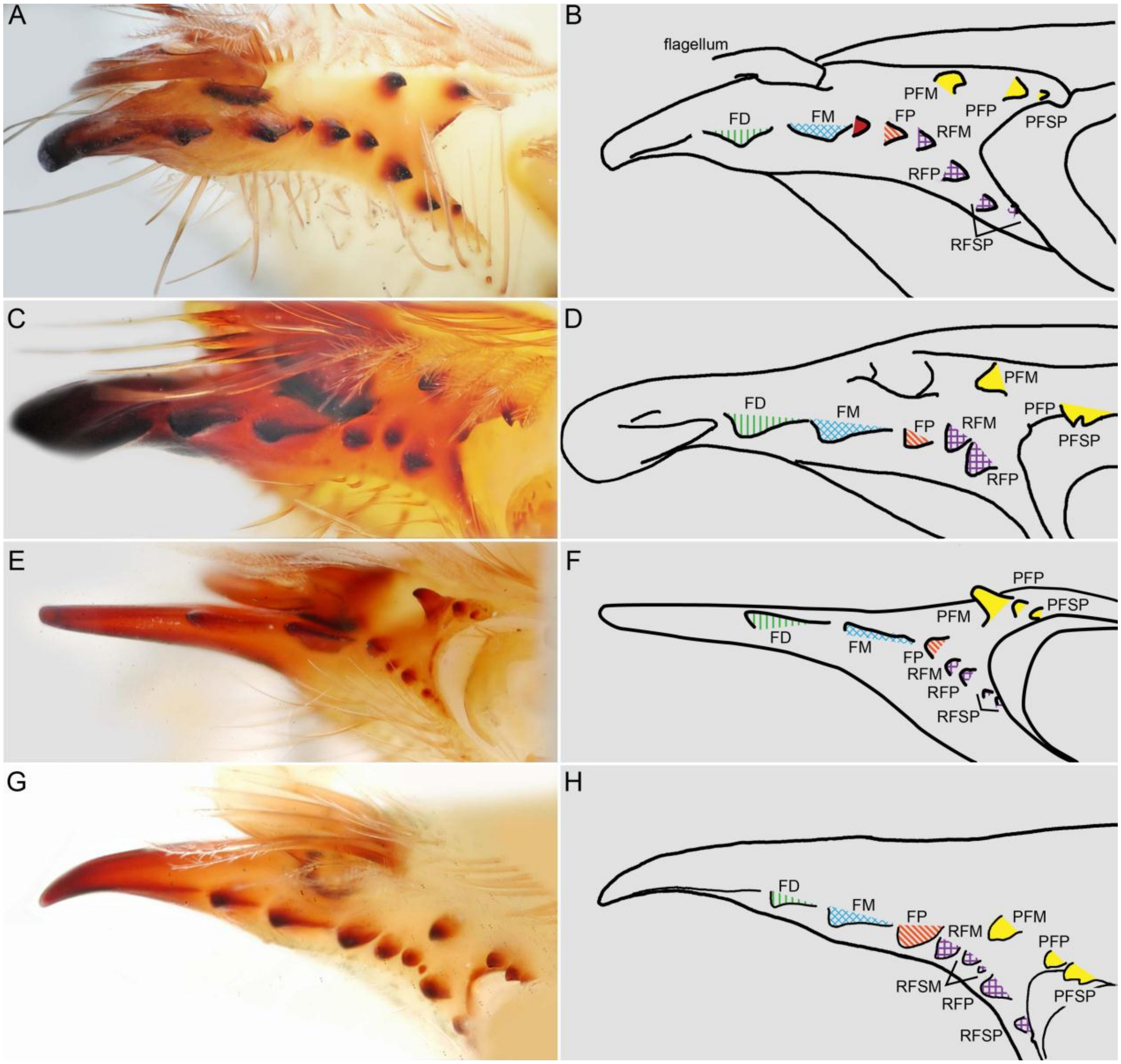

Plate 96. Ceromidae Roewer, 1933, cheliceral fixed fingers, proventral views illustrating fondal area. **A, B.** *Ceroma inerme* Purcell, 1899, ♂ (AMNH [LP 9864]). **C, D.** *Ceroma ornatum* Karsch, 1885, ♂ (MRAC 213.106). **E, F.** *Ceroma swierstrae* Lawrence, 1935, ♂ (NCA 2009/4355). **G, H.** *Ceromella* sp. n., ♂ (AMNH [LP 8527]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; PFM, profondal medial tooth; PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial teeth; RFSP, retrofondal subproximal teeth.

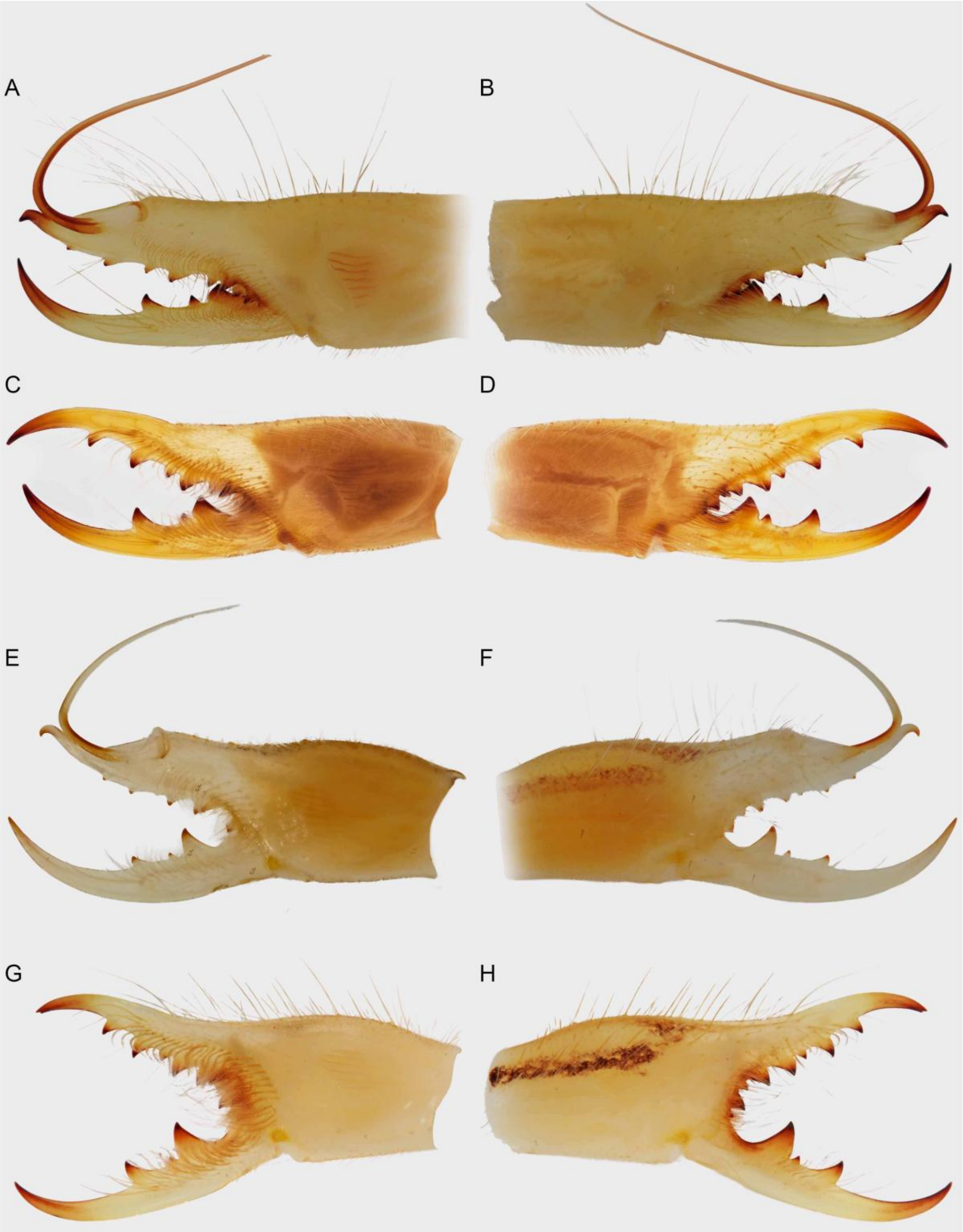

Plate 97. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A–D.** *Metasolpuga picta* (Kraepelin, 1899). **A, B.** ♂ (AMNH [LP 10719]). **C, D.** subad. ♂ (AMNH), Namibia: Gobabeb plains. **E–H.** *Prosolpuga schultzei* (Kraepelin, 1908). **E, F.** ♂ (NMNW 13759). **G, H.** ♀ (AMNH [LP 3605]).

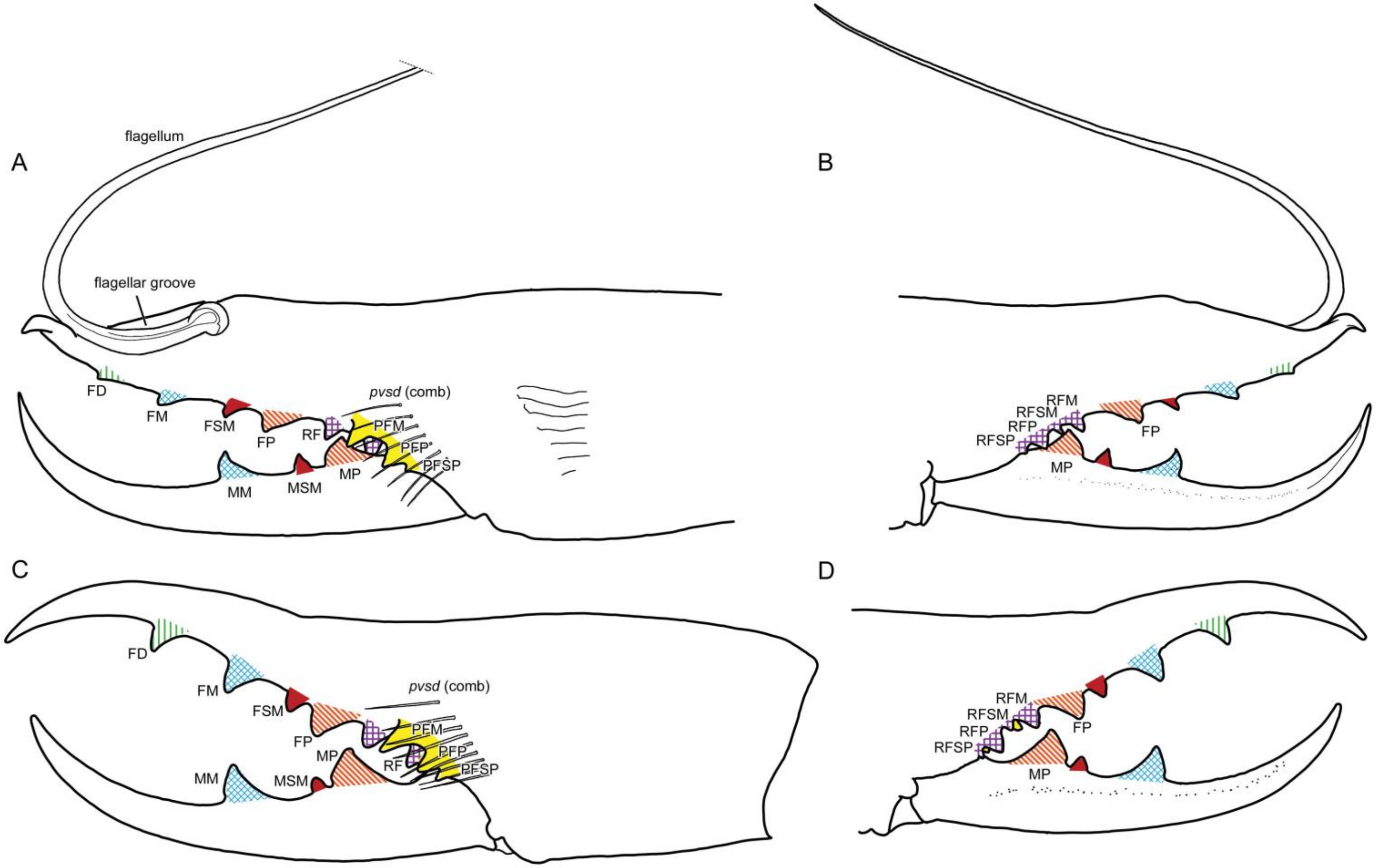

Plate 98. Solpugidae Leach, 1815, *Metasolpuga picta* (Kraepelin, 1899), chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 10719]). **C, D.** subad. ♂ (AMNH), Namibia: Gobabeb. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only).

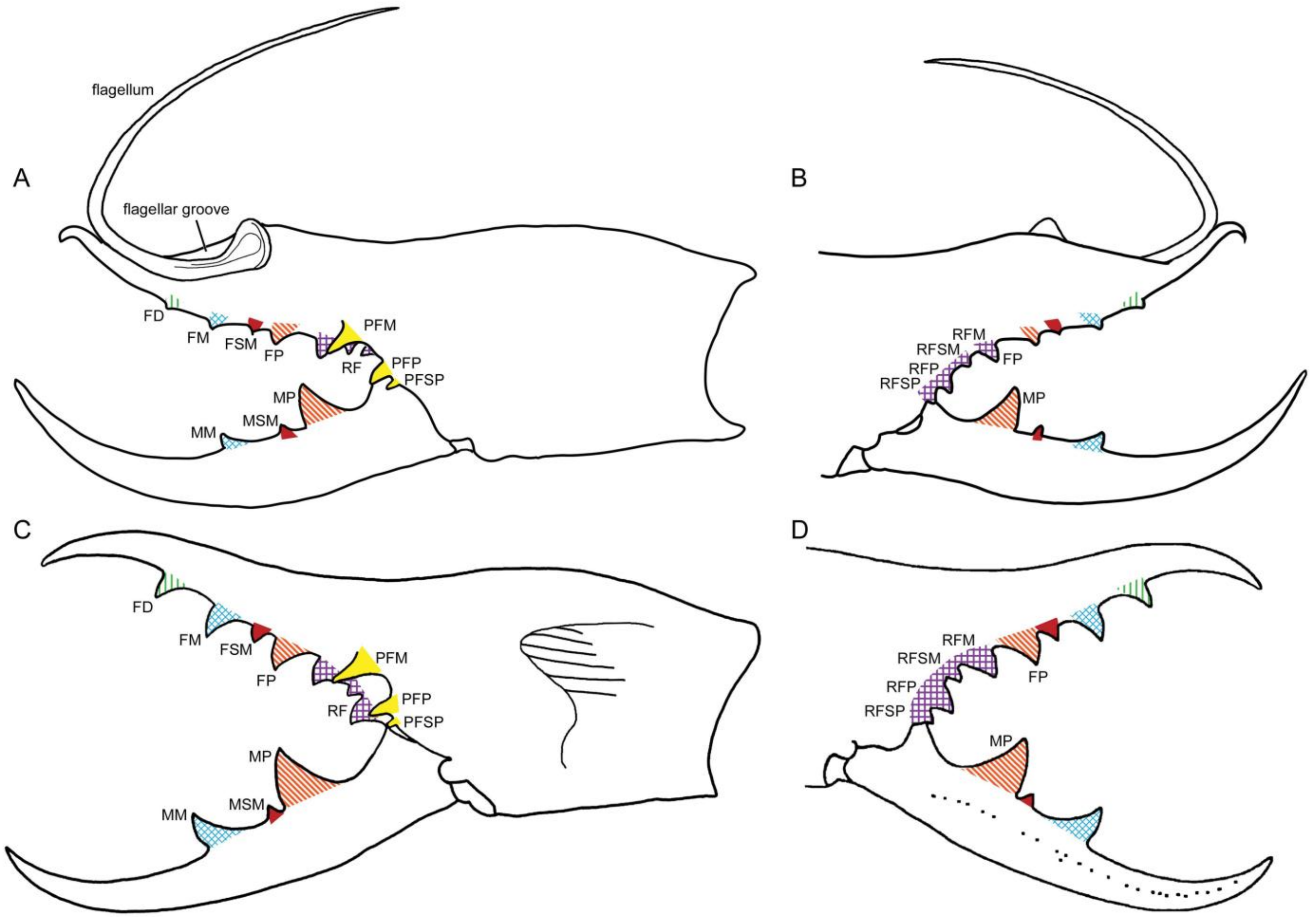

Plate 99. Solpugidae Leach, 1815, *Prosolpuga schultzei* (Kraepelin, 1908), chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (NMNW 13759). **C, D.** ♀ (AMNH [LP 3605]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal teeth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth.

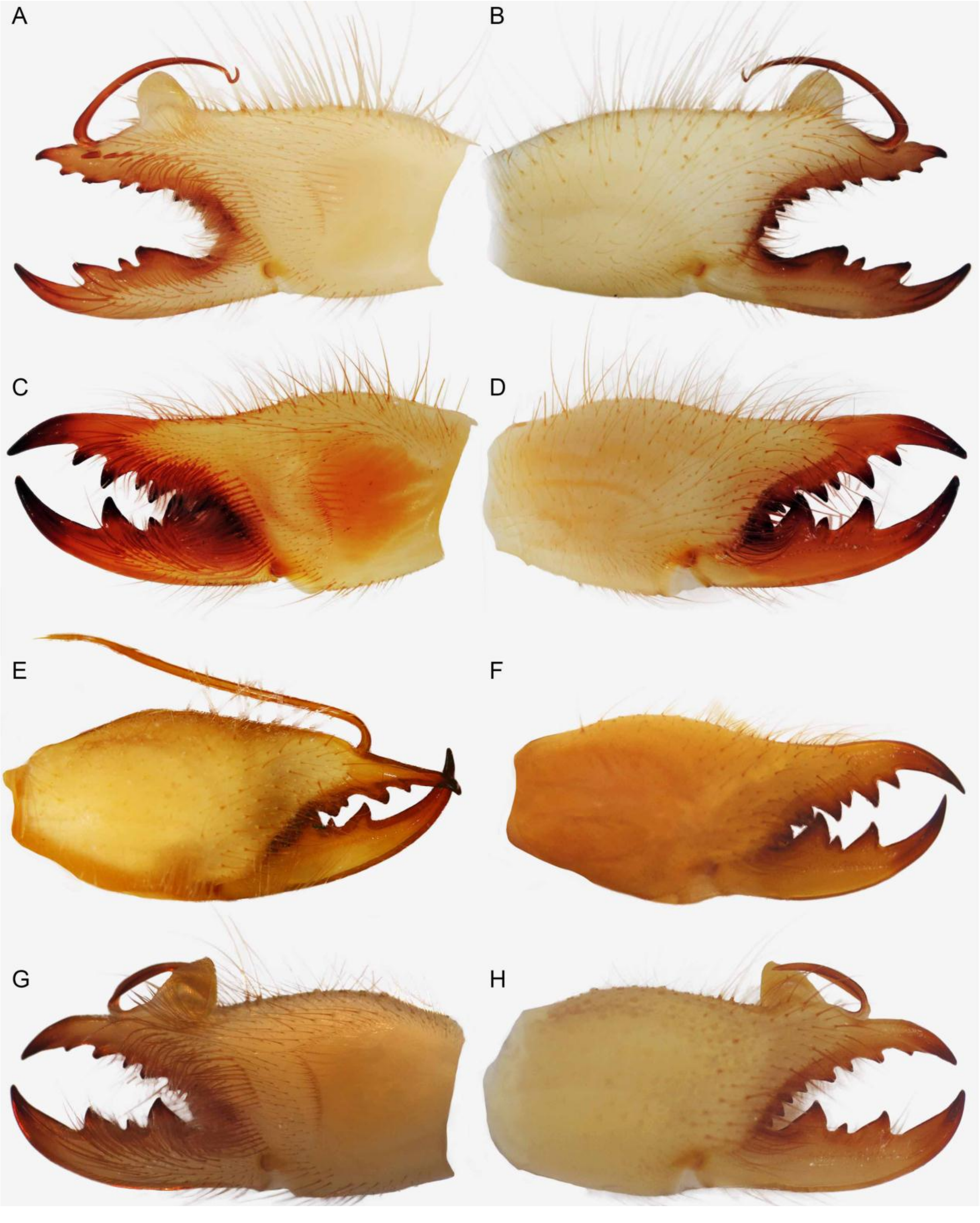

Plate 100. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, G**) and retrolateral (**B, D–F, H**) views. **A–D.** *Oparba asiatica* (Turk, 1948). **A, B.** ♂ (HUJI 684). **C, D.** ♀ (TAU 50313). **E, F.** *Oparbella flavescens* (C.L. Koch, 1842). **E.** ♂ (MCZ 102912). **F.** ♀ (MCZ 102912). **G, H.** *Oparbella* sp., ♂ (MRAC 230.211).

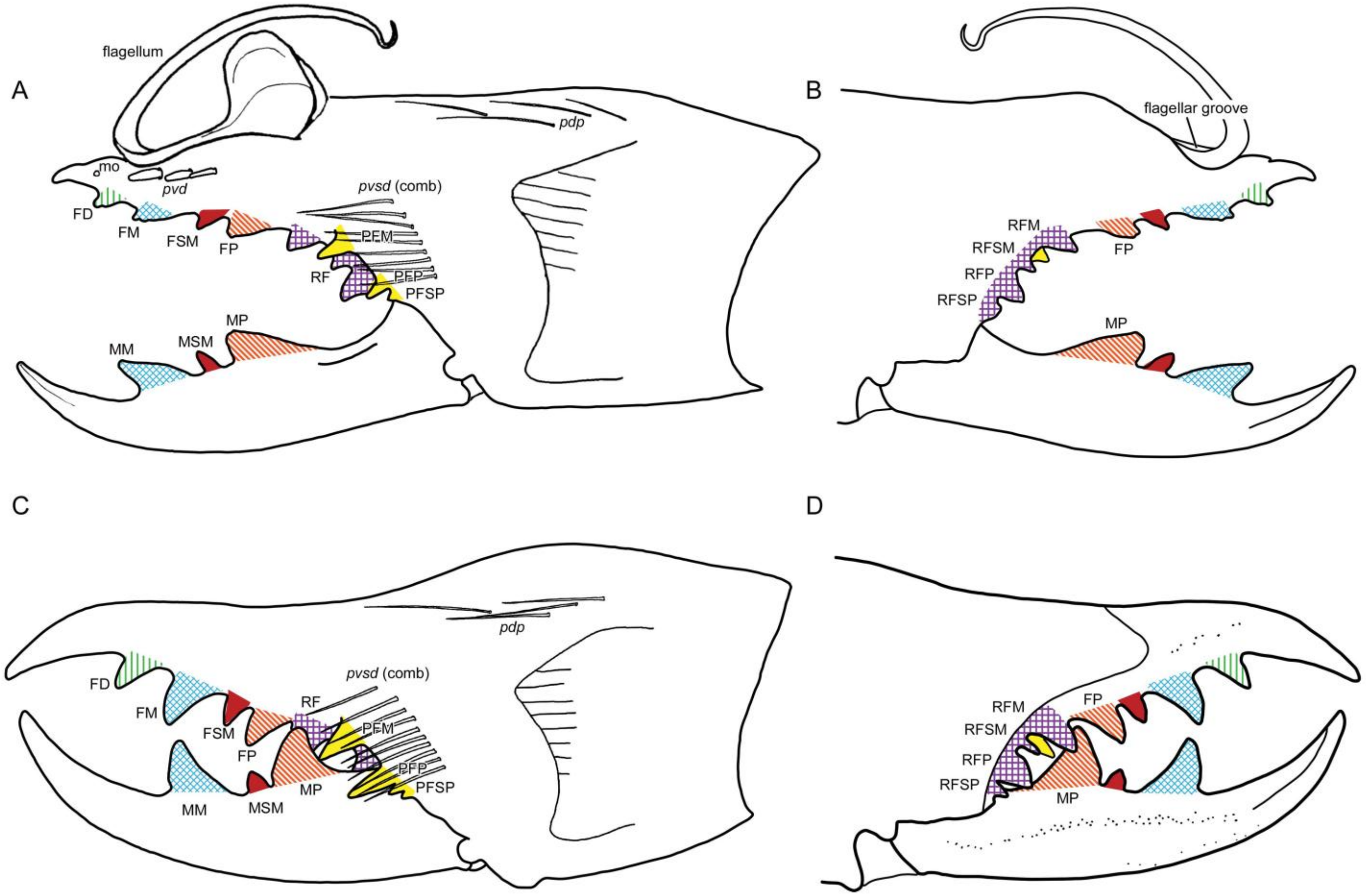

Plate 101. Solpugidae Leach, 1815, *Oparba asiatica* (Turk, 1948), chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (HUJI 684). **C, D.** ♀ (TAU 50313). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pdp*, prodorsal proximal setae; *fcp*, flagellar complex plumose setae (modified proventral distal, *pvd*, setae); *pvsd*, proventral subdistal setae (setal comb only); mo, mucron organ.

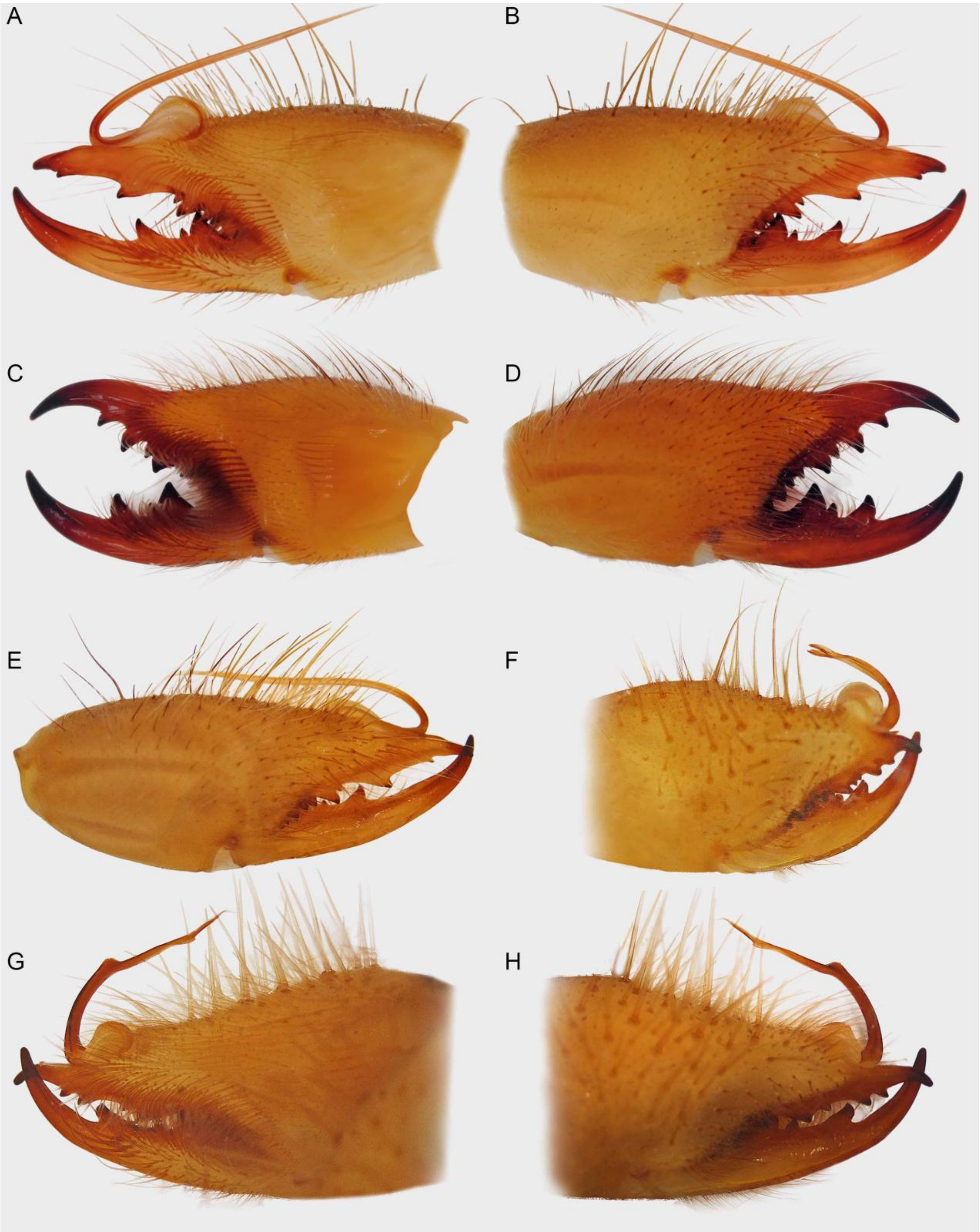

Plate 102. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, G**) and retrolateral (**B, D–F, H**) views. **A–D, E.** *Solpuga chelicornis* Lichtenstein, 1796. **A, B.** ♂ (AMNH [LP 8158]). **C, D.** ♀ (NCA 2008/3524). **E.** ♂ (NCA 2008/3524). **F.** *Solpuga massaica* Roewer, 1941 ♂ (SMF R 7391). **G, H.** *Solpuga roeweri* Fage, 1936, ♂ (MCZ 126317).

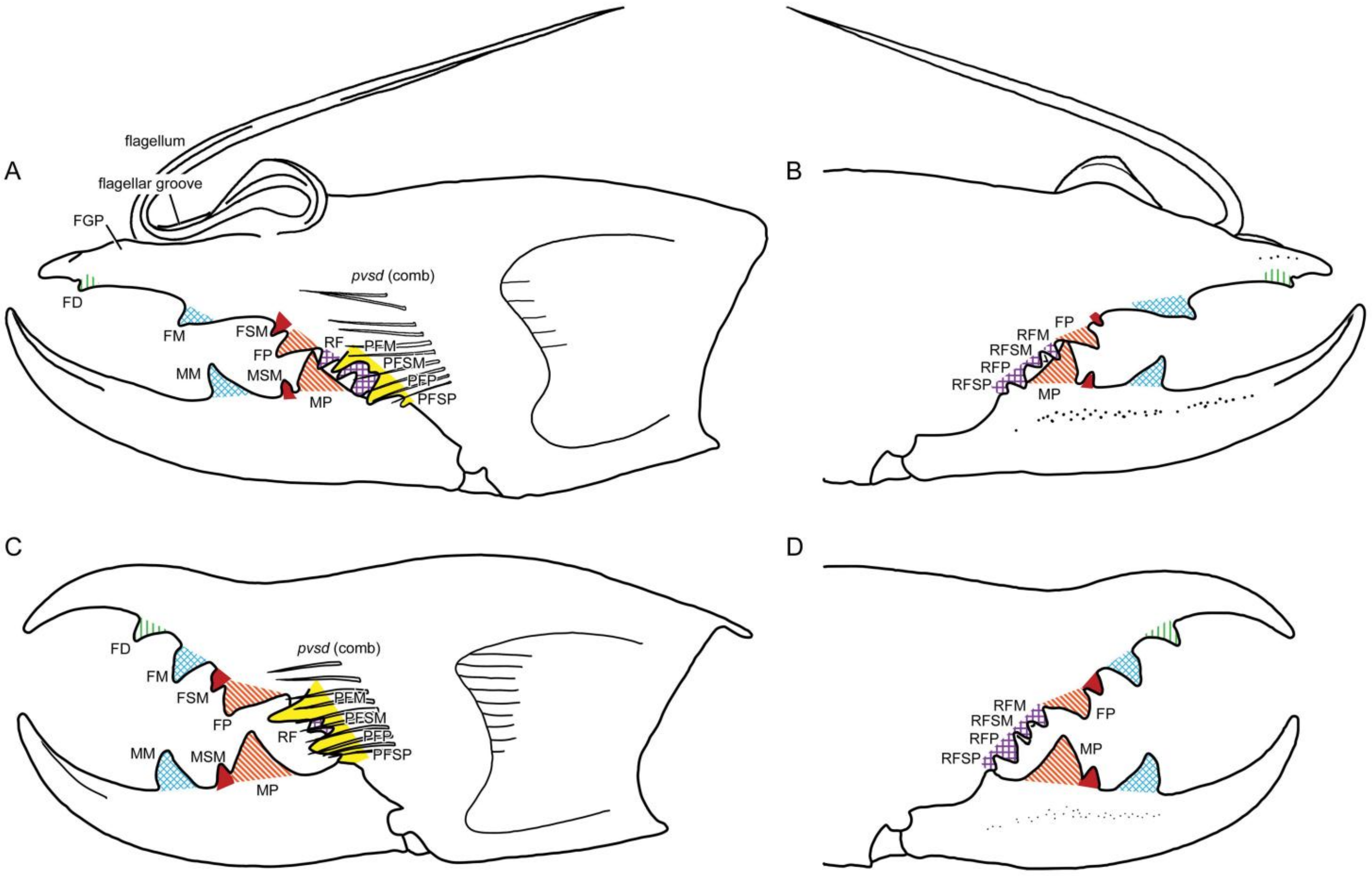

Plate 103. Solpugidae Leach, 1815, *Solpuga chelicornis* Lichtenstein, 1796, chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 8158]). **C, D.** ♀ (NCA 2008/3524). Abbreviations: FD, fixed finger, distal tooth; FGP, flagellar groove process; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only).

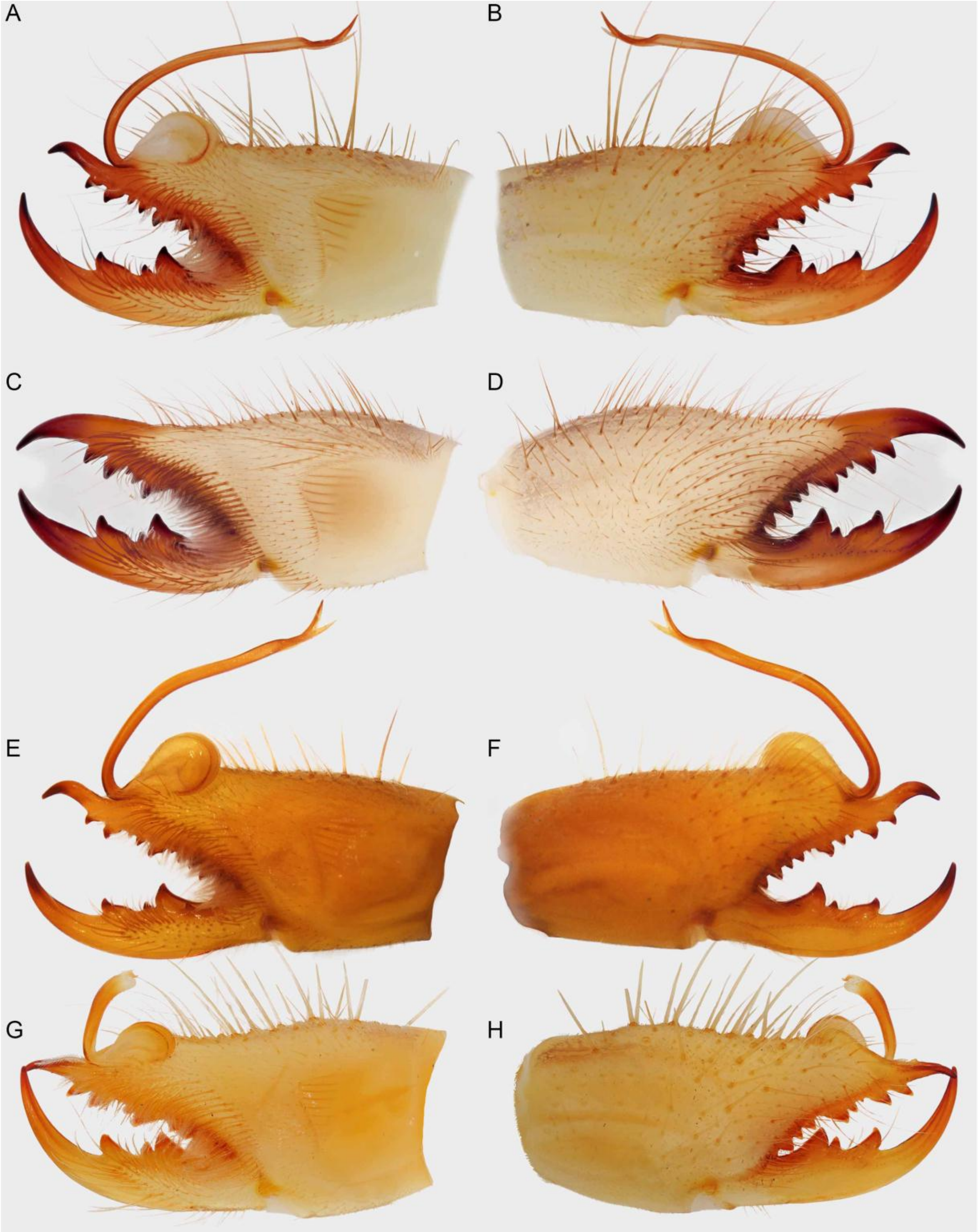

Plate 104. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A–D.** *Solpugassa furcifera* (Kraepelin, 1899). **A, B.** ♂ (AMNH [LP 3632]). **C, D.** ♀ (AMNH [LP 3632]). **E, F.** *Solpugassa furcifera* (Kraepelin, 1899), holotype ♂ (TM 8843) of *Solpugassa kochi* Lawrence, 1959. **G, H.** *Solpugella* sp., ♂ (NMNW 11097).

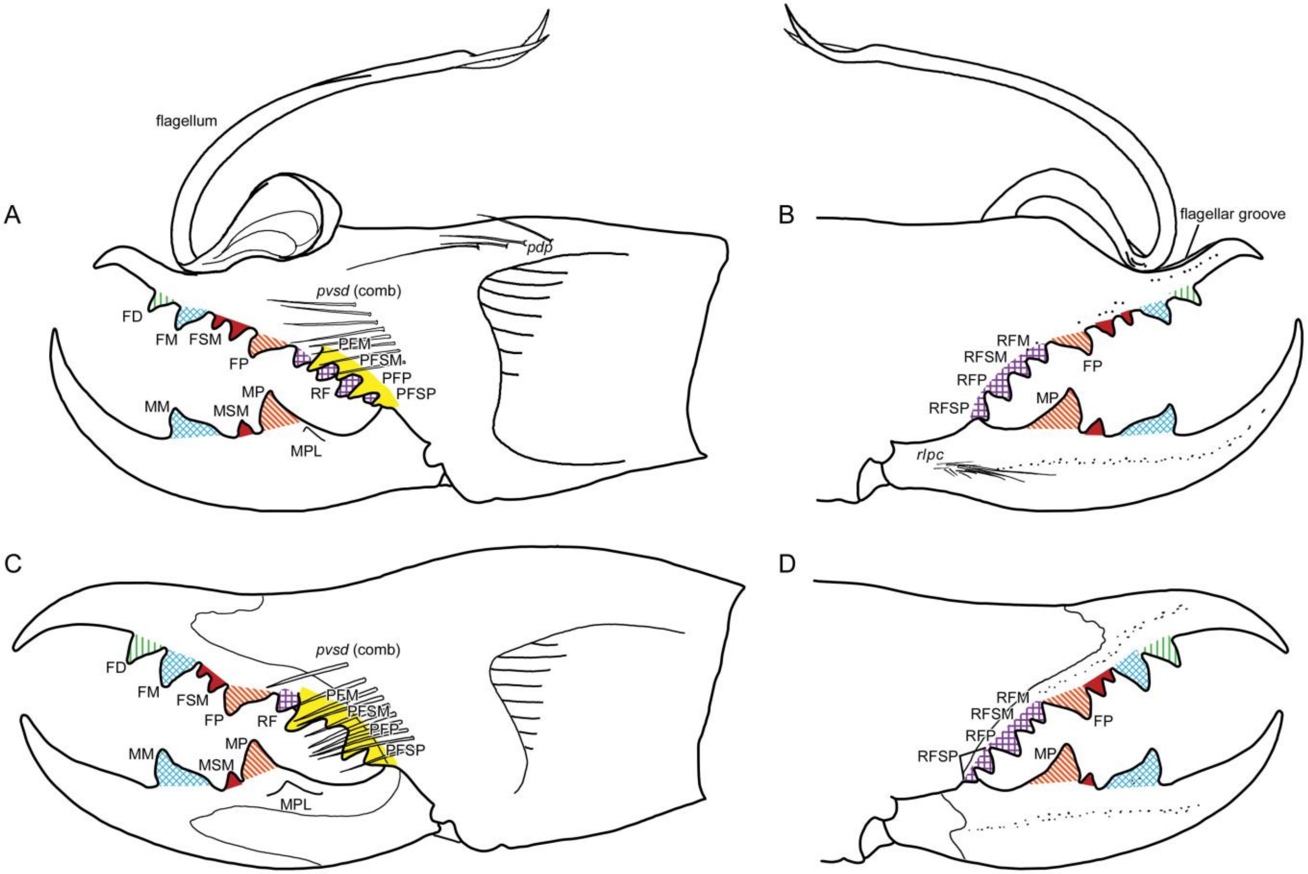

Plate 105. Solpugidae Leach, 1815, *Solpugassa furcifera* (Kraepelin, 1899), chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 3632]). **C, D.** ♀ (AMNH [LP 3632]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MPL, movable finger, prolateral tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth; PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pdp*, prodorsal proximal setae; *pvsd*, proventral subdistal setae (setal comb only); *rlpc*, retrolateral proximal cluster of setae.

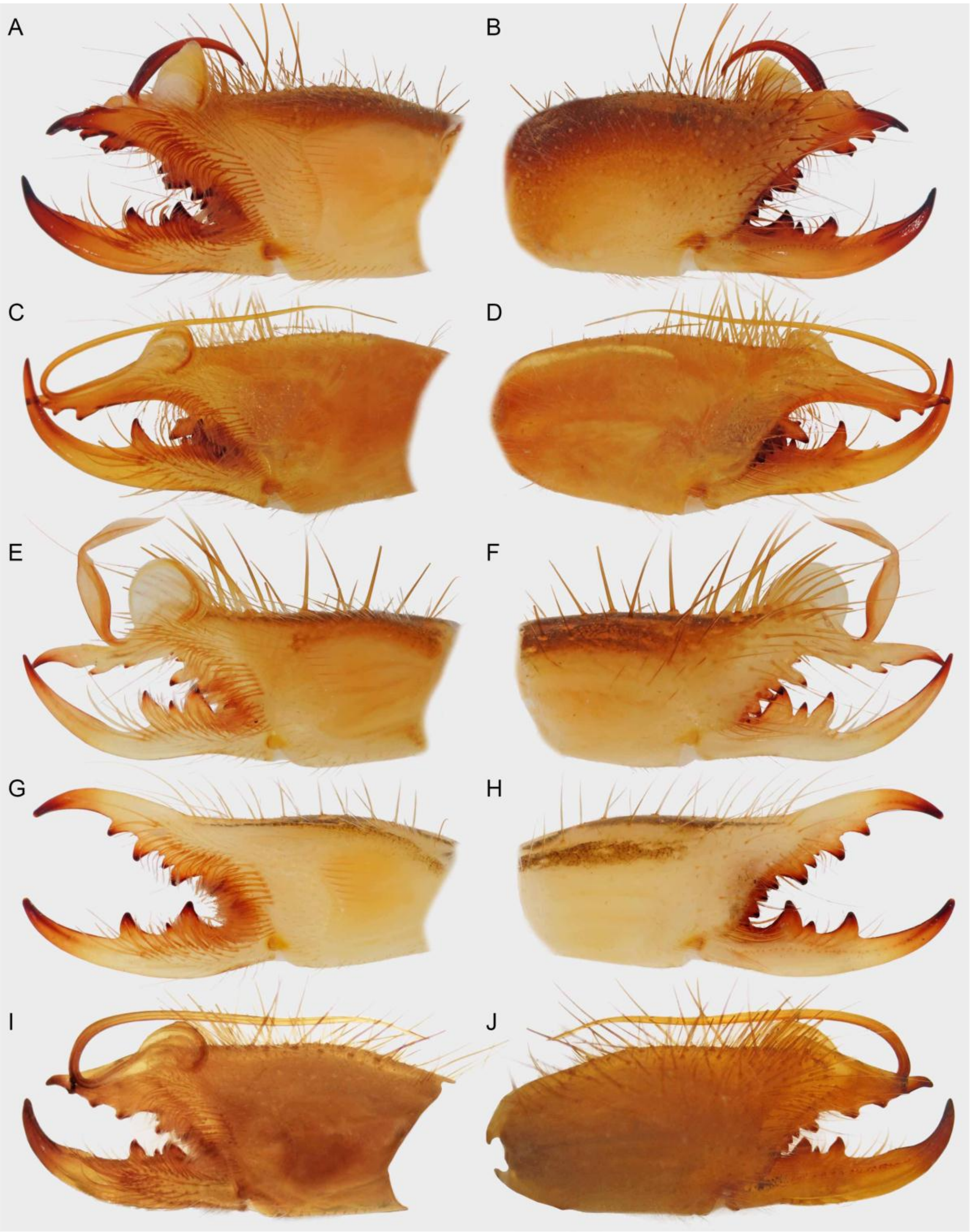

Plate 106. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Solpugema brachyceras* (Lawrence, 1931), ♂ (AMNH [LP 1960B]). **C, D.** *Solpugema derbiana* (Pocock, 1895), ♂ (AMNH [LP 7709]). **E–H.** *Solpugema genucornis* (Lawrence, 1935). **E, F.** ♂ (AMNH [LP 8167]). **G, H.** ♀ (AMNH [LP 10292]). **I, J.** *Solpugema hamata* (Hewitt, 1914), ♂ (TM 6632).

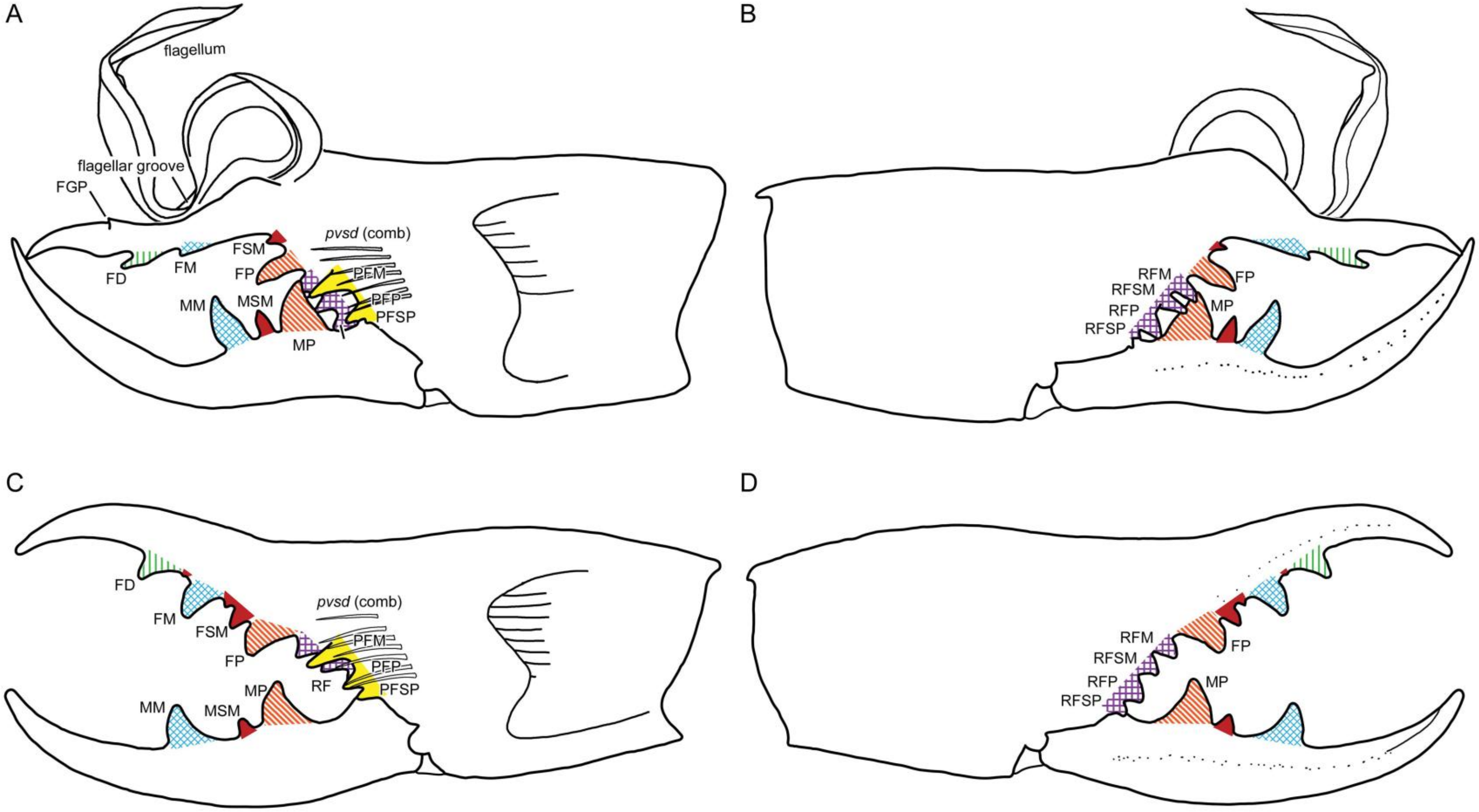

Plate 107. Solpugidae Leach, 1815, *Solpugema genucornis* (Lawrence, 1935), chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 8167]). **C, D.** ♀ (AMNH [LP 10292]). Abbreviations: FD, fixed finger, distal tooth; FGP, flagellar groove process; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only).

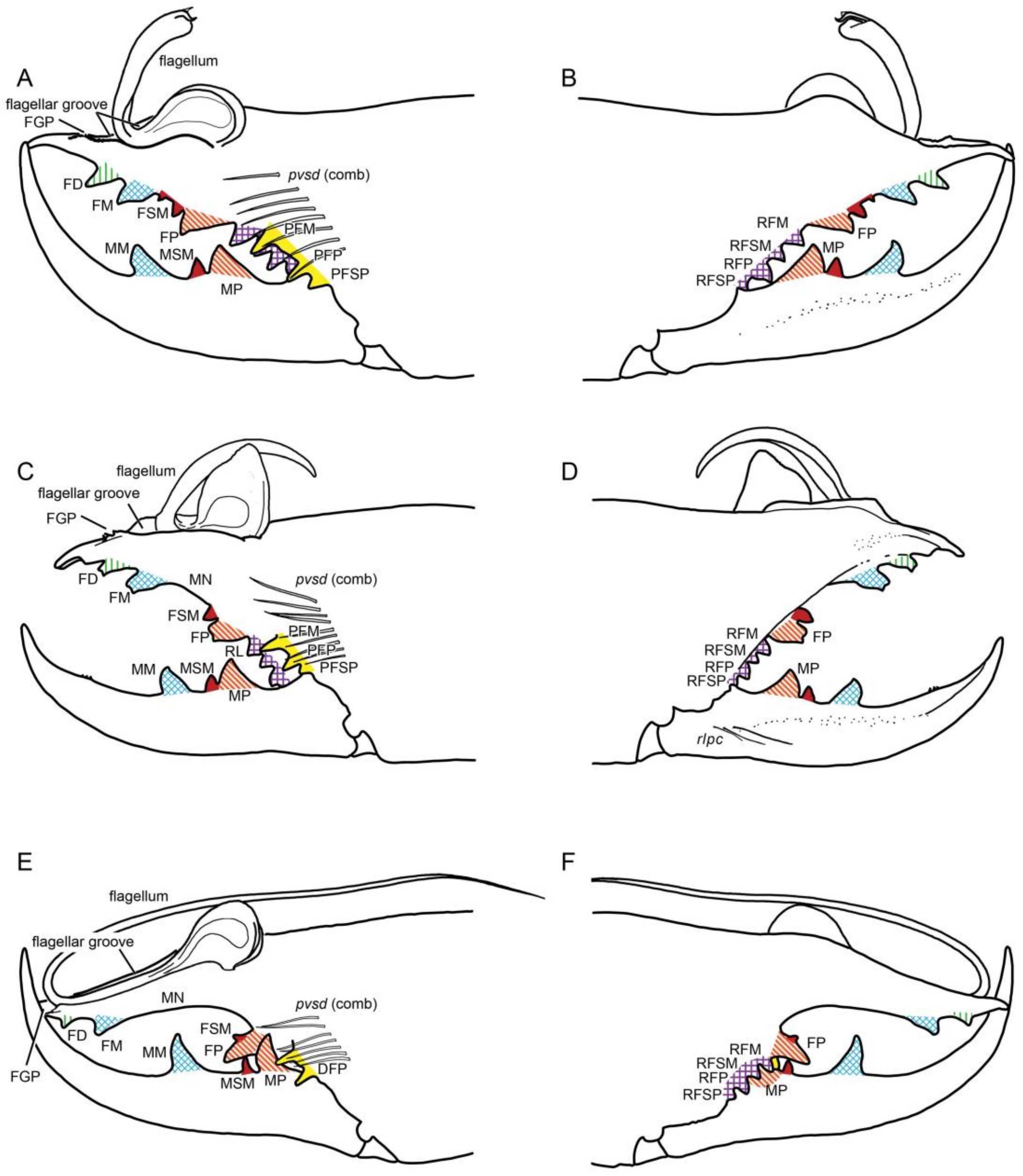

Plate 108. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E**) and retrolateral (**B, D, F**) views, illustrating dentition, setae, and male flagellum. **A, B.** *Solpugella* sp., ♂ (NMNW 11097). **C, D.** *Solpugema brachyceras* (Lawrence, 1931), ♂ (AMNH [LP 1960B]). **E, F.** *Solpugema derbiana* (Pocock, 1895), ♂ (AMNH [LP 7709]). Abbreviations: FD, fixed finger, distal tooth; FGP, flagellar groove process. FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only); *rlpc*, retrolateral proximal cluster of setae

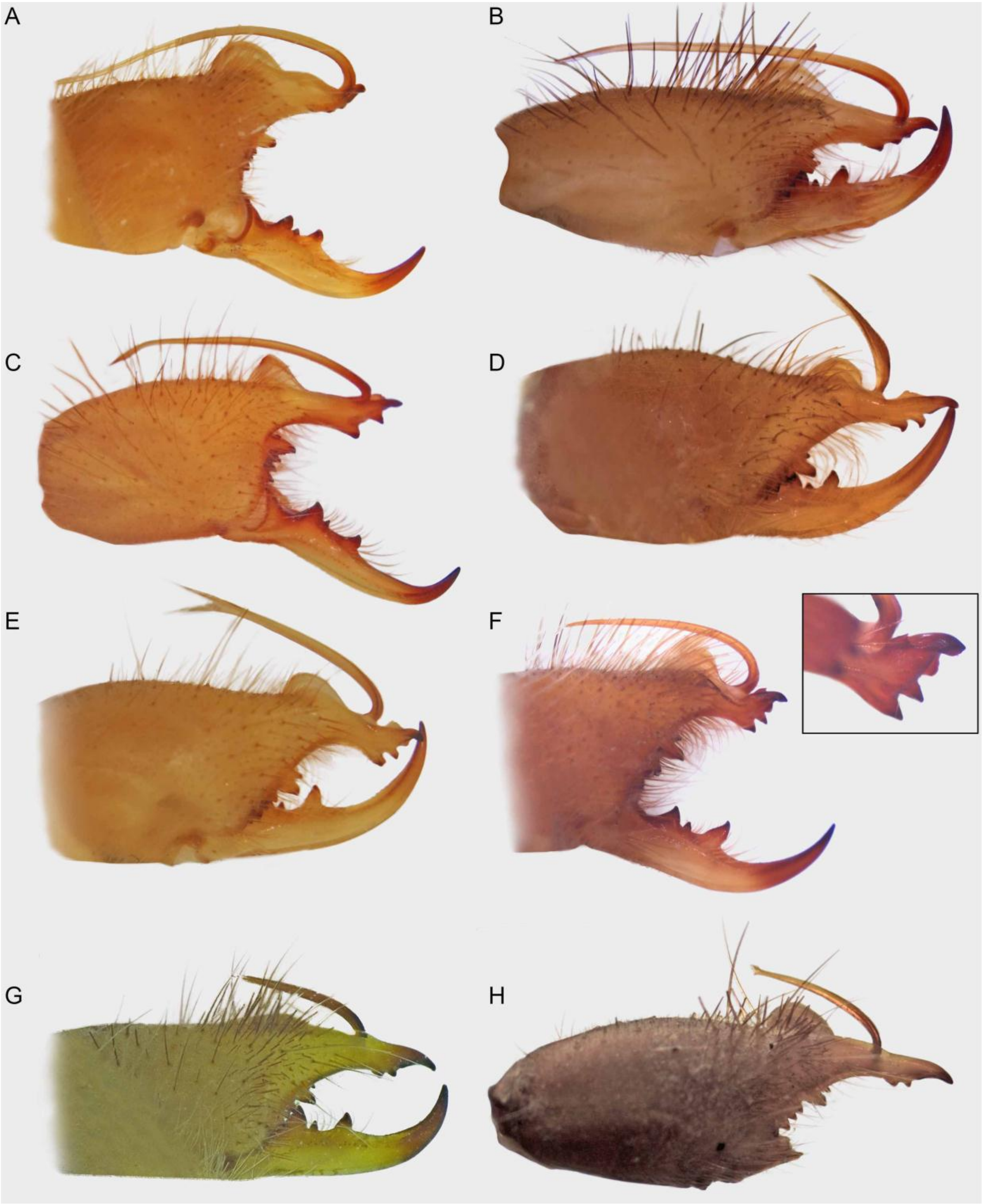

Plate 109. Solpugidae Leach, 1815, chelicerae, retrolateral views. **A, B.** *Solpugema hostilis* (White, 1846). **A.** ♂ (SMF R 3117). **B.** ♂ (NCA 2009/2817). **C.** *Solpugema* sp., ♂ (NCA 97/821). **D.** *Solpugema phylloceras* (Lawrence, 1929), ♂ (TM 8606). **E.** *Solpugema montana* (Lawrence, 1929), ♂ (SMF R 2904). **F.** *Solpugema intermedia* (Lawrence, 1929), ♂ (NCA 2009/4482). Insert: distal part of fixed (dorsal) finger. **G, H.** *Solpugema tubicen* (Kraepelin, 1911). **G.** Syntype ♂ (ZMUH [R9503]), **H.** ♂ (TM 2643).

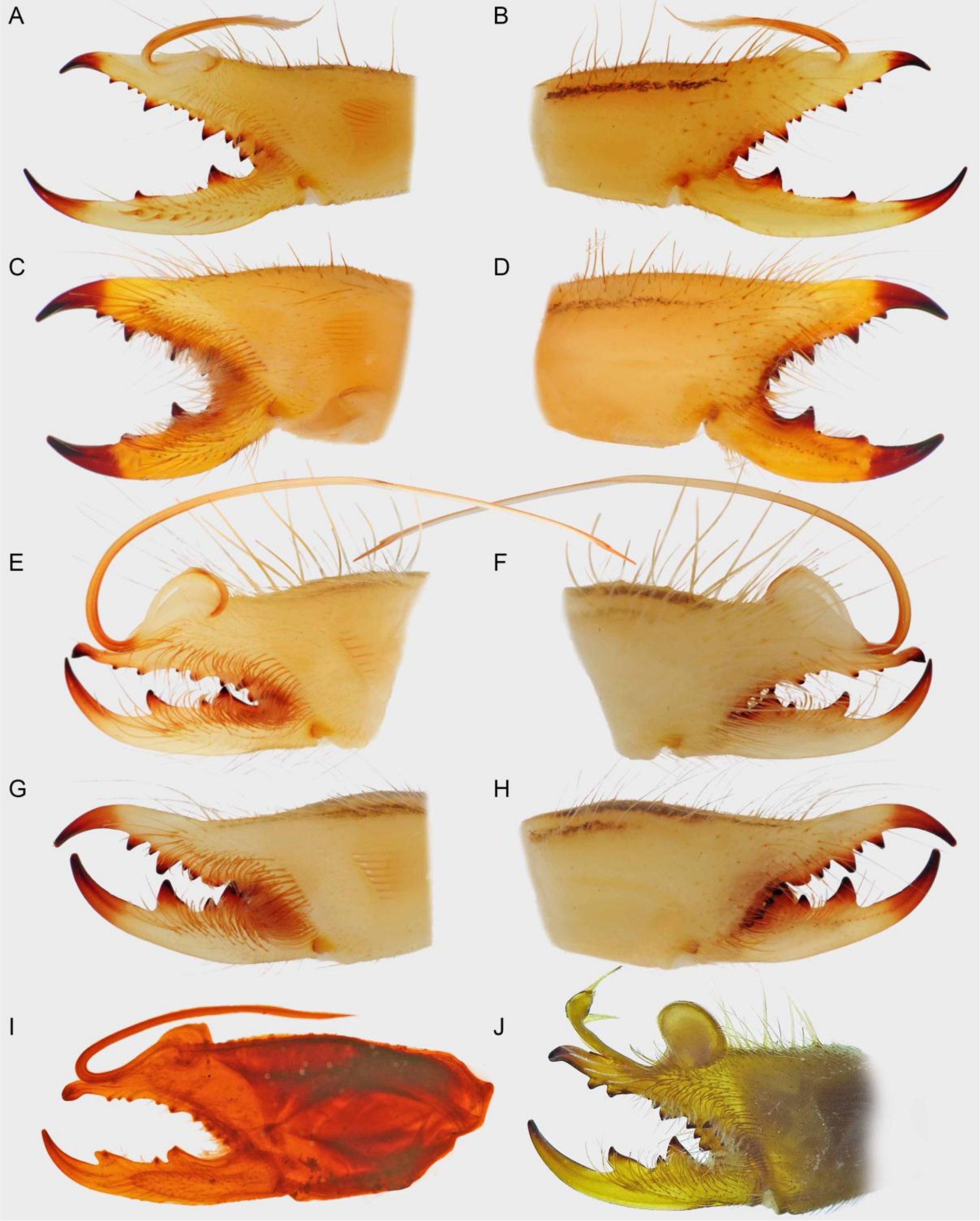

Plate 110. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G, I, J**) and retrolateral (**B, D, F, H**) views. **A–D.** *Solpugiba lineata* (C.L. Koch, 1842). **A, B.** ♂ (AMNH [LP 5919]). **C, D.** ♀ (AMNH [LP 5919]). **E–H.** *Solpugista bicolor* (Lawrence, 1953). **E, F.** ♂ (AMNH [LP 7933]). **G, H.** ♀ (AMNH [LP 9879]). **I.** *Solpugista hastata* (Kraepelin, 1899), holotype ♂ (SMF R6918). **J.** *Solpuguna alcicornis* (Kraepelin, 1914), syntype ♂ (ZMUH [R8515]).

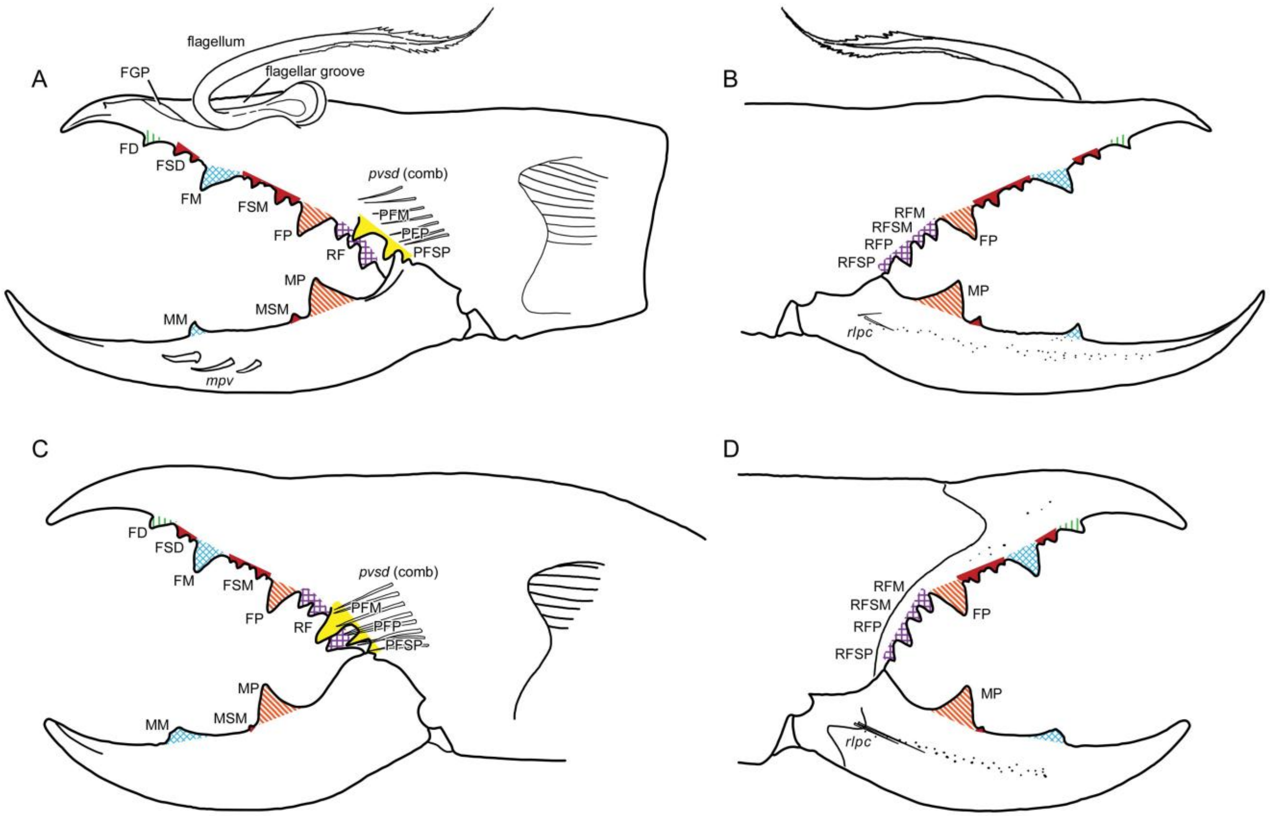

Plate 111. Solpugidae Leach, 1815, *Solpugiba lineata* (C.L. Koch, 1842), chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and male flagellum. **A, B.** ♂ (AMNH [LP 5919]). **C, D.** ♀ (AMNH [LP 5919]). Arrow indicates mucron organ (mo) apically on flagellar groove process (FGP). Abbreviations: FD, fixed finger, distal tooth; FGP, flagellar groove process; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal teeth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal tooth; *mpv*, movable finger, proventral setae (three apicalmost *mpv* setae illustrated in **A**); *pvsd*, proventral subdistal setae (setal comb only); *rlpc*, retrolateral proximal cluster of setae.

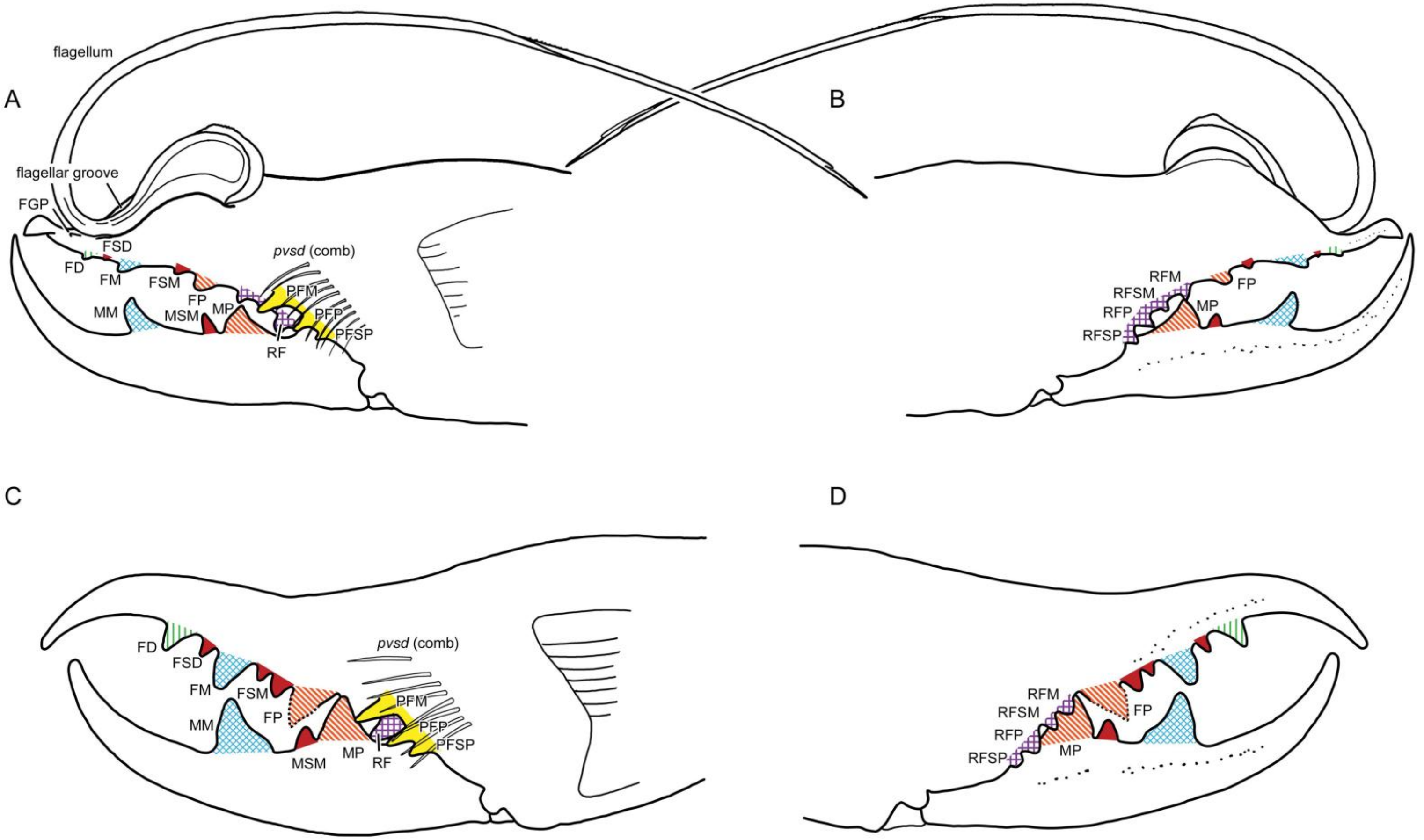

Plate 112. Solpugidae Leach, 1815, *Solpugista bicolor* (Lawrence, 1953), chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 7933]). **C, D.** ♀ (AMNH [LP 9879]). Abbreviations: FD, fixed finger, distal tooth; FGP, flagellar groove process; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only).

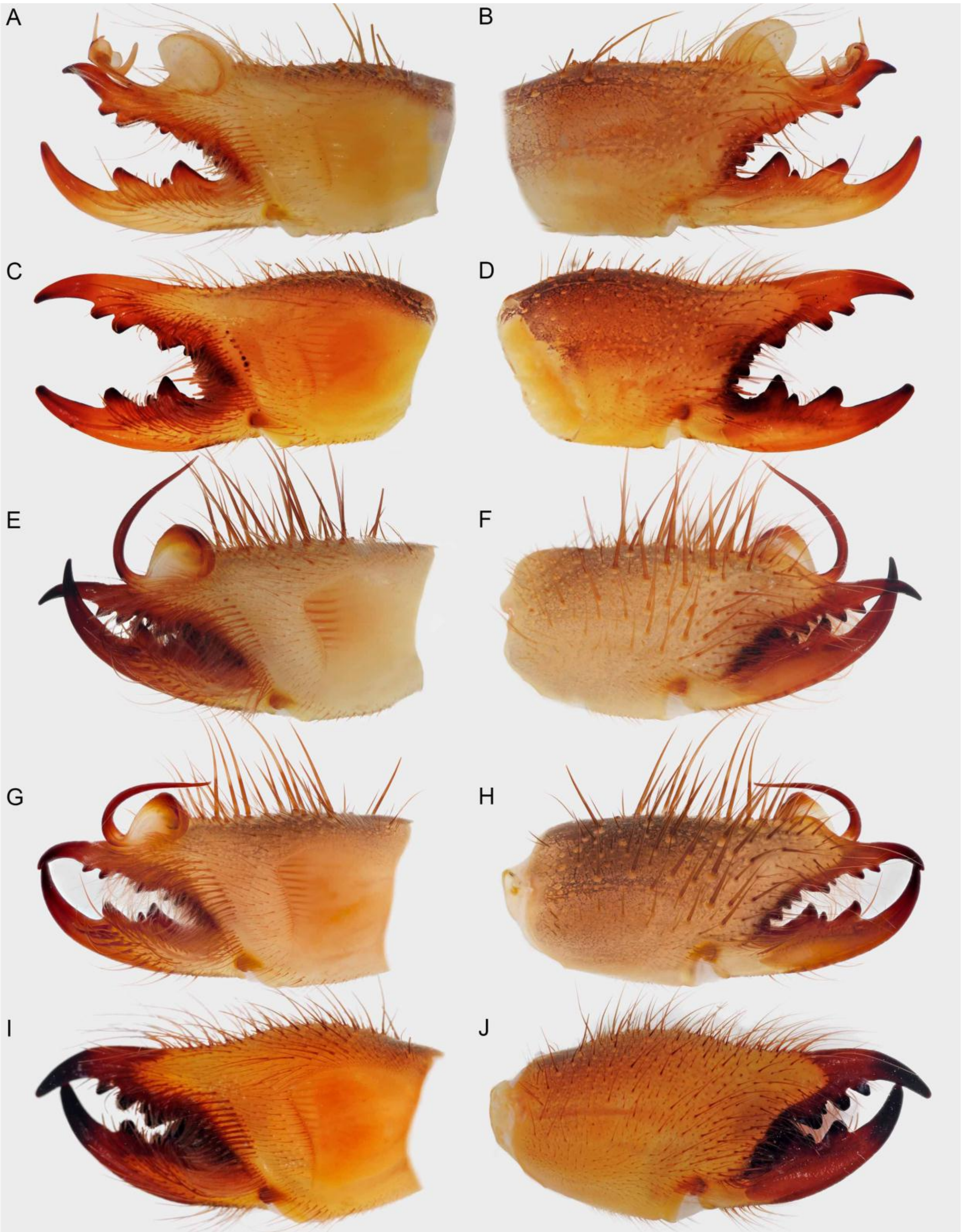

Plate 113. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A–D.** *Solpuguna* cf. *orangica.* **A, B.** ♂ (AMNH [LP 5969]). **C, D.** ♀ (AMNH [LP 5969]). **E–J.** *Solpugyla* sp. **E, F.** ♂ (AMNH [LP 8138]). **G, H.** ♂ (AMNH [LP 10764]). **I, J.** ♀ (AMNH [LP 10764]).

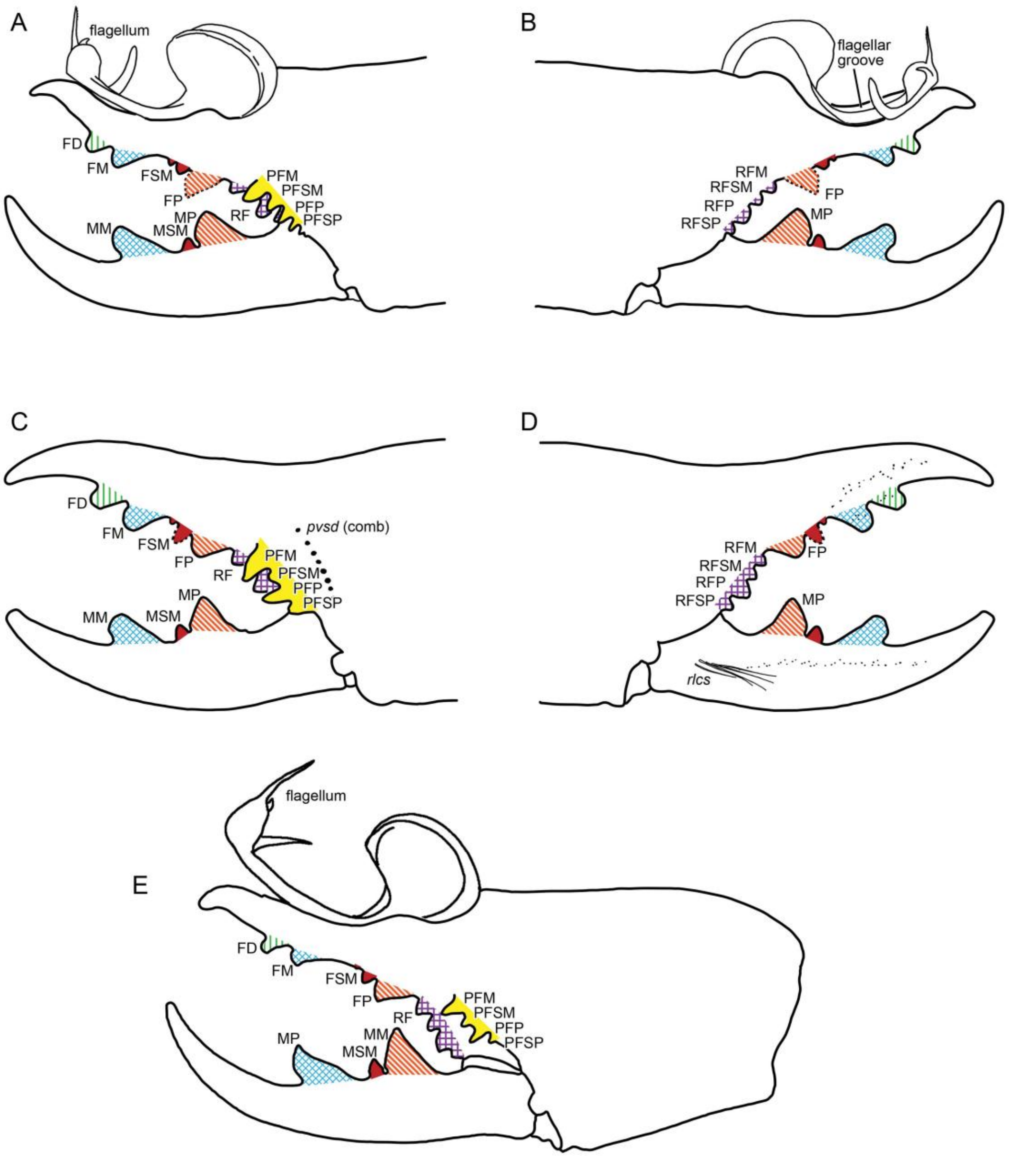

Plate 114. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A–D.** *Solpuguna* cf. *orangica*. **A, B.** ♂ (AMNH [LP 5969]). **C, D.** ♀ (AMNH [LP 5969]). **E.** *Solpuguna alcicornis* (Kraepelin, 1914), syntype ♂ (ZMUH [R8515]). Abbreviations: F D, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal (sockets of setal comb only); *rlpc*, retrolateral proximal cluster of setae.

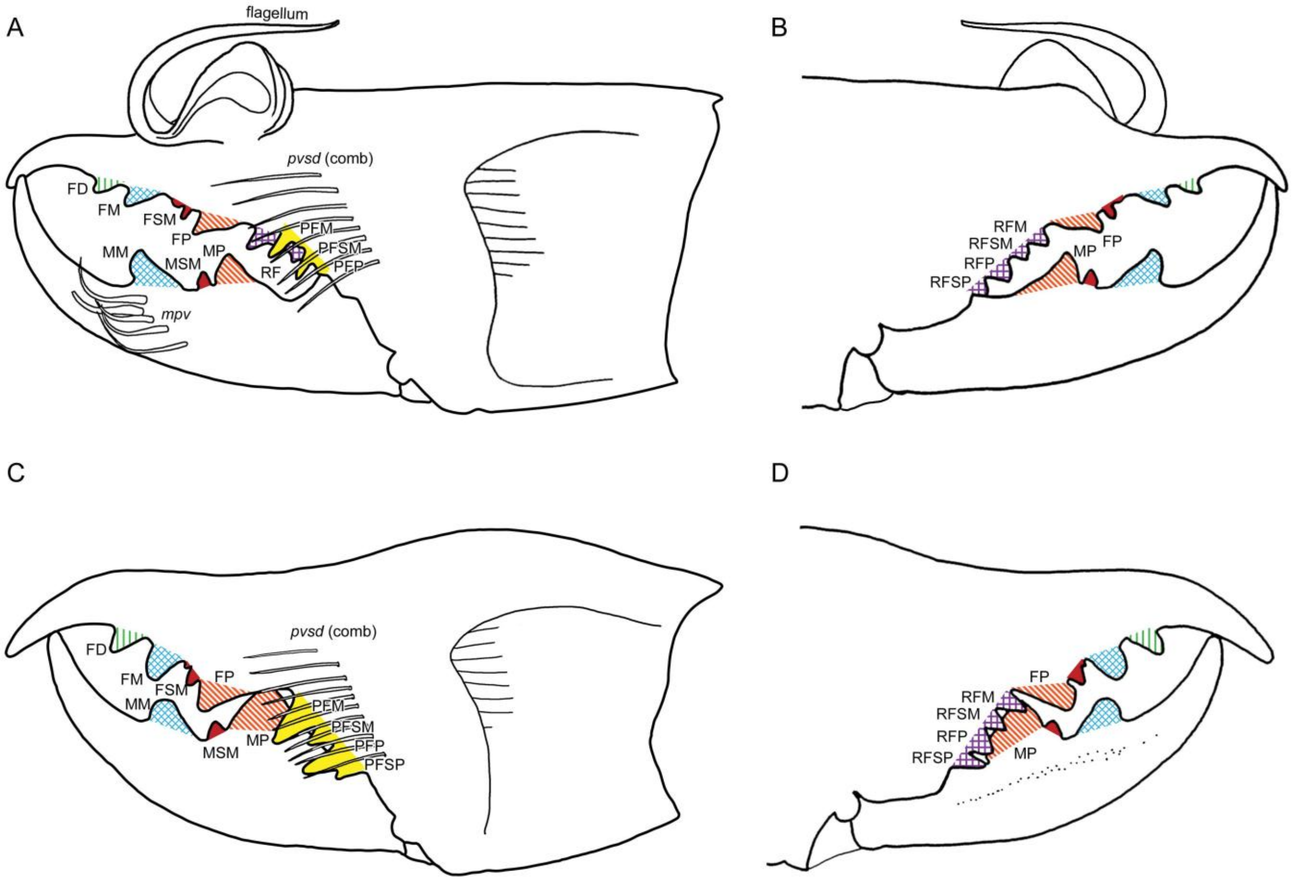

Plate 115. Solpugidae Leach, 1815, *Solpugyla* sp., chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 10764]). **C, D.** ♀ (AMNH [LP 10764]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *mpv*, movable finger, proventral setae (four apicalmost *mpv* setae illustrated in **A**); *pvsd*, proventral subdistal setae (setal comb only).

Plate 116. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A–D.** *Zeria fusca* (C.L. Koch, 1842). **A, B.** ♂ (AMNH [LP 1473]). **C, D.** ♀ (AMNH [LP 1472]). **E–H.** *Zeria sericea* (Pocock, 1897). **E, F.** ♂ (NMNW 13801). **G, H.** ♀ (NMNW 13801).

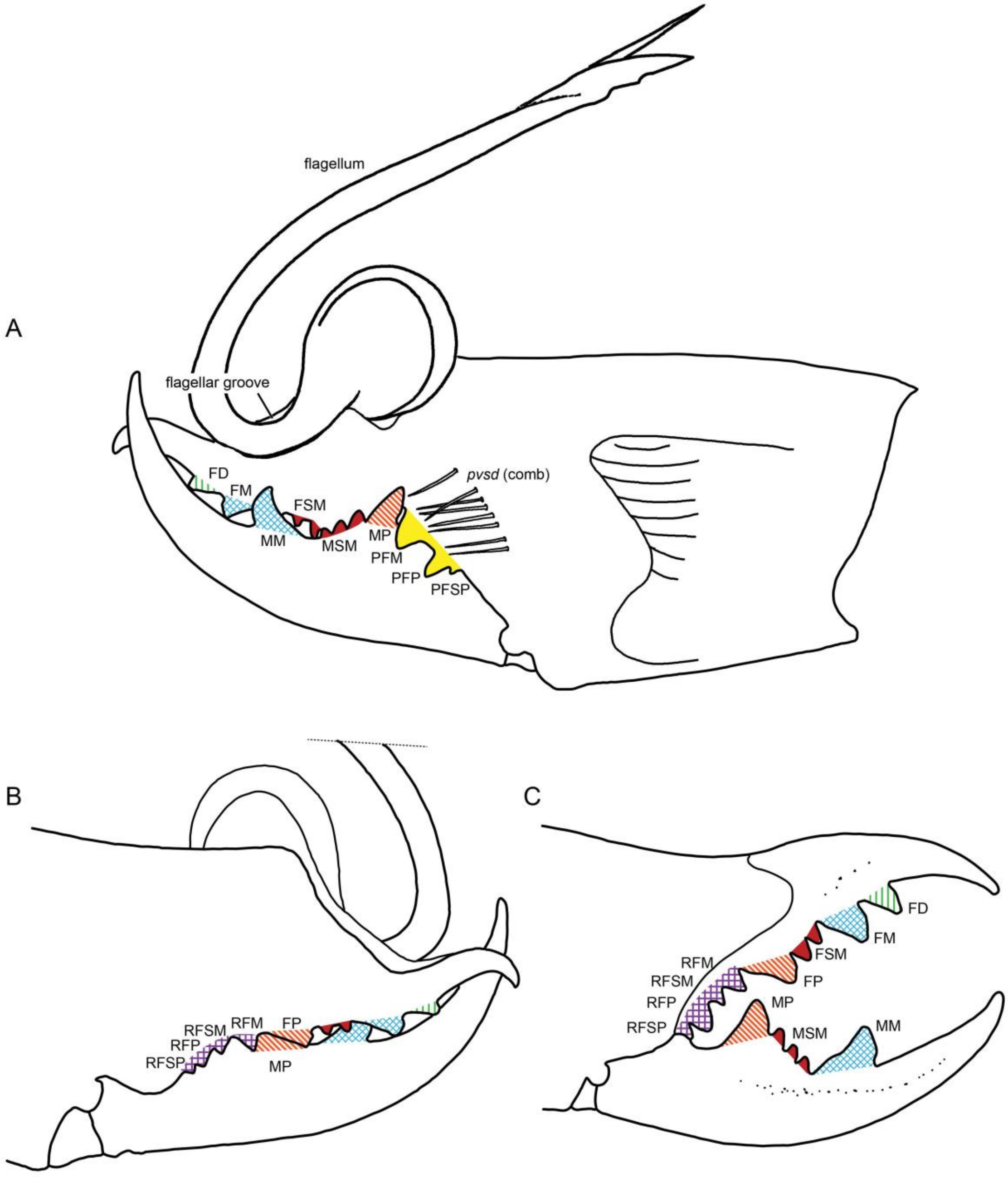

Plate 117. Solpugidae Leach, 1815, *Zeria fusca* (C.L. Koch, 1842), chelicerae, prolateral (**A**) and retrolateral (**B, C**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 1473]). **C.** ♀ (AMNH [LP 1472]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; PF, profondal teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only).

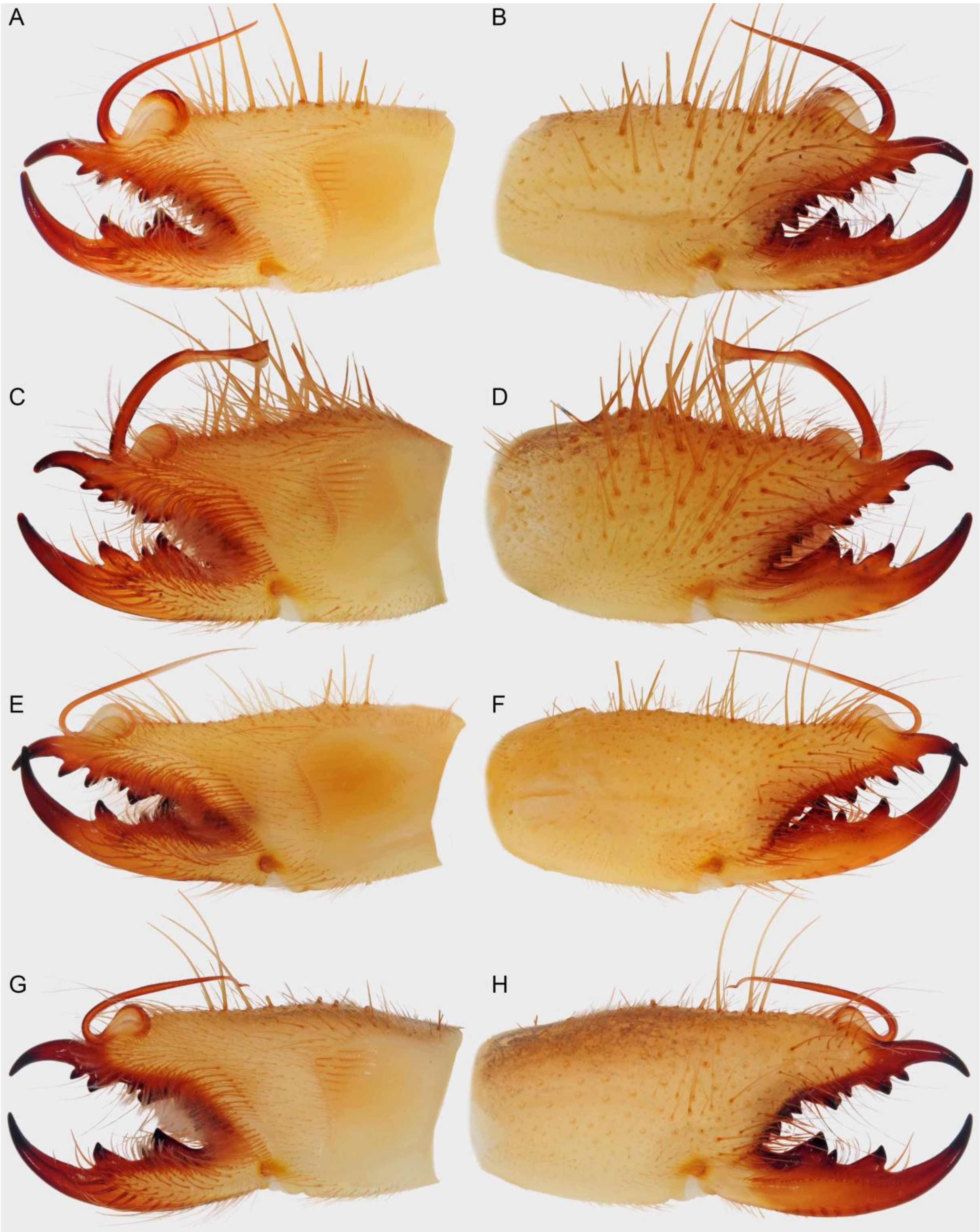

Plate 118. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A, B.** *Zeria adunca* (Roewer, 1933), ♂ (MRAC 216.105). **C, D.** *Zeria fordi* (Hirst, 1907), ♂ (AMNH [LP 9090]). **E, F.** *Zeria glabricornis* (Lawrence, 1928), ♂ (AMNH [LP 3614]). **G, H.** *Zeria keyserlingi* (Pocock, 1895), ♂ (AMNH [LP 4632]).

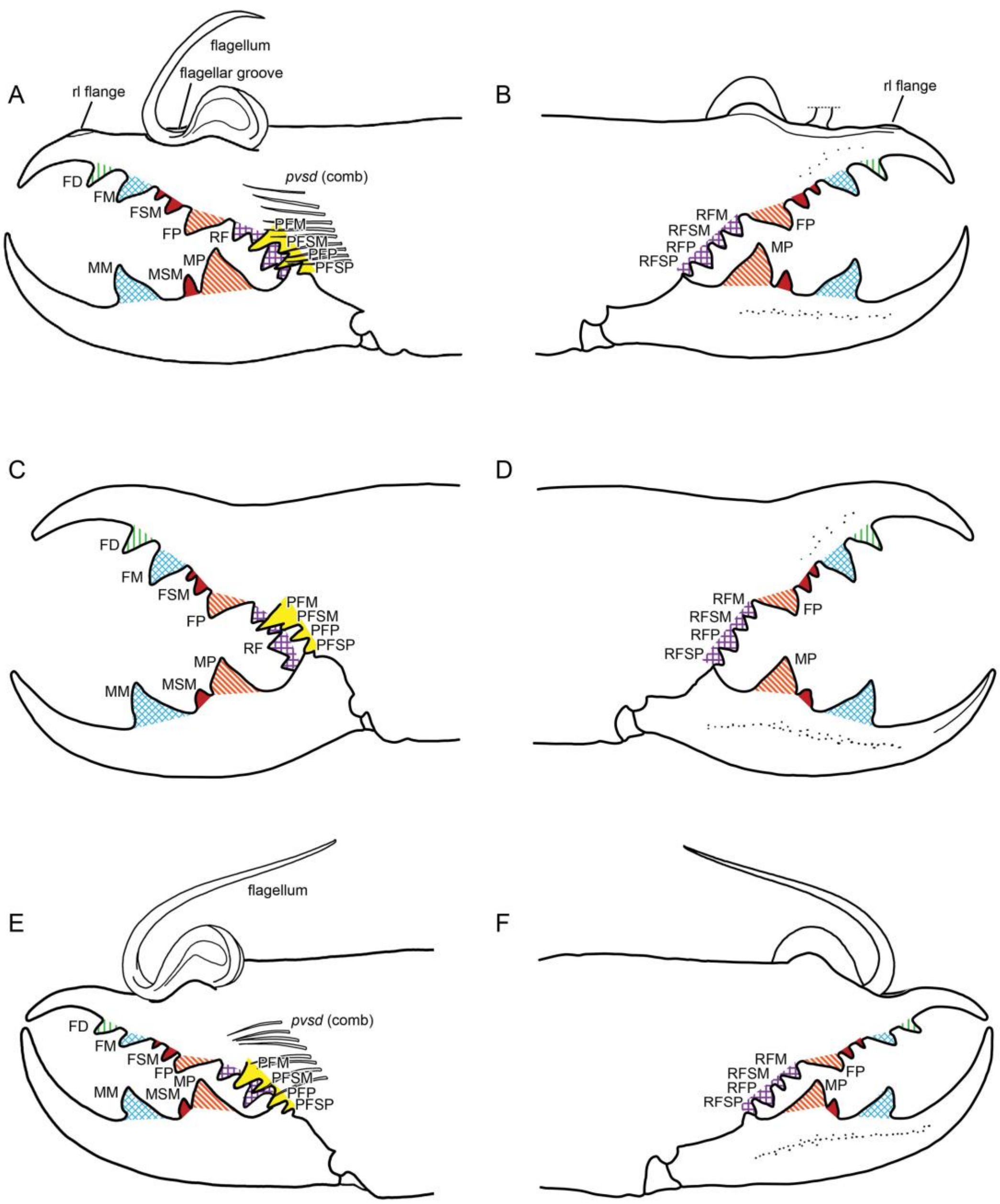

Plate 119. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E**) and retrolateral (**B, D, F**) views, illustrating dentition, setae, and flagellum. **A–D.** *Zeria sericea* (Pocock, 1897). **A, B.** ♂ (NMNW 13801). **C, D.** ♀ (NMNW 13801). **E, F.** *Zeria adunca* (Roewer, 1933), ♂ (MRAC 216.105). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only); rl, retrolateral.

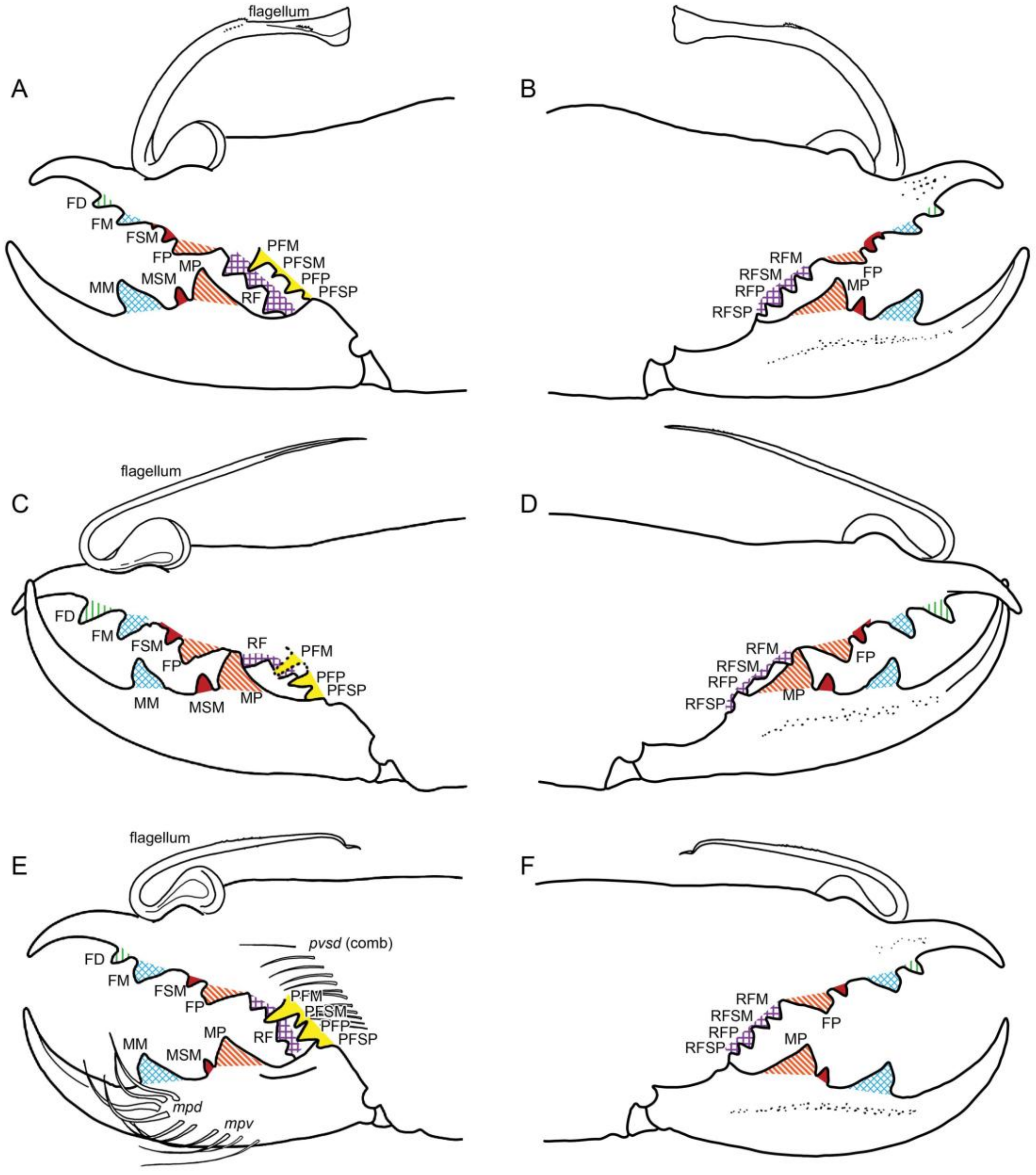

Plate 120. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E**) and retrolateral (**B, D, F**) views, illustrating dentition, setae, and flagellum. **A, B.** *Zeria fordi* (Hirst, 1907), ♂ (AMNH [LP 9090]). **C, D.** *Zeria glabricornis* (Lawrence, 1928), ♂ (AMNH [LP 3614]). **E, F.** *Zeria keyserlingi* (Pocock, 1895), ♂ (AMNH [LP 4632]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *mpv*, movable finger, proventral setae (not all setae indicated); *mpd*, movable finger, proventral setae (only two distalmost indicated); *pvsd*, proventral subdistal setae (setal comb only).

Plate 121. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A, B.** *Zeria carli* (Roewer, 1933), ♂ (AMNH [LP 7915]). **C–F.** *Zeria lawrencei* (Roewer, 1933). **C, D.** ♂ (AMNH [LP 9906]). **E, F.** ♀ (NMNW 13820). **G, H.** *Zeria venator* (Pocock, 1897), ♂ (AMNH [LP 5952]).

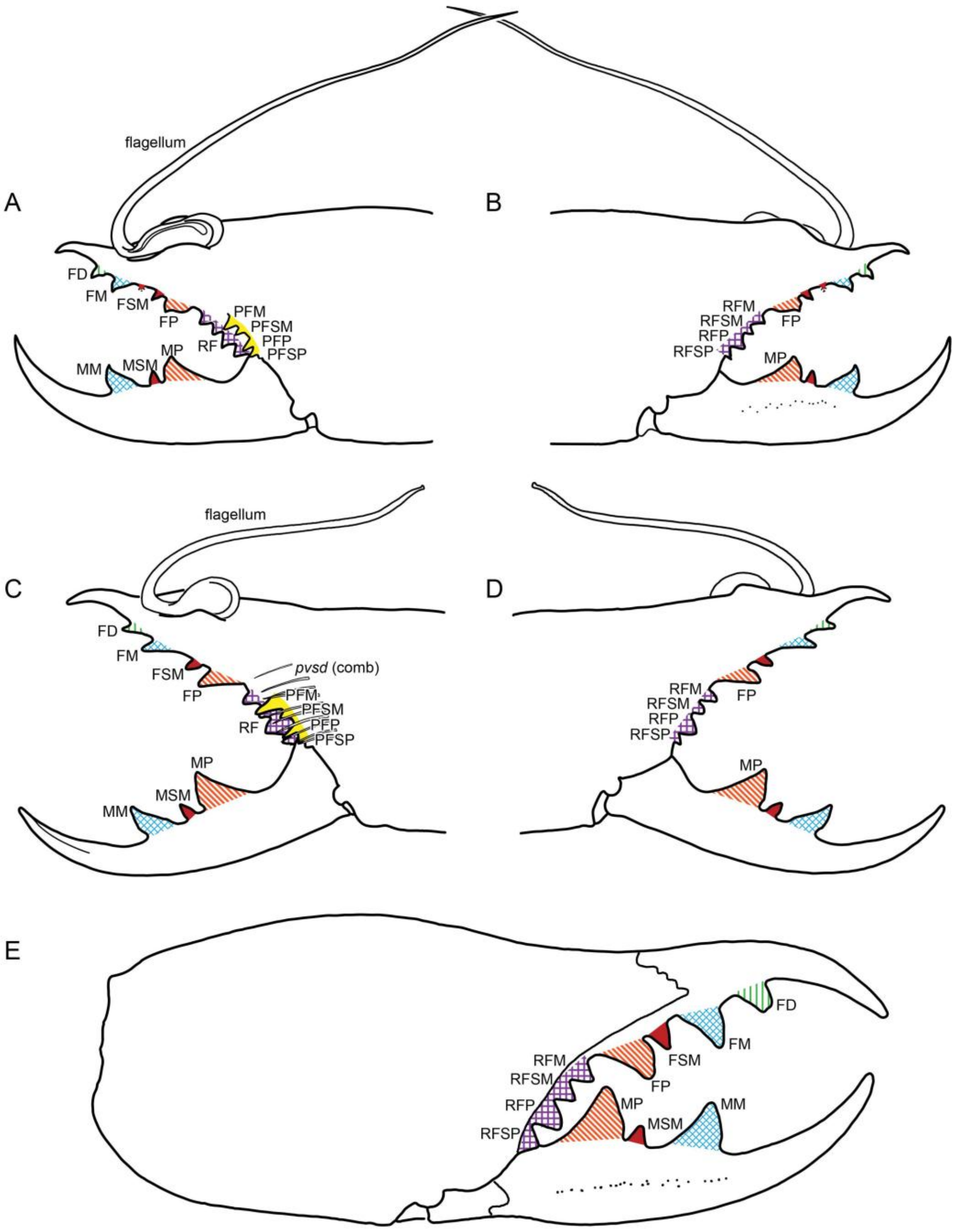

Plate 122. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C**) and retrolateral (**B, D, E**) views, illustrating dentition, setae, and flagellum. **A, B.** *Zeria carli* (Roewer, 1933), ♂ (AMNH [LP 7915]). **C–E.** *Zeria lawrencei* (Roewer, 1933). **C, D.** ♂ (AMNH [LP 9906]). **E.** ♀ (NMNW 13820). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only).

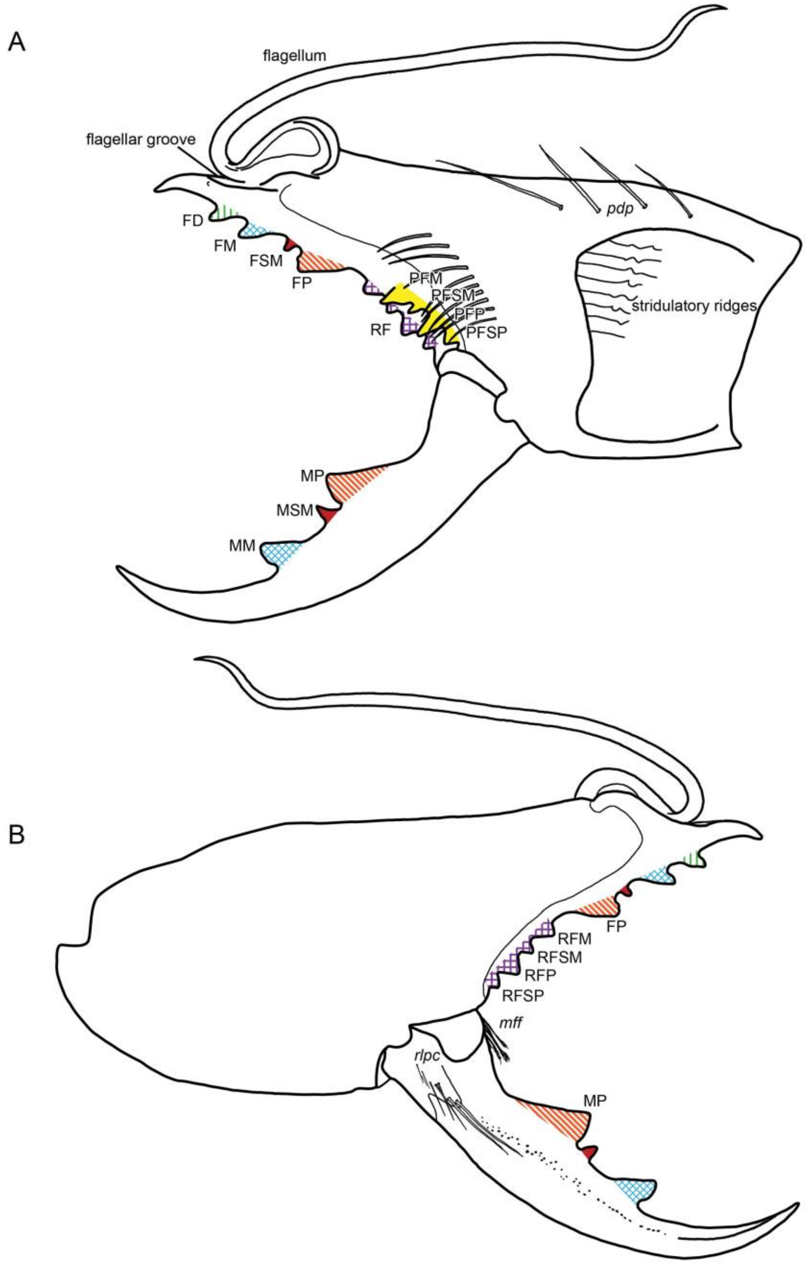

Plate 123. Solpugidae Leach, 1815, *Zeria venator* (Pocock, 1897), ♂ (AMNH [LP 5952]), chelicerae, prolateral (**A**) and retrolateral (**B**) views, illustrating dentition, setae, and flagellum. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *mff*, movable finger, fondal setae; *pdp*, prodorsal proximal setae; *pvsd*, proventral subdistal setae (setal comb only); *rlpc*, retrolateral proximal cluster of setae.

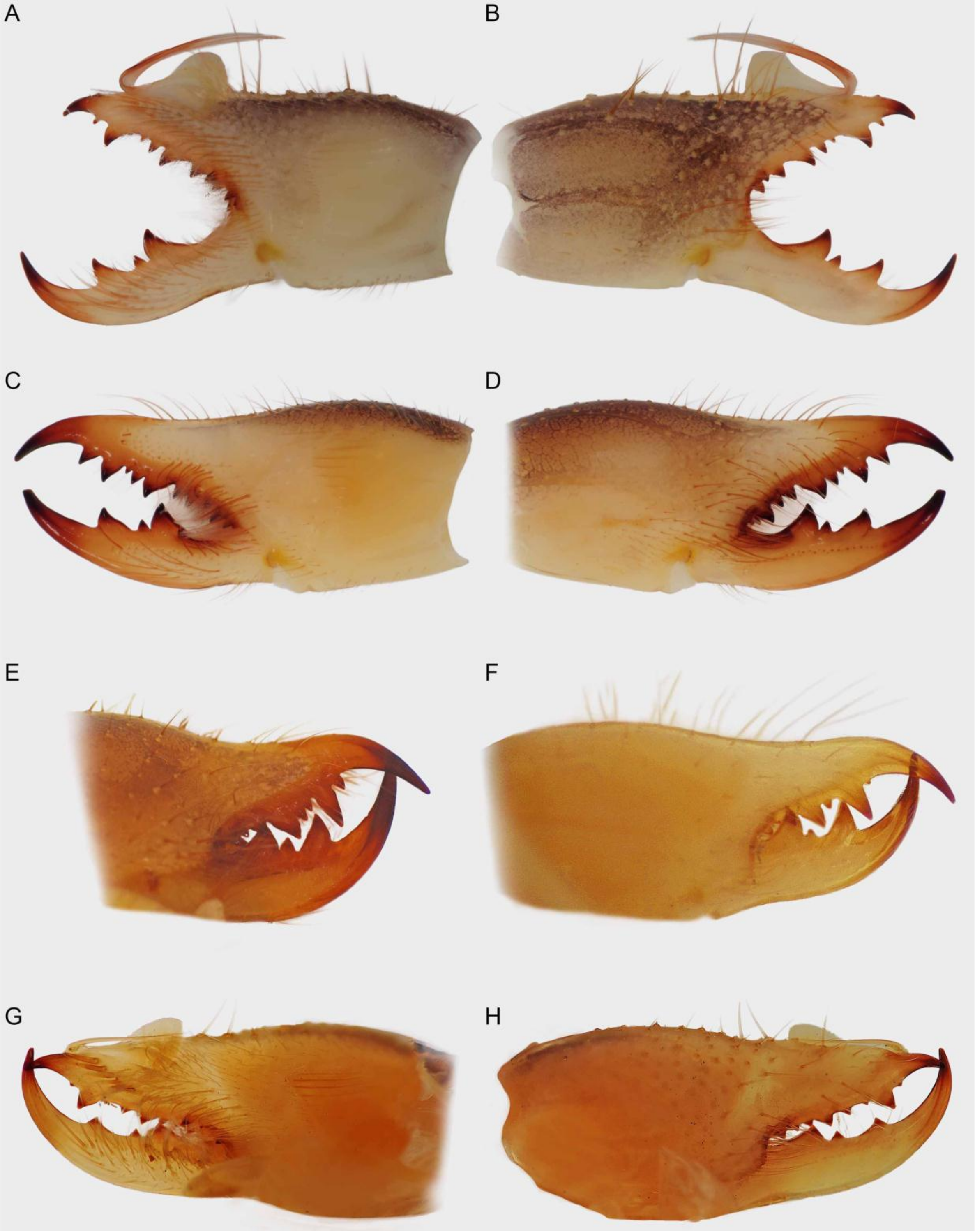

Plate 124. Solpugidae Leach, 1815, chelicerae, prolateral (**A, C, G**) and retrolateral (**B, D–F, H**) views. **A–D.** *Zeriassa furcicornis* Lawrence, 1929. **A, B.** ♂ (AMNH [LP 3612]). **C, D.** ♀ (AMNH [LP 9848]). **E.** *Zeriassa* sp., ♀ (MCZ 126318). **F.** *Zeriassa* sp., 3-claw stage juv. (MCZ 126318). **G, H.** *Solpugisticella kenyae* Turk, 1960, holotype ♂ (HUJI).

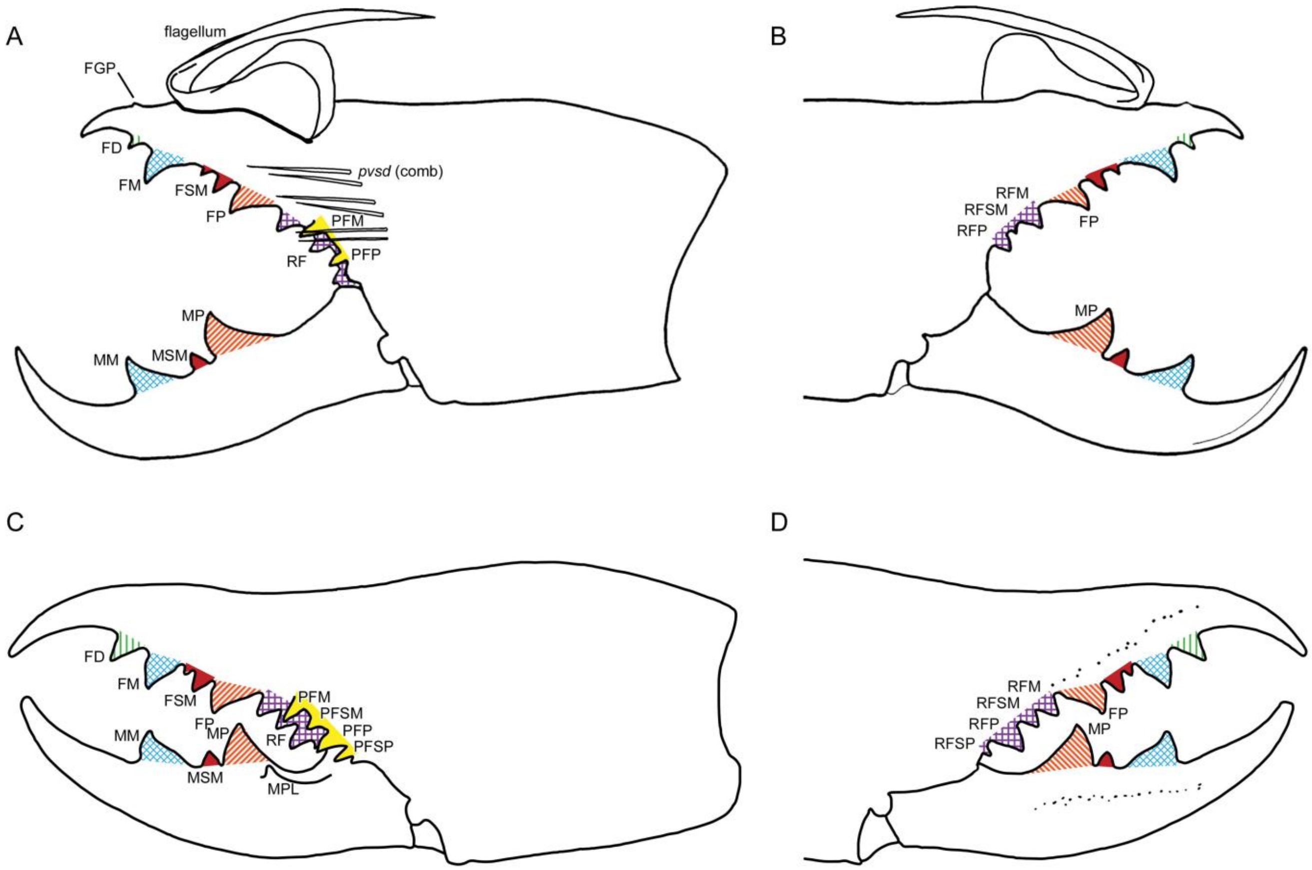

Plate 125. Solpugidae Leach, 1815, *Zeriassa furcicornis* Lawrence, 1929, chelicerae, prolateral (**A, C**) and retrolateral (**B, D**) views, illustrating dentition, setae, and flagellum. **A, B.** ♂ (AMNH [LP 3612]). **C, D.** ♀ (AMNH [LP 9848]). Abbreviations: FD, fixed finger, distal tooth; FGP, flagellar groove process; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MPL, movable finger, prolateral tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only).

Plate 126. Hexisopodidae Pocock, 1897, chelicerae, prolateral (**A**) and retrolateral (**B, F–H**) views, fixed finger, ventral view (**C**), movable finger, retrodorsal view (**D**), and fondal area, ventral view (**E**). **A, B.** *Hexisopus pusillus* Lawrence, 1962, ♂ (NMNW 11426). **C–E.** *Hexisopus lanatus* (C.L. Koch, 1942), ♂ (NMNW 10795). **F, G.** *Hexisopus* sp., juv. (NMNW 11098). **H.** *Hexisopus aureopilosus* Lawrence, 1968, ♀ (NMNW 11203).

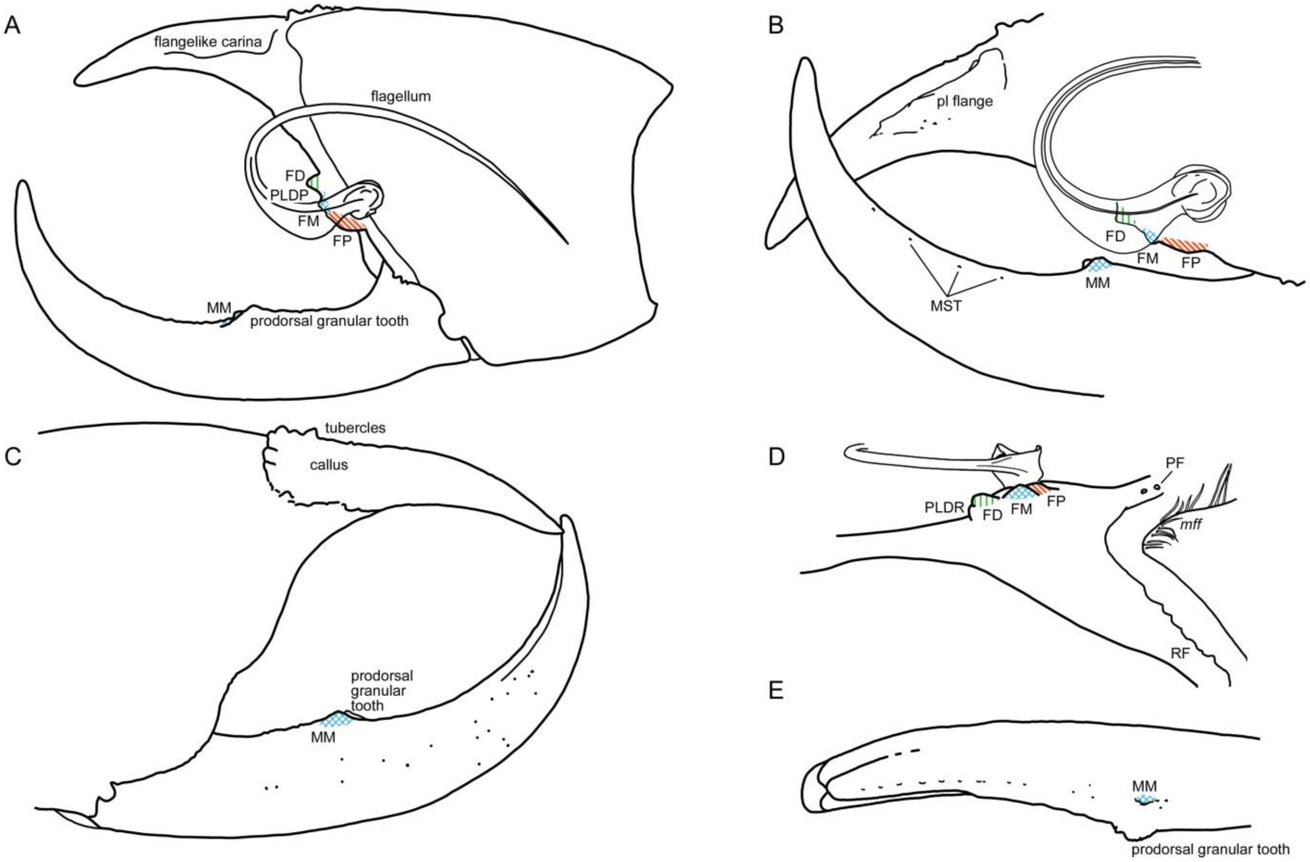

Plate 127. Hexisopodidae Pocock, 1897, *Hexisopus pusillus* Lawrence, 1962, ♂ (NMNW 11426), chelicerae, prolateral (**A, B**) and retrolateral (**C**) views, fixed finger fondal area, ventral view (**D**), and movable finger, retrodorsal view (**E**), illustrating dentition, setae, and flagellum. Arrows indicate hypothesized prolateral dental ridge fused with primary teeth. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; MM, movable finger, medial tooth; MST, movable finger, subterminal teeth (denticle-like serrations on cutting edge of finger); PLDP, prolateral dental process (hypothesized to be fused with teeth), PF, profondal teeth; RF, retrofondal teeth; *mff*, movable finger, fondal setae; pl, prolateral..

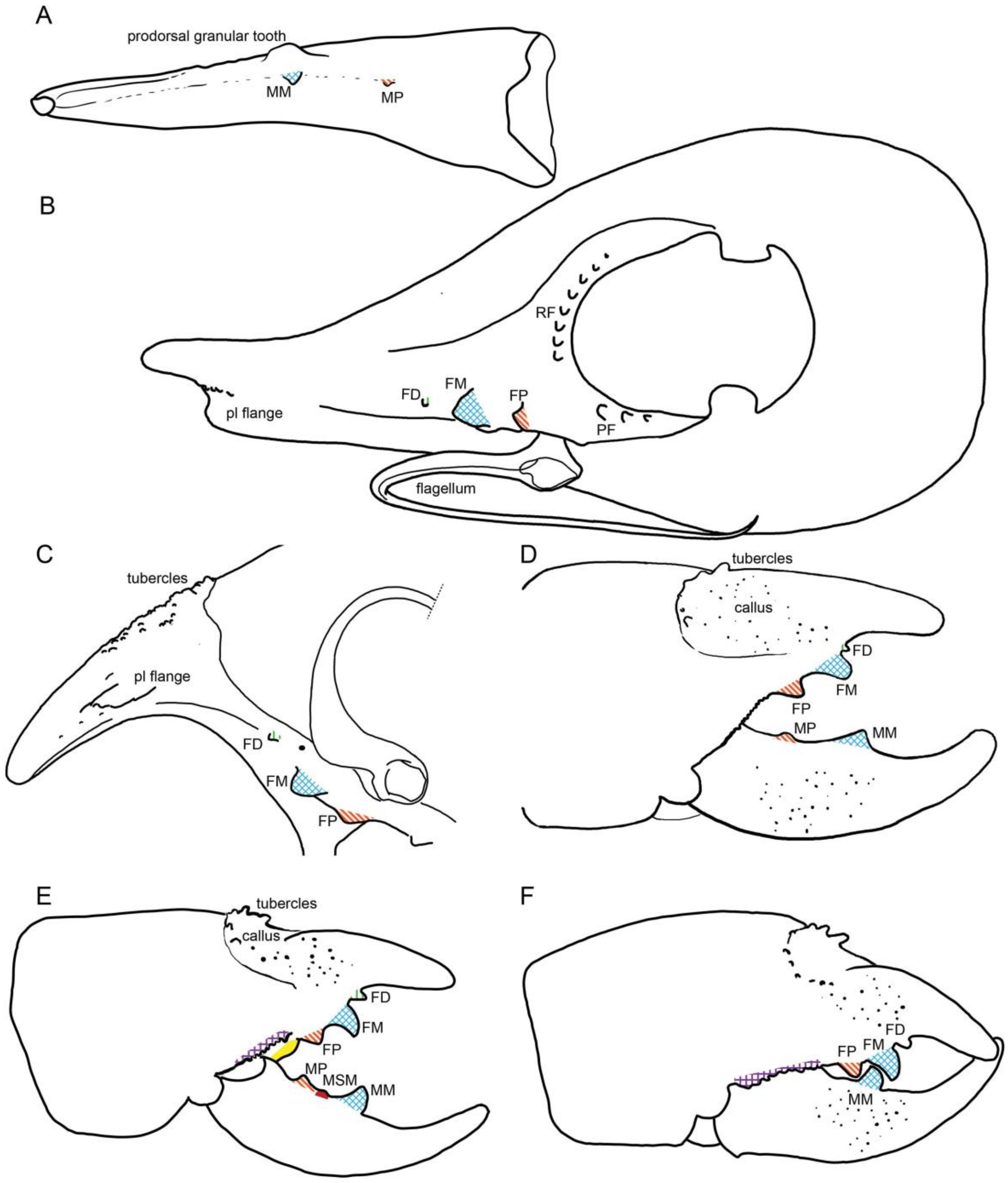

Plate 128. Hexisopodidae Pocock, 1897, movable finger, dorsal view (**A**), cheliceral manus and fixed finger, ventral view (**B**), fixed finger, prolateral view (**C**), and chelicerae, retrolateral view (**D–F**), illustrating dentition, setae, and flagellum. **A–C.** *Hexisopus lanatus* (C.L. Koch, 1942), ♂ (NMNW 10795). **D.** *Hexisopus* sp., juv. (NMNW 11098). **E, F.** *Hexisopus aureopilosus* Lawrence, 1968, ♀ (NMNW 11203). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; PF, profondal teeth; RF, retrofondal teeth; PLDP, prolateral dental process (hypothesized to be fused with teeth), pl, prolateral..

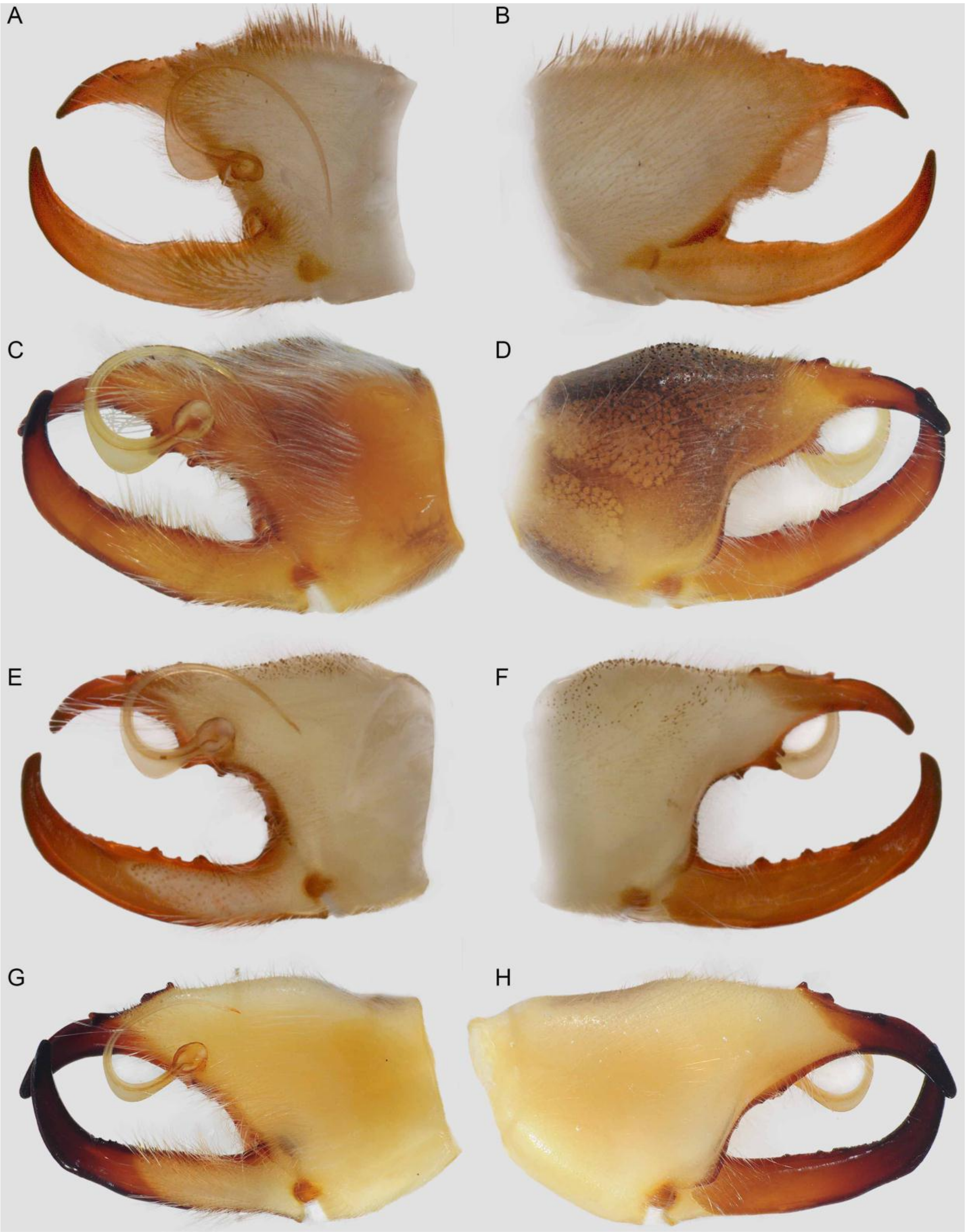

Plate 129. Hexisopodidae Pocock, 1897, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A, B.** *Hexisopus psammophilus* Wharton, 1981, ♂ (AMNH [LP 9858]). **C–F.** *Chelypus hirsti* Hewitt, 1915. **C, D.** ♂ (NMNW 10804). **E, F.** ♂ (NMNW 11202). **G, H.** *Chelypus shortridgei* Hewitt, 1931, ♂ (NMNW 12632).

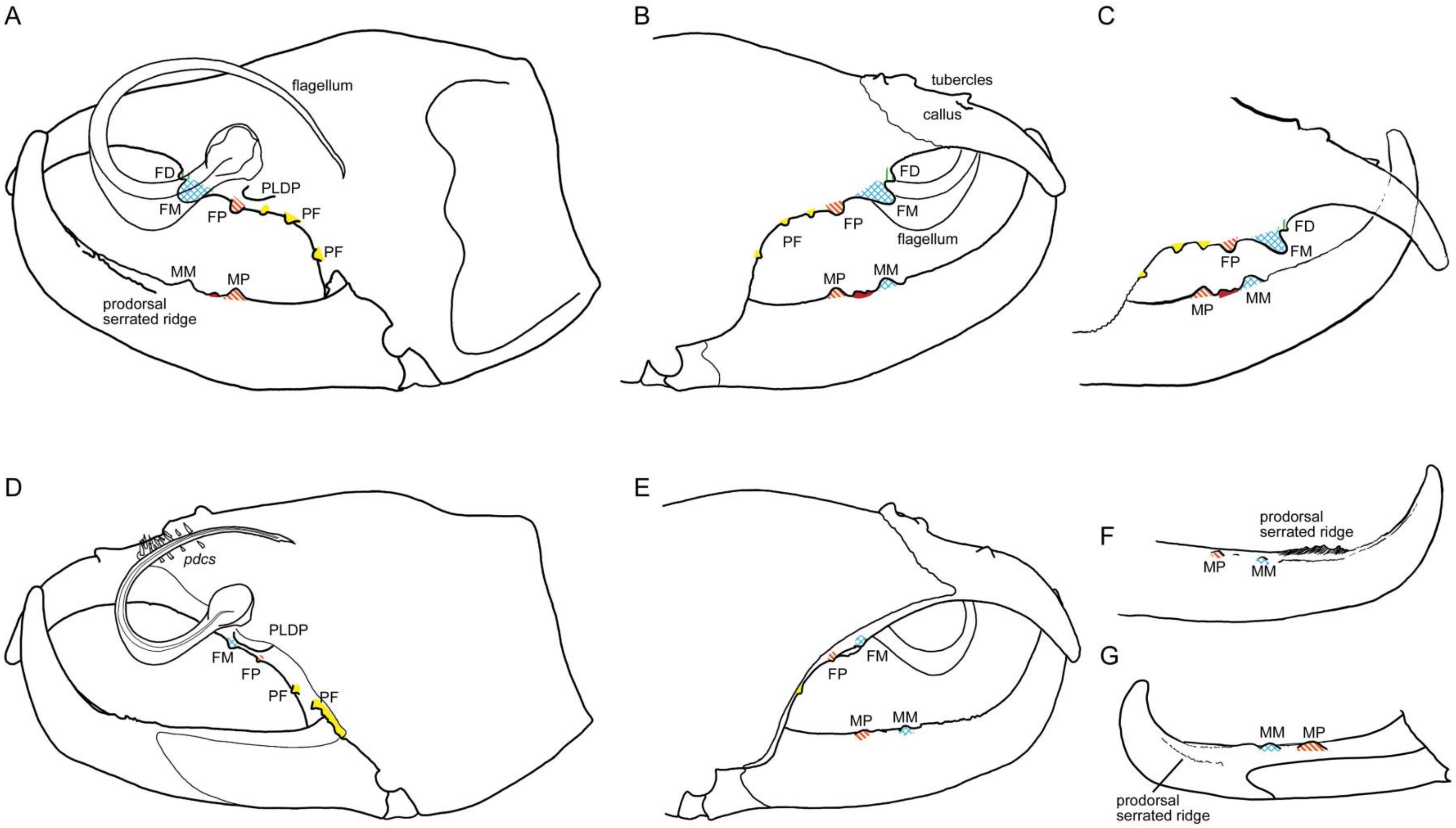

Plate 130. Hexisopodidae Pocock, 1897, chelicerae, prolateral (**A, D**) and retrolateral views (**B, C, E**), and movable finger, retrodorsal (**F**) and prodorsal views (**G**). **A–C, F.** *Chelypus hirsti* Hewitt, 1915, ♂ (NMNW 10804). **D, E, G.** *Chelypus shortridgei* Hewitt, 1931, ♂ (NMNW 12632). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; PF, profondal teeth; PLDP, prolateral dental process; *pdcs*, prodorsal cluster of spiniform setae.

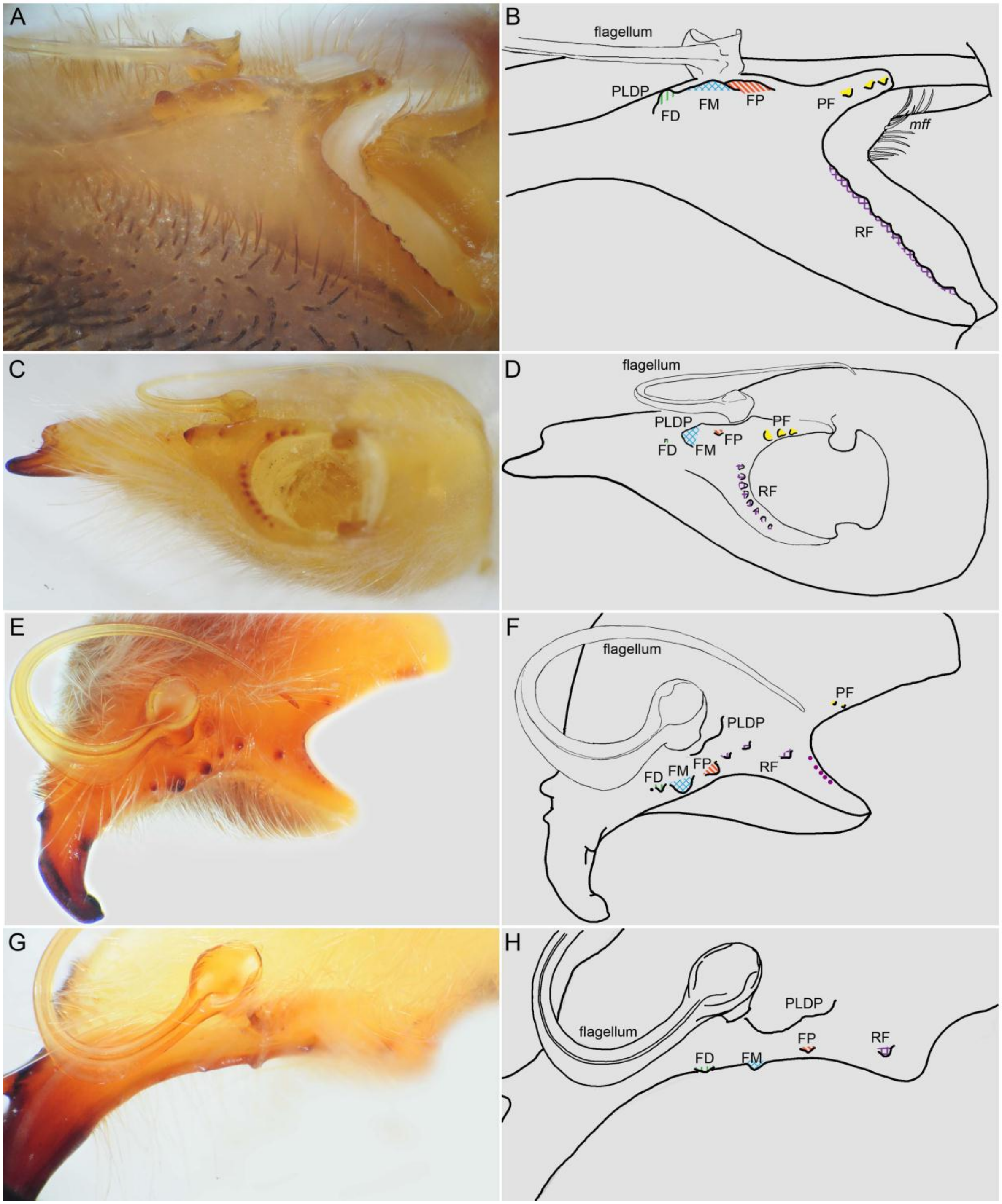

Plate 131. Hexisopodidae Pocock, 1897, cheliceral fixed fingers, ventral (**A–D**) and proventral (**E–H**) views illustrating fondal area. **A, B.** *Hexisopus pusillus* Lawrence, 1962, ♂ (NMNW 11426). **C, D.** *Hexisopus lanatus* (C.L. Koch, 1942), ♂ (NMNW 10795). **E, F.** *Chelypus hirsti* Hewitt, 1915, ♂ (NMNW 10804). **G, H.** *Chelypus shortridgei* Hewitt, 1931, ♂ (NMNW 12632). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; PLDP, prolateral dental process; PF, profondal teeth; RF, retrofondal teeth; *mff*, movable finger, fondal setae...

Plate 132. Daesiidae Kraepelin, 1899 (**A–J**), including Namibesiinae Wharton, 1981 (**A–D**), chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A–D.** *Namibesia pallida* Lawrence, 1962. **A, B.** ♂ (AMNH [LP 10721]). **C, D.** ♀ (AMNH [LP 4017]). **E–H.** *Ammotrechelis goetschi* Roewer, 1934. **E, F.** ♂ (AMNH [LP 10673]). **G, H.** ♀ (AMNH [LP 10673]). **I, J.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]).

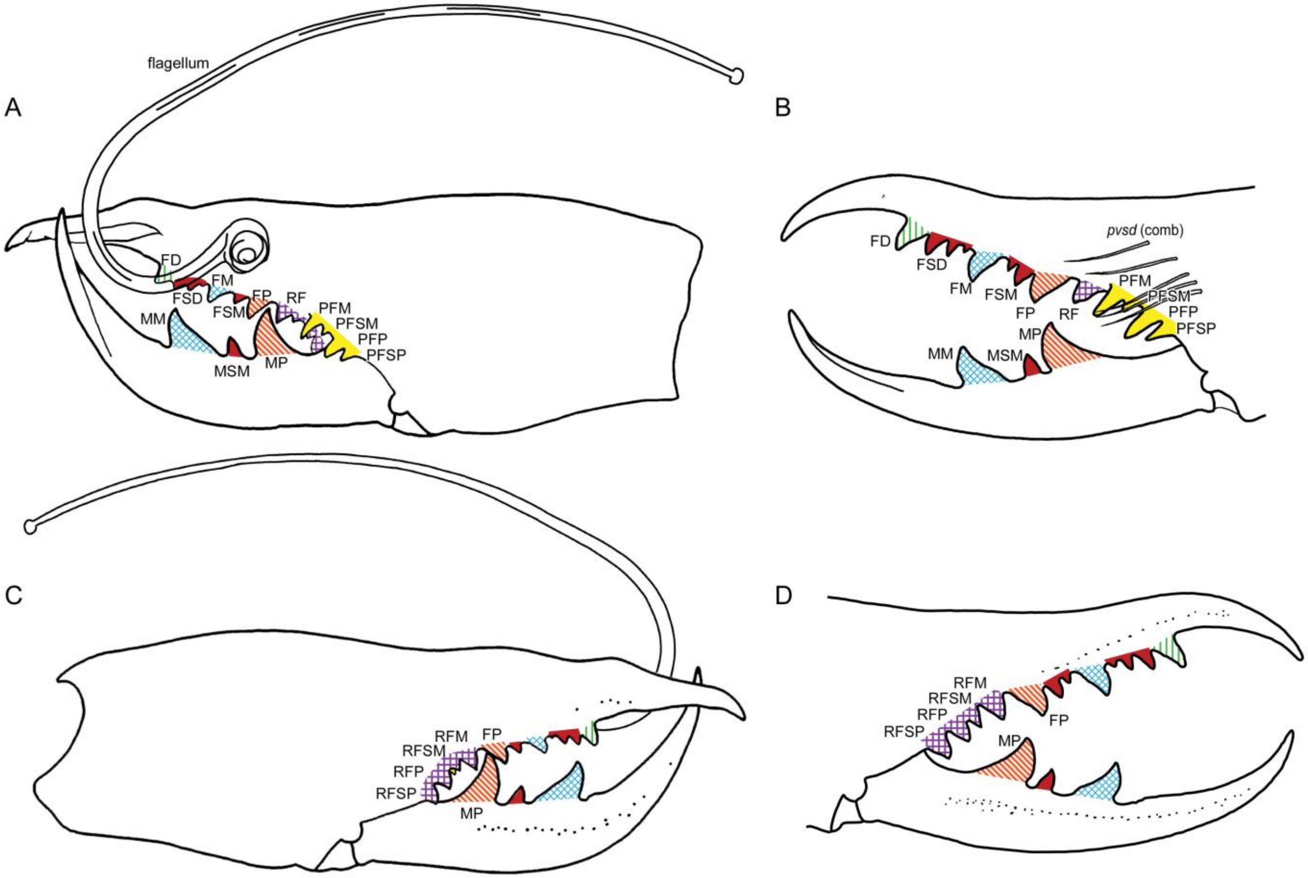

Plate 133. Daesiidae Kraepelin, 1899, Namibesiinae Wharton, 1981, *Namibesia pallida* Lawrence, 1962, chelicerae, prolateral (**A, B**) and retrolateral (**C, D**) views illustrating dentition, setae, and flagellum. **A, C.** ♂ (AMNH [LP 10721]). **B, D.** ♀ (AMNH [LP 4017]). Arrow indicates concave terminal tooth of movable (ventral) finger (**A**). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal teeth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only).

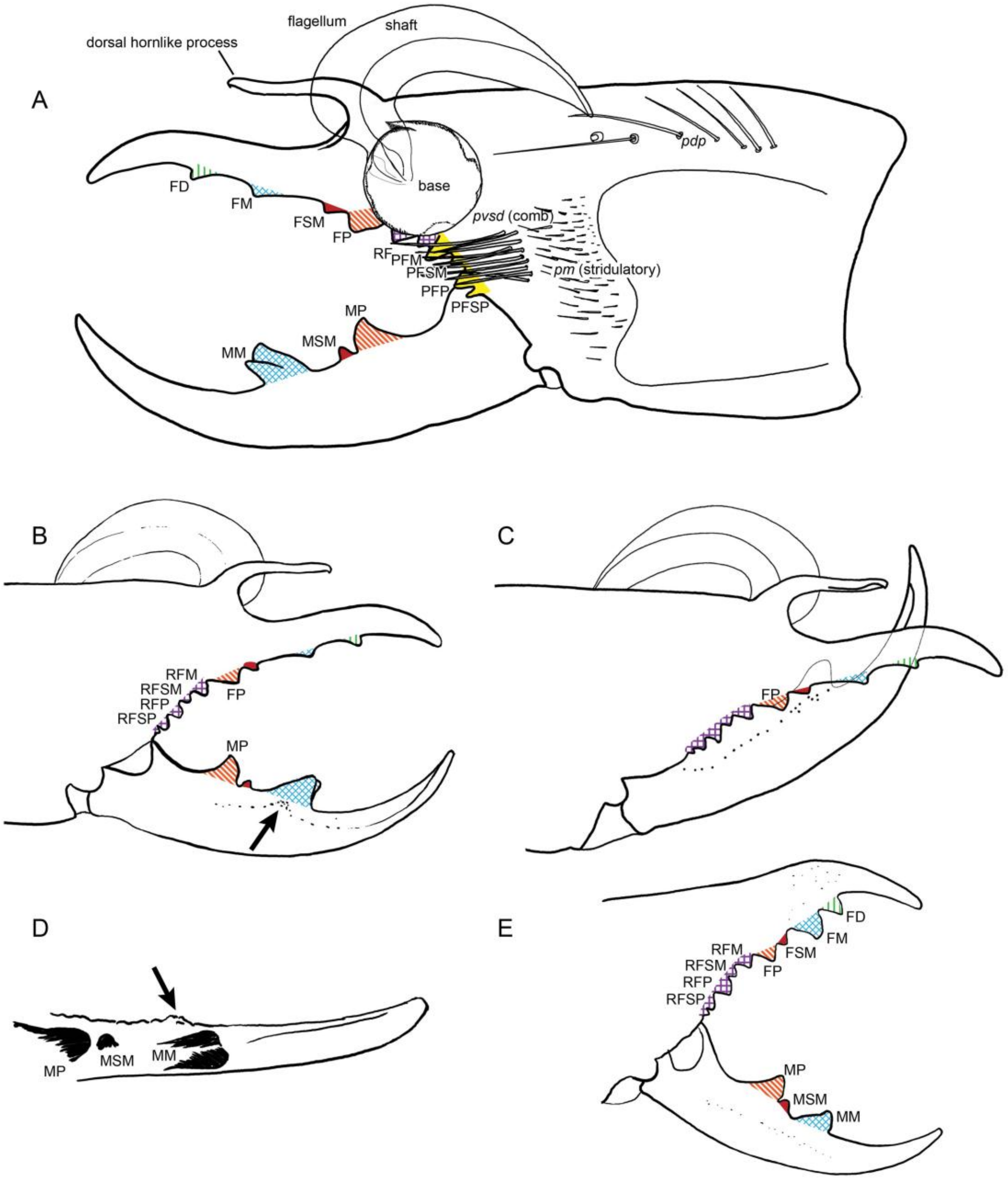

Plate 134. Daesiidae Kraepelin, 1899, *Ammotrechelis goetschi* Roewer, 1934, chelicerae, prolateral (**A**) and retrolateral (**B, C, E**) views, and movable finger, prodorsal view (**D**), illustrating dentition, setae, and flagellum. **A–D.** ♂ (AMNH [LP 10673]). **E.** ♀ (AMNH [LP 10673]). Arrows indicate blunt retrolateral granular tubercle. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pdp*, prodorsal proximal setae; *pm*, promedial setae (stridulatory setae only); *pvsd*, proventral subdistal setae (setal comb only).

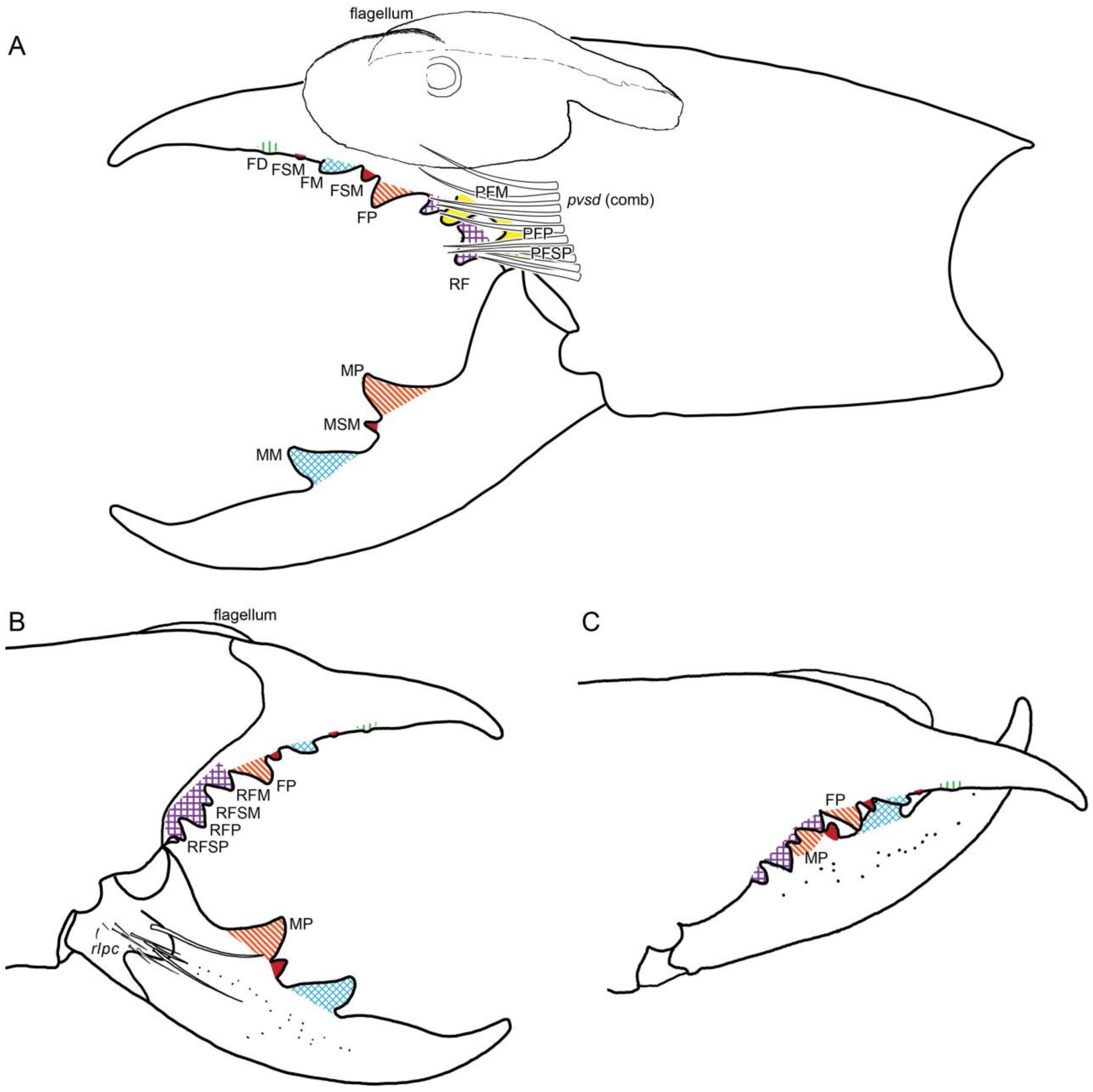

Plate 135. Daesiidae Kraepelin, 1899, *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]), chelicerae, prolateral (**A**) and retrolateral (**B, C**) views, illustrating dentition, setae, and flagellum. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger subdistal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only); *rlpc*, retrolateral proximal cluster of setae.

Plate 136. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Gluviopsilla discolor* (Kraepelin, 1899), ♂ (AMNH [LP 7516]). **C, D.** *Gnosippus klunzingeri* Karsch, 1880, ♂ (HUJI 770). **E–H.** *Biton* (*B.*) *rossicus* (Birula, 1905). **E, F.** ♂ (AMNH [LP 3959]). **G, H.** ♀ (AMNH [LP 3959]). **I, J.** *Biton* (*B.*) *browni* (Lawrence, 1963), ♂ (AMNH [LP 3633]).

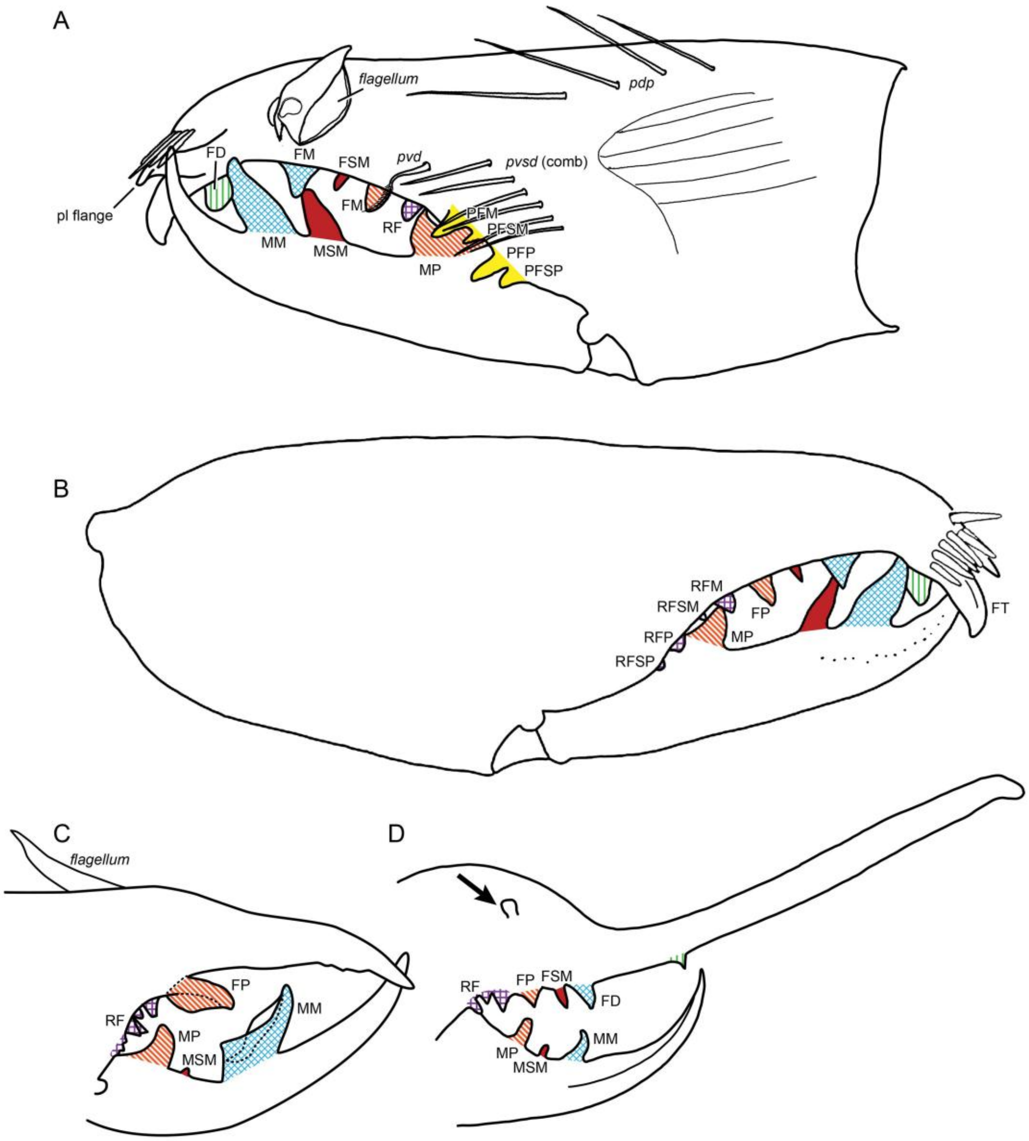

Plate 137. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**A**) and retrolateral (**B–D**) views, illustrating dentition, setae, and flagellum. **A, B.** *Gnosippus klunzingeri* Karsch, 1880, ♂ (HUJI 770). **C.** *Biton* (*B.*) *truncatidens* Lawrence, 1954, ♂, adapted from Lawrence (1954a: 115, fig. 3D). **D.** *Ceratobiton styloceros* (Kraepelin, 1899), ♂ (HUJI 55), with elongated fixed (dorsal) finger. Arrow indicates flagellar attachment point visible retrolaterally through cuticle of dorsal finger. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pdp*, prodorsal proximal setae; *pvsd*, proventral subdistal setae (setal comb only); rl, retrolateral.

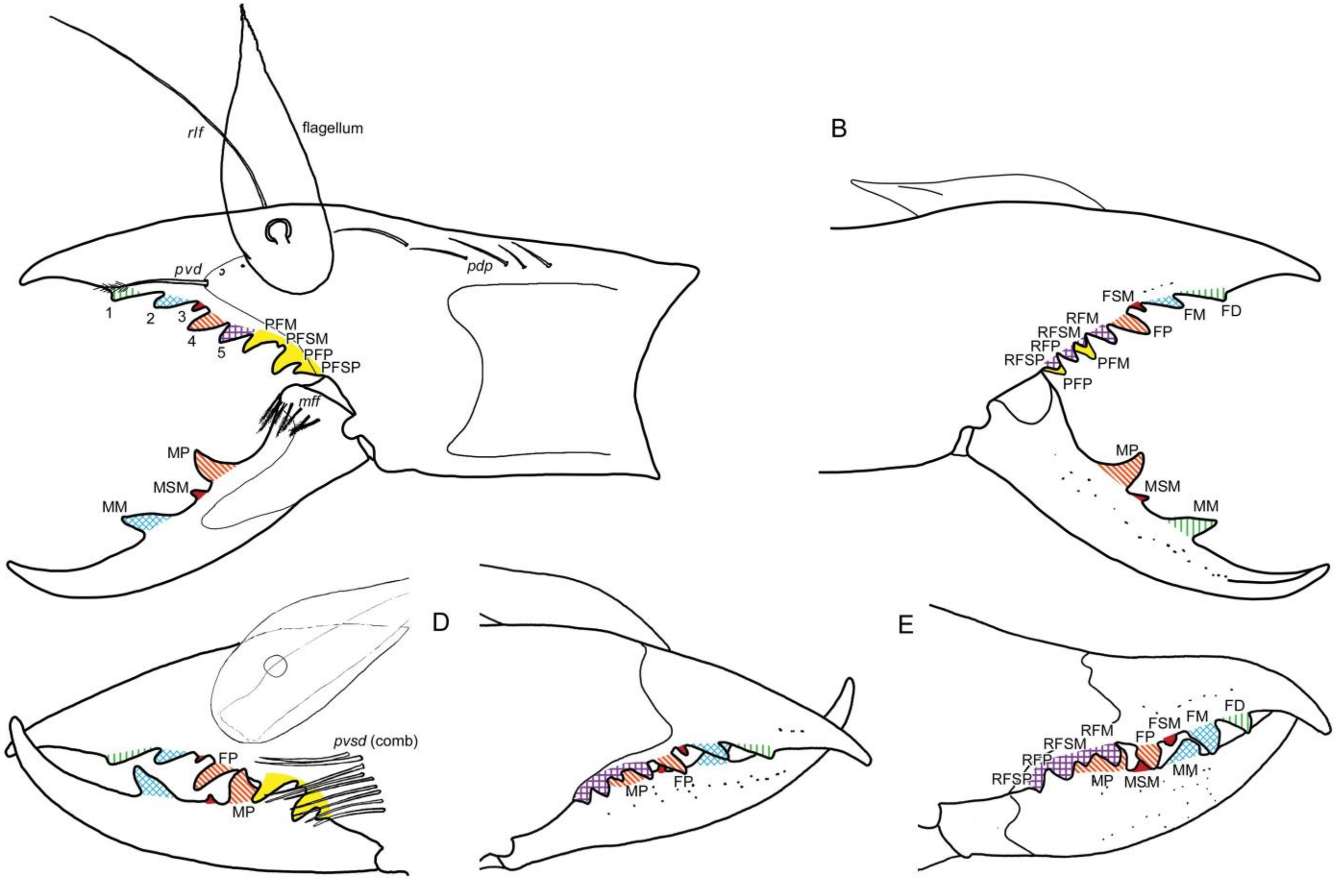

Plate 138. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**A, C**) and retrolateral (**B, D, E**) views, illustrating dentition, setae, and flagellum. **A–E.** *Biton* (*B.*) *rossicus* (Birula, 1905). **A–D.** ♂ (AMNH [LP 3959]). Numbers indicate five distalmost toothlike structures. **E.** ♀ (AMNH [LP 3959]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pdp*, prodorsal proximal setae; *mff*, movable finger, fondal setae; *pvsd*, proventral subdistal setae (setal comb only); *rlf*, retrolateral finger seta.

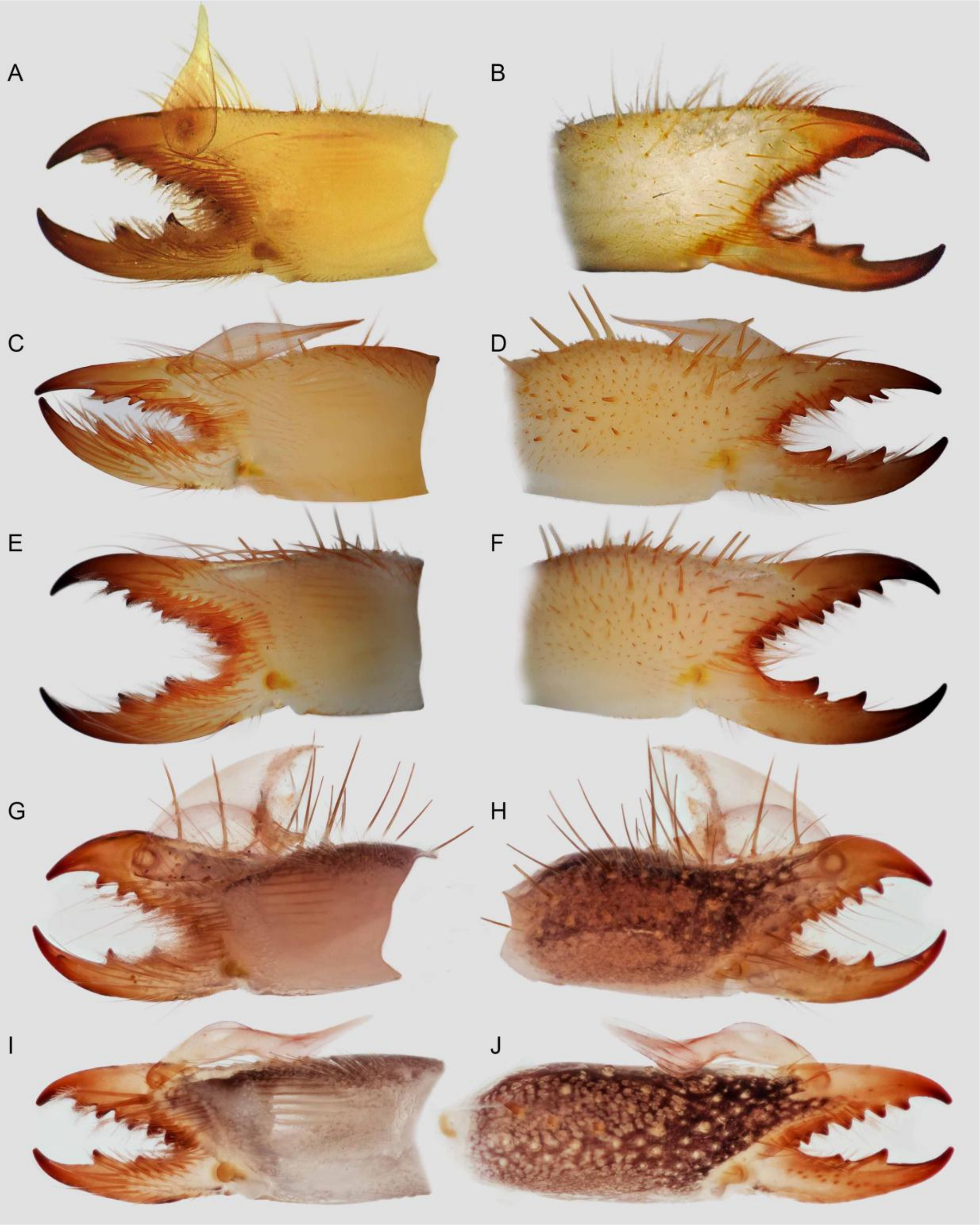

Plate 139. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A, B.** *Biton* (*B.*) *zederbaueri* (Werner, 1905), ♂ (KU), Turkey: Hasançali. **C–F.** *Blossia grandicornis* Lawrence, 1929. **C, D.** ♂ (AMNH [LP 5905]). **E, F.** ♀ (AMNH [LP 5905]). **G, H.** *Hemiblossia etosha* Lawrence, 1927, ♂ (AMNH [LP 9854]). **I, J.** *Hemiblossia australis* (Purcell, 1902), ♂ (AMNH [LP 9866]).

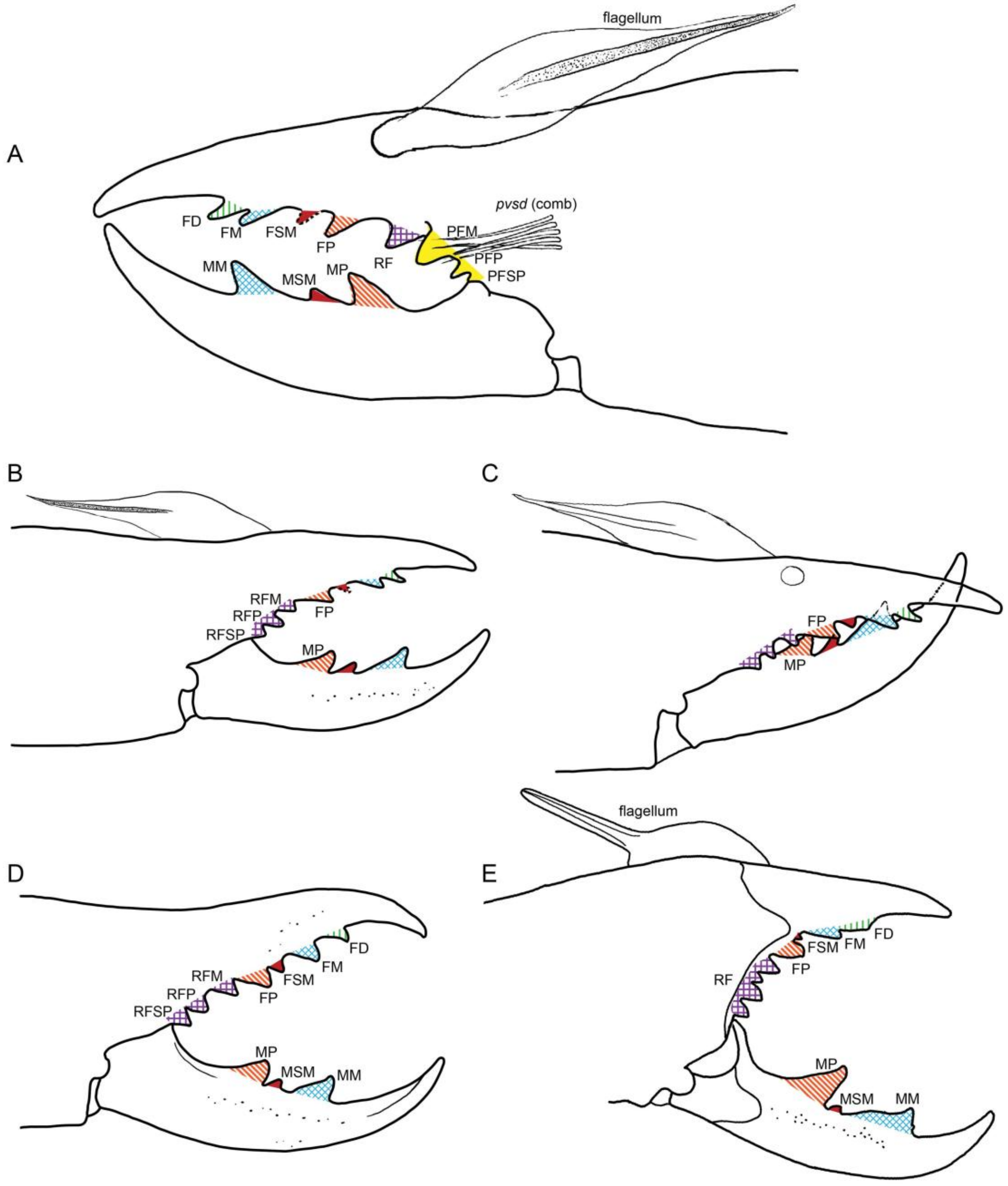

Plate 140. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**A**) and retrolateral (**B–E**) views, illustrating dentition, setae, and flagellum. **A–D.** *Blossia grandicornis* Lawrence, 1929. **A–C.** ♂ (AMNH [LP 5905]). **D.** ♀ (AMNH [LP 5905]). **E.** *Biton* (*B.*) sp. 6 (*namaqua* group), ♂ (NMNW), Namibia: Windhoek, Auas Mountains. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth; PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only).

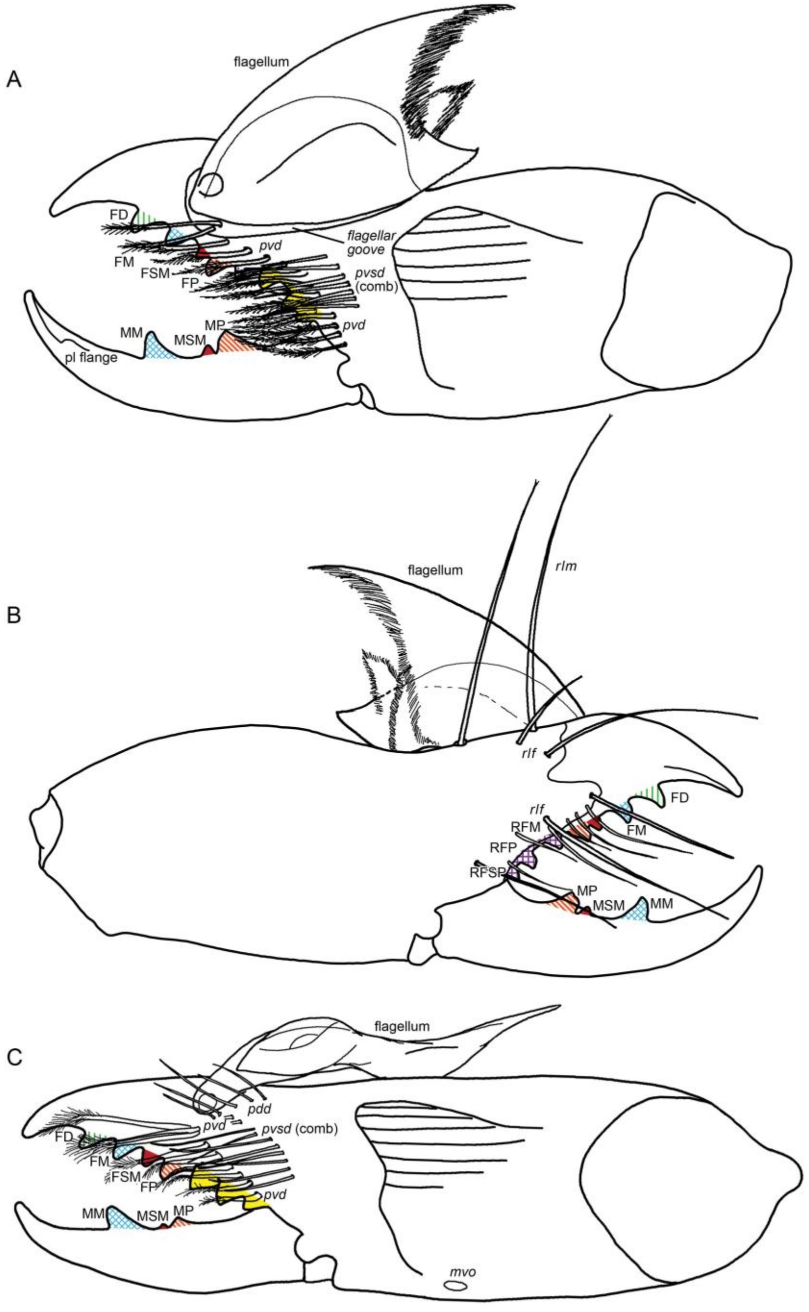

Plate 141. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**A, C**) and retrolateral (**B**) views, illustrating dentition, setae, and flagellum. **A, B.** *Hemiblossia etosha* Lawrence, 1927, ♂ (AMNH [LP 9854]). **C, D.** *Hemiblossia australis* (Purcell, 1902), ♂ (AMNH [LP 9866]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MPL, movable finger, prolateral tooth; MSM, movable finger, submedial tooth; PF, profondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal tooth; *pdd*, prodorsal distal setae; *pvd*, proventral distal setae; *pvsd*, proventral subdistal setae (setal comb only); *rlf*, retrolateral finger setae; mvo, medioventral organ.

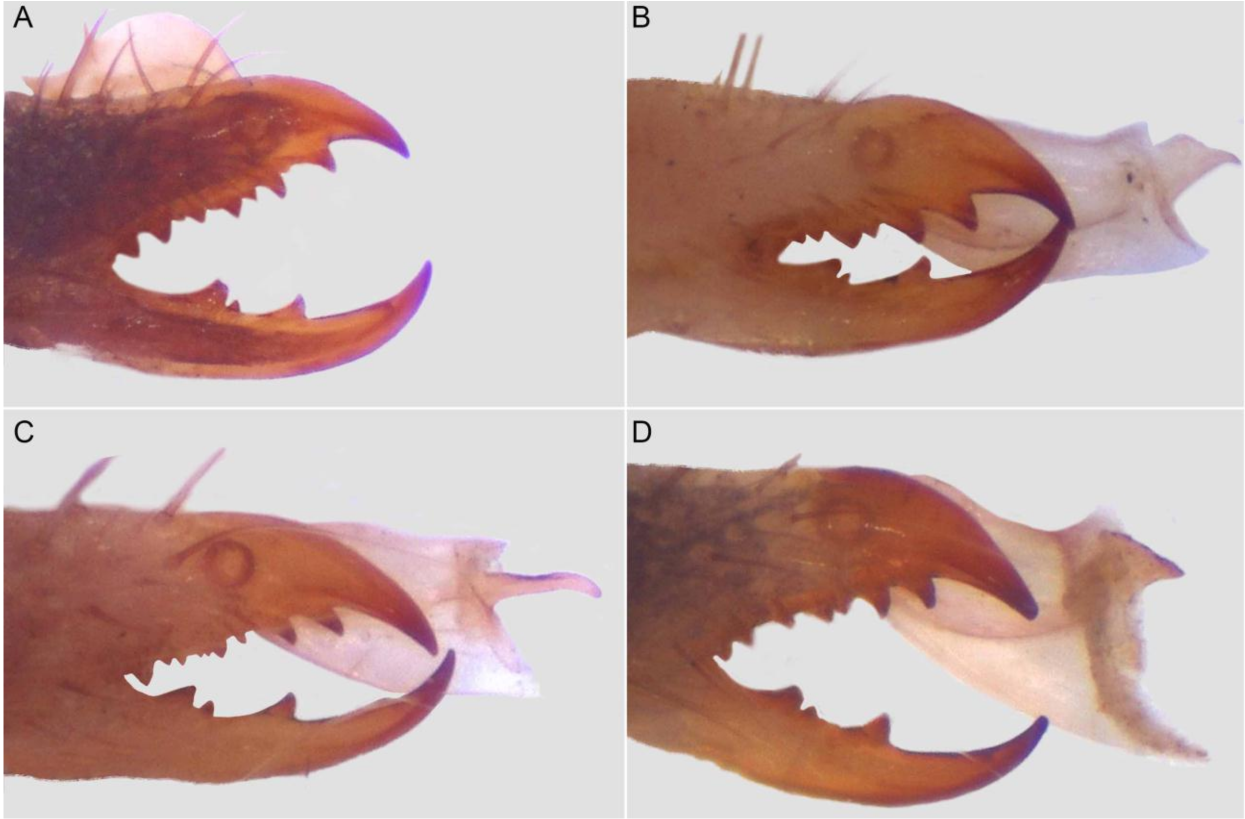

Plate 142. Daesiidae Kraepelin, 1899, chelicerae, retrolateral views. **A.** *Hemiblossia oneili* Purcell, 1902, ♂ (NMNW), Namibia: Gondwana Cañon Park (SNAP; Site G31). **B, C.** *Hemiblossia* sp. (*bouvieri* group), ♂ (NMNW), Namibia: Gondwana Cañon Park (SNAP; Site G30) (**B**), and ♂ (NMNW), Namibia: Gondwana Cañon Park (SNAP; Site G29) (**C**). **D.** *Hemiblossia etosha* Lawrence, 1927, ♂ (NMNW 13798).

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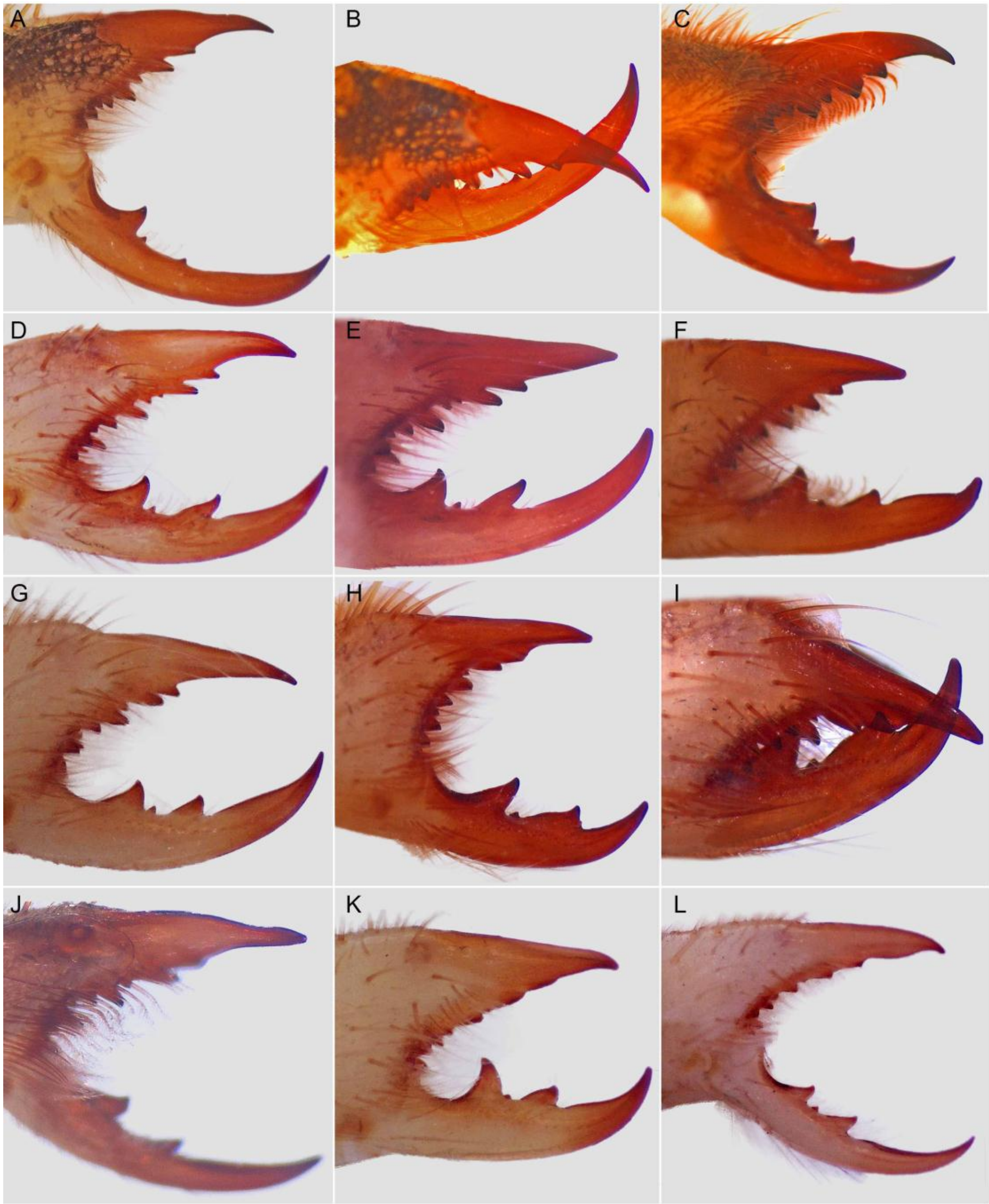

Plate 143. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**J**) and retrolateral (**A–I, K, L**) views. **A, B.** *Biton* (*B.*) sp. 1, ♂ (NMNW 13278). **C.** *Biton* (*B.*) sp. 1, ♀ (NMNW 13278). **D.** *Biton* (*B.*) sp. 2, ♂ (NMNW), Namibia: Gondwana Cañon Park, with two FSM teeth (within same collecting series, one specimen with single FSM on both chelicerae). **E.** *Biton* (*B.*) sp. 3, ♂ (AMNH [LP 9852]), left chelicera with two FSM, right chelicera (not shown) with single FSM. **F.** *Biton* (*B.*) sp. 4, ♂ (NMNW), Namibia: Gondwana Cañon Park (SNAP; Site G29). **G.** *Biton* (*B.*) sp. 5, ♂ (NMNW 12228). **H, I.** *Biton* (*B.*) sp. 6 (*namaqua* group), ♂ (NMNW), Namibia: Windhoek, Auas Mountains. **J.** *Biton* (*B.*) sp. 7, ♂ (LP 9853). **K.** *Biton* (*B.*) sp. 8, ♂ (NMNW 12336)(sp. 8). **L.** *Eberlanzia flava* Roewer, 1941, ♂ (NMNW 11175).

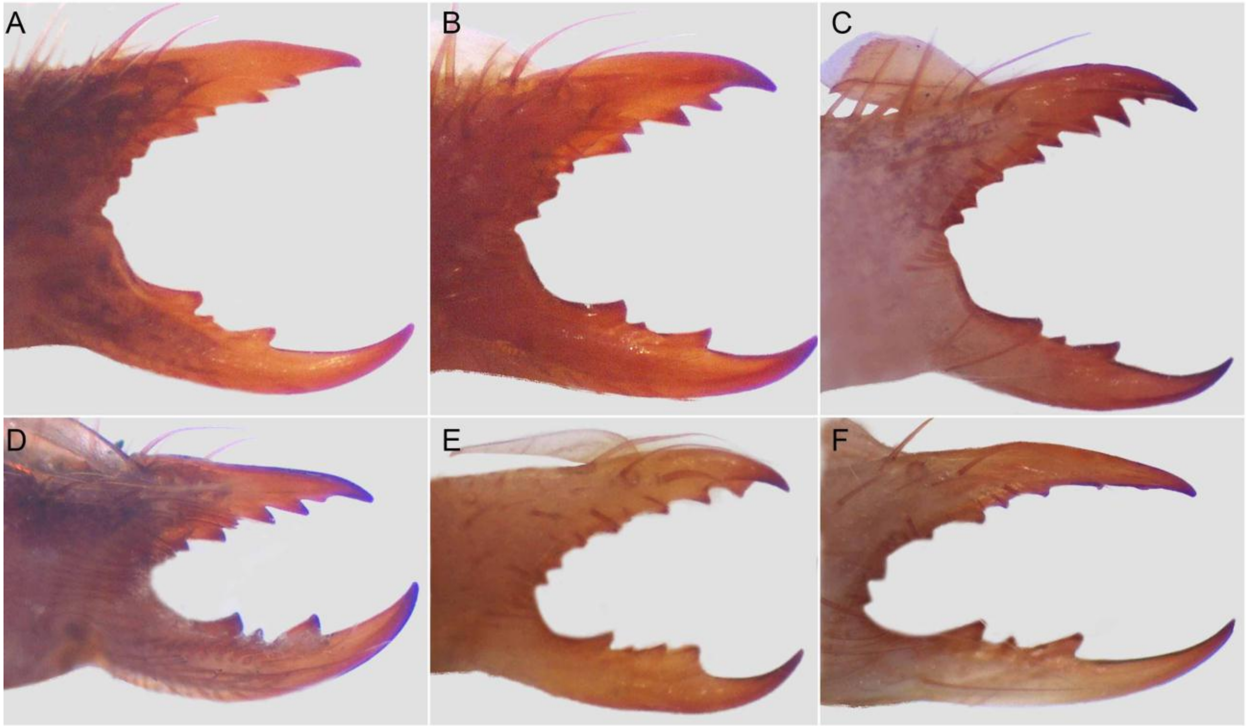

Plate 144. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**D**) and retrolateral (**A–C, E, F)** views. **A.** *Blossia* sp., ♂ (NMNW), Namibia: Namib-Naukluft Park (SNAP; Site S26). **B.** *Blossia tricolor* Hewitt, 1914, ♂ (NMNW), Namibia: Gondwana Cañon Park (SNAP; G29). **C.** *Blossia* cf. *purpurea*, ♂ (NMNW 13893). **D.** *Blossia spinicornis* Lawrence, 1928, ♂ (NMNW), Namibia: Windhoek (NARREC). **E.** *Blossia* cf. *rooica*, ♂ (NMNW), Namibia: Gondwana Cañon Park (SNAP; Site G29). **F.** *Blossia sabulosa* (Lawrence, 1972), ♂ (NMNW), Namibia: Namib-Naukluft Park (SNAP; Site N26).Arrow indicate subterminal flange.

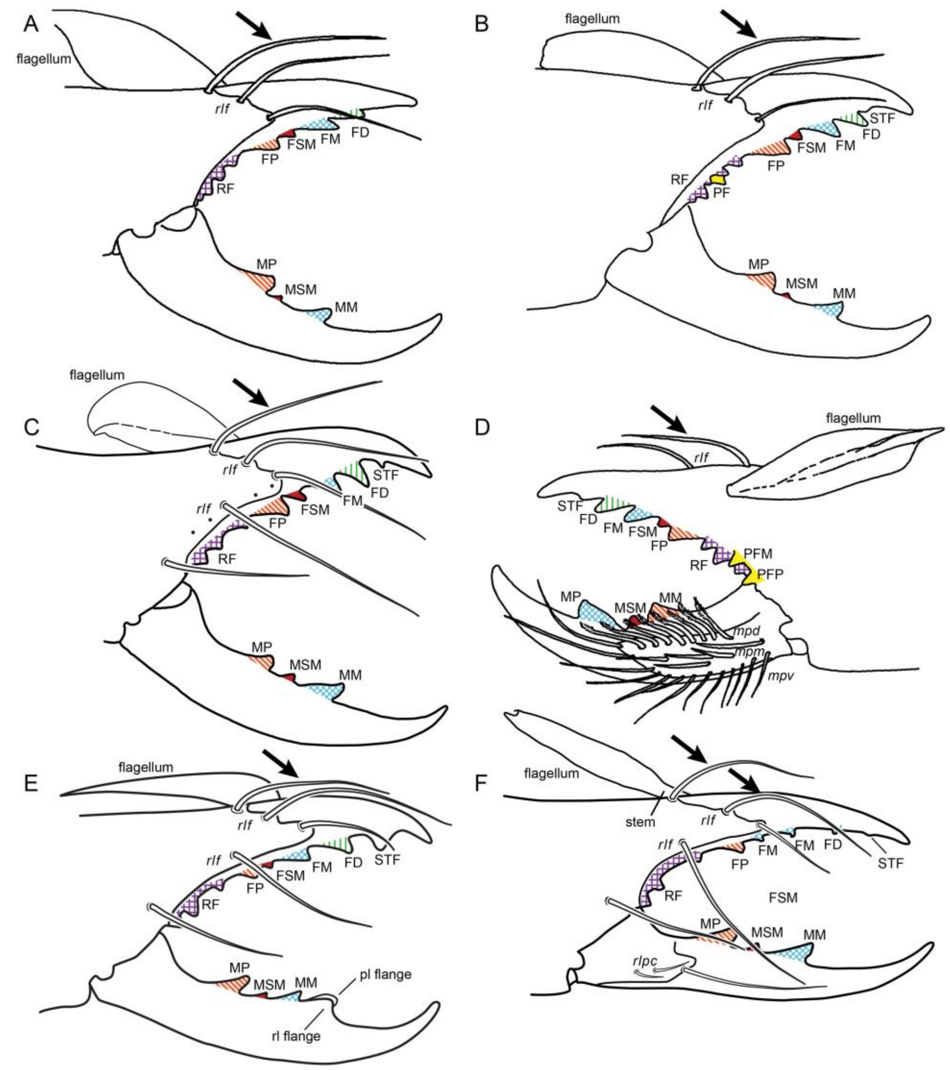

Plate 145. Daesiidae Kraepelin, 1899, chelicerae, prolateral (**D**) and retrolateral (**A–C, E, F**) views, illustrating dentition, setae, and flagellum. **A.** *Blossia* sp., ♂ (NMNW), Namibia: Namib-Naukluft Park (SNAP; Site S26). **B.** *Blossia tricolor* Hewitt, 1914, ♂ (NMNW), Namibia: Gondwana Cañon Park (SNAP; G29). **C.** *Blossia* cf. *purpurea*, ♂ (NMNW 13893). **D.** *Blossia spinicornis* Lawrence, 1928, ♂ (NMNW), Namibia: Windhoek (NARREC). **E.** *Blossia* cf. *rooica*, ♂ (NMNW), Namibia: Gondwana Cañon Park (SNAP; Site G29), with prolateral and retrolateral flanges forming toothlike structure distal to MM. **F.** *Blossia sabulosa* (Lawrence, 1972), ♂ (NMNW), Namibia: Namib-Naukluft Park (SNAP; Site N26). Arrows indicate modified *rlf* (i.e., *principal rlf*). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth; PFP, profondal proximal tooth; RF, retrofondal teeth; STF, subterminal flange; *mpd*, movable finger, prodorsal setae; *mpm*, movable finger, promedial setae; *mpv*, movable finger, proventral setae; *rlpc*, retrolateral proximal cluster of setae; *rlf*, retrolateral finger setae; pl, prolateral; rl, retrolateral.

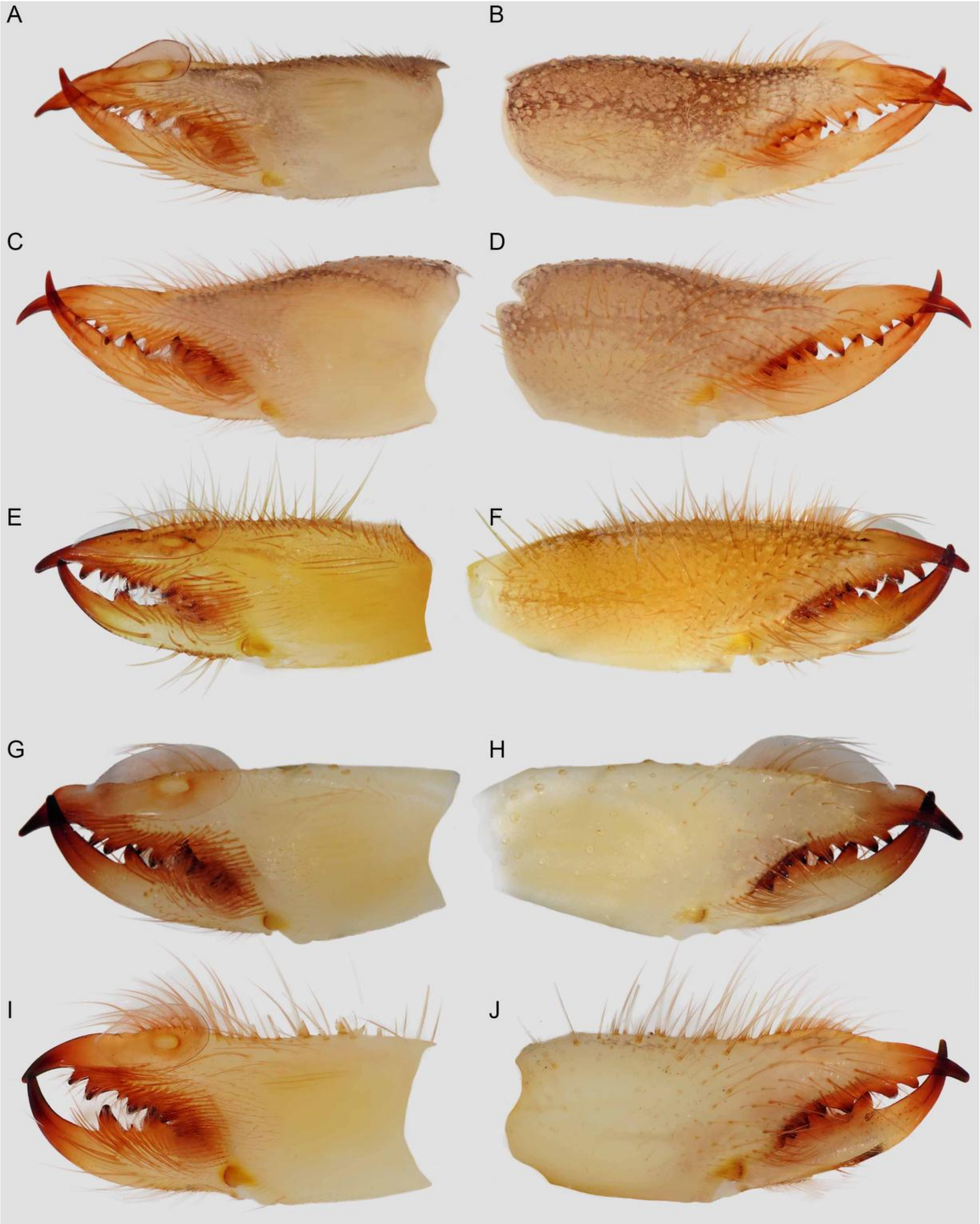

Plate 146. Ammotrechidae Roewer, 1934, chelicerae, prolateral (**A, C, E, G, I**) and retrolateral (**B, D, F, H, J**) views. **A–D.** *Pseudocleobis andinus* (Pocock, 1899). **A, B.** ♂ (AMNH [LP 2384]). **C, D.** ♀ (AMNH [LP 2384]). **E, F.** *Ammotrecha stollii* (Pocock, 1895), ♂ (AMNH [LP 8605]). **G, H.** *Nothopuga cuyana* Maury, 1976, ♂ (AMNH [LP 2263]). **I, J.** *Oltacola gomezi* Roewer, 1932, ♂ (AMNH [LP 2262A]).

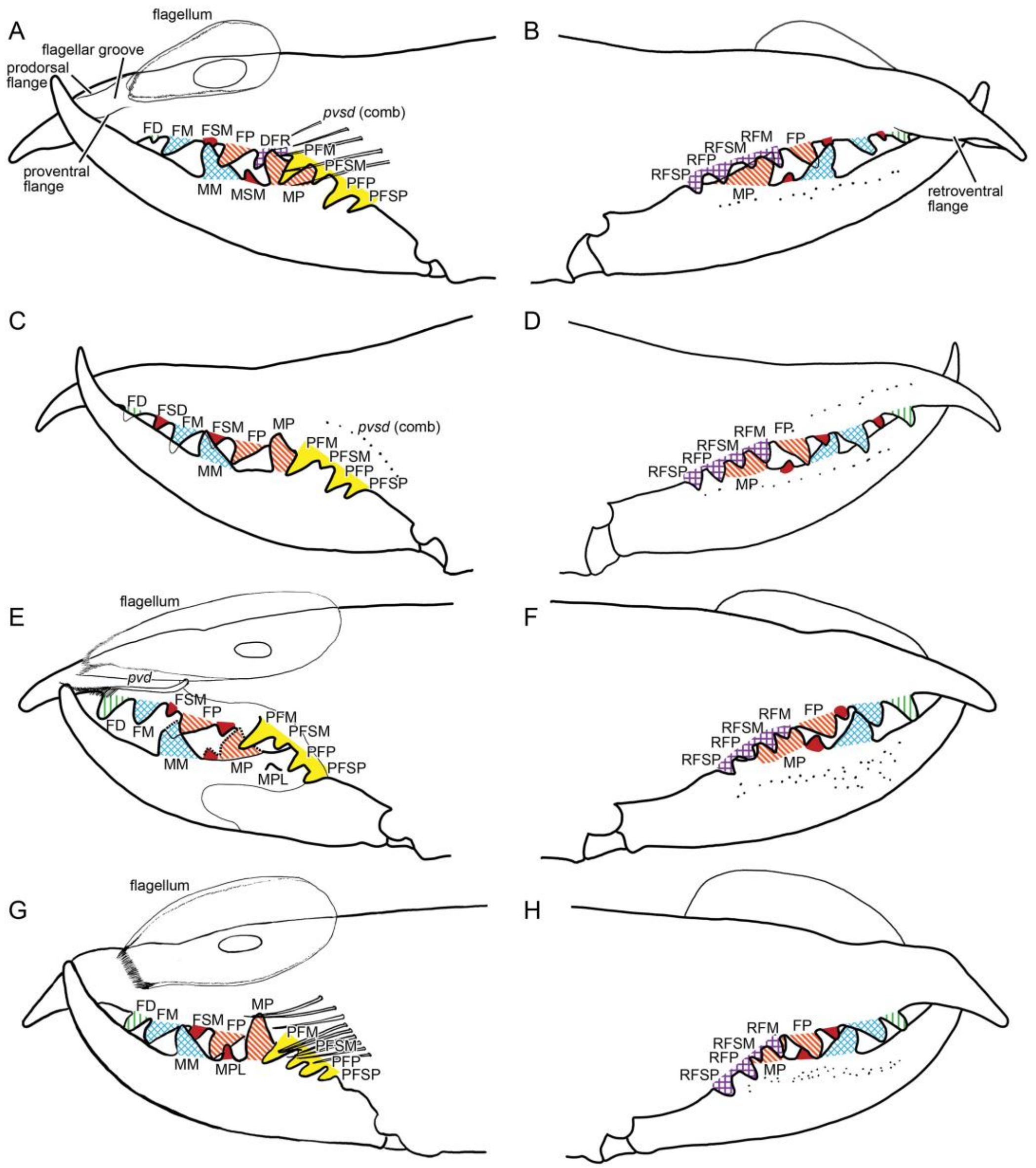

Plate 147. Ammotrechidae Roewer, 1934, chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views, illustrating dentition, setae, and flagellum. **A–D.** *Pseudocleobis andinus* (Pocock, 1899). **A, B.** ♂ (AMNH [LP 2384]). **C, D.** ♀ (AMNH [LP 2384]). **E, F.** *Ammotrecha stollii* (Pocock, 1895), ♂ (AMNH [LP 8605]). **G, H.** *Nothopuga cuyana* Maury, 1976, ♂ (AMNH [LP 2263]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSD, retrofondal subdistal; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvd*, proventral distal (apicalmost setae only); *pvsd*, proventral subdistal setae (setal comb only).

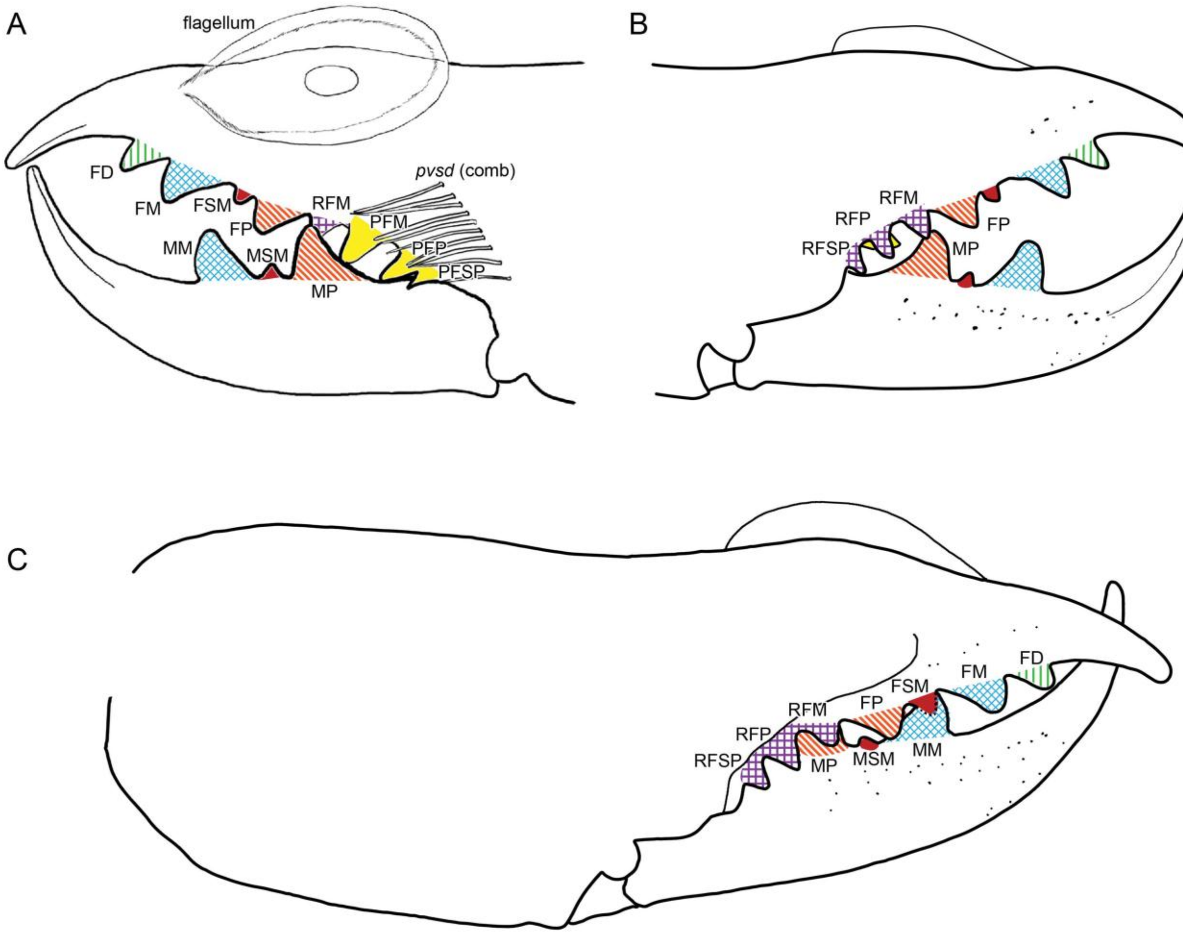

Plate 148. Ammotrechidae Roewer, 1934, chelicerae, prolateral (**A**) and retrolateral (**B, C**) views, indicating dentition, setae, and flagellum. **A–C.** *Oltacola gomezi* Roewer, 1932. **A, B.** ♂ (AMNH [LP 2262A]), with cheliceral fingers open. **C.** ♂ (AMNH [LP 10681]), with fingers closed, illustrating shape of chelicera and indistinct margin of sclerotized area on fixed finger. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only).

Plate 149. Ammotrechidae Roewer, 1934 (**A–D**) and Mummuciidae Roewer, 1934 (**E–H**), chelicerae, prolateral (**A, C, E, G**) and retrolateral (**B, D, F, H**) views. **A, B.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). **C, D.** *Sedna pirata* Muma, 1971, ♀ (AMNH [LP 2362]). **E, F.** *Gaucha fasciata* Mello-Leitão, 1924, ♂ (AMNH [LP 5858]). **G, H.** *Uspallata pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]).

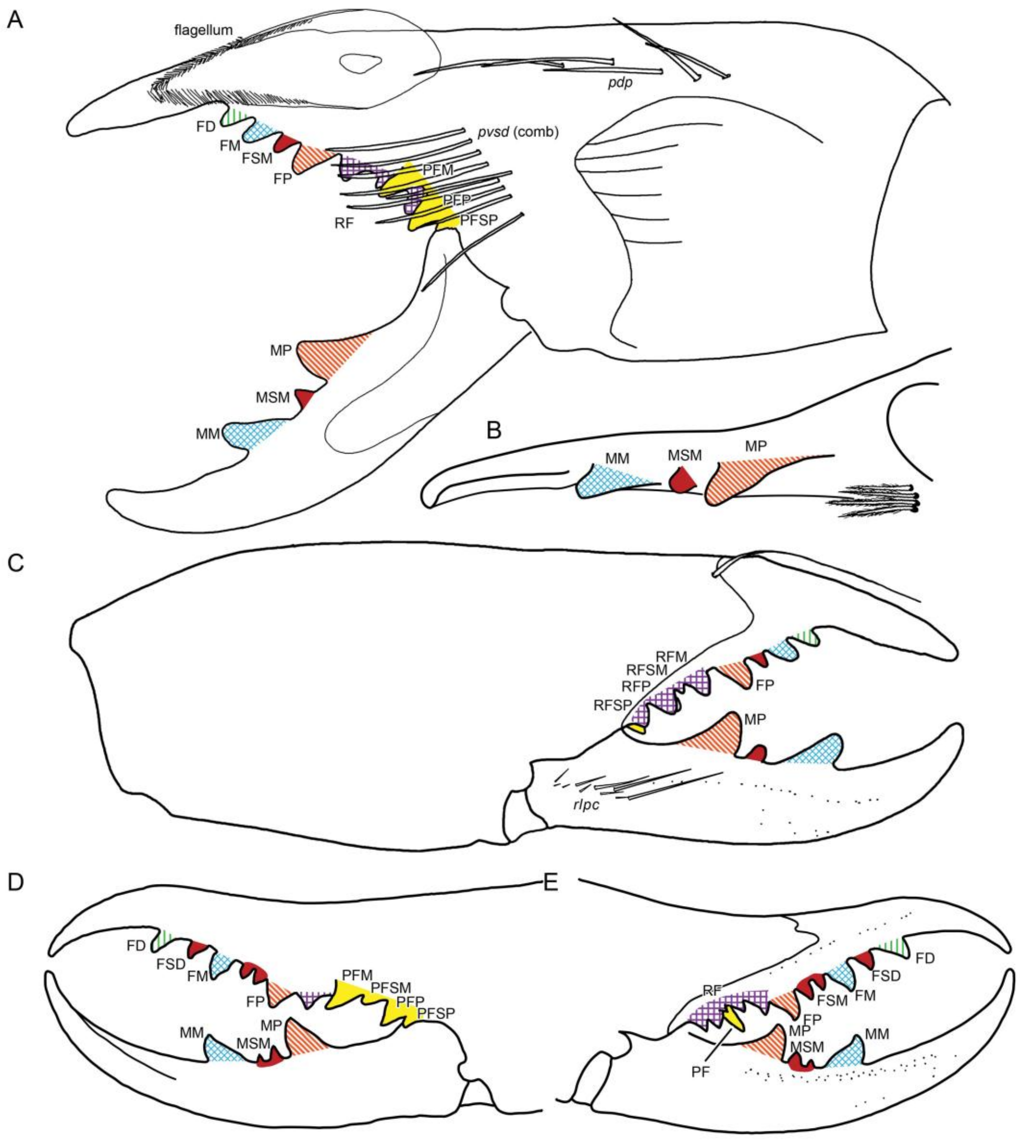

Plate 150. Ammotrechidae Roewer, 1934, chelicerae, prolateral (**A**) and retrolateral (**C–E**) views, and movable finger, retrodorsal view (**B**), illustrating dentition, setae, and flagellum. **A–C.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). Flagellum not shown in (**C**). **D, E.** *Sedna pirata* Muma, 1971, ♀ (AMNH [LP 2362]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; PF, profondal teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pdp*, prodorsal proximal setae; *mff*, movable finger, fondal setae; *pvsd*, proventral subdistal setae (setal comb only); *rlpc*, retrolateral proximal cluster of setae..

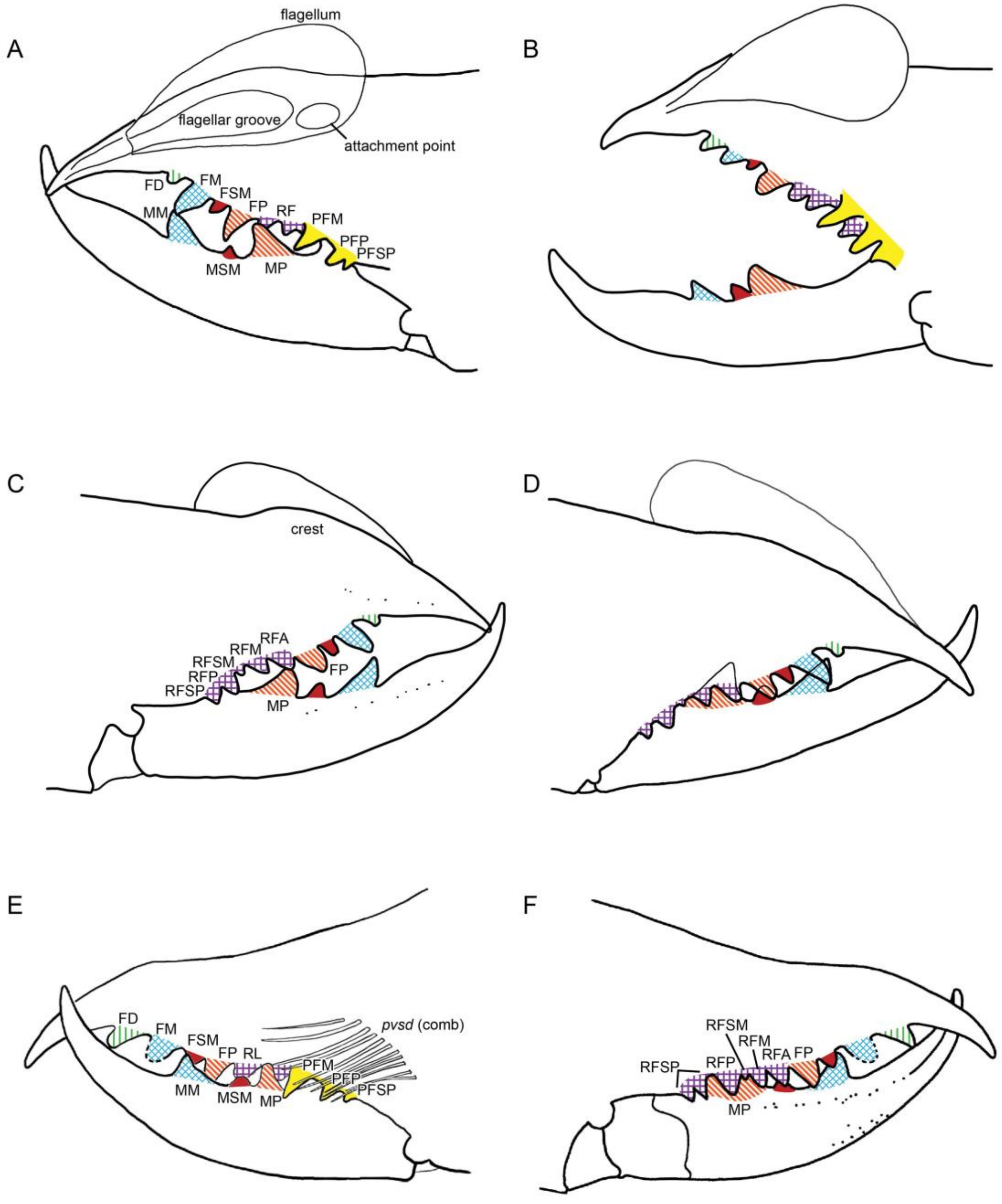

Plate 151. Mummuciidae Roewer, 1934, chelicerae, prolateral (**A, B, E**) and retrolateral (**C, D, F**) views, illustrating dentition, setae, and flagellum. **A–F.** *Gaucha fasciata* Mello-Leitão, 1924. **A, C, D.** ♂ (AMNH [LP 5858). **B.** ♂, adapted from Maury (1970: 360, fig. 2). **E, F.** ♀ (AMNH [LP 10699]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RF, retrofondal teeth; RFA, retrofondal apical tooth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only); *rlpc*, retrolateral proximal cluster of setae.

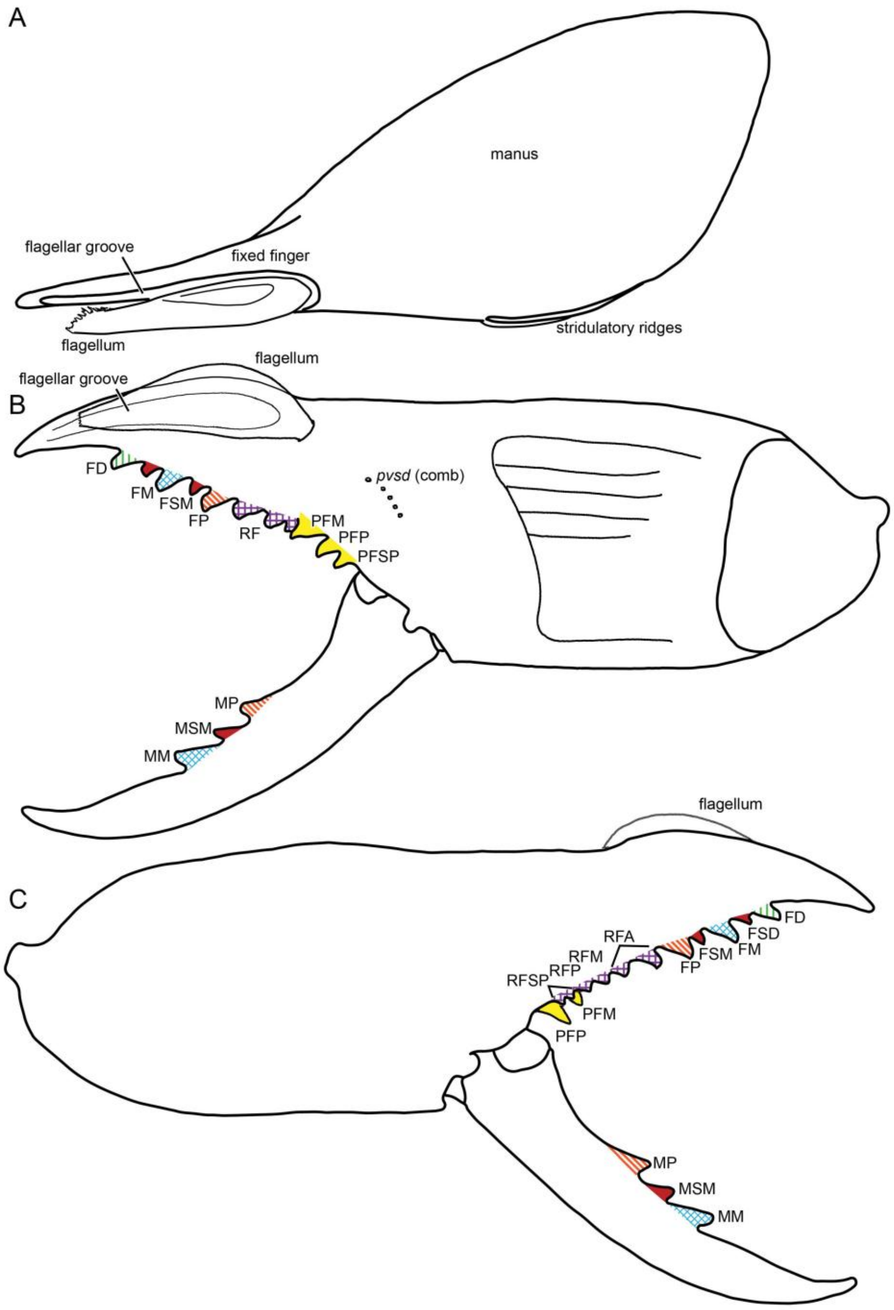

Plate 152. Mummuciidae Roewer, 1934, *Uspallata pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]), chelicerae, dorsal (**A**), prolateral (**B**), and retrolateral (**C**) views, illustrating dentition, setae, and flagellum. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; PFM, profondal medial tooth; PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RFA, retrofondal apical teeth, RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only).

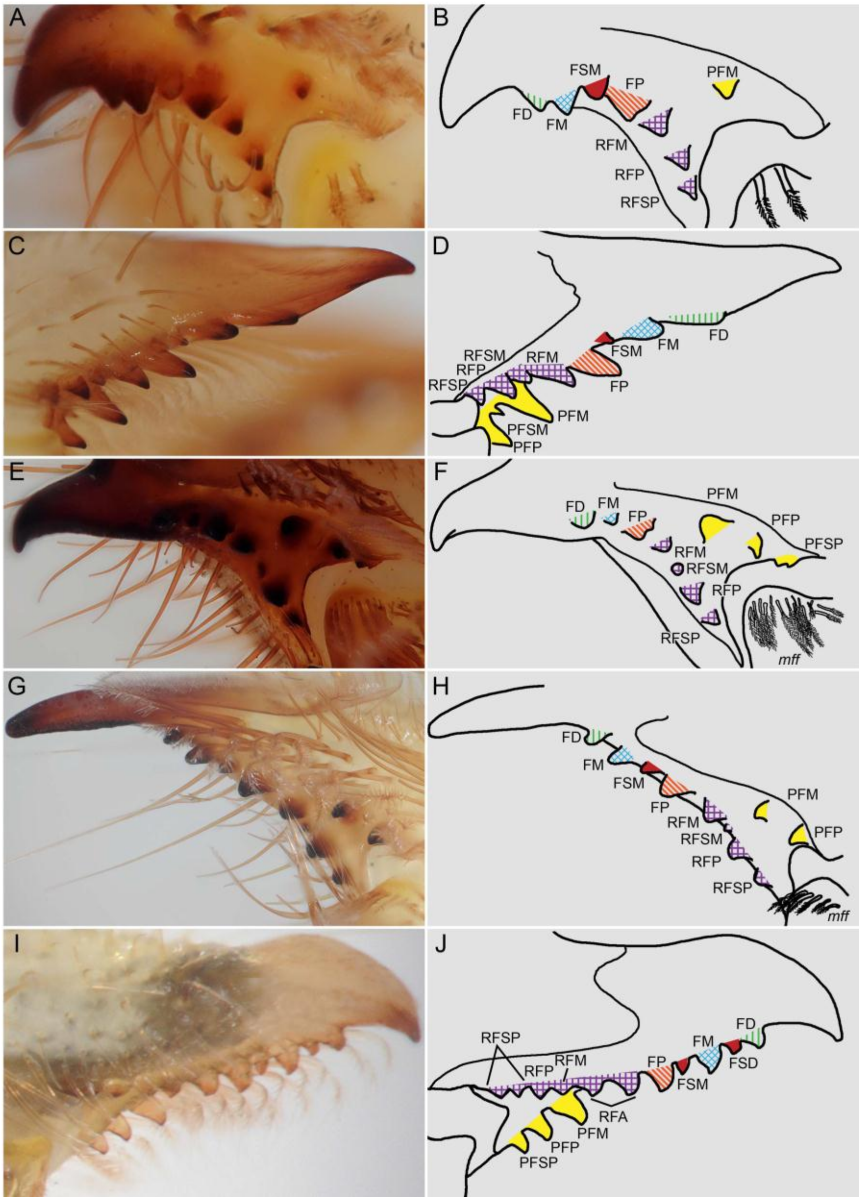

Plate 153. Daesiidae Kraepelin, 1899 (**A–F**), Ammotrechidae Roewer, 1934 (**G, H**), and Mummuciidae Roewer, 1934 (**I, J**), cheliceral fixed fingers, proventral (**A, B, E–H**) and retroventral (**C, D, I, J**) views illustrating fondal area. **A, B.** *Blossia grandicornis* Lawrence, 1929, ♂ (AMNH [LP 5905]). **C, D.** *Biton* (*B.*) *rossicus* (Birula, 1905), ♂ (AMNH [LP 3959]). **E, F.** *Gluvia dorsalis* (Latreille, 1817), ♂ (AMNH [LP 6093]). **G, H.** *Procleobis patagonicus* (Holmberg, 1876), ♂ (AMNH [LP 4235]). **I, J.** *Uspallata pulchra* Mello-Leitão, 1938, ♂ (AMNH [LP 2403]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial tooth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSM, profondal submedial tooth; PFSP, profondal subproximal tooth; RFA, retrofondal apical teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSM, retrofondal submedial tooth; RFSP, retrofondal subproximal tooth; *mff*, movable finger, fondal setae.

Plate 154. Melanoblossiidae Roewer, 1933, Melanoblossiinae, chelicerae, prolateral (**A, C, E, G, I**), retrolateral (**B–D, F, H, J–L**), views. **A–D.** *Melanoblossia braunsi*, Purcell, 1903. **A, B** ♂ (AMNH [LP 10737]). **C, D.** ♀ (AMNH [LP 10737]), sinistral chelicera with bifid (**C**), and dextral chelicera with regular (**D**) fixed finger medial (FM) tooth. **E, F.** *Melanoblossia* cf. *braunsi*, ♂ (AMNH [LP 8550]). **G, H.** *Melanoblossia* sp., ♂ (AMNH [LP 9857]). **I, J.** *Lawrencega procera* Wharton, 1981, ♂ (AMNH [LP 9863]). **K, L.** *Lawrencega minuta* Wharton, 1981. **K.** Paratype ♂ (CAS 9033898). **L.** ♀ (CAS 9033898).

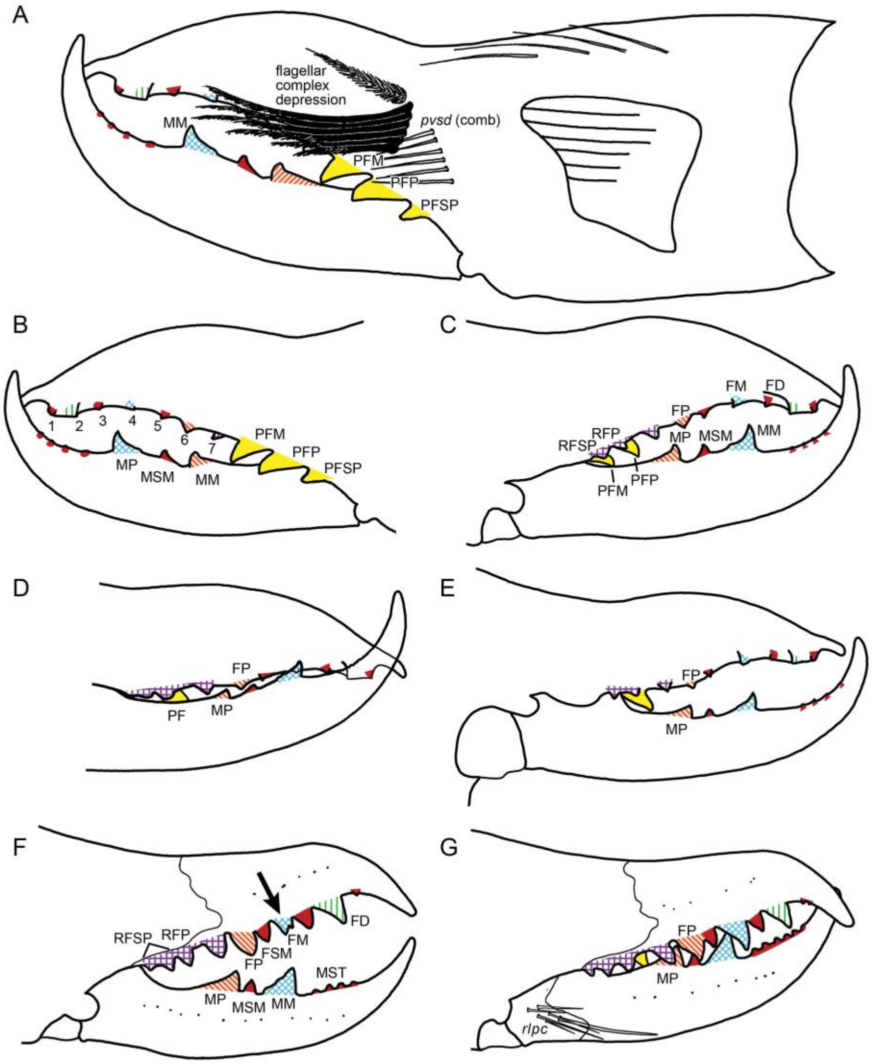

Plate 155. Melanoblossiidae Roewer, 1933, Melanoblossiinae, *Melanoblossia braunsi* Purcell, 1903, chelicerae, prolateral (**A, B**), retrolateral (**C, D, F, G**), and proventral (**E**) views, illustrating dentition, setae, and flagellar complex. **A–E.** ♂ (AMNH [LP 10737]), with (**A**) and without (**B**) flagellar setal complex illustrated, with cheliceral fingers open (**C**) and closed (**D**), and illustrating positions of fondal teeth relative to median series (**E**). Arrow indicates possible flagellum. Numbers indicate seven distalmost toothlike structures. **F, G.** ♀ (AMNH [LP 10737]), illustrating apparently aberrant bifid tooth (arrow). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial tooth; FST, fixed finger, subterminal tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; MST, movable finger, subterminal teeth (denticles); PF, profondal teeth; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal teeth; *pdp*, prodorsal proximal setae; *pvsd*, proventral subdistal setae (setal comb only); *rlpc*, retrolateral proximal cluster of setae.

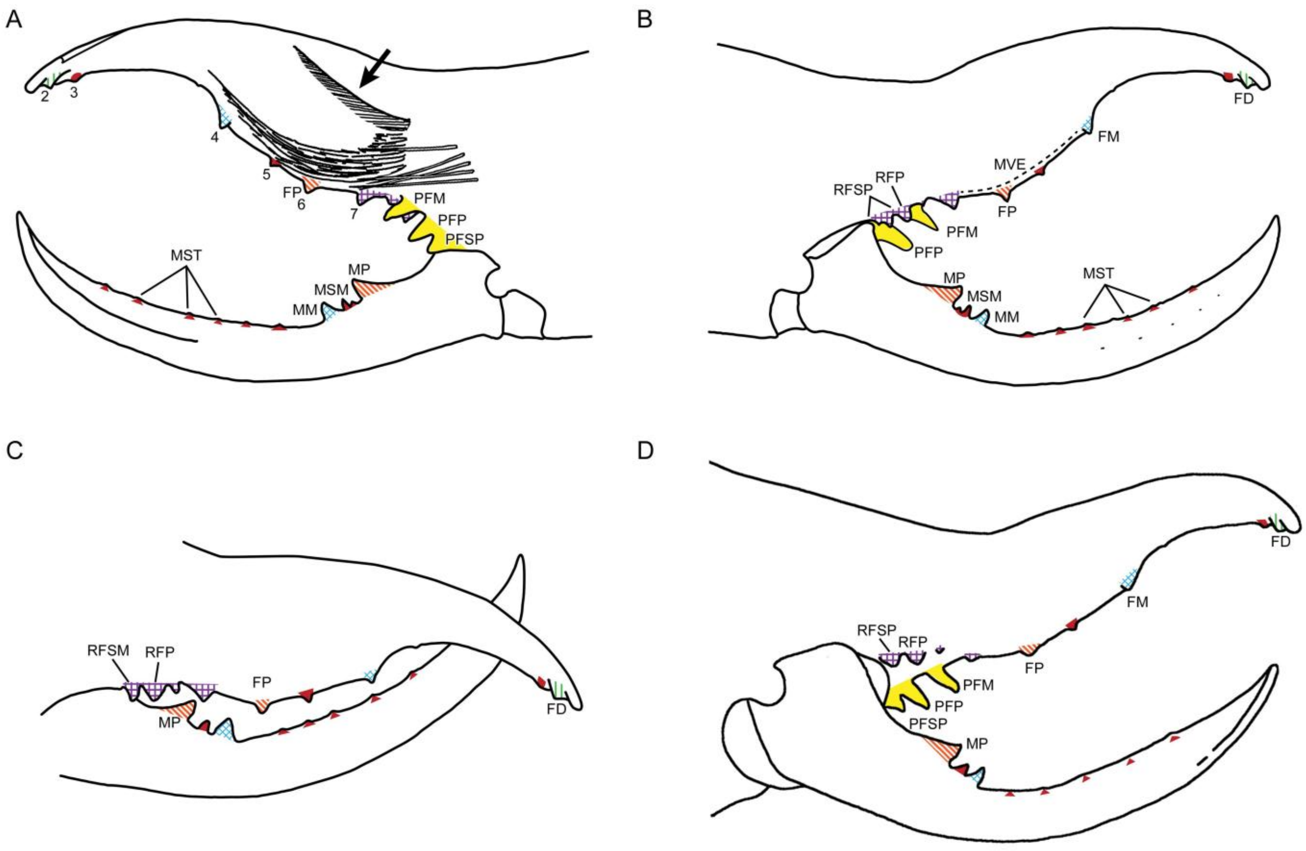

Plate 156. Melanoblossiidae Roewer, 1933, Melanoblossiinae, *Melanoblossia* cf. *braunsi*, ♂ (AMNH [LP 8550]), chelicerae, prolateral (**A**), retrolateral (**B, C**), and proventral (**D**) views, illustrating dentition, setae, and flagellar complex with cheliceral fingers open (**A, B**), closed (**C**), and illustrating fondal teeth (**D**). Arrow indicates differentiated flagellar complex seta. Numbers indicate seven distalmost toothlike structures. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; MST, movable finger, subterminal tooth; MVE, medioventral excrescence; PFM, profondal medial tooth; PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only); *sfc*, setiform flagellar complex.

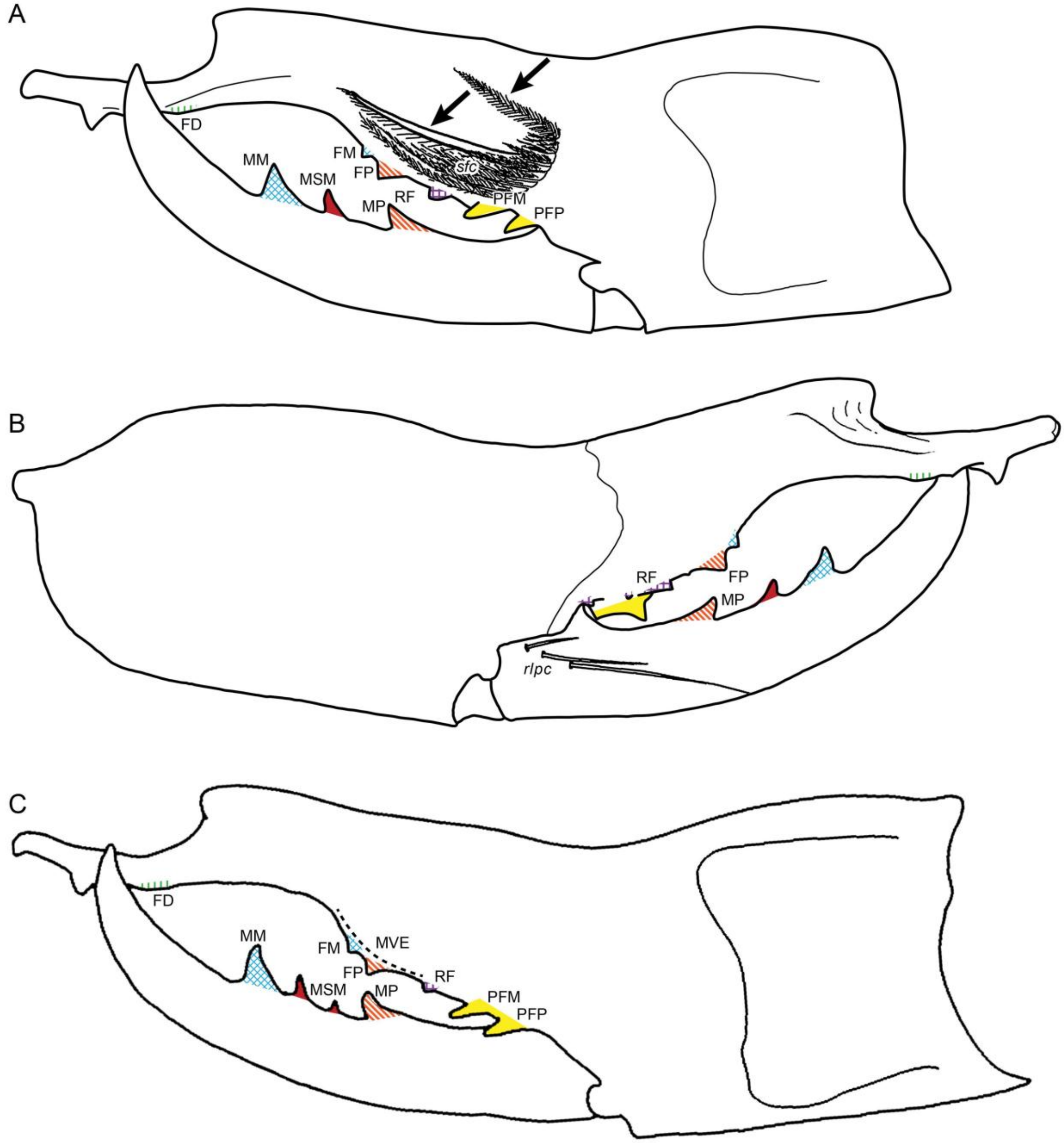

Plate 157. Melanoblossiidae Roewer, 1933, Melanoblossiinae, chelicerae, prolateral (**A, C**) and retrolateral (**B**) views, illustrating flagellar complex, and population variation in dentition (arrowhead). **A–C.** *Melanoblossia* sp. **A, B.** ♂ (AMNH [LP 9857]). **C.** ♂ (NMNW 13396). Arrows indicate possible flagella. Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSM, fixed finger, submedial tooth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial tooth; MVE, medioventral excrescence; PF, profondal teeth; PFM, profondal medial tooth; PFP, profondal proximal tooth; RF, retrofondal teeth; *pvd*, proventral distal setae; *rlpc*, retrolateral proximal cluster of setae; *sfc*, setiform flagellar complex.

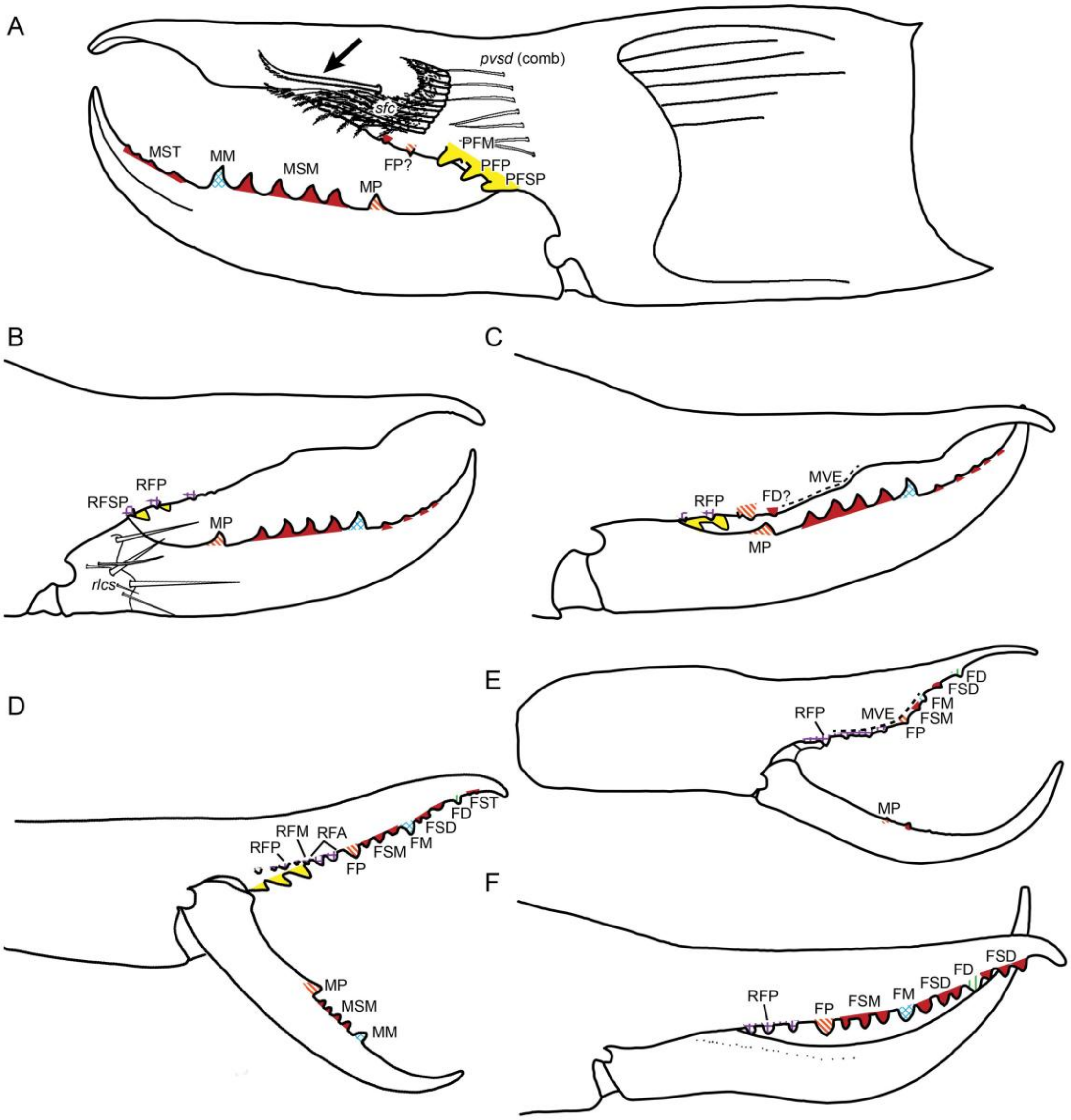

Plate 158. Melanoblossiidae Roewer, 1933, Melanoblossiinae, chelicerae, prolateral (**A**) and retrolateral (**B–F**) views, illustrating dentition, setae, and flagellar complex. **A–C.** *Lawrencega procera* Wharton, 1981, ♂ (AMNH [LP 9863]). **D.** *Lawrencega trispilosa* Lawrence, 1968, ♀ (NMNW 11118). **E, F.** *Lawrencega minuta* Wharton, 1981. **E.** Paratype ♂ (CAS 9033898), flagellar complex not illustrated. **F.** Paratype ♀ (CAS 9033898). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal teeth; FSM, fixed finger, submedial teeth; FST, fixed finger, subterminal teeth; MM, movable finger, medial tooth; MP, movable finger, proximal tooth; MSM, movable finger, submedial teeth; MST, movable finger, subterminal tooth; MVE, medioventral excrescence; PFM, profondal medial tooth, PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RFS, retrofondal apical teeth; RFM, retrofondal medial tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal tooth; *pvsd*, proventral subdistal setae (setal comb only); *rlpc*, retrolateral proximal cluster of seta, *sfc*, seriform flagellar complex..

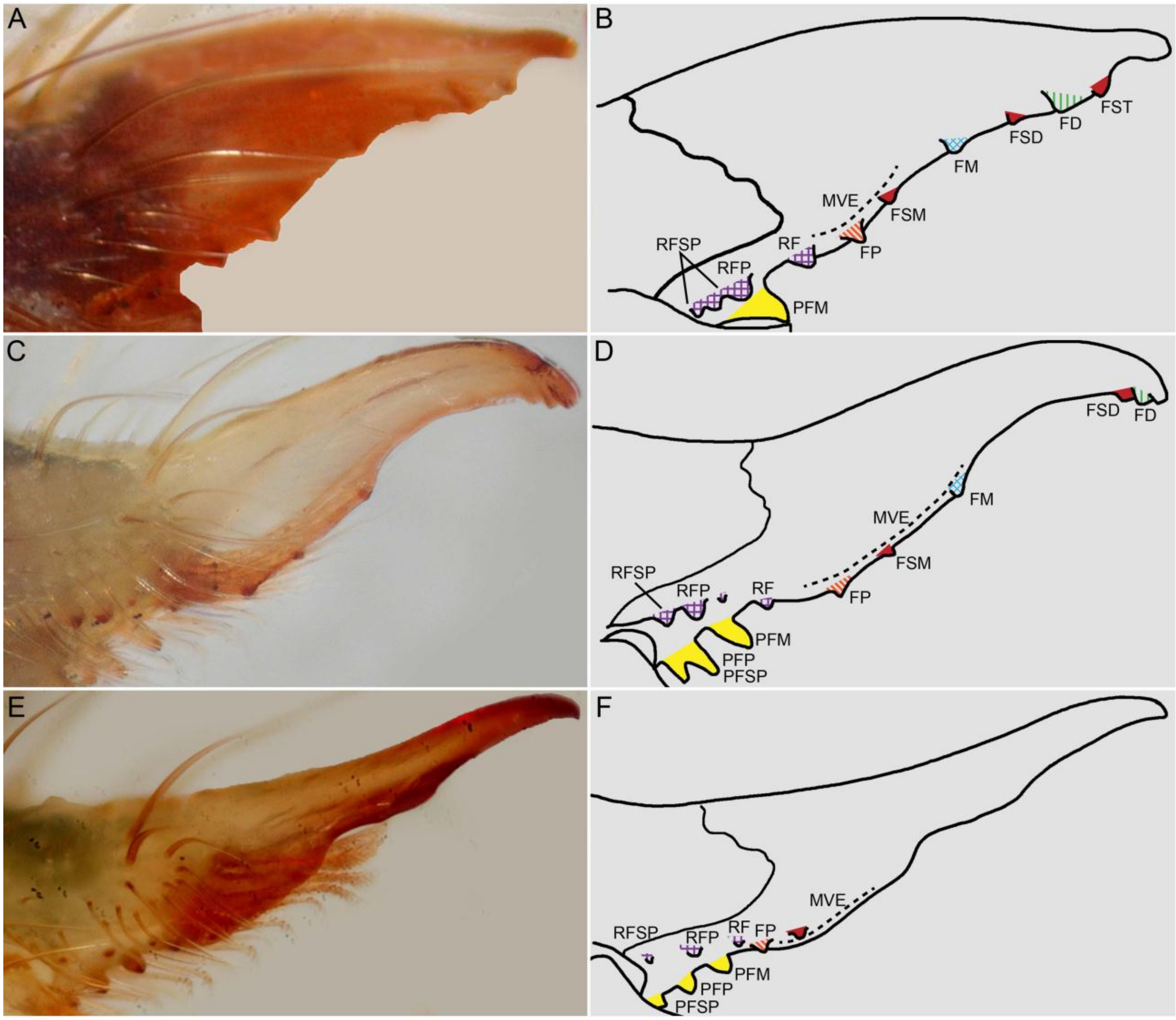

Plate 159. Melanoblossiidae Roewer, 1933, Melanoblossiinae, cheliceral fixed fingers, retroventral views illustrating fondal area. **A, B.** *Melanoblossia braunsi*, Purcell, 1903, ♂ (AMNH [LP 10737]). **C, D.** *Melanoblossia* cf. *braunsi*, ♂ (AMNH [LP 8550]). **E, F.** *Lawrencega procera* Wharton, 1981, ♂ (AMNH [LP 9863]). Abbreviations: FD, fixed finger, distal tooth; FM, fixed finger, medial tooth; FP, fixed finger, proximal tooth; FSD, fixed finger, subdistal tooth; FSM, fixed finger, submedial tooth; FST, fixed finger, subterminal tooth; MVE, medioventral excrescence; PFM, profondal medial tooth; PFP, profondal proximal tooth; PFSP, profondal subproximal tooth; RFP, retrofondal proximal tooth; RFSP, retrofondal subproximal teeth.

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APPENDIX 1

SOLIFUGAE SUNDEVALL 1833 TAXONOMY AND MATERIAL EXAMINED.

Currently, 12 extant families comprising 139 genera (Harvey, 2003a; Prendini, 2011) and 1103 species are recognized within Solifugae. Thirty-three species have been added to the 1075 species listed by Harvey (2003a), six species of Ammotrechidae Roewer, 1934, one species of Daesiidae Kraepelin, 1899, 17 species of Eremobatidae Kraepelin, 1899, five species of Karschiidae Kraepelin, 1899 and four species of Mummuciidae Roewer, 1934, while five species of Eremobatidae were synonymized (Brookhart and Cushing, 2002; 2004; 2005; 2008; Gromov, 2003a; Martins et al., 2004; Armas and Teruel, 2005; Rocha and Carvalho, 2006; Ballesteros and Francke, 2007; Catenazzi et al., 2009; Carvalho et al., 2010; Reddick et al. 2010; González Reyes and Corronca, 2013; Karataş and Uçak, 2013; Iuri, et al., 2014). The most speciose families are Galeodidae Sundevall, 1833 (199 species), Solpugidae Leach, 1815 (191 species), Daesiidae (190 species), and Eremobatidae (186 species). Understanding the current family, subfamily, and generic level taxonomy of the group is necessary for evaluating patterns of character variation. A list of taxa and material examined follows the family discussions.

AMMOTRECHIDAE ROEWER, 1934

Ammotrechidae (Pls. 146–148, 149A–D, 150, 153G, H) are restricted to the New World, the southern half of the U.S.A. (northern California to Florida), Mexico, the

Caribbean, and South America, with greatest diversity in the arid to semi-arid northern and western parts of South America. Ammotrechidae is defined primarily on the immovable, membranous, elliptical and bowl-shaped flagellum. The family is divided into five subfamilies, Ammotrechinae Roewer, 1934, Mortolinae Mello-Leitão, 1938, Nothopuginae Maury, 1976, Oltacolinae Roewer, 1934, Saronominae Roewer, 1934, and includes some genera of uncertain placement (Harvey, 2003a). Harvey's (2003a) list of 22 extant genera did not reflect the transfers of *Mummuciona* Roewer, 1934 and *Sedna* Muma, 1971 from Mummuciidae to Ammotrechidae (Maury, 1976, 1982, 1987) which, together with the subsequent synonymy of *Ammotrechella* Roewer, 1934 with *Ammotrechona* Roewer, 1934 by Armas (2004), brings the number of extant ammotrechid genera to 23. The fossil species *Happlodontus proterus* Poinar and Santiago-Blay, 1989, described from Dominican amber, is also placed in Ammotrechidae. According to Muma (1971), the flagellum is the only character by means of which Daesiidae and Ammotrechidae (and Mummuciidae) can be differentiated, rendering identifications of singleton females almost impossible, even to family. Six ammotrechid species have been described, four by Armas and Teruel (2005), one by Catenazzi et al. (2009), and one by Iuri, et al. (2014) since Harvey's (2003a) catalogue. Four subfamilies, six genera and six species were examined during the present study.

AMMOTRECHINAE ROEWER, 1934

Ammotrecha stollii (Pocock, 1895): **NICARAGUA: Chinandega Province:** El Viejo, Hacienda (Hostal) Cosiquina, 12°54'33.0"N 87°30'40.0"W, 18 m, 27.xi.2007, C.

Viquez and J. Mata, 5 ♂ (AMNH [LP 8605]).

Pseudoclobis andinus (Pocock, 1899): **ARGENTINA: Mendoza Province:** Puente del Inca, 32°49.568'S 69°54.606'W, 2759 m, 2.xi.2003, C. Mattoni, L. Prendini, and J. Ochoa, 2 ♂, 1 ♀, 2 juv. (AMNH [LP 2384]).

NOTHOPUGINAE MAURY, 1976

Nothopuga cuyana Maury, 1976: **ARGENTINA: Córdoba Province:** 20 km N of San José de las Salinas, E border of Salinas Grandes, 15.xi.2002, C. Mattoni, J. Ochoa, and M. Moyano, 1 ♂, 2 juv. (AMNH [LP 2263]).

OLTACOLINAE ROEWER, 1934

Oltacola gomezi Roewer, 1932: **ARGENTINA: Córdoba Province:** 20 km N of San José de las Salinas, E border of Salinas Grandes, 15.xi.2002, C. Mattoni, J. Ochoa, and M. Moyano, 2 ♂ (AMNH [LP 2262A, 10681]).

SARONOMINAE Roewer, 1934

Procleobis patagonicus (Holmberg, 1876): **ARGENTINA: Neuquen Province:** Picun Leufu, 39°32'13.5"S 69°13'21.8"W, 399 m, 25.i.2005, M. Magnanelli and E.G. López, 1 ♂ (AMNH [LP 4235]).

INCERTAE SEDIS

Sedna pirata Muma, 1971: **CHILE: Region IV (Coquimbo):** *Choapa Province*: Caleta Totoralillo, 32°01.569'S 71°30.889'W, 5 m, 4.xi.2003, L. Prendini, C. Mattoni, and

J. Ochoa, 1 ♀ (AMNH [LP 2362]).

CEROMIDAE ROEWER, 1933

Ceromidae (Pls. 91–96) is a small family, currently containing three extant genera, recorded from southern and eastern Africa, and the fossil *Cratosolpuga wunderlichi* Selden, 1996, from the Crato Formation in Brazil. *Ceroma* Karsch, 1885 and *Ceromella* Roewer, 1933 show clear affinities including dentition and a distinct flagellar complex comprising an elongated, paraxially rotatable flagellum with a vesicular base situated behind a row of stiff modified setae (flagellar complex plumose, *fcp*, setae). *Toreus* Purcell, 1903 is a monotypic genus of unclear affinities (Muma, 1976; Wharton, 1981), known from a single specimen. A flagellum is absent in the type species, *Toreus capensis* (Purcell, 1899), but the dorsal cheliceral fingers are highly modified. Lawrence (1962b) suggested that the holotype is a female, the male being the paratype of *Solpuga grindleyi* Brown, 1961 (currently in synonymy with *Blossia litoralis* Purcell, 1903), a species originally placed in Solpugidae notwithstanding that the flagellum and associated setae being consistent with the flagellar complex of Ceromidae. Lawrence (1962b) did not formally synonymize these taxa, however, and it is unlikely, based on the extreme modification of the cheliceral fingers, that the holotype of *Toreus*, which was not examined during the present study, is female. If the holotype is indeed male, the absence of a flagellum suggests an affinity with Lipophaginae Wharton, 1981 (*vide* Wharton, 1981), but Muma (1976) retained *Toreus* in Ceromidae presumably based on characters shared with ceromids, notably two claws on the tarsi of leg I*. Toreus capensis* may prove to be an intermediate form between Ceromidae and Lipophaginae.

According to Hewitt (1919b: 63), the dorsal finger is “divided into two portions.”. This seems to resemble the dorsal hornlike process which is fused to the fixed (dorsal) finger in *Trichotoma michaelseni* (Kraepelin, 1914) (Pl. 88C). Additional specimens of *Toreus* are required to resolve its phylogenetic position. Two genera and four species of Ceromidae were examined during the present study.

Ceroma inerme Purcell, 1899: **NAMIBIA: Karas Region:** *Luderitz District*: Diamond Area: Sperrgebiet National Park: Bogenfels, 27°27'27.6"S 15°23'28.6"E, 31.viii.2006, EduVentures 9 Expedition, 1 ♀ (AMNH [LP 8425]); S of Bogenfels Arch, 27°27'36.2"S 15°23'38.6"E, 9 m, 14–16.vi.2008, C. Kaapehi and B. Muramba, 8 ♂, 1 ♀ (NMNW 13632), S of beach, 27°27'36.2"S 15°23'38.6"E , 9 m, 14–18.vi.2008, C. Kaapehi and B. Muramba, 2 ♂ (AMNH [LP 9864]).

Ceroma ornatum Karsch, 1885: **KENYA:** Mount Kasigau, Jora Village, xii.2001, E. Selempo, 1 ♂ (MRAC 2013.106).

Ceroma swierstrae Lawrence, 1935: **SOUTH AFRICA: Western Cape Province:** *Bredasdorp District*: De Hoop Nature Reserve, 26.iii.2005, C. Haddad, 1 ♂ (NCA 2009/4355]).

Ceromella sp. n.: **SOUTH AFRICA: Western Cape Province:** *Vredendal District*: Farm Perseel Weskus 197, 31°29.038'S 18°01.367'E, 16 m, 21–26.ix.2007, C. Lyons, J. Mingo, and R. Lyons, 1 ♂ (AMNH [LP 8527]).

DAESIIDAE KRAEPELIN, 1899

Daesiidae (Pls. 132–145, 153A–F) is a large, diverse family, with a broad distribution including Africa, southern Europe, the Middle East, central Asia, and South

America (Argentina and Chile), and is the only family occurring in the New World and the Old World. Daesiidae is probably paraphyletic, however. The family is currently divided into six subfamilies, Daesiinae Kraepelin, 1899, Gluviinae Roewer, 1933, Gluviopsinae Roewer, 1933, Gnosippinae Roewer, 1933, Namibesiinae Wharton, 1981, and Triditarsinae Roewer, 1933, which do not accommodate all taxa, and have been largely ignored in the taxonomic literature (for details, see Wharton, 1981). Wharton (1981) described Namibesiinae Wharton, 1981 to accommodate the Old World genus *Namibesia* Lawrence, 1962 (Pls. 132A–D, 133). The monotypic *Syndaesia* Maury, 1980, restricted to the New World, resembles *Namibesia* but Maury (1985) suggested that these similarities are superficial and the two genera are not closely related. Generic definitions within Daesiidae remain untested, and various workers have called for re-evaluation of generic characters (Delle Cave and Simonetta, 1971; Wharton, 1981; Muma, 1982; Reddick et al., 2010). For example, two distinct species groups are recognized within *Hemiblossia* Kraepelin, 1899, the *bouveri* group (Pls. 139G, H, 141A, B, 142) and the *australis* group (Pls. 139I, J, 141C) (Wharton, 1981). Wharton (1981) suggested these groups may be united by convergent characteristics based on shared termitophilous habits. Tarsal segmentation (tarsi of legs II and III are one or two segmented, of leg IV one to four segmented), the absence of claws on leg I, and the form of the flagellum played an important role in the classification of Daesiidae (Roewer, 1934: 346). Kraepelin (1899) established subfamily Daesiinae within Solpugidae, based partly on the husk-, bladder- or vase-shaped flagellum. Roewer (1934: 344) elevated Daesiinae to family rank, again mostly on the basis of the rotation, shape, and membranous character of the flagellum.

Family Amacataidae Muma, 1971 was created to accommodate *Amacata penai* Muma, 1971, a New World species later synonymized with *Ammotrechelis goetschi* Roewer, 1934 by Maury (1985) (Pls. 132E–H, 134). Muma (1971: 17) separated Amacataidae from Ammotrechidae on the basis of the complex, rotatable cheliceral flagellum and from Daesiidae on the basis of the “distinctive flagellum … [and] … unusual tarsal segmentation and spinelike setal armature of the tarsi”. Arguing that the flagellum is not that different and that the tarsal segmentation and “spination” of legs II–IV falls within the range of variation observed within Daesiidae, Maury (1980a) synonymized Amacataidae with the latter. The Baltic amber fossil *Palaeoblossia groehni* Dunlop et al., 2004 is placed within Daesiidae. Only one extant species of Daesiidae has been described (Reddick et al., 2010) since Harvey’s (2003a) catalogue. Five of the six subfamilies, 10 genera and 30 species were examined during the present study.

DAESIINAE KRAEPELIN, 1899

Biton (*Biton*) *browni* (Lawrence, 1963): **NAMIBIA: Karas Region:** *Keetmanshoop District*: Kokerboom Forest on Farm Gariganus 157, 14 km NE of Keetsmanshoop, 26°28.914'S 18°14.660'E, 1092 m, 25.i.2004, L. Prendini and E. Scott, 1 ♂, 1 juv. (AMNH [LP 3633]).

Biton (*Biton*) *rossicus* (Birula, 1905): **UZBEKISTAN: Surkhandarya Area:** *Angor District*: Kattakum Desert, 4.5 km NE of Uchkyzyl, 37°22.549'N, 67°16.618'E, 331 m, 19.v.2003, L. Prendini and A.V. Gromov, 1 ♂, 1 ♀ (AMNH [LP 3959]).

Biton (*Biton*) *zederbaueri* (Werner, 1905): **TURKEY: Kilis Province:** *Musabeyli District*: Hasançali Village, 36°53'30"S 36°47'35"E, 27.v.2006, E.A. Yağmur, 1 ♂ (KU).

Biton (*Biton*) sp. 1: **NAMIBIA: Kunene Region:** *Opuwo District*: Kaokoland, Baynes Mountains, Okaombo Valley, 17°02'44.7"S 13°03'51.9"E, 985 m, 18.iv.2006, EduVentures 8 Expedition, 10 ♂, 1 ♀ (NMNW 13278).

Biton (*Biton*) sp. 2: **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park, Farm: Gaap River, viii.2005, EduVentures 7 Expedition, 1 ♂ (NMNW).

Biton (*Biton*) sp. 3: **NAMIBIA: Karas Region:** *Lüderitz district:* Farm: Klein Aus 8, 26°39'06.9"S, 16°14'38.0"E, 1382 m, 31.x.2008, T. Greyling, 1 ♂ (AMNH [LP 9852]).

Biton (*Biton*) sp. 4: **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park, Farm: Stamprivier 108 (SNAP; Site G29), 27°28'06.8"S 17°52'29.8"E, 888 m, 6.xi–15.xii.2008, R & D.R. Brand, 1 ♂ (NMNW).

Biton (*Biton*) sp. 5: **NAMIBIA: Khomas Region:** *Windhoek District*: Farm Gocheganas 26, 20.xii–20.i.1982, M.L. Penrith, 1 ♂ (NMNW 12228).

Biton (*Biton*) sp. 6 (*namaqua* group): **NAMIBIA: Khomas Region:** *Windhoek District*: Auas Mountains, Farm: Regenstein 32, 22°42'39.0"E 17°02'21.8"E, 2022 m, 16.ii–16iv.2009, J.F. Kaudinge, B.K. Muramba, T.L.Bird, 1 ♂ (NMNW).

Biton (*Biton*) sp. 7: **NAMIBIA: Khomas Region:** *Windhoek District*: Windhoek, Ludwigsdorf, 22°33'37.1"S 17°06'41.7"E, 1715 m, 16.vi.2009, J. Walter and U. Kirchner, 1 ♂ (AMNH [LP 9853]).

Biton (*Biton*) sp. 8: **NAMIBIA: Khomas Region:** *Windhoek District*: Farm Gocheganas 26, 22.iv–20.v.1982, M.L. Penrith, 3 ♂ (NMNW 12336).

Blossia grandicornis Lawrence, 1929: **SOUTH AFRICA: Northern Cape Province:** *Prieska District*: Farm Good Hope, ca. 30 km SW of Prieska, 29°49'11"S 22°31'42"E, 9–18.i.2006, M. Burger, D. Haarmeyer, and D. Massyn, 4 ♂, 1 ♀ (AMNH

[LP 5905]).

Blossia sabulosa Lawrence, 1972: **NAMIBIA:** *Lüderitz District*: Diamond Area: Namib-Naukluft Park: Garub Plains (SNAP; Site N26), 26°31'35.1"S 16°04'44.9"E, 910 m, 14.xii.2008–25.i.2009, T.L. Bird; L. Prendini; J. Huff, 1 ♂ (NMNW).

Blossia spinicornis Lawrence, 1928: **NAMIBIA: Khomas Region:** *Windhoek District*: Farm Brakwater 48, NARREC, 22°25'27.0"S 17°02'09.2"E, 1516 m, 20.ii–14.iv.2009, J.F. Kaudinge, B.K. Muramba, and T.L. Bird, 1 ♂ (NMNW).

Blossia tricolor Hewitt, 1914: **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park: Farm Stamprivier 108 Stamprivier 108 (SNAP; Site G29), 27°28'06.8"S 17°52'29.8"E, 888 m, 6.xi–15xii.2008, R. and D.R. Brand, 1 ♂ (NMNW).

Blossia cf. *purpurea* Wharton, 1981: **NAMIBIA: Erongo Region:** *Swakopmund District*: Namib-Naukluft Park: Ganab, 4.5 km S, 23°08'37.4"S 15°31'17.3"E, 1045 m, 20.i.2009, T.L. Bird, J. Huff, and L. Prendini, 1 ♂ (NMNW 13893).

Blossia cf. *rooica*: **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park: Farm Stamprivier 108 (SNAP; Site G29), 27°28'06.8"S 17°52'29.8"E, 888 m, 6.xi–15xii.2008, R. and D.R. Brand, 1 ♂ (NMNW).

Blossia sp.: **NAMIBIA: Karas Region:** *Lüderitz District*: Diamond Area: Namib-Naukluft Park: Garub (SNAP; Site S26), 26°31'35.1"S 16°04'44.9"E, 910 m, 14.xii.2008–20.i.2009, T.L. Bird; J. Huff; L. Prendini, 1 ♂ (NMNW).

GLUVIINAE ROEWER, 1933

Eberlanzia flava Roewer, 1941: **NAMIBIA: Erongo Region:** *Walvis Bay District*: Kuiseb Delta, 16.viii.1976, S. Louw, 9 ♂, 1 ♀, 1 juv (NMNW 11176).

Gluvia dorsalis (Latreille, 1817): **PORTUGAL: Évora:** Herdade da Mitra, 38°31.937'N 08°01.096'W, 12.vii.2006, S. Henriques, 1 ♂ (AMNH [LP 6093]).

GLUVIOPSINAE ROEWER, 1933

Gluviopsilla discolor (Kraepelin, 1899): **TURKEY:** Yeniyat, 37°42'25.4"N 44°00'34.1"E, 1535 m, 22.vi.2007, A.V. Gromov and H. Koç, 1 ♂ (AMNH [LP 7516]).

GNOSIPPINAE ROEWER, 1933

Gnosippus klunzingeri Karsch, 1880: **ISRAEL:** Arava Valley, 30°43.645'N 035°12.091'E, 17.vi.2009, T. Hacket, 1 ♂ (HUJI 770).

Hemiblossia australis (Purcell, 1902): **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park: Farm Holoog 106, 27°24'06.9"S 17°47'17.5"E, 793 m, 16.xii.2008, R. Brand, 1 ♂, 1 juv. (AMNH [LP 9866]).

Hemiblossia etosha Lawrence, 1927: **NAMIBIA: Otjozondjupa Region:** *Grootfontein District*: Farm Uisib 427, 19°32'54.1"S 17°14'06.8"E, 1343 m, 29.xii.2008–2.i.2009, T.L. and C. Bird and C. Schoeman, 1 ♂ (AMNH [LP 9854]), 1 ♂, 1juv. NMNW 13798).

Hemiblossia oneili Purcell, 1902: **NAMIBIA: Karas Region:** *Karasburg District*: Gondwana Cañon Park, Farm Karios 8 (SNAP; Site G31), 27°40'28.3"S 17°49'10.6"E, 896 m, 7.xi–12.xii.2008, R. and D.R. Brand, 1 ♂ (NMNW).

Hemiblossia sp.: **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park: Farm Holoogberg 107 (Middelpos, SNAP Site G30), 27°32'40.9"S 17°53'36.6"E, 965 m, , 6.xi–13xii.2008, R. and D.R. Brand,1 ♂ (NMNW); Farm

Stamprivier 108 (SNAP; Site G29), 27°28'06.8"S 17°52'29.8"E, 888 m, 6.xi–15xii.2008, R. and D.R. Brand, 1 ♂ (NMNW).

NAMIBESIINAE WHARTON. 1981

Namibesia pallida Lawrence, 1962: **NAMIBIA: Erongo Region**: *Omaruru District*: Brandberg, base of Ga-Aseb Gorge, 21°13'41.6"S 14°34'44.1"E, 781 m, 21.xii.2003, L. Prendini, T.L. Bird, and N. Krone, 1 ♂ (AMNH [LP 10721]). **SOUTH AFRICA: Northern Cape Province:** *Namaqualand District*: Farm Goodhouse 23, 1 km W of turnoff to Goodhouse, on Pella–Concordia road, 28°58.684'S 18°13.337'E, 450 m, 2–3.iii.2005, L. Prendini and E. Scott, 1 ♀ (AMNH [LP 4017]).

INCERTAE SEDIS

Ammotrechelis goetschi Roewer, 1934: **CHILE: Region IV (Coquimbo):** *Choapa Province*: Quereo, 19.viii.2009, J. Pizarro, 2 ♂, 1 ♀ (AMNH [LP 10673]).

Ceratobiton styloceros (Kraepelin, 1899): **ISRAEL:** Big Crater, 21.i.1962, 1 ♂ (HUJI 55).

EREMOBATIDAE KRAEPELIN, 1899

Eremobatidae (Pls. 65–84), restricted to North America, i.e., southeastern Canada, the U.S.A. west of the Missouri-Mississippi rivers (Maury, 1984), and Mexico, is the most speciose family of Solifugae in the New World (Harvey, 2003a). Muma (1951, 1989) recognized two subfamilies, based mainly on number of claws on tarsus I: Eremobatinae Kraepelin, 1901, comprising *Eremobates* Banks, 1900, *Eremocosta*

Roewer, 1934, *Eremorhax* Roewer, 1934, *Eremothera* Muma, 1951, *Horribates* Muma, 1962; and Therobatinae Muma, 1951, comprising *Chanbria* Muma, 1951, *Eremochelis* Roewer, 1934, synonymized with *Therobates* Muma, 1951 by Muma (1970a), and *Hemerotrecha* Banks, 1903. Muma (1989) provided a historical synopsis of the taxonomy of Eremobatidae post-Roewer (1934). This was supplemented by the annotated checklist of Brookhart and Brookhart (2006). Seventeen species have been described and five synonymized since Harvey's (2003a) catalogue (Brookhart and Cushing, 2002, 2004, 2005, 2008; Ballesteros and Francke, 2007), resulting in 186 species currently described. The presence of a dorsal terminal spiniform macroseta on tarsi II and III (Muma, 1976) may be a synapomorphy for the family. Both eremobatid subfamilies, 8 genera and 33 species were examined for the present study.

EREMOBATINAE KRAEPELIN, 1899

Eremobates actenidia Muma, 1989: **U.S.A.: Utah:** *Emery County*: 38.7256°N 110.4323°W, 1394 m, 8–9.vi.2013, P.E. Cushing, L. Petrie, R. Wicker, and J. Brainard, 6 ♂, 1 ♀ (DMNS ZA.33522).

Eremobates ajoanus Muma and Brookhart, 1988: **U.S.A.: Arizona:** *Pima County*: Ajo Road S of Ajo, 32.67°N 112.86°W, 335 m, 4.vi.1975, C. Moss, paratype ♀ (DMNS ZA.17311); Ajo, 10 mi. N, 32.34°N 112.85°W, 16.v.1972, C. Moss, paratype ♂ (DMNS ZA.17384); 31.942726°N 112.811093°W, 8.vi.2013, 2 ♂ (DMNS ZA.33218, ZA.33222); 31.941989°N 112.811877°W, 9.vi.2013, 1 ♂ (DMNS ZA.33219).

Eremobates angustus Muma, 1951: **U.S.A.: Arizona:** *Cochise County*: Huachuca Mountains, Ramsey Canyon, 31.450081°N 110.305752°W, 1494 m, 10 vii.1941, paratype ♂ (DMNS ZA.16789).

Eremobates ascopulatus Muma, 1951: **U.S.A.: Nevada:** *White Pine County*: Great Basin National Park, 39.01511°N 114.12556°W, 1631 m, 7–8.vi.2013, P.E. Cushing, 4 ♂, 1 ♀ (DMNS ZA.33524). Great Basin National Park, 39.01511°N 114.12556°W, 1631 m, 9.vii.2013, P.E. Cushing and P. Gorring, 5 ♂ (DMNS ZA.33529).

Eremobates bajadae Muma and Brookhart, 1988: **U.S.A.: New Mexico:** 10 mi. W of Carlsbad, 1.5 mi. N on Dark Canyon Road after second cattle guard, 32°17.082'N 104°18.000'W, 7–10.vi.2004, J. Huff and R. West, 1♂ (AMNH [LP 5740]).

Eremobates bixleri Muma and Brookhart, 1988: **U.S.A.: Arizona**: *Pima County*: Tucson, 32.22167°N 110.92583°W, 20.iv.1968, 896 m, D.E. Bixler, paratype ♂ (DMNS ZA.17386).

Eremobates chihuaensis Brookhart and Cushing, 2002: **MEXICO: Chihuahua:** Chihuahua, 22 mi. S, 4400 ft, 25 viii.1980, J.B. Karren, holotype ♂ (DMNS ZA.10002).

Eremobates corpink Brookhart and Cushing, 2004: **U.S.A.: Utah:** *Kane County*: Coral Pink sand dunes, 21.vii.1998, R.W. Baumann, holotype ♂ (DMNS ZA.17380); Coral Pink sand dunes, Ponderosa Grove campground, 37°05'N 112°40'W, 11.vi.2002, S.M. Clark, paratype ♀ (DMNS ZA.17379); Off Hwy 276, S of junction Hwy 95, 37.54738°N 110.04059°W, 1868 m, 28.v.2012, P.E. Cushing, L. Petrie, B. Trierweiler, and A. McMichael, 1 ♂ (DMNS ZA.33748).

Eremobates gerbae Brookhart and Cushing, 2002: **U.S.A.: Arizona:** *Pima County*: Mack Burn Area, 32.13194°N 110.51889°W, 30.viii.1994, P. Gerba, holotype ♂ (DMNS ZA.10000), 8.x.1995, P. Gerba, paratype ♀ (DMNS ZA.10001), 29.iii.1995, P. Gerba, 1 ♂, 1 ♀ (DMNS ZA.16189).

Eremobates icenoglei Brookhart and Cushing, 2004: **U.S.A.: California:** *Riverside County*: Winchester, 33°42'N 117°05'W, 22.viii.1968, W. Icenogle, holotype ♂ (DMNS ZA.17376), 29.viii.1996, W. Icenogle, paratype ♀ (DMNS ZA.17377).

Eremobates inkopaensis Brookhart and Cushing, 2005: **U.S.A.: California:** *Imperial County*: Meyer Gorge, Ko Pah Valley, 32.68°N 116.06°W, 570 m, 27.iii.1982, J. Berrian, paratype ♂ (DMNS ZA.17381), 32°43'N 116°02'W, 17.iv.1982, J. Berrian, paratype ♀ (DMNS ZA.17310).

Eremobates kiseri Muma and Brookhart 1988: **U.S.A,: Texas**: Turkey, 6 mi. SE, 6.v.1970, D. Kiser, paratype ♀ (DMNS ZA.17385), 1 ♀ (DMNS ZA.16791).

Eremobates norrisi Muma and Brookhart 1988: **U.S.A.: New Mexico:** *Hidalgo County*: Lordsburg, 32.345639°N 108.6957°W, 1306 m, 15.v.1975, M.H. Muma, paratype ♀ (DMNS ZA.17383).

Eremobates pallipes (Say, 1823): **U.S.A.: New Mexico:** *Socorro County*: Sevilleta National Wildlife Refuge, Long Term Ecological Survey Station, 34.350°N 106.883°W, 1471 m, 31.vii.1991, J.O. Brookhart, 1 ♂ (DMNS ZA.16258). **Utah:** *San Juan County*: 4 mi. S of Blanding, State Rt 210 and Hwy 191, 10.vi–26.viii.2000, J.O. and I.P. Brookhart, 1 ♀ (DMNS ZA.15662).

Eremobates palpisetulosus Fichter, 1941: **U.S.A.: Colorado:** *Denver County*, Denver, 135 S Taylor Ave, 17.vii.2003, B. Tiemann, 1 ♂ (DMNS ZA.15683). *Fremont County*: Phantom Canyon Road, 4.5 mi. from Hwy 50, 38.512°N 105.112°W, 1829 m, 10.v–10.vii.1999, J.O. and I.P. Brookhart, 1 ♀ (DMNS ZA.15686).

Eremobates polhemusi Muma and Brookhart, 1984: **U.S.A.: Utah:** *San Juan County*: 4 mi. N of Bluff, Hwy 191 and UT 240, 10.vi–26.viii.2000, J.O. and I.P.

Brookhart, 1 ♀ (DMNS ZA.10004).

Eremobates socal Brookhart and Cushing, 2004: **U.S.A.: California:** *San Bernardino County*: Joshua Tree National Park, 29 Palms, Park Headquarters, 34.128042°N 116.040437°W, 1070 m, 22.viii.1994, paratype ♀ (DMNS ZA.17378).

Eremobates tuberculatus (Kraepelin, 1899): **U.S.A.:** Mokelumne Hill, 1 ♂ (AMNH).

Eremobates cf. *palpisetulosus*: **U.S.A.:** 1 ♂ (AMNH).

Eremocosta gigasella (Muma, 1970): **U.S.A.: New Mexico:** *Socorro County*: Sevilleta Long Term Ecological Research Center, 34°21'10.8"N 106°52'55.2"W, 1478 m, 26.vii.1993, 1 ♀ (DMNS ZA.17350).

Eremocosta titania (Muma, 1951): **U.S.A.: California:** *Imperial County*: Ogilby Road, N of Hwy 8, 32°46.180'N 114°50.209'E, 74 m, D. Wood, DAW02-009, 1 ♂ (DMNS ZA.16319). *Inyo County*: Death Valley National Park, Saline Valley Dunes, just off Saline Valley Road, 36°45.188'N 117°51.795'W, 343 m, 4.ix.2005, L. Prendini and R. Mercurio, 1 ♂ (AMNH [LP 5035]). *San Bernardino County*: 29 Palms, 5 mi. NW Sunshine Peak, 34.700°N 116.479°W, 914 m, 17.v.2004, G. Pratt, C. Pierce, and Tilborg, 1 ♂ (DMNS ZA.16320).

Eremothera drachmani Muma, 1986: **U.S.A.: Arizona:** *Pima County*: Catalina State Park, campsite A and B, 32.42445°N 110.92271°W, 822 m, 28–29.vii.2011, P.E. Cushing, 1 ♂ (DMNS ZA.28156).

Eremothera sculpturata Muma, 1951: **U.S.A.: Arizona:** *Pima County*: 1.3 mi. S State 86 on road to Pisinimo, 32.099°N 112.296°W, 624 m, 1.ix.1965, T. Briggs, 1 ♀ (DMNS ZA.16477). *Yavapai County*: Congress, 9 mi. W, 34.113°N 112.976°W, 914 m, 30.vii–24.viii.1998, R.S. Beal, 1 ♂ (DMNS ZA.16475); 6 mi. from Wickenburg, 13.viii.1976, V. Roth, 1 ♂ (DMNS ZA.16476).

Horribates bantai Muma, 1989: **U.S.A.: California:** *San Bernardino County*: Granite Cove, 5 mi. N I-40 on Kelbaker Road, 34.78°N 115.65°W, 1341 m, 2.vii.1998, E. Fessler, 1 ♀ (DMNS ZA.17691).

THEROBATINAE MUMA, 1951

Chanbria regalis Muma, 1951: **U.S.A.: California:** *Imperial County*: Algodones Dunes, at junction of Olgiby Road (S34) and Interstate Hwy 8, 32°45.454'N 114°50.203'W, 50 m, 31.viii.2005, R. Mercurio and L. Prendini, 1 ♂, 3 ♀ (AMNH [LP 10746]).

Eremochelis acrilobatus (Muma, 1962): **U.S.A.:** 1 ♂ (DMNS ZA.16067).

Eremochelis albaventralis Brookhart and Cushing, 2005: **MEXICO:** Juchitipec, 7 km (air) WSW, 19.085887°N 98.946848°W, 2734 m, 24.vii.1987, J. Doyen, paratype ♂ (DMNS ZA.17382).

Eremochelis andreasana (Muma, 1962): **MEXICO: Baja California Sur:** San Ignacio, 27°18'04"N 112°53'11.1"W, 125 m, 17.vii.2004, O. Francke, W. Savary, E. González, and A. Valdez, 1 ♂ (AMNH [LP 3184]). **U.S.A.: California:** *Riverside County*: Andreas Canyon, 24.iv.1954, J.G. Rozen, holotype ♂ (AMNH).

Eremochelis bilobatus (Muma, 1951): **U.S.A.: Colorado:** *Douglas County*: Roxborough State Park, Willow Creek Trail, 1.25 mi. S of Visitor Center, 39.420°N 105.065°W, 1926 m, 18.vi.1999, B. Nelson, 1 ♂ (DMNS ZA.16039).

Eremochelis insignatus Roewer, 1934: **U.S.A.: California:** *San Bernardino*

County: Joshua Tree National Monument, 33.9476°N 116.1717°W, v.2000, USGS-San Diego, 1 ♂, 1 ♀ (DMNS ZA.16136). **California:** *Imperial County*: Hwy 78 at Junct. San Felipe Creek, 10.5 mi. W of Junct. Hwy 86, 33°07.538'N 116°02.660'W, 4.vi.2008, W. Icenogle, 5 ♂, 1 ♀ (DMNS ZA.25434).

Eremochelis oregonensis Brookhart and Cushing, 2002: **U.S.A.: Colorado:** 6 mi. N of Valley, Falls, Hwy 31, Lake City, 26.v.1999, Opler and Buckner, holotype ♂ (DMNS ZA.10008).

Eremorhax joshui (Brookhart and Muma, 1987): **U.S.A.: California:** *Kern County*: Dove Springs 2, 34.4237°N 118.0176°W, vi.2004, USGS-San Diego, 1 ♂ (DMNS ZA.16416). *San Bernardino County*: Marine Corps Air Ground, 34.2834°N 116.2998°W, vi.2000, USGS-San Diego, 1 ♀ (DMNS ZA.16415).

Hemerotrecha branchi Muma, 1951: **U.S.A.: California:** *San Bernardino County*: Wonder Valley, Amboy Road, 8.5 mi. E of 29 Palms, 34°09.942'N 115°54.203'W, 1600 m, 14.vii.2006, W. Icenogle, 2 ♂ (DMNS ZA.17234), 30–31.vii.2006, W. Icenogle, 1 ♂, 1 ♀ (DMNS ZA.16786).

Hemerotrecha cornuta Brookhart and Cushing, 2002: **U.S.A.: Colorado:** *Pueblo County*: Boone, 6 mi. NE, 38.310095°N 104.183558°W, 1504 m, 15.viii.1970, J.O. Brookhart, paratype ♀ (DMNS ZA.17367), 20.vi.1976, J.O. Brookhart, holotype ♂ (DMNS ZA.10005).

Hemerotrecha fruitanta Muma, 1951: **U.S.A.: Colorado:** *Arapahoe County*: Byers, 10 mi. SW, 39.61°N 104.36°W, 1722 m, 24.v.1974, J.O. Brookhart, 1 ♂ (DMNS ZA.17312), 1 ♀ (DMNS ZA.17313).

Hemerotrecha hanfordana Brookhart and Cushing, 2008: **U.S.A.: Washington:**

Franklin County: Hanford National Monument, Wahlike WL Area, White Bluff Ferry, 46°04.541"N 119°26.949"W, 21–28.vi.2002, R.S. Zack, holotype ♂ (DMNS ZA.21371), 6–12.vii.2002, R.S. Zack, paratype ♀ (DMNS ZA.19402).

Hemerotrecha marginata (Kraepelin, 1911): **U.S.A.: California:** San Pedro, vi.1907, syntypes, 2 ♂, 2 ♀ (ZMUH [R8376]).

Hemerotrecha prenticei Brookhart and Cushing, 2008: **U.S.A.: California:** *Riverside County*: Multispecies Reserve (Lake Skinner), 22.3806°N 117.0022°W, 9–12.v.2000, T. Prentrice, holotype ♂ (DMNS ZA.21376), 15–18.v.2000, T. Prentrice, paratype ♀ (DMNS ZA.21366).

Hemerotrecha sevilleta Brookhart and Cushing, 2002: **U.S.A.: New Mexico:** *Socorro County*: Sevilleta LTER Wild Fire Exp. Area, cell #11, 29.vi.1991, LTER staff, holotype ♂ (DMNS ZA.10006), paratype ♀ (DMNS ZA.10007).

Hemerotrecha vetteri Brookhart and Cushing, 2008: **U.S.A.: California:** *Santa Barbara County*: Vandenburg Air Force Base, 34.76°N 120.14°W, Abela, Pierce, and Pratt, holotype ♂ (DMNS ZA.21377).

GALEODIDAE SUNDEVALL, 1833

Galeodidae (Pls. 59-63, 64K, L) is currently the most speciose family of Solifugae, with largely a Palearctic distribution in north Africa, the Middle East, and central Asia, extending to the Indian subcontinent. No subfamilial divisions are recognized. Nine genera are recognized, with 173 of the 199 current galeodid species placed in *Galeodes* Olivier, 1791. Five galeodid genera, *Galeodumus* Roewer, 1960, *Gluviema* Caporiacco, 1937, *Paragaleodiscus* Birula, 1941, *Roeweriscus* Birula, 1937, and *Zombis* Simon, 1882, are monotypic. *Gluviema migiurtina* Caporiacco, 1937, described on the basis of a single female, was erroneously placed in Daesiidae, and Della Cave and Simonetta (1971) speculated it should be transferred to *Galeodellus* Roewer, 1934, formerly a subgenus of *Galeodes*. The validity of *Paragaleodiscus aflagellatus* Birula, 1941, described on the basis of 7 males, 18 females and 10 juveniles, and the only galeodid apparently lacking a flagellum in the adult male, requires further investigation. Turk (1960) did not recognize *Roeweriscus* as the diagnostic characters are not unique. *Zombis* is probably a senior synonym of *Paragaleodes* Kraepelin, 1899 (Harvey, 2002a), which contains 12 diurnal species, and is the most speciose galeodid genus after *Galeodes*. The remaining genera, *Galeodopsis* Birula, 1903 and *Othoes* Hirst, 1911, comprise five and four species, respectively. Galeodidae are probably monophyletic. Potential synapomorphies include the presence of setae on the basal claw segment, a comb-like structure protecting the abdominal spiracles, and a leaf-shaped, paraxially and partly diaxially (Muma, 1976) rotatable flagellum. However, few morphological characters have been identified on which to base a natural generic division within Galeodidae (Turk, 1960) and species delimitation is hampered by the relative uniformity of the male flagellum. Two genera and eight species were examined for the present study.

Galeodes arabs C.L. Koch, 1842: **UNITED ARAB EMIRATES:** Dubai Desert Conservation Reserve, 24°49'27.5"N 55°39'40.7"E, 17.vi.2003, P. Roosenschoon, 1 ♂ (AMNH [LP 9123]).

Galeodes araneoides (Pallas, 1772): **TURKEY:** Gurgen, 39°53'59.2"N 44°18'12.3"E, 889m, 15.vi.2007, A.V. Gromov and H. Koç, 1 ♂, 1 ♀ (AMNH).

Galeodes olivieri Simon, 1879: **SENEGAL:** Ndioum, 16°30'48.2"N 14°39'50.5"W, 7 m, 6.vii.2005, J. Huff and V. Vignoli, 1 ♂ (AMNH [LP 4630]); Ourosogui, 24 km N, 15°48'24.6"N 13°26'43.2"W, 41 m, 5.vii.2005, J. Huff and V. Vignoli, 1 ♀ (AMNH [LP 4628]).

Galeodes toelgi Werner, 1922: **TURKEY:** Ortaoba, 36°25'41.3"N 36°14'14.5"E, 200 m, 31.v.2007, A.V. Gromov, 1 ♂ (AMNH [LP 7536]).

Galeodes sp.: **ISRAEL:** *Southern District*: Ashdod Nitzanim Nature Reserve, near Nitzan, 31°44'09.0"N 34°37'11.4"E, 17 m, 29.viii.2011, L. Prendini and T.L. Bird, 2 ♂ (AMNH [LP 11204]). **NIGER:** Birni N'kare, 120 km W, savannah, R. Brinckerhoff, 1 ♀ (MCZ).

Paragaleodes nesterovi Birula, 1916: **TURKEY:** Sinidagi Mt., 37°26'48.6"N 42°39'55.1"E, 26.vi.2007, A.V. Gromov and H. Koç, 1 ♂ (AMNH [LP 7480]).

Paragaleodes pallidus (Birula, 1890): **KAZAKHSTAN: South Kazakhstan Area:** *Otrar District*: Akkum, ca. 2–3 km W, 42°22'53"N 68°10'25"E, 202 m, 21.vi.2003, L. Prendini and A.V. Gromov, 1 ♂ (AMNH [LP 3922]).

Paragaleodes sp.: **ISRAEL:** Sede Boqer, viii.2009, Y. Lubin, 1 ♀ (AMNH [LP 10550]).

GYLIPPIDAE ROEWER, 1933

As currently defined, Gylippidae comprises two diverse groups of taxa with a disjunct distribution. Wharton (1981) placed the Middle Eastern/Asian genera, *Acanthogylippus* Birula, 1913 and G*ylippus* Simon, 1879, in subfamily Gylippinae Roewer, 1933 and the southern African genera, *Lipophaga* Purcell, 1903, *Trichotoma*

Lawrence, 1968, and the monotypic *Bdellophaga* Wharton, 1981, in Lipophaginae Wharton, 1981. The subfamilial classification of Wharton (1981) was not mentioned by Harvey (2003a) but is reflected in Harvey (2013). Gylippinae and Lipophaginae share prominent features such as the number of leg tarsal segments, the claw on leg I, and the separation of the lateral propeltidial lobe from the propeltidium (Wharton, 1981) as well as more subtle features such as similar stridulatory setae and the number and placement of eyespots (unpublished data). However, they differ considerably, especially in the nature of the flagellar complex and the presence of prominent spiniform setae in Gylippinae. Due to the morphological disparity between Gylippinae and Lipophaginae, they are treated separately in the study presented here.

GYLIPPINAE ROEWER, 1933

Gylippinae (Pls. 85A–F, 86, 90A, B) comprises only 19 described species, restricted to the Middle East and central Asia. Birula (1913) divided *Gylippus* into four subgenera, *Gylippus*, *Acanthogylippus*, *Anoplogylippus* Birula, 1913 and *Hemigylippus* Birula, 1913, based mainly on the dental papillae and the presence and number of dorsomedial spiniform setae, i.e., the flagellar complex spiniform setae (*fcs*) and the robust retrolateral spiniform seta or retrolateral manus spiniform seta (*rlms*). These taxa alternated between genera and subgenera. Roewer (1934: 310) elevated Birula's (1913) subgenera to genera and added a fifth genus, *Paragylippus* Roewer, 1933. Birula (1938) again treated these taxa, including *Paragylippus*, as subgenera whereas Roewer (1960) treated the taxa occurring in Afghanistan, i.e., *Gylippus*, *Paragylippus* and *Anoplogylippus*, as genera. Gromov and Kopdykbaev (1994) again treated the taxa occurring in Kazakhstan, i.e., *Anoplogylippus* and *Hemigylippus*, as subgenera. As a consequence, two genera are currently recognized, *Acanthogylippus* and *Gylippus*, the latter comprising four subgenera, i.e., *Gylippus* (*Gylippus*), *G.* (*Anoplogylippus*), *G.* (*Hemigylippus*), and *G.* (*Paragylippus*). Two species in different subgenera of *Gylippus* were examined for the present study.

Gylippus (*Anoplogylippus*) *ferganensis* Birula, 1893: **UZBEKISTAN: Jizzax Area:** *Farish District*: Nuratau Nature Reserve: Nuratau Mountains, N slopes, ca. 1 km NW of Khayat village, 40°31'42"N 66°46'28"E, 978 m, 6–7.vi2003, A.V. Gromov, 1 juv. (AMNH [LP 3921]).

Gylippus (*Paragylippus*) *monoceros* Werner, 1905: **TURKEY: Isparta Province:** between Karamik and Sağir, 38°26.307'N 30°50.864'E, 1643 m, 13.v.2004, H. Koç, 1 ♂ (AMNH [LP 5437]). **Kayseri Province:** Lifos Mount, 38°35'22,8"N 35°27'59,4"E, 2100 m, 24.v.2013, M. Erdek, 1 ♀ (KU).

LIPOPHAGINAE WHARTON, 1981

Lipophaginae (Pls. 85G, H, 87–89, 90C–F) comprises seven described species, restricted to southern Africa. No male flagellum, defined as a single modified primary or secondary flagellar seta, is present, but a cluster of similarly modified setae, including the ventral flagellar seta (vfs) on the fixed finger, forms a setiform flagellar complex (type B). The extent to which these setae are differentiated from the surrounding setae varies from very weak, e.g., in *Trichotoma michaelseni*, to strong, e.g., in *Bdellophaga angulata* Wharton, 1981. All three genera and five species were examined for the present study.

Bdellophaga angulata Wharton, 1981: **NAMIBIA: Khomas Region:** *Windhoek District*: Farm Gocheganas 26, 22°50'S 17°11'E, 1–20.vi.1981, S. Louw and M.-L. Penrith, 53 ♂ (NMNW 11601), 20–22.vi.1982, M.-L. Penrith,18 ♂, 1 ♀ (NMNW 12240).

Lipophaga trispinosa Purcell, 1903: **SOUTH AFRICA: Western Cape Province:** *Prince Albert District*: Tierberg, old lands, 10.v.1990, West Cape Survey, W.R. Dean, 1 ♂ (NMNW 12503).

Trichotoma brunnea Lawrence, 1968: **NAMIBIA: Erongo Region:** *Swakopmund District*: Swakopmund, 30.v.2009, E. and B. Roxin, 1 ♀ (LP 9870).

Trichotoma michaelseni (Kraepelin, 1914): **NAMIBIA: Erongo Region:** *Swakopmund District*: Namib-Naukluft Park: Gobabeb, ca. 600 m N, 23°33'06"S 15°02'50"E, 395 m, 27.iii.2006, L. Prendini, T. Bird, and S.K. Uunona, 1 ♂ (AMNH [LP 5724]). **Karas Region:** *Lüderitz District*: Diamond Area: Sperrgebiet National Park: Scorpion Mine site, 27°49'S 16°35'E, 28.vii.1997, E. Griffin, 10 ♂, 1 ♀ (NMNW 12757); South of Bogenfels Arch, 27°27'36.2"S 15°23'38.6"E, 9 m, 14–16.vi.2008, C.M. Kaapehi and B. Muramba, 1 ♂ (NMNW).

HEXISOPODIDAE POCOCK, 1897

Hexisopodidae (Pls. 126–131) is a small, psammophilous family endemic to southern Africa, comprising 23 described species (Harvey, 2003a). The small number of species is almost probably an artifact of their cryptic, fossorial habits. The family is defined by a number of unique characters probably related to burrowing (Wharton, 1981). The two genera currently recognized, *Chelypus* Purcell, 1902 and *Hexisopus* Karsch, 1879, are separated by various characters, including the presence of spiniform setae on the pedipalp (Lamoral, 1973) and cheliceral characters described in the present study. Both genera and nine species were examined for the study.

Chelypus hirsti Hewitt, 1915: **NAMIBIA: Hardap Region:** *Rehoboth District*: Farm Willies Rest 391, 10.vi.1966, C. van der Hoven, 2 ♂ (NMNW 10804). **Karas Region:** *Keetmanshoop District*: Farm Wildheim Ost 384, 1–30.iv.1977, S. Louw and M-L. Penrith (NMNW 11202).

Chelypus shortridgei Hewitt, 1931: **NAMIBIA: Karas Region:** *Lüderitz District*: Diamond Area: Sperrgebiet National Park: Obib Dunes, 27°53'S 16°32'E, 19.xi.1992, Huns Expedition, 1 ♂ (NMNW 12632).

Chelypus sp.: **NAMIBIA: Hardap Region:** *Mariental District*: Chulon, on Narib Ost 602, Gibeon, Penrith, M.J. and M.-L. Penrith, 16.v.1980, 1 ♂ (NMNW 11329). **Karas Region:** *Keetmanshoop District*: Tses, 25°55'12.5"S 18°10'54.5"E, R. Poller, F. van Deventer, J. Irish, and E. Marais, 4–7.iv.2003, 1 ♂ (NMNW 13475).

Hexisopus aureopilosus Lawrence, 1968: **NAMIBIA: Erongo Region:** *Karibib District*: Farm Emeritus 123, 1.vi.1967, Capt. Peterson, 1 ♀ (NMNW 11203).

Hexisopus lanatus (C.L. Koch, 1942): **NAMIBIA: Karas Region:** *Karasburg District*: Goodhouse, Warmbad, 14.xi.1963, L. Blom, 2 ♂ (NMNW 10795).

Hexisopus moiseli Lamoral, 1972*:* **NAMIBIA: Erongo Region:** *Karibib District*: Farm Emeritus 123, 9.vi. 1967, Capt. Peterson, 1♂ (NMNW 10918).

Hexisopus psammophilus Wharton, 1981: **NAMIBIA: Erongo Region:** *Swakopmund District*: Namib-Naukluft Park: Gobabeb, 23°34'40.5"S 15°02'33.3"E, 412 m, 28–29.vii.2008, R.A. Wharton and T.L. Bird, 1 ♂ (AMNH [LP 9858]).

Hexisopus pusillus Lawrence, 1962: **NAMIBIA: Erongo Region:** *Swakopmund*

District: Namib-Naukluft Park: Gobabeb, 2–14.v.1979, R.A. Wharton (NMNW 11426).

Hexisopus sp.: **NAMIBIA: Khomas Region:** *Windhoek District*: Farm Solitaire 412, 9.v.1975, E. Griffin, 1 juv. (NMNW 11098).

KARSCHIIDAE KRAEPELIN, 1899

Karschiidae (Pls. 50–55, 64A–F) is a small family comprising four genera and 45 species with a Palaearctic distribution in north Africa, the Middle East, and central Asia. *Barrus* Simon, 1880, *Barrussus* Roewer, 1928, and *Eusimonia* Kraepelin, 1899 are similar in dentition and flagellar morphology, and distinctly different from *Karschia* Walter, 1889 (Pls. 1, 2). *Karschia* is divided into two subgenera, *Karschia* and *Rhinokarschia* Birula, 1935. Two species of *Eusimonia* (Gromov, 2003a), four species of *Karschia* (Gromov, 2003a), and one species of *Barrussus* (Karataş and Uçak, 2013) have been described since Harvey's (2003a) catalogue. Three genera and six species were examined for the present study.

Barrussus pentheri (Werner, 1905): **TURKEY: Kayseri Province:** Hisarcik, 38°36'44.7"N 35°31'09.5"E, 1739 m, 6–7.vii.2007, A.V. Gromov and E.A. Yağmur, 1 juv. (AMNH [LP 10693]).

Eusimonia divina Birula, 1935: **UZBEKISTAN: Navoiy Area:** *Tamdy District*: Kyzylkum Desert, foothills of Tamdytau Mountain Range, 2.5 km NW of Zarafshan, 41°35'47"N 64°11'05"E, 366 m, 3.vi.2003, L. Prendini and A.V. Gromov, 3 ♂, 7 ♀, 1 juv. (AMNH [LP 4098]).

Eusimonia nigrescens Kraepelin, 1899: **TURKEY: Mardin Province:** Yolbaşi, 37°16'00.8"N 40°48'00.0"E, 663 m, 26.v.2007, A.V. Gromov and H. Koç, 1 ♂ (AMNH [LP

7473]).

Eusimonia turkestana Kraepelin, 1899: **UZBEKISTAN: Fergana Area:** *Beshariq District*: Kairakkum sands/hills, 13 km WNW of Beshariq (Kirovo), 40°28.684'N 70°27.448'E, 365 m, 14.v.2003, L. Prendini and A.V. Gromov, 1 ♀ (AMNH [LP 4097]). **Khorezm Area:** *Hazorasp District*: Kyzylkum Desert, Uchizhak Hills, ca. 19 km N of Turpakkala, ca. 10 km E of Lebap [Turkmenistan], 41°01.673'N 62°00.361'E, 227 m, 31.v.2003, L. Prendini and A.V. Gromov, 1 ♂ (AMNH [LP 4096]).

Karschia (*Karschia*) *mastigofera* Birula, 1890: **TURKEY: Iğdir Province:** Yenidoğan, 39°47'12.3"N 44°23'36.9"E, 1563 m, 16.v–17.vi.2007, A.V. Gromov and H. Koç, 1 ♂ (AMNH [LP 7474]). **Van Province:** Muradiye, 38°59'26.2"N 43°44'33.9"E, 1680 m, 19–20.vi.2007, A.V. Gromov and H. Koç, 2 ♀ (AMNH [LP 7476]).

Karschia (*Karschia*) *tibetana* Hirst, 1907: **TIBET:** *Lang County*: 22.vi.2004, Y. Ba and A. Shi, 1 ♂ (AMNH [LP 7719]).

MELANOBLOSSIIDAE ROEWER, 1933

Melanoblossiidae is a small family restricted to southern Africa, with the exception of the monotypic *Dinorhax* Simon, 1879. The inclusion of *Dinorhax* in Melanoblossiidae probably renders this family polyphyletic.

DINORHAXINAE ROEWER, 1933

The monotypic subfamily Dinorhaxinae (Pls. 56A, B, 57A, B) contains the enigmatic *Dinorhax rostrumpsittaci* (Simon, 1877), the only solifuge species occurring in South-East Asia (Indonesia and Vietnam). This species was initially placed within

Rhagodidae Pocock, 1897, in the genus *Rhax* Hermann, 1804, which was suppressed in favor of *Rhagodes* Pocock, 1897 (ICZN, 2005 by Roewer (1934: 340), a position that is unlikely to be upheld by phylogenetic analysis. The monotypic genus, *Dinorhax*, was examined for the present study.

Dinorhax rostrumpsittaci (Simon, 1877): Cauda Nhatray, 28.x.1931, Ilawydoff; **VIETNAM: Ba Ria-Vung Tau Province:** Binh Chau-Phuoc Buu Nature Reserve, 10°32'N 107°29'E, ca. 50 m, vi.2007, A.V. Abramov (expedition of Russia-Vietnam Tropical Centre), 1 ♂ (AMNH [LP 7537]).

MELANOBLOSSIINAE ROEWER, 1933

Melanoblossiinae (Pls. 154–159) currently contains 15 species restricted to southern Africa. All species appear to be diurnal. Melanoblossiids tend to be small in body size, and include the smallest Solifugae described to date, i.e., *Lawrencega minuta* Wharton, 1981, with adult males measuring 5–8 mm. Adult males are unknown in two of the five genera, i.e., *Daesiella* Hewitt, 1934, and *Unguiblossia* Roewer, 1941. A third genus, *Microblossia* Roewer, 1941, is characterized in part by an unmodified flagellar setal complex (Roewer, 1941) comprising three plumose setae at the apex, resembling the flagellar setal complex of Lipophaginae. Three species of *Lawrencega* Roewer, 1933 and three species of *Melanoblossia* Purcell, 1903, the most speciose melanoblossiid genera, known from both sexes, were examined in the present study.

Lawrencega minuta Wharton 1981: **NAMIBIA: Erongo Region:** *Swakopmund District*: Namib-Naukluft Park: Gobabeb dunes, 24.ix.1979, R.A. Wharton, 3 ♂, 1 ♀ (CAS 9033898).

Lawrencega procera Wharton, 1981: **NAMIBIA: Kunene Region:** *Khorixas District*: Farm Losberg 449, 6.7 km N intersection with D2612 on C35, 20°39'12.6"S 14°51'05.1"E, 888 m, 18.i.2009, T.L. Bird, J. Huff and L. Prendini, 1 ♂ (AMNH [LP 9863]).

Lawrencega tripilosa Lawrence, 1968: **SOUTH AFRICA: Northern Cape Province**: *Namaqualand District*: Richtersveld, Amnisfontein, opposite Cornellskop, 23.xi.1975, 1 ♂ (NMNW 11118).

Melanoblossia braunsi Purcell, 1903: **SOUTH AFRICA: Western Cape Province:** *Beaufort West District*: Farm Vaalkuil, Area 1, Site 4, 32.8139°S 22.7818°E, 3–6.xii.2007, D.H. Jacobs, 4 ♂, 1 ♀ (AMNH [LP 10737]).

Melanoblossia cf. *braunsi*: **SOUTH AFRICA: Northern Cape Province:** *Calvinia District*: Farm Springbokpan (Springboktand), N of Loeriesfontein, 30°23'23"S 19°24'09"E, 5–12.x.2006, M. Burger, D. Massyn and J. Sakwa, 1 ♂ (AMNH [LP 8550]).

Melanoblossia sp. n.: **NAMIBIA: Karas Region:** *Lüderitz District*: Diamond Area: Sperrgebiet National Park: Tsaukhaib Mountain, old transport route, 26°42'58.0"S 15°40'12.6"E, 906 m, 24–30.viii.2006, EduVentures 9 Expedition, 5 ♂ (AMNH [LP 9857]; NMNW 13396).

MUMMUCIIDAE ROEWER, 1934

Mummuciidae (Pls. 149E–H, 150–152, 153I, J) is restricted to South America and comprises 22 species. The family was initially created as a subfamily of Ammotrechidae (Roewer, 1934: 582) but later elevated to family rank (Maury, 1984: 74) on the basis of the following characters: a vesicular flagellum with an anterior opening ("*una vesicula* *ovoide, con una pequeña abertura anterior*"), the absence of pairs of spiniform setae on the pedipalps; and the absence of a movable finger prolateral tooth ("*diente basal interno*"). Three *Mummucia* Simon, 1879 species (Martins et al., 2004; Rocha and Carvalho, 2006; Carvalho et al., 2010) and one *Mummucina* Roewer 1934 species (González Reyes and Corronca, 2013) have been described since Harvey's (2003a) catalogue. The transfer of *Mummuciona* (in Maury 1976, 1982) and *Sedna* (in Maury, 1987) to Ammotrechidae reduced the ten genera reported by Harvey (2003a) to eight genera in Mummuciidae. *Cordobulgida* Mello-Leitão, 1938, *Gaucha* Mello-Leitão, 1924, *Gauchella* Mello-Leitão, 1937, *Metacleobis* Roewer, 1934, *Mummucipes* Roewer, 1934, and *Uspallata* Mello-Leitão, 1938 are monotypic. Most species in the family are placed in the two remaining genera, *Mummucia* (comprising eight species) and *Mummucina* Roewer, 1934 (comprising six species) but mummuciid genera are poorly defined (Maury, 1998) and recent authors followed a conservative approach, placing new species within the type genus, *Mummucia* pending are generic revision of the family (Xavier and Rocha, 2001; Martins et al. 2004; Rocha and Carvalho, 2006). Two genera and species were examined during the present study.

Gaucha fasciata Mello-Leitao, 1924: **URUGUAY: Rivera Department:** Route 30, km 233, ca. 100 km SE of Artigas, 31°08'25.692"S 55°55'11.280"W, 345 m, 13.xii.2005, C. Mattoni, A. Ojanguren, and F. Labarque, 1 ♂ (AMNH [LP 5858]), 1 ♀ (AMNH [LP 10699]).

Uspallata pulchra Mello-Leitao, 1938: **CHILE: Region IV (Coquimbo):** *Elqui Province*: Mangueras, Mina el Indio, ca. 4200 m, 7.xi.2003, L. Prendini, C. Mattoni, and J. Ochoa, 28 ♂ (AMNH [LP 2403]).

RHAGODIDAE POCOCK, 1897

Members of the Rhagodidae (Pls. 56CH, 57, 58, 64I, J), broadly distributed across north Africa, the Middle East, Asia, and the Indian subcontinent, and characterized by a cylindrical abdomen, short, robust legs, and robust chelicerae, were recognized as a distinct group early on (Pocock, 1897). Thirteen of the 27 current rhagodid genera are monotypic, often based on females and juveniles (Roewer, 1934; Harvey, 2003a). Cheliceral structure and dentition are very similar among rhagodid species, often even between the sexes (Pls. 3C-H; 50-51). There is no apparent interspecific variation in the male flagellum. Few characters exist to diagnose species and the taxonomy of Roewer (1934: 264–288) is uninformative for species identification (Lawrence, 1956; Levy and Shulov, 1964). Lawrence (1956: 120) noted that many specimens key to different genera, depending on whether a left or right appendage is examined during the identification process. Identifying genera is thus often impossible for Rhagodidae (e.g., Levy and Shulov, 1964). As with Galeodidae, the other morphologically uniform family of Solifugae, rhagodid taxonomy relies heavily on color patterns (Roewer, 1934) which appear to be "remarkably constant for most of the Galeodidae and Rhagodidae" (Turk, 1960: 107). Two genera and three species were examined during the present study.

Rhagoderma tricolor Roewer, 1941: **TURKEY:** Yedi Tepe M. Sehir ici Sahinbey, G. Antep, 1.vii.2005, E.A. Yağmur, 1 ♂ (AMNH [LP 5435]).

Rhagodes melanus (Olivier, 1807): **EGYPT:** vii.2003, 1 ♂ (AMNH [LP 2293]). **ISRAEL:** Agur sand dunes, near Egyptian border, viii.2009, B. Shacham, 1 ♀ (AMNH

[LP 10549]), 5 ♂, 1 ♀ (NMNW).

Rhagodes sp.: **KENYA:** Kenya, Kalabata River where Lokori–Lodwan road crosses SE of Loperot, Turkana, 30.vi–26.vii.1965, B. Patterson Expedition, 1 ♂ (MCZ 126321).

SOLPUGIDAE LEACH, 1815

Solpugidae (Pls. 90G–L, 97–125) is a speciose family, occurring throughout Africa and the Middle East, easily identified by the six- to seven segmented tarsus of leg IV (all other families possess one to four true segments) and a unique flagellar configuration consisting of a bulbous base fixed immovably to the fixed finger, and a chitinous, usually whip-like shaft. Solpugidae is divided into two subfamilies, Ferrandiinae Roewer, 1933, containing a single genus, *Ferrandia* Roewer, 1933, and Solpuginae Leach, 1897, containing the other 16 genera, based on the number of leg IV tarsal segments (six and seven, respectively). Some of the characters presented by Roewer (1934: 420–421), e.g. shape of the deuterosternum, and presence of scopula and spiniform setae on the pedipalpal metatarsus, appear to identify broad groups that may prove to be natural (Turk, 1960; Wharton, 1981). However, the overt reliance on variable characters, particularly spiniform setae on the legs, resulted in most of the 17 currently recognized genera (Harvey, 2003a) being poorly defined. This is especially true for the large genus *Zeria* Simon, 1879, comprising 59 species. Other genera, e.g., *Zeriassa* Pocock, 1897, the fourth largest genus of Solpugidae, comprising 17 species, appear to be better defined. *Zeriassa* is one of the most distinct genera in the family, supported by a suite of characters including the shape of the deuterosternum, the propeltidium, and the epistosomal-labral plate of the rostrum, etc. These characters are, however, shared with the monotypic *Solpugisticella* Turk, 1960. Several authors (Lawrence, 1955; Turk, 1960; Simonetta and Della Cave, 1968) have identified Solpugidae as one of the families in most urgent need of revision. A synopsis of Solpugidae taxonomy was provided by Wharton (1981). Both subfamilies, 16 genera and 42 species were examined during the present study.

FERRANDIINAE ROEWER, 1933

Ferrandia robusta Lawrence, 1954: **SOMALIA:** Burao, P.E. Glovere, 1 ♀ (MCZ 126329).

SOLPUGINAE LEACH, 1815

Metasolpuga picta (Kraepelin, 1899): **NAMIBIA: Erongo Region:** *Swakopmund District*: Namib-Naukluft Park: Gobabeb plains, 16.xi.1979, V. Gray, 1 subad. ♂ (AMNH); Gobabeb, 23°34'40.5"S 15°02'33.3"E, 412 m, 28–29.vii.2008, R.A. Wharton and T.L. Bird, 1 ♂ (AMNH [LP 10719]).

Oparba asiatica (Turk, 1948): **EGYPT:** Qassassin, vi.1942, Buxton, holotype ♂ (HUJI); Sheikh el Karai, Sinai, 8.iv.1968, 1 ♂ (HUJI 360). **ISRAEL:** Ezuz, 22.iv.2012, A. Novikova, 1 ♂ (HUJI 684); Negev, Retanim, 2.vii.2012, S. Aharon, 1 ♂ (TAUZM 50313).

Oparbella flavescens (C.L. Koch, 1842): **TUNISIA:** Tunis, Central-gebirge, N. Banks, 1 ♂, 1 ♀ (MCZ 102912).

Oparbella sp.: **MOROCCO:** Tata, 14.ii.2007, R. Bosmans, 1 ♂ (MRAC 230.211).

Prosolpuga schultzei (Kraepelin, 1908): **NAMIBIA: Erongo Region:**

Swakopmund District: Namib-Naukluft Park: Homeb, 23°38.785'S 15°11.424'E, 409 m, 30.xii.2003, L. Prendini and E. Scott, 1 ♀, 1 juv. (AMNH [LP 3605]). **Karas Region:** *Lüderitz District*: Diamond Area: Sperrgebiet National Park: E of Oranjemund, 8–11.xi.1986, E. Griffin, 3 ♂ (NMNW 13759).

Solpuga chelicornis Lichtenstein, 1796: **SOUTH AFRICA: Northern Cape Province:** *Britstown District*: Farm Kareebosch Poort, 0.9 km SE railway intersection with N10 (Prieska–Britstown) on gravel road (Voëlgeraas–Broken Dam), 30°26.831'S 23°21.883'E, 1066 m, 30.xii.2007, L. Prendini and M. Cooper, 1 ♂ (AMNH [LP 8158]).

Solpuga c. carlkochi Harvey, 2002: **SOUTH AFRICA: Western Cape Province:** *Beaufort West District*: Farm Vaalkuil, Area 1, Site 4, 32.8139°S 22.7818°E, 3–6.xii.2007, D.H. Jacobs, 1 ♂ (AMNH [LP 10285]), 1 ♀ (NCA 2008/3524).

Solpuga massaica Roewer, 1941: Massai Steppe, East Africa, 1 ♂, 1 subad. ♂ syntypes (SMF 9907391 [RII/7391/450]).

Solpuga roeweri Fage, 1936: **KENYA:** Loperot, viii.1964, B. Patterson, 1 ♂, 1 juv. (MCZ 126317).

Solpugassa furcifera (Kraepelin, 1899): **NAMIBIA: Kunene Region:** *Opuwo District*: Kaokoveld, Ohopoho [Opuwo], viii.1956, C. Koch, holotype ♂ [*Solpugassa kochi* Lawrence, 1959] (TM 8843); Puros, 5 km N, on E side of Hoarusib riverbed, at W edge of Etendeka Mountains, 18°43.461'S 12°56.879'E, 320 m, 19.i.2004, L. Prendini, E. Scott, T. and C. Bird, Q. and N. Martins, 3 ♂, 2 ♀ (AMNH [LP 3632]).

Solpugella asiatica Roewer 1933: **ISRAEL: Gaza:** vi.1942, 1 ♀ (HUJI).

Solpugella sp.: **ANGOLA: Cunene Province:** Cahama, 15 km E of Cunene River, 4–6.xii.1974, M.-L. Penrith, 1 ♂ (NMNW 11097).

Solpugema brachyceras (Lawrence, 1931): **SOUTH AFRICA: Western Cape Province:** *Paarl District*: Mont Rochelle Nature Reserve, Perdekop trail, Franschhoek, 33°54.102'S 19°09.531'E, 5.xi.2000, L. Prendini, E. Scott, R. and K. Lynch, 1 ♂ (AMNH [LP 1960B]).

Solpugema derbiana (Pocock, 1895): **SOUTH AFRICA: Northern Cape Province:** *Hay District*: Farm Boseekoebaard, SE of Groblershoop, 29°02'00"S 22°17'19"E, 4–13.xii.2005, M. Burger, H. Janse van Vuuren, C. Lyons, and S. Ward, 1 ♂ (AMNH [LP 7709]).

Solpugema genucornis (Lawrence, 1935): **NAMIBIA: Karas Region:** *Keetmanshoop District*: Gondwana Cañon Park: Farm Holoog 106 (Holoog boma site), 27.41098°S 17.96102°E, 809 m, 29.i.2009, R. and D.R. Brand, 1 ♀ (AMNH [LP 10292]). **SOUTH AFRICA: Northern Cape Province:** *Namaqualand District*: Farm Gemsbokvlei 571, 7.8 km N turnoff from R382 (Port Nolloth–Steinkopf) on road to Lekkersing, 29°15.16'S 17°06.377'E, 181 m, 3.i.2008, L. Prendini and M. Cooper, 1 ♂ (AMNH [LP 8167]).

Solpugema hamata (Hewitt, 1914): **SOUTH AFRICA: Mpumalanga Province:** *Barberton District*: Barberton, xii.1922, G.P.F. van Dam, 1 ♂ (TM 6632 old 856).

Solpugema hostilis (White, 1846): 1 ♂ (SMF [R3117]), 1 ♂ (NCA 2009/2817).

Solpugema intermedia (Lawrence, 1929): **SOUTH AFRICA: Western Cape Province:** *Laingsburg District*: Anysberg Nature Reserve, 33°28.759'S 20°34.610'E, 9–13.xii.2008, R. Lyle, D. du Plessis, H. van As, V. Butler, and J. Terblanche, 1 ♂ (NCA 2009/4482), 1 ♂ (AMNH [LP 10249]).

Solpugema montana (Lawrence, 1929): **SOUTH AFRICA: Western Cape**

Province: *Worcester District*: Matroosberg Mountains, syntype ♂ (SMF 9902904 [RII/2904/32]).

Solpugema phylloceras (Lawrence, 1929): **SOUTH AFRICA: Northern Cape Province:** *Heidelberg District*: Grootvadersbosch, ix.1940, V. Fitzsimons, 1 ♂ (TM 8606).

Solpugema tubicen (Kraepelin, 1911): **SOUTH AFRICA:** 1 ♂ (TM 2643 old 769); Transvaal, 1910, 1 ♂, 2 ♀ syntypes (ZMUH [R9503]).

Solpugema sp.: 1 ♂ (NCA 97/821).

Solpugiba lineata (C.L. Koch, 1842): **NAMIBIA: Hardap Region:** *Maltahöhe District*: Namib Rand Nature Reserve: Farm: Aandster 147, 25°22'04.14"S 16°04'56.04"E, 2.i.2000, E. Griffin, 2 ♂(NMNW 13814). **SOUTH AFRICA: Northern Cape Province:** *Hay District*: Farm Koedoesnek, E of Langberge, NEE of Groblershoop, 28°46'27"S 22°31'01"E, 14–22.xii.2005, M. Burger, D. du Toit, and R. James, 2 ♂, 1 ♀, 2 juv (AMNH [LP 5919]).

Solpugista hastata (Kraepelin, 1899): **NAMIBIA:** Groß Namaqualand, holotype, chelicera only, ♂ (SMF [R6918]).

Solpugista bicolor (Lawrence, 1953): **NAMIBIA: Erongo Region:** *Swakopmund/Karibib Districts*: Swakopmund–Usakos, 14.ix.2007, J. Visser, 1 ♂ (AMNH [LP 7933]). *Swakopmund District*: Namib-Naukluft Park: Gorob mine, 23°34'11.6"S 15°15'29.1"E, 603 m, 20.i.2009, T.L. Bird, J. Huff, and L. Prendini, 1 ♀ (AMNH [LP 9879]).

Solpugisticella kenyae Turk, 1960: **KENYA:** holotype ♂ (HUJI).

Solpuguna alcicornis (Kraepelin, 1914): **NAMIBIA: Karas Region:**

Keetmanshoop District: Keetmanshoop, viii.1912, W. Krause, 1 ♂, 1 ♀ (ZMUH [R8515]).

Solpuguna cf. *orangica*: **SOUTH AFRICA: Northern Cape Province:** *Prieska District*: Farm Good Hope, ca. 30 km SW of Prieska, 29°51'38"S 22°31'29"E, 9–18.i.2006, M. Burger, D. Haarmeyer and D. Massyn, 2 ♂, 1 ♀ (AMNH [LP 5969]).

Solpugyla sp.: **MALAWI: Southern (Blantyre) Region:** *Balaka District*: Liwonde National Park, Chinguni Hills Camp (Chinguni Lodge), at base Mount Chinguni, 15°00'49"S 35°15'40"E, 519 m, 12.xii.2007, L. Prendini and W.R. Schmidt, 5 ♂, 3 ♀ (AMNH [LP 10764]). **MOZAMBIQUE: Tete Province:** *Tete District*: Tete, close to top of hill with communications tower overlooking town, 16°12'01.7"S 33°33'57.9"E, 400 m, 9–10.xii.2007, L. Prendini and W.R. Schmidt, 1 ♂ (AMNH [LP 8138]).

Zeria adunca (Roewer, 1933): **ZAMBIA:** Mpulungu, Nkupi Lodge, 24.x.2001, J. Snoeks and M. Hansens, 1 ♂ (MRAC 216.105).

Zeria carli (Roewer, 1933): **MOZAMBIQUE:** Blue Anchor Inn, near Marracuene, 25°35.124'S 32°39.568'E, 50 m, 28.xi.2007, C. Haddad and R. Fourie, 1 ♂ (AMNH [LP 7915]).

Zeria fordi (Hirst, 1907): **KENYA: Rift Valley Province:** Lake Bogoria National Reserve Chemurak Valley, 00.355250°S 36.064944°E, 27.iv.2007, K. Reddick and J. Mugambi, 1 ♂ (AMNH [LP 9090]).

Zeria fusca (C.L. Koch, 1842): **SOUTH AFRICA: Western Cape Province:** *Wynberg District*: Newlands Forest, x.1997, L. Prendini, E. Scott and J. Knight, 1 ♂ (AMNH [LP 1473]); Newlands Forest, E slope Table Mountain, 26.xi.2000, L. Prendini and E. Scott, 2 ♀ (AMNH [LP 1472]).

Zeria glabricornis (Lawrence, 1928): **NAMIBIA: Kunene Region:** *Opuwo District*:

Ruacana, 5 km NNE, 17°25.869'S 14°21.522'E, 1109 m, 6.i.2004, L. Prendini, E. Scott, T. and C. Bird, Q. and N. Martins, 1 ♂ (AMNH [LP 3614]).

Zeria keyserlingi (Pocock, 1895): **GUINEA-BISSAU:** Bambadinca, property of Riverzoo Farm, 12°00'09.0"N 14°53'25.9"W, 28 m, 29.vi–2.vii.2005, J. Huff and V. Vignoli, 1 ♂ (AMNH [LP 4632]).

Zeria lawrencei (Roewer, 1933): **NAMIBIA: Hardap Region:** *Maltahöhe District*: Namib-Naukluft Park: Sossusvlei, Elim Dune, 24°27'35.0"S 15°46'33.2"E, 827 m, 2.xi.2009, T.L. Bird, J. Huff, and L. Prendini, 1 ♂ (AMNH [LP 9906]), 2 ♂, 1 ♀ (NMNW 13820).

Zeria sericea (Pocock, 1897): **NAMIBIA: Otjozondjupa Region**: *Grootfontein District*: Farm Uisib 427, 19°33'19.9"S 17°11.53.3"E, 1343 m, 31.xii.2008, T.L. Bird, J. Lukas and K. Schoeman, 7 ♂, 1 ♀ (NMNW 13801); 19°32'54.1"S 17°14.06.8"E, 1343 m, 29.xii.2008-2.i.2009, T.L. & C. Bird; K. Schoeman 6 ♂ (NMNW 13800).

Zeria strepsiceros (Kraepelin, 1899): **MOZAMBIQUE: Maputo Provice:** *Matutuine District*: Delagoa Bay, 7.x.1893, W. Joost, holotype ♂ (ZMUH [R9500]).

Zeria venator (Pocock, 1897): **SOUTH AFRICA: Northern Cape Province:** *Britstown District*: Farm De Put, ca. 30 km SE of Britstown, 30°48'53"S 23°40'58"E, 20–29.i.2006, M. Burger, M. Carstens, K. Jacobs, and A. Pretorius, 3 ♂, 1 ♀ (AMNH [LP 5952]).

Zeria sp.: **KENYA: Eastern Province:** *Kibwezi District*: Tsavo National Park, Kitani Lodge, 2 ♂ 2 ♀ (CAS).

Zeriassa cf. *furcicornis*: **NAMIBIA: Otjozondjupa Region:** *Grootfontein District*: Farm Uisib 427, red sandy flats in valley, 19°32'54.3"S 17°14'08.8"E, 1340 m, 3.i.2004,

L. Prendini, E. Scott, T. and C. Bird, Q. and N. Martins, 1 ♂ (AMNH [LP 3612]); Farm Uisib 427, 19°32'54.1"S 17°14'06.8"E, 1343 m, 29.xii.2008–2.i.2009, T.L. and C. Bird and K. Schoeman, 1 juv. (AMNH [LP 9848]).

Zeriassa sp.: **KENYA:** Kalabata River where Lokori–Lodwan road crosses SE of Loperot, Turkana, 30.vi–26.vii.1965, B. Patterson Expedition, 1 juv. (MCZ [unaccessioned ex MCZ 126321]); Kanebi, Pleist., 27.vii–8.viii.1965, B. Patterson Expedition, 1 ♀, 1 juv. (MCZ 126318).

APPENDIX 2

GLOSSARY OF TERMINOLOGY

Terms in languages other than English are in italics except for descriptive phrases, which are in inverted commas. Direct translations are in square brackets.

A/CP ratio: Ratio indicating size of body appendages (A = sum of pedipalp, leg I, and leg IV lengths) to body length (CP = length of chelicera plus length of propeltidium) (Fig. 5F; Brookhart and Muma, 1981; Muma and Brookhart, 1988).

alembic lumen: Lumen in flagellum of Ceromidae Roewer, 1933 and Solpugidae Leach, 1815 (Pl. 41) but hypothesized to occur in all flagella with a shaft, including wide shaft of the daesiid *Ammotrechelis*. In Solpugidae, comprises alembic canal in flagellar shaft which terminates proximally in a blind pouch (alembic pouch; basal pouch *sensu* Lamoral, 1975); transition from pouch to canal flask shaped (hence alembic), visible through cuticle of bulbous base of flagellum (Pls. 33K, L, 45A). Open externally. Lined by epicuticle; hypothesized to have formed by longitudinal invagination of seta (Lamoral, 1975: 138, fig. 1). Function unknown. No connection between alembic canal and hemolymph. Historical use: alembic lumen (Lamoral, 1975).

alveolus: deep flagellar socket in Galeodidae Sundevall, 1833, *Karschia* Walter, 1889 and Rhagodidae Pocock, 1897 (Pl. 40A–C).

anterolateral propeltidial lobe: Lateral lobes partially or entirely fused to propeltidium (Fig. 1A, Pl. 3A, B) in Ammotrechidae Roewer, 1934, Ceromidae, some

Daesiidae Kraepelin, 1899 (e.g., *Ammotrechelis*, *Namibesia* Lawrence, 1962, *Biton* Karsch, 1880), Eremobatidae Kraepelin, 1899, Karschiidae Kraepelin, 1899, Melanoblossiidae Roewer, 1933 (Melanoblossiinae), Mummuciidae Roewer, 1934, and Solpugidae, but completely separated from propeltidium in some Daesiidae (e.g., *Hemiblossia* Kraepelin, 1899), Gylippidae, Hexisopodidae Pocock, 1897 (but see Roewer, 1934: 42; Muma, 1976), Melanoblossiidae (Dinorhaxinae Roewer, 1933), and Rhagodidae (based on Muma, 1976; Wharton, 1981). Each lobe contains anterolateral cheliceropeltidial articulation (anterolateral chelicerocarapacal articulation of Shultz, 1990) and lateral eyespots (Bernard, 1894a). Similar articulation present in Pseudoscorpiones de Geer, 1778 except for some species of superfamily Chthonioidea Daday, 1888 (Chamberlin, 1931; Shultz, 1990). Pocock (1893) misinterpreted as basal sclerite of chelicera, hence argument for three-segmented chelicera in Solifugae, but presence of eyespots indicates a "carapacal" origin" (Shultz, 1990: 11). Historical use: buttress to which the mandible is articulated [on each side of the head] (Pocock, 1900b: 133); *Lobus exterior* [exterior lobe] (Roewer, 1934; Muma, 1976; Wharton, 1981); lateral lobe (e.g., Carvalho et al., 2010).

asetose areas: Distinct areas devoid of setae and more sclerotized than surrounding areas (Fig. 1B, C, Pl. 4). Includes terminal tooth, area extending along cutting edges of fingers and including teeth, stridulatory plate, interdigital and cheliceropeltidial condyli, and ventral digital (vdp) and ventral manus (vmp) plagula (Fig. 2, Pl. 6). Generally dark reddish brown. Historical use (relevant only to asetose areas of fingers): hardened points of digit (Bernard, 1896: 323); *besonders dicker Chitinregionen* (Roewer, 1934: 118).

atrium: Narrow, longitudinal “chamber” of hemolymph below bulbous base of flagellum in Solpugidae (Fig. 22D). Connected to hemolymph lumen of base through longitudinal valve extending along base of bulb. Not mentioned by Lamoral (1975) in treatment of Solpugidae flagellum. Historical use: *atrium* (Sørensen, 1914).

basal cheliceral apodeme: Collar-like ingrowth of exoskeleton at base of chelicera at articulation with propeltidium (Pl. 3D–I). Forms rim of basal cheliceropeltidial foramen. Separated from external cheliceral surfaces by cheliceropeltidial articular membrane. Site of cheliceral muscle attachment (Roewer, 1934: 52; Van der Meijden et al., 2012). Historical use: *Chitinwulst-Umrandung* [chitinous lipped rim] (Roewer, 1934: 53); basal ring, but apparently in broader sense than used here (Van der Meijden et al., 2012).

basal fondal margin: Basal margin of strongly sclerotized, asetose fond (Pl. 2A, B). Historical use: edge of mandibular joint (Birula, 1926: 196); *Gelenksrande* [margin of joint] (Birula, 1937a); socket margin of movable finger (Muma, 1951: 39, 43).

basal peg: Swelling at base of flagellum of *Karschia* (Karschiidae) (Pl. 40C). Might be homologous to base of compound flagellum and previously suggested to be homologous with base of flagellum of Ceromidae (Roewer, 1934: 148). Hypothesized to prevent movement at base during extension of flagellum (Roewer, 1934: 146). Historical use: *petite apophyse* [small apophysis] (Sørensen, 1914: plate II, fig. 14); *Zapfen* [spigot] (Roewer, 1934: 142).

basifondal (BF) teeth: Small to minute, but distinct teeth medially on basal fondal margin forming third row of fondal teeth. Most pronounced in Galeodidae (Pl. 64K, L) and Rhagodidae (Pl. 64I, J), present but reduced in some Eremobatidae (Pl.

84I, J), absent but vestigial signs of BF teeth present in, e.g., Ceromidae (e.g., Pl. 96A, C). Historical use: *Gelenksrande sitzenden Zähnchen* (Birula, 1937a).

bifid setae: Apically forked setae (Fig. 10A). One of most common setal types in Solifugae, present on retrolateral surface of chelicera, but absent on prolateral surface. Historical use: *Gabelborsten und Gabelhaare* (Kraepelin, 1901); cleft apically (Hewitt, 1934; Lawrence, 1935).

bulbous base: Swollen base of flagellum of Solpugidae (Fig. 25, Pl. 45). Immovably fixed dorsally to prodorsally along its length (above atrium) to chelicera. Contains alembic pouch. Historical use: proximal portion of flagellum (Pocock, 1895); basal enlargement of flagellum (Purcell, 1903c: 305); basal lamina of flagellum (Pocock, 1897); *Grundschwiele* (Kraepelin, 1901, 1908a); basal lobe (Hirst, 1911b); *ballon* (Sørensen 1914); basal enlargement (Hewitt, 1919b); *Blase*, *Basalblase des Flagellum* (Roewer, 1934: 154, 444); enlarged ovate to globular base (Muma, 1976); flagellar base, bulbous base (Wharton, 1981).

bulbous base carinae: Moderately to strongly sclerotized, smooth to jagged, dorsal to proximodorsal ridge along bulbous base of male flagellum in Solpugidae (Fig. 25, Pl. 33L). May prevent bulbous base yielding during expansion of flagellum, thus increasing hemolymph pressure (Sørensen, 1914: 168). Historical use: *carène* [carina] (Sørensen, 1914); *Dorsalrippe* [dorsal ridge of bulbous base] (Roewer, 1934: 153).

chaetotaxy: Arrangement, nomenclature and classification of setae (Gordh and Headrick, 2001), e.g., Pls. 12–14. Pending further study, cuticular processes pertaining to chelicera here categorized into spines (rare in Solifugae *vide* Lamoral, 1973) and setae. See macrosetae, microsetae, spines and processes. Historical use: Kraepelin

(1901: 8) defined nine types of setae in Solifugae, i.e., *Dornen* [spines], *Dornenborsten* [spinose bristles], *Borsten* [Bristles], *Haare* [hairs], *Abgestutzte Borsten* [bristles abruptly narrowing at apex, e.g., stridulatory setae], *Gabelborsten und Gabelhaare* [bifid bristles and hairs], *Cylinderborsten* [cylindrical bristles], *Tubenhaare und Tubenborsten* [ctenidia], *Papillen* [papillae]. All except ctenidia and papillae occur on the chelicera. Roewer (1934: 121) recognized and defined these types as *Dornen* [spines] when shaft inflexible, *Borsten* [setae/bristles] when slightly flexible, *Haaren* [hairs] when very flexible, and *ctenidien* [ctenidia] and *papillae* [papillae] when unsclerotized. El-Hennawy (1998: 6, fig. 5) largely followed Kraepelin's (1901) distinction between "spines", "bristles", "spinous-bristles" and "sense hairs". Lawrence (1956: 120) used translations spinose setae (for *Dornenborsten*) and spines (for *Dornen*) to refer to different setae, but in discussion on rhagodid taxonomy emphasized that it is often impossible to assign setae to one category or another, and hence often used spine-like setae for those not rigid enough to be referred to as spines (Lawrence, 1956: 129). Lamoral (1973) noted correct definition of "spine" is outgrowth of cuticle whereas "seta" is outgrowth of epidermis with some flexibility and connected to cuticle by means of membrane. Lamoral (1973) noted true spines rare in Solifugae, rejected use of "spine", and suggested use of "spine-like" setae for rigid setae, a suggestion followed by some (e.g., Muma, 1976; Wharton, 1981) but not all (e.g., Maury, 1985; Gromov, 2003b; Reddick et al., 2010; Cushing and Castro, 2012) subsequent workers.

callus: Strongly sclerotized, lobate asetose area on fixed finger of both sexes in Hexisopodidae (Fig. 6A; Pls. 127C, 128D, E), usually with blunt spines (outgrowths or tubercles). Historical use: hairless area at base of fang (Purcell, 1899); sclerotized patch

(Lamoral, 1973); callus (Wharton, 1981).

chelicera (-ae): First pair of appendages in Chelicerata (Fig. 1); large, two-segmented, and chelate in Solifugae. Each solifuge chelicera comprises two segments, first (basal) segment compriing manus and fixed (dorsal) finger, second (terminal) segment referred to as movable (ventral) finger. Historical use: *Fangscheeren* [scissor fang] (Pallas in Lichtenstein and Herbst, 1758); *mandibules en pinces* (Latreille, 1796: 188); *mandibules* (Blanchard, 1847; Dufour, 1861: 348; Pavesi, 1897); mandibles (Putnam, 1883: 257; Pocock, 1895; Purcell, 1899; Hewitt, 1914a, 1919b; Lawrence, 1927); *Mandibeln* (Mdb,) (Kraepelin, 1901: 5; Heymons, 1902; Birula, 1916, 1937a); *Fresszangen* [fang scissors] (Koch, 1842); *antenne-pinces* [antennal clamps] (Latreille, 1829: 212); *chélicères* (Latreille, 1829: 212); chelicera (Pocock, 1889; Heymons, 1902; Hewitt,1914a, 1919b; Panouse, 1960b); *queliceros* (Maury, 1970); *Cheliceren* (Roewer, 1934: 53; Lamoral, 1975); *de forcipules* [claspers] (Savigny, 1809: 176); chela (Hutton, 1843), *Kiefer* [jaw]/*Oberkiefer* [maxilla] (Kraepelin, 1899); *les antennes/*"*chélicères*" (Sørensen, 1914: 158).

cheliceral fingers: On chelicera, two opposable, distal digits, bearing teeth (Fig. 1), i.e., fixed (dorsal) and movable (ventral) fingers.

cheliceral mill: Behavioral term referring to combination of movements made by chelicerae and cheliceral fingers during feeding (e.g,. Muma, 1966c); involves scissor-like movements of cheliceral fingers, and forward-backward, up-and-down movements of entire chelicerae, presumed to grind food between stridulatory ridges.

cheliceropeltidial articular membrane (cpam): Membrane around cheliceral foramen (Fig. 1A, Pl. 3A, B) which connects chelicera to prosoma. Historical use: *la* *membrane conjonctive* (Sørensen, 1914); flexible membrane (Dunlop, 2000); connective membranes (Van der Meijden et al., 2012).

cheliceropeltidial condyle (cpc): Condyle at proximal end of chelicera (Pl. 3); articulates with prosoma to form anterolateral cheliceropeltidial articulation in anterolateral propeltidial lobe of prosoma (Roewer, 1934: 32). Historical use: *condyle* (Sørensen, 1914: 158); *hintere Apophyse* [posterior apophysis] (Roewer, 1934: 52, fig. 47).

cheliceropeltidial foramen: Rounded-triangular proventral-basal opening on chelicera where attaches to prosoma through cheliceropeltidial connective membrane, and articulates with prosoma through cheliceropeltidial condyle (Pl. 3). Historical use: *une cavité articulaire* … [termed] *un segment de surface sphérique* (Sørensen, 1914).

CH/FFH (cheliceral height/fixed finger height) ratio: Ratio indicating height of fixed finger relative to height of paturon . Utility in taxa without fondal notch unknown. Historical use: cheliceral width/fixed finger width (CW/FFW, CW/WFF) (Brookhart and Cushing, 2004).

CL/CW (cheliceral length/cheliceral width) ratio: Ratio indicating length relative to width of paturon (Fig. 5E); one of two indices measuring volume of paturon.

CL/CH (cheliceral length/cheliceral height) ratio: Aspect ratio, indicating length relative to height of paturon (Fig. 5D); one of two measures indicating relative volume of paturon. Historical use: jaw index (jaw length/jaw breadth) (Cloudsley-Thompson, 1961); L/W (length/width) (Brookhart and Muma, 1981).

condyle: round, strongly sclerotized process by which fixed (dorsal) finger articulates into a socket (Fig. 2A) with movable (ventral) finger (pro- and retrolateral interdigital condyli, pic, ric; Fig. 1, Pl. 2), and chelicera with propeltidial lobe (cheliceropeltidial condyle, cpc; Fig. 3).

cuticular canals: Narrow canals approximately perpendicular to axis of finger, extending to cuticular surface, often clearly visible through cuticle of asetose areas of fingers. Some appear to terminate in granules (Pl. 5A).

dental formulae: Formulae used to describe solifuge dentition. Two types, i.e., dental pattern formula (Tables 7, 8) describing pattern of dentition, and size grading formula, usually applied only to fondal teeth (e.g., Maury, 1982), but sometimes to median series and fondal teeth (e.g., Xavier and Rocha, 2001).

dental papillae: Papillae situated prolaterally on chelicera of male *Gylippus* (*Anoplogylippus*) species (Gylippinae), at base of teeth on fixed finger (Birula, 1938: 93, 96, figs. 64, 61); may be simple (*zp.a – einfachen sensu* Birula, 1913: 329, fig. 8a) or comb-shaped (*zp – kammförmigen sensu* Birula, 1913: 329, fig. 8b). Historical use: *Zahnpapillen* (1913); [dental papillae] (*pa* in Birula, 1938: 93, 96, fig. 61, 64).

denticles: Minute teeth (Figs. 19, 20, arrows) often variable in presence/absence. Historical use: granuliform teeth (Lawrence, 1962a, 1965b); denticles/denticules (Muma, 1951). Birula (1926) used denticles as synonym for teeth.

diploflagellum: Composite primary and secondary flagella in male Rhagodidae; superficial appearance of single structure (Pls. 30F, 31D). Historical use: flagellum (e.g., Roewer, 1934); bifid flagellum (Cloudsley-Thompson and Constantinou, 1984).

dorsal cheliceral spine: Posterodorsally to dorsally projecting, apically pointed spine in males of some *Karschia* (Karschiidae). His torical use: *Horn* or *processus rostralis* (Roewer, 1934: 291; Birula, 1935b: 302, fig 2); *r, rh* (Birula, 1938: 44, 50, 58, 60, figs. 18, 24, 34, 36). In *Biton* (*B.*) *gariesensis* (Lawrence, 1931) as *Daesia gariesensis*, pointed tooth directed slightly outwards (Lawrence, 1931: 134, fig. 3b).

dorsal flagellar seta (*dfs*): Apicalmost seta of prolateral dorsal distal (*pdd*) series, situated directly dorsal or proximodorsal to ventral flagellar seta (v*fs*) (Pls. 12A, 13, 46C, 47); hypothesized precursor to secondary flagellum in Rhagodidae and most Karschiidae (*Barrussus* Roewer, 1905 and *Eusimonia* Kraepelin, 1899).

dorsal hornlike process: Hornlike processes situated dorsally on fixed finger in males of some karschiids, i.e. *Barrus* Simon, 1880, *Barrussus*, *Eusimonia* (anterodorsal projecting process, e.g., Pls. 30D, 31B), some Daesiidae (anterior projecting protuberance, e.g., Pls. 132F, 134A, and Lawrence, 1931: 134, fig. 3a, b) and *Trichotoma michaelseni* (Kraepelin, 1914) (anterior projecting protuberance fused dorsally to fixed finger, e.g., Pls. 87A–D, 88C). Historical use: In *Eusimonia*: *crochet fixe, profondément bifurqué* (Simon, 1879: 128, 129); *Horn* or *Hornfortsatz* (Kraepelin, 1901: 140, 1908a); horn (Hirst, 1908); dorsal process of immovable finger (Hirst, 1910); *Horn* or *Processus rostralis* (Birula, 1935a: 1218); Gabelhaken des Chelicerenfingers or *Chelicerenfingergabel* (Roewer, 1934: 143, 144); dorsal cheliceral horn (Muma, 1976: 6); *Finger ist gegabelt* (Pieper, 1977). In *Ammotrechelis*: anteriorly projecting dorsal process (Muma, 1971).

external cheliceropeltidial condylar attachment (ecpca): Pale area visible on anterolateral propeltidial lobes (Figs. 1A, 3A, B); external indication of where condyle is attached inside lobe.

fang: Obsolete term, commonly used in older literature. Different usages of "fang". Fang often synonymous with movable finger (e.g., Pocock, 1893: 10: "terminal segment [movable finger] or fang") or teeth (Pocock, 1895: 84). Most common usage describes dorsal finger (usually as "upper fang") or some more distal part of dorsal finger (usually as "terminal fang"). Terminal fang usually synonymous with mucron (e.g., Purcell, 1899; Pocock, 1900b: 133; Hewitt, 1921, 1923), but limits arbitrarily defined. In Hexisopodidae, "fang" used as reference to toothless, or apparently toothless section of finger with callus or denticular ridge at flagellar base indicated to be at base of fang (Purcell, 1902; Lamoral, 1972). Also often used to describe part of dorsal finger distal to fondal teeth (Lawrence, 1928: 262, apparent in reference to median series as "fang series"), especially in modified chelicera where refers to larger toothless areas (e.g., Purcell, 1899: 394, in a modified Daesiidae chelicera). Not always restricted to toothless areas. "Basal portion" of fang described to "commence at first [distalmost] tooth of inner series [profondal row]" in *Toreus capensis* (as *Ceroma capense*; Purcell, 1899: 100). Although neither Purcell (1899) nor Hewitt (1921, 1923) defined "fang", extent thereof apparent from their usage. For example, Hewitt (1921: 9) described "terminal fang of lower jaw strong, the distance from its tip to the tip of the first tooth scarcely 1¼ times the distance between the first and third teeth" and Hewitt (1923: 56) described dentition on fixed finger as "...with two large teeth in front, behind the long terminal fang". These distances are measured using apex of medial (MM) tooth to tip of finger (e.g., Hewitt, 1919b: 31).

fixed (dorsal) finger: Distal part of first, or basal, cheliceral segment (Fig. 1A). Fixed finger possesses two basal condyli, viz. the prolateral (pic) and retrolateral (ric) interdigital condyli (Figs. 1B, C, 2) responsible for articulation of fingers relative to each other (see *manus* for division between manus and fixed finger). Birula (1937a) divided fixed finger of galeodids into *Endteil*, toothless area distal to median row of teeth, or *mucron*, and *Basalteil*, measured from distal end of median series of teeth to insertion point of flagellum, approximately between medial (FM) and proximal (FP) teeth of fixed finger.

fixed finger crimp: A slight to marked upturn in largely stylet-like fixed finger of Eremobatidae (Pl. 67A). Historical use: crimp (Brookhart and Cushing, 2004: 294, fig. 31).

fixed finger distal (FD) tooth: Distalmost primary tooth on fixed finger and thus also distalmost tooth on finger (but see multidentate taxa, and discussion of daesiid dentition) (Pls. 21, 22A–D). Historical use: *dent distale* (*dd*) [distal tooth] (Vachon, 1950: 101, fig. 13); *première dent antérieure* (*DA1)* [first anterior tooth] (Panouse, 1956: 212); anterior tooth (e.g., Muma, 1951; Lawrence, 1968);. On fixed finger, anterior teeth commonly used by various authors as encompassing distal and medial teeth as well as secondary teeth situated between them, e.g., *Vorderzähne* [anterior teeth] (Kraepelin, 1899, 1901; Roewer, 1934: 53); *dent antérieure* (Panouse, 1960b: 176, fig. 2); *anterior* (*A*) (Maury, 1982, 1984), anterior teeth (Martins et al., 2004) anterior teeth, as Fa_1, Fa_2, Fa_3 (Botero-Trujillo, 2014). Muma (1951) differentiated between two anteriormost primary teeth on fixed finger, and introduced terms medial tooth (MT) for most proximal thereof, and “intermediate teeth” for teeth situated between them.

fixed finger medial (FM) tooth: First primary tooth distal to proximal tooth on fixed finger (Pls. 21, 22A–D; Muma, 1951). Historical use: *seconde dent antérieure* (*DA2*) [second anterior tooth] (Panouse, 1956: 212); medial tooth (MT) (Muma, 1951). Historically usually referred to as one of anterior teeth (see historical use under distal tooth). Kraus (1966: 183, figs. 1–4) labelled both the medial tooth (FM) and the submedial tooth (FSM) on fixed finger as *Zwischenzähne* [intermediate teeth].

fixed finger proximal (FP) tooth and movable finger proximal (MP) tooth: Proximalmost primary tooth on fixed and movable fingers, respectively (Pls. 21, 22A–D); often largest tooth on finger. Historical use: principal tooth (Pocock, 1889; Muma, 1951; Brookhart & Cushing, 2002); *Hauptzahn* [main tooth] (Kraepelin, 1899, 1901; Roewer, 1934: 53); chief tooth (Birula, 1926); terminal tooth of fang series (Lawrence, 1928: 262); *dent principale* (*DP*) [principal tooth] (Vachon, 1950; Panouse, 1956, 1960b); main tooth (Turk, 1960; Van der Meijden et al., 2012); main basal tooth (Wharton 1981: 69); *principal* (*P*) (Maury, 1984); central tooth (El-Hennawy, 1998); primary tooth (Brookhart and Cushing, 2004; Catenazzi et al., 2009); posterior tooth (Bayram, 2011); principal tooth, as *Fp* and *Mp* respectively (Botero-Trujillo, 2014).

fixed finger subdistal (FSD) tooth/teeth: One or more secondary teeth situated between fixed finger medial (FM) and fixed finger distal (FD) teeth (Pls. 21, 22A, D). Also see fixed finger distal (FD) tooth.

fixed finger submedial (FSM) tooth/teeth: One or more secondary teeth situated between fixed finger proximal (FP) and fixed finger medial (FM) teeth (Pls. 21, 22A–D). Historically usually referred to as intermediate tooth/teeth on fixed finger (e.g., Kraepelin, 1899, 1901; Roewer, 1934: 53; Panouse, 1960b: 176, fig. 2; Maury, 1982, 1984; Martins et al., 2004), intermediate teeth, Fi_1, Fi_2 (Botero-Trujillo, 2014).

fixed finger subterminal (FST) tooth/teeth: One or more secondary teeth situated on fixed finger mucron, i.e. between fixed finger distal (FD) and fixed finger terminal (FT) teeth (Pl. 158D, F). Uncommon.

fixed finger terminal (FT) and movable finger terminal (MT) teeth: Tip of finger, i.e., distalmost part of mucron (Pls. 21, 22A–D), traditionally interpreted either as section of mucron, e.g., "terminal fang [mucron] of moderate length, the apex [terminal tooth] suddenly and strongly curved downwards … " (Hewitt 1913: 479), or as structure equivalent to mucron (e.g., Pocock, 1895). Historical use: apex [of finger] (Purcell, 1899); "*Endspitze des Oberfinger*" (Birula, 1937a); tip (Van der Meijden et al., 2012: 3412, fig. 1).

flagellar attachment point: Point of attachment through which flagellum attaches to, or point around which it rotates in the fixed finger (Pl. 40); in socket or modified socket. If present, area through which lumen of flagellum connects with hemolymph in chelicera. Fixed (Ammotrechidae, Eremobatidae, Karschiidae, Melanoblossiidae, Mummuciidae, Rhagodidae and Solpugidae) or rotatable (Ceromidae, Daesiidae, Galeodidae and Hexisopodidae). Absent in Gylippinae. Inner surface of socket strongly sclerotized in Ceromidae (Pl. 96A). Attachment oval in Ammotrechidae (Pls. 34E, F35G); round in Mummuciidae (Pls. 34G, H, 35H). Historical use: In Ammotrechidae: *anillo de fijación* [attachment ring] (Maury, 1982: 136). Daesiidae: *chitinösen Fixationspunkt* (Kraepelin, 1908a: 220); rotatory centre (Lawrence, 1956: 123; 1965a: 55); *kreisrunden Chitinring der Anheftung* or *kreisrunden Anheftungsring* [circular attachment ring] (Roewer, 1934: 150). In Karschiidae: *Basalring* (Roewer, 1934: 146). In Mummuciidae: attachment base, attaching ring (Xavier and Rocha, 2001: 129, 132, fig. 10), probably refering to short stalk. Mostly used broadly in literature, with little distinction between inner margin of socket, general reference to "attachment point", and hairpin pattern made by stalk transitioning into base, e.g., “rotatory axis … as an ill-defined longish triangular marking” (Lawrence, 1928: 266, plate XXIII, fig. 48).

flagellar base: Section of flagellum distal to stalk and proximal to shaft, if present (Pls. 32A–G, 33A-H, K–M). Bulbous base in Solpugidae, cup-shaped base in Hexisopodidae and *Namibesia,* swollen structure in Ceromidae, main membranous structure (i. e. “flagellum”) in Ammotrechidae, Mummuciidae and typical Daesiidae. Absent in Eremobatidae, Karschiidae, Melanoblossiidae and Rhagodidae. May be homologous to collar at flagellar base in Galeodidae. Historical use: In Ceromidae: basal enlargement of flagellum (Purcell, 1899: 395). In Solpugidae: see bulbous base.

flagellar complex: All projections and modified setae situated apically on prolateral surface of male cheliceral fixed finger. Includes flagellum, if present, and associated flagellar complex plumose (*fcp*) setae and flagellar complex subspiniform or spiniform (*fcs*) setaein addition to various cuticular processes. In Ceromidae, consists of rotatable whip-like flagellum, two to three spiniform setae (*fcs*), and row of stiff, often pipette-shaped setae (*fcp*) at flagellar base (Pls. 32A, B, 33A–C; Roewer, 1934: 147, 1941: 117). In Galeodidae, consists of rotatable, spoonshaped flagellum, a stout plumose seta (*fcp*), and one to four spiniform setae (*fcs*) at flagellar base (Pls. 30G, H, 31E, F; Turk, 1960: 109). In Karschiidae, consists of fixed, coiled, filiform flagellum, two subspiniform setae (*fcs*) near flagellar base, and suit of similarly or differently modified proventral distal (*pvd*) setae (*fcp*) in *Karschia* (Pls. 30A–C, 31A; Panouse, 1955; Roewer, 1934: 144; Pieper 1977), or a fixed ventral primary and fixed dorsal secondary flagellum, and one or two subspiniform (*fcs*) setae near base of cheliceral hornlike process in *Barrussus* and *Eusimonia* (Pls. 30D, 31B; Panouse, 1955; Roewer, 1934:

144; Pieper 1977). When setae, including flagellum if present, of flagellar complex retain setiform appearance, as in Eremobatidae (Pls. 37–39; Muma, 1970a, Brookhart and Cushing, 2004), Lipophaginae (Pl. 36A–F), and Melanoblossiinae (Pl. 36G–I; Roewer, 1941:127), flagellar complex is referred to as “setiform” (see setiform flagellar complex, *sfc*). “Flagellar complex” has elsewhere been equated with flagellum, especially in Melanoblossiinae and Eremobatidae (e.g., Lawrence, 1972: 98; Wharton, 1981: 53; Gromov, 2003b: 199, El-Hennawy, 1990: 26). Historical use: *zusammengesetzten Natur des Flagellums* (Kraepelin, 1908a: 222); *Flagellumapparatus* [of *Karschia*] (Roewer, 1934: 146); *complexe flagellaire* [of *Eusimonia*] (Panouse: 1955: 347, figs. 2–4).

flagellar complex depression: Prolateral depression in fixed finger, which accommodates setiform flagellar complex in male Melanoblossiinae (Fig. 26, Pl. 36G–I).

flagellar complex plumose (*fcp*) seta(e): One or more slightly to distinctly modified proventral distal (*pvd*) setae, situated proximoventral or ventral to flagellar base in several taxa. Differ in shape, robustness, and position relative to flagellar base, but hypothesized to be homologous, modified *pvd* setae. In Ceromidae, smooth or plumose, often pipette-shaped *pvd* setae situated in short, closely spaced row at flagellar base (Pls. 32A, B, 33A–C). In Galeodidae, stout, plumose seta situated directly proximoventral to base of flagellum (Pls. 4C, 30G, H, 31E, F; Birula, 1936a: 48, fig., 1937a, b, 1938; Panouse, 1960b: 178, fig. 4), not obviously connected to *pvd* row (Pl. 62A, E, G, I). In Solpugidae, weak to moderately differentiated single plumose seta situated directly distal to base of flagellum, and apically in *pvd* row (Pl. 45B); robust *pvd* setae near apex in several other Solpugidae (Pl. 27). In some *Blossia* Simon, 1880 (Daesiidae), two to four distalmost *pvd* setae slightly more differentiated, but equally so, compared to more proximally situated *pvd* setae (Pl. 47D; Hewitt 1921: 10, fig. 4). In *Karschia* (Karschiidae), plumose setae increasing in length towards flagellum (Pls. 30A, 31A, 50A, E), apical one or two setae often more robust or modified into various shapes (see *i*, *f* in Birula, 1938: 58, fig. 34; Gromov, 1998: 181, figs. 1f–l). Historical use: In Ceromidae: radiating tuft of spiniform setae at flagellar base (Pocock, 1897: 254); "row of stiff bristles", "long stiff feathery hairs which reach to the apex of the fang [in *Ceroma sclateri* Purcell, 1899]", "row of stiff feathery bristles, which do not…reach the apex of the jaw [in *Ceroma inerme* Purcell, 1899]" (Purcell, 1899: 395, 399); "fan-like row of feather bristles" (Hewitt, 1919b: 23); "row of … very stout, smooth, basally expanded spines" (Lawrence, 1954: 114); "enlarged setae [associated with flagellum]" (El-Hennawy, 1990: 22; Muma, 1976: 10); "cluster of thickened setae arising from small tubercle" (Wharton, 1981: 11). In Galeodidae: *hintere gefiederte Borste*, *St.p.* to distinguish from other plumose setae in *pvd* series labelled "*vordere gefiederte Borsten*, *St.a.*" (Birula, 1937a: 595, fig. 17, 1938: 155, fig. 87). In *Karschia* (Karschiidae): *Säbelborsten* (Kraepelin, 1908a); mandible bristles (*i* and *f* in Birula, 1938: 58, fig. 34); dorsal modified setae (Gromov, 1998: 181, figs. 1f–l). In Solpugidae: *une grade soie droite plumeuse*, (*ibid. s*); *s*, *une soie plumeuse*, *probablement un organe sensitif* (Sørensen, 1914: 173, 212, fig. 10).

flagellar complex subspiniform to spiniform (*fcs*) seta(e): One to five (depending on taxon) subspiniform to spiniform setae, presumably modified prodorsal distal setae (*pdd*), at flagellar base; part of male flagellar complex. Differ in shape, robustness, and position among taxa. In Ceromidae, two or three spiniform setae situated dorsally on chelicera near flagellar base in some species (Pls. 32B, 33C), important for species diagnosis. In Galeodidae, intraspecifically variable row of one to four (Birula, 1937a: 594) spiniform setae situated proximoventral to base of flagellum (Pls. 4C, 30G, H, 31E, F). In Gylippinae, one or two robust spiniform setae situated prodorsally on chelicera (Pls. 32H, 33I, 85A, B); presence/absence and number important for species diagnosis (Birula, 1913). In *Eusimonia* (Karschiidae), one or two subspiniform setae situated dorsally near base of cheliceral hornlike process, e.g., *Eusimonia furcillata* (Simon, 1872) (Roewer, 1934: 143, fig. 141A), *E. nigrescens* Kraepelin, 1899 (Pls. 30D, 31B). In *Karschia* (Karschiidae), subspiniform setae situated dorsoproximal to flagellar base; often originating within spiral formed by flagellum near base of flagellar shaft (Pls. 30B, C, 31A). Historical use: In Ceromidae: *Oberfingerdornen* (Roewer, 1934: 148). In *Karschia: einem dicken*, *gekrümmten Dorn* [hypothesized to keep flagellum in place: "*wie von einer seitlichen Klammer*, *in seiner Lage fest gehalten wird*"] (Kraepelin, 1901: 145); *spinae flagelli* [flagellar spines] (Roewer, 1934: 291; Lawrence, 1954: 113); spine (*k* and *c* in Birula, 1938: 60, fig. 36). In Galeodidae: *Stiftdornen* (Birula, 1905a, 1929a: 164, fig. 1), "*Dornen unter dem Insertionspunkte des Flagellums*" (Birula, 1929b: 276, fig. 2); "*Sp - Hinterdornen des Flagellums*" (Birula, 1937a: 595, fig. 17, 1938: 155, fig. 87); *Nebendornen* (Birula, 1913: 332, 1937a); note: Birula (1937a: 593) also used *Nebendornen* to refer to the retrolateral manus spiniform (*rlm*) setae of Gylippinae; "a very stout and conical spine" (Lawrence, 1954). In Gylippinae: *Fingerdorn* (Birula, 1907b), *Oberfingerdorn* (*ofd* in Birula, 1913: 331, fig. 9); *Spina digitalis* [digital spines] (Roewer, 1934: 308); digital spine (Koç, 2011: 120, fig. 3); anterior main spine (Lawrence, 1953); principal spine-like setae (Wharton, 1981).

flagellar groove (fg): Prolateral to dorsal groove or longitudinal depression which accommodates flagellum. Different expressions of flagellar groove may or may not be homologous. In Eremobatidae: Longitudinal, prolateral to proventral groove, usually well defined, on fixed finger of male Eremobatidae (Pls. 38, 39A–E, H). Usually associated with male flagellum (see Brookhart and Muma, 1981: 291, figs. 2, 3); may comprise long (*Eremobates* Banks, 1900; Pl. 66C) or short (some *Eremochelis* Roewer, 1934 species) longitudinal groove, or series of distinct (*bilobatus* group of *Eremochelis*, e.g., Pl. 78A) or indistinct (*imperialis* group of *Eremochelis*, e.g., Muma, 1951) creases and folds. Longitudinal groove may be enlarged proximally to form a cuplike enlarged proximal concavity (Pl. 39B). Carinae (ridges) may be present inside groove (Pl. 39H). Also see **ventrodistal cheliceral concavity**. In Ammotrechidae and Mummuciidae: Prodorsal groove on fixed finger which accommodates flagellum; broad basally, narrowing apically to fit vesicular, or tapered bowl-shaped flagellum (Pls. 34G, H, 35H, I; see González Reyes and Corronca, 2013: 542, fig. 4). In Ammotrechidae only: Formed by prodorsal and proventral flanges, the former a prolateral curvature of the laterally-compressed dorsal margin of the fixed finger. In Daesiidae: Shallow prolateral depression along prodorsal distal margin (pddm) of asetose area of fixed finger which accommodates flagellum in some Daesiidae (Pls. 139G, 141A; also see Klann & Alberti, 2010: 226, fig. 1A); groove less distinct than other types of flagellar grooves. In Gylippinae: Shallow dorsal groove in asetose area of fixed finger with which proximal part of flagellum is fused in Gylippidae (Pl. 32H). In Solpugidae: Prodorsal to dorsal groove in asetose area of fixed finger in which base of flagellar shaft situated before curving dorsally (Pls. 32G, 33K, 48). Prolateral margin of groove associated with various proventral to dorsal elongate, jagged, flange-like, or toothlike carinae in adult male (Pl. 20). Historical use, in Eremobatidae: “longitudinal groove on median face” (Fichter, 1941); mesal groove (Muma, 1951); mesoventral groove (Brookhart & Brookhart, 2006: 301).

flagellar groove process (FGP): Flanges and carinae formed by anterior extension and modification of prolateral rim of flagellar groove in Solpugidae (Pl. 20). Historical use: e.g., *zahnartig vorspringendem Grat* [toothlike protruding ridge] (Kraepelin, 1901: 64); tooth, keel, ridge (Lawrence, 1929); *Zahnhöcker* or *gezähnelter erhabener* [toothed, raised keel] (Roewer, 1934: 468).

flagellar hemolymph lumen: Lumen between flagellar membranes (e.g., Pl. 30D) or in canal parallel to alembic canal, if present (e.g., Pl. 41). Hypothesized to be connected proximally to hemolymph (through atrium in Solpugidae; Sørensen, 1914); blind ending apically. Possibility of hemolymph entering flagellum recognized by Sørensen (1914: 164), Roewer (1934: 135–155) and Lamoral (1975). First histological studies by Lamoral (1975).

flagellar shaft: Section of flagellum distal to base (Pls. 32, 33A–H, K–M). Usually chitinous and rod-like. Present in Ceromidae, Daesiidae (*Ammotrechelis, Namibesia, Syndaesia*), Hexisopodidae and Solpugidae. Gylippinae flagellum (Pls. 32H, 33J) hypothesized to be homolog of shaft. Historical use: *partie corniforme*, or *corne* (“horn”) (Sørensen 1914: 165); shaft (Hewitt, 1919b; Purcell, 1899); *Schaft* (Roewer, 1934: 154); U-shaped crest of *Ammotrechelis goetschi* Roewer, 1934 (as *Amacata penai* Muma, 1971) (Muma, 1971).

flagellar stalk: Short section of flagellum connecting attachment point on fixed finger to flagellar base (Pls. 32D, 33D–F). Facilitates location of flagellum parallel to prolateral surface of chelicera. Manner in which stalk transitions to base in many Daesiidae hairpin shaped (Pls. 34A, B, 35A, B), e.g., *Biton tenuifalcis* (*vide* Lawrence, 1962b: 198, fig. 1c). Reference to “stalk” for flagella of certain daesiids, e.g., *Blossia litoralis* (Purcell, 1903a: 5, fig. 3), and Birula’s (1935a) use of short *Füsschen* which attaches dorsal flagellum of *Eusimonia* to chelicera, not interpreted as homologous to stalk as defined here.

flagellar stem: Stem section of leaf-like flagellum in some *Blossia* (Daesiidae) (Pl. 145F). Not considered homologous to flagellum stalk.

flagellar tip: Arbitrarily defined apex of flagellum. May be acuminate, bifid, fringed, etc. (Pl. 49D–L). Open to the exterior in flagella of Ceromidae (Pl. 41E), the daesiids *Ammotrechelis goetschi* (Pls. 32F, 33H, arrows; Maury, 1980a: 64, fig. 11) and *Syndaesia mastix* Maury, 1980 (Maury, 1980a: 64, figs. 3, 4), Solpugidae Lamoral (1975), and perhaps other rod-shaped flagella. Usually refers to tip of shaft of sclerotized rod-shaped flagellum; not homologous to tip of membranous bowl-, husk- or vesicular-shaped flagella (Ammotrechidae, Mummuciidae, and most Daesiidae) as shaft absent and tip refers to tip of base in these flagella.

flagellum, or male flagellum: Distinctly modified, strongly differentiated seta, or two setae in Rhagodidae and most Karschiidae (*Barrussus* and *Eusimonia*), originating prolaterally or prodorsally on fixed (dorsal) finger of chelicera (Pls. 30–35, 36G–I, 38). Present only in adult males. Primary flagellum, assumed to be homologous across Solifugae (Pl. 43), derived from apicalmost seta, i.e., ventral flagellar seta (*vfs*) in proventral distal (*pvd*) series (Pls 12A, 46, 47). Secondary flagellum, when present, assumed to be homologous in respective taxa, and derived from apicalmost seta in prodorsal distal (*pdd*) series, i.e. dorsal flagellar seta (*dfs*) (Pls. 12, 47). In Rhagodidae, primary and secondary flagella appear to form a single structure, referred to as diploflagellum (Pls. 30F, 31D). Flagellum absent in some taxa, notably Lipophaginae (Pl. 36A–C) and some Eremobatidae, e.g., *Chanbria regalis* Muma, 1951 and *Eremocosta titania* (Muma, 1951) (Pls. 37, 39I, J). If flagellum absent, its putative homolog, an unmodified ventral flagellar seta, presumed to be present. Historical use: *cirrhe* [cirrus] (Latreille in Dufour, 1861: 428); *un petit appendice mobile* (Savigny, 1816: 178). In Gylippinae: Simon (1879: fig. 15) labelled structure now recognized as flagellum, as *lamelle transparente*, and retrolateral manus spiniform (*rlms*) seta as *flagellum*. In *Eusimonia* (Karschiidae): earlier workers (Simon, 1879; Kraepelin, 1901; Hirst, 1908; Birula, 1913; but not Kraepelin, 1908a; Roewer, 1934: 299; Birula, 1935a) labelled primary flagellum as *flagellum* and secondary flagellum as *Plättchen*, *Lamelle*, or *Bläschenflagellum* (see also Table 12); *seta principalis* has also been used for Karschiidae (Birula, 1918; Roewer, 1934: 291). In Rhagodidae: references to the *flagellum* (e.g., Roewer, 1934: 55, fig. 50) concerned the apparently single structure comprising the primary and secondary flagella (referred to here as the diploflagellum). Primary and secondary flagella referred to as *Stab* and *Schuppe*, respectively, by Kraepelin (1908a), and plaques by Sørensen (1914: 169). In Eremobatidae: single flat bristle of flagellar complex (Fichter, 1941); apical and subapical plumose bristles in *Eremobates* (*vide* Muma, 1951: 61, fig. 48); apical plumose spine in *Eremorhax* Roewer, 1934 (*vide* Muma, 1951: 61); apically plumose seta in *Eremothera* Muma, 1951 (*vide* Muma, 1961); plumose apical bristle (e.g., Muma, 1970a; Brookhart and Cushing, 2002). In Melanoblossiinae: *Seta principalis des Flagellum-Komplexes* (Roewer, 1941: 1247); flagellum (Purcell, 1903a); *Flagellum* (Roewer, 1941:127); *appendice mobile* (Savigny, 1809).

FNL/FNH (fondal notch length/fondal notch height) ratio: Ratio indicating dimensions of fondal notch in Eremobatidae (Fig. 5H). Fondal length measured across maximum distance; width measured from "fondal tooth 1", i.e., retrofondal medial tooth (RFM) to ventral margin of fixed finger (Brookhart and Muma, 1987). Historical use: FN ratio (Brookhart and Muma, 1987); LFN/WFN (Muma and Brookhart, 1988: 3, plate 1); FL/FW (Brookhart and Cushing, 2004).

FNH/FFH (fondal notch height/fixed finger height) ratio: Ratio indicating height of fondal notch relative to height of fixed finger in Eremobatidae (Fig. 5H). Historical use: Introduced as fixed finger width/fondal notch width (FF/FN) by Brookhart and Muma (1987), followed by fixed finger width/fondal width (WFF/FW) of Brookhart and Cushing (2002) and later calculated as fondal notch width/fixed finger width (FW/FFW), requiring a switch between numerator and denominator, by Brookhart and Cushing (2004).

fond: Derived from *fundus* = base. Triangular broadening of base of fixed finger between two diverging rows of fondal teeth (Fig. 2A, Pls. 2A, B, 22E, F, 64); not to be confused with usage "FW = fond width" (Brookhart and Cushing, 2002) which indicates width of fondal notch, not width of fond. Historical use: *fond de la pince* (Simon, 1879: 126, 1880: 402); fond (Putnam, 1883: 257; Fichter, 1941; Muma, 1951, 1970); *Wangenteil* [cheek part] (Kraepelin, 1901: 99; Birula, 1937a: 568); *Kauflache* [chewing surface] (Roewer, 1934).

fondal interdigital articular membrane (fiam): See interdigital articular membrane (iam).

fondal notch (FN): Shallow to deep notch in fixed (dorsal) finger situated proximal to proximal tooth (FP) in male Eremobatidae (Muma, 1951) (Fig. 7A, B). Historical use: *Basalbuckel* (Roewer, 1934: 570); space between base of dorsal finger and first tooth of fond (Fichter, 1941); fond, fondal notch (Muma, 1951; Brookhart and Muma, 1981, 1987).

fondal teeth: Diverging rows of small teeth at base of fixed (dorsal) finger, comprising profondal row (PF) and retrofondal row (RF) which converge towards median series (Pl. 22E, F; Muma, 1951); in addition, basifondal row (BF) on basal fondal margin forms third "row" of teeth (*Gelenksrande sitzenden Zähnchen,* Birula, 1937a) connecting pro- and retrofondal rows into triangle delimiting fond, e.g., Eremobatidae (Pl. 84I, J), Galeodidae (Pl. 64K, L) and Rhagodidae (Pl. 64I, J). Basifondal (BF) teeth probably originated as proximal fondal teeth shifted along basal fondal articulation margin, based on position of reduced proximalmost profondal (PF) and retrofondal (RF) teeth, e.g., in *Eusimonia* (Pl. 64C, D), and basifondal teeth. Vestigial bead-like teeth of Hexisopodidae (Pl. 131) probably reduced fondal teeth, based on larger number of "beads" retrolaterally (more teeth are often found in the retrofondal (RF) row than in the profondal (PF) rows) and similarity to serrated basal fondal margin in, e.g., Eremobatidae (Muma, 1951: 39). Furthermore, distinct fondal teeth often grade into a "denticulate mound" (Wharton, 1981: 42) of indistinct teeth forming ridge-like surface proximally along edge of fondal area. Historical use (for fondal teeth in general): *molars* (Dufour, 1861); *Wangenzähne* [cheek teeth], e.g., "laterale (äussere) und mediale (innere) Wangenzähne” (Kraepelin 1899, 1901; Roewer, 1934: 58); cheek teeth (translation from German by Turk, 1948; Lawrence, 1962a; Levi and Shulov, 1964; Wharton, 1981; El-Hennawy, 1998), double series of teeth, as opposed to “single series”, or median series (Hewitt, 1914a: 152); “jugales latérales” and “jugales internes” (Vachon, 1950); *dent jugale* (*DJ*; *DJ int & DJ ext*) [cheek teeth] (Panouse, 1960b); *basal externo* (*BE*) and *basal interno* (*BI*) (Maury, 1984).

granulation: Arrangement of small, round structures situated retrolaterally on asetose areas of cheliceral fingers (Fig. 8, Pl. 5). Most prominent on pro- and retrolateral surfaces of movable finger where arranged in row from base to apex. With few exceptions (e.g., Pl. 5B), less distinct and randomly distributed on fixed finger and towards apex of movable finger. Historical use: granular area (Purcell, 1899: 385); granulations (Lawrence, 1972: 99); setal pores (Bernard, 1896: 323). Presence on prolateral surface only mentioned by Bernard (1896).

interdigital articular membrane (iam): Membrane connecting fixed and movable cheliceral fingers at joint, visible proximally adjacent to fond (fondal interdigital articular membrane, fiam) and ventrally between cheliceral segments (ventral interdigital articular membrane, viam) (Fig. 2B, Pl. 2); involved in articulation of fixed and movable fingers (Van der Meijden et al. 2012). Historical use: *weiche Bindehaut* (Roewer, 1934: 54, fig. 48); “less sclerotized cuticle”, referring to viam only (Klann and Alberti, 2010: 227, fig. 226E, G).

interdigital condyli: Two distinct, semi-circular articulation sclerites (condyli), devoid of setae (asetose areas), situated prolaterally (prolateral interdigital condyle, pic) and retrolaterally (retrolateral interdigital condyle, ric) at base of fixed (dorsal) finger

(Fig. 1, Pl. 2). Together forming bicondylar hinge through which fixed finger articulates with movable finger (Fig. 2A). Condyli connected to each other via the ventral manus plagula (vmp) (Fig. 2A). Historical use: *condyles* (Sørensen, 1914); *Condylus des Endringes* (Roewer, 1934: 54); external articulation sclerites (Muma, 1985: 2); two articulation points (Van der Meijden, 2012).

interdigital foramen: Circular opening on paturon where movable (ventral) finger attaches to manus through interdigital articular membrane, and articulates with manus through interdigital condyli (Pl. 3D–I).

macrosetae: Darker, more sclerotized setae that may be spiniform (rigid) or setiform (flexible). Historical use (spiniform setae): *Dornen* (Kraepelin, 1901: 8; Roewer, 1934: 121); spines (translation from German by Turk, 1960; used by Lawrence, 1956; Maury, 1985; Gromov, 2003b; Reddick et al., 2010; Cushing and Castro, 2012); spine-like setae (Muma, 1976; Wharton, 1981); spiniform (Botero-Trujillo, 2014), denticulate or spiculate, referring to “very short spine-like setae” (Wharton 1981: 9).

manus: Broad, largely setose, basal section of paturon (Fig. 1A). Use of manus consistent with usage in some arthropods (e.g., crustaceans). Transition from manus to fixed finger historically vague and arbitrarily defined. Roewer (1934: 152, fig. 154) described placement of bulbous base in Solpugidae as approximately where finger meets manus, shown in examples to be approximately dorsal to fondal teeth. Based on division of galeodid finger into *Endteil* and *Basalteil*, Birula (1937a) evidently regarded point between fixed finger proximal (FP) and fixed finger medial (FM) as start of finger. Wharton (1981: 42) considered fixed finger to start at distal end of fondal teeth. In present study, both fondal and median series teeth considered part of fixed finger, whereas interdigital condyli regarded as transition between manus and fixed finger (Fig. 1A). Retrolateral interdigital condyle (ric), a well defined landmark to indicate start of fixed finger, is critical for objective and repeatable comparisons of finger length. Historical use: bases of falces (Putnam, 1883: 255); *Stamm der Mandibeln* [base of chelicera] (Kraepelin, 1901); *Hand* (Roewer, 1934: 53); "verdickten Teil beider Mandibeln" (Birula, 1937a: 568); *mano* (Mello-Leitao, 1938); trunk (Fichter, 1940); *main* (Panouse, 1960b); basal segment (Van der Meijden et al., 2012).

medial notch (MN): Large toothless space on fixed finger, between fixed finger medial (FM) tooth and single fixed finger submedial (FSM) tooth situated close to fixed finger proximal (FP) tooth (Fig. 7C, D). Notch not considered homologous to eremobatid fondal notch because medial notch situated distal to proximal tooth (FP), i.e. within median series of teeth, and fondal notch situated proximal to fixed finger proximal (FP) teeth. Most prominent in Solpugidae (Fig. 7C). Diagnostic character for *Solpugema* Roewer, 1933 (Roewer, 1934: 420). Similarly positioned, but less pronounced toothless spaces in other Solpugidae, e.g., see use of *Zahnlücke* by Kraepelin (1901: 59) to describe small toothless spaces such as in *Solpugista hastata* (Kraepelin, 1899). Also present in Ammotrechidae (Fig. 7D), e.g., *Antillotrecha disjunctodens* Armas and Teruel, 2005, *Branchia angustus* Muma, 1951, *Branchia brevis* Muma, 1951, and apparently Karschiidae, e.g., *Eusimonia mirabilis* Roewer, 1932 (Roewer, 1934: 143, fig. 141C; Muma, 1951: 136, figs. 305, 306, 311; Armas and Teruel, 2005: 161, fig. 9C; Armas, 2010: 522, fig. 1F). Historical use: In Solpugidae: *Zahnlücke* (Kraepelin, 1901, 1908a); *weiten, zahnlosen Lücke* (Roewer, 1934: 420). In Ammotrechidae: "*el diastema entre los dientes anteriores y el intermedio*" (Armas, 2010: 522, fig. 1F).

median series teeth: All teeth on chelicera except fondal teeth on fixed finger; median series of fixed and movable fingers, respectively (Fig. 1A). Previously referred only to teeth on fixed finger, but also applied here to teeth on movable finger. Historical use: *canines plus incisives* (Dufour, 1861); distal series (Purcell, 1899: 404); single series (Purcell, 1899, 1902; Hewitt, 1914a: 155); outer/external series/row, including fondal teeth (Pocock, 1895; Birula, 1916; Lawrence, 1972); fang series (Lawrence, 1928: 262), median series (Wharton, 1981).

medioventral excrescence (MVE): Excrescence on ventral surface of fixed finger in male Melanoblossiinae (Pls. 156B, 157C, 158E, 159). Accommodates male flagellar complex and associated flagellar complex depression. Depending on species, excrescence may be slightly (Pl. 158C) or markedly (Pl. 156B) developed.

medioventral organ: Round to oval depression(s) situated medioventrally on stridulatory plate (Fig. 1C, Pl. 6B–D).

microsetae: Pale or transparent, weakly sclerotized setae. Uncommon or absent on chelicera.

movable finger fondal (*mff*) setae: Short series of plumose setae situated within fond (Pls. 2B, 12A, 13A); arise on proximal margin of movable finger, and more dense on prolateral surface of fond.

movable finger medial (MM) tooth: First primary tooth distal to proximal tooth, i.e., distalmost primary tooth, on movable finger (Pls. 21, 22A–D). Introduced for movable finger to correspond to terminology of fixed finger based on relative positions of fixed finger medial (FM) and movable finger medial (MM) teeth when fingers closed (Pl. 29). Historical use: *Vorderzähn* (Kraepelin, 1899, 1901; Roewer, 1934: 53; Kraus, 1966); “anterior tooth on movable finger” (Lawrence, 1968); fore tooth (El-Hennawy, 1998), anterior tooth, as *Ma* (Botero-Trujillo, 2014).

movable finger prodorsal (*mpd*) setae: Series of prolateral setae lining dorsal margin of setose area on movable finger, directly ventral to asetose area (Fig. 13, Pls. 12A, 13A, 24A, 15). Setae plumose or acuminate, usually directed anterodorsally at base.

movable finger prolateral setae: Prolateral setae on setose area of movable finger (Figs. 12, 13, Pls. 12A, 13A, C, 14A, 15). Comprises three series, i.e., movable finger prodorsal (*mpd*), promedial (*mpm*) and proventral (*mpv*) series. Historical use: mesal setae of movable finger (Muma, 1951); median patch of bristles (Wharton, 1981: 51).

movable finger prolateral (MPL) tooth: Small to well developed tooth situated prolaterally on movable (ventral) finger (Pls. 15B, 22C), slightly proximal to movable finger proximal (MP) tooth in both sexes of Ammotrechidae (Roewer, 1934: 54; Muma 1951; Armas, 1994), most Eremobatidae (Muma, 1951), Rhagodidae (Roewer, 1934: 54; pl. 3C), and few species of Solpugidae (Pls. 56A, C, 76C; Lawrence, 1954; 1961; Roewer, 1934: 429; Wharton, 1981). Historical use: “small tooth behind and on inner side of large tooth” (Pocock, 1889: 474), *Nebenzahn* (Kraepelin, 1901); *medialen Wangenzahn* [medial cheek tooth of movable finger] (Roewer, 1934); mesal tooth (Muma, 1951); “third tooth proximal to [rest of teeth on ventral finger] below level of anterior teeth” (Lawrence, 1954, for *Ferrandia robusta*); supernumerary tooth (Brookhart, 1965), not to be confused with mesal tooth referring to movable finger medial (MM) tooth in description of *Hemerotrecha fruitana* Muma, 1951; *diente parietal* *interno* (Maury, 1980a); *diente basal interno* (Maury, 1982); *basal interno* (*BI*) [of movable finger] (Maury, 1984); median tooth (Wharton, 1981).

movable finger promedial (*mpm*) setae: Series of prolateral setae situated between movable finger prodorsal (*mpd*) and movable finger proventral (*mpv*) setae on setose area of movable finger (Figs. 12, 13, Pls. 12A, 13A, C, 14A, 15). Setae acuminate, usually directed distally at base.

movable finger proventral (*mpv*) setae: Series of prolateral setae situated ventrally on setose area of movable finger (Figs. 12, 13, Pls. 12A, 13A, C, 14A, 15). Setae acuminate, sometimes more differentiated towards distal end of series (Fig. 13), often directed ventrodistal at base.

movable finger submedial (MSM) tooth/teeth: One or more secondary teeth situated between movable finger proximal (MP) and movable finger medial (MM) tooth (Pls. 21, 22A–D). Historical use: intermediate teeth (e.g., Kraepelin, 1899, 1901; Roewer, 1934: 53; Panouse, 1960b: 176, fig. 2; Maury, 1982, 1984; Martins et al., 2004); intermediate teeth, as Mi_1, Mi_2 (Botero-Trujillo, 2014).

movable finger subproximal (MSP) teeth: Secondary teeth situated proximal to movable finger prximal (MP) tooth (Pl. 22D).

movable finger subterminal (MST) teeth: Secondary teeth situated on movable finger mucron, i.e. between movable finger medial (MM) and movable finger terminal (MT) teeth (Pl. 22D).

movable (ventral) finger: Second (ventral) segment of chelicera; articulates with first (basal) cheliceral segment (paturon), opposing fixed finger (Fig. 1A). Historical use: See table 5.

mucron: Distal, usually toothless section of finger (Fig. 1A, 22D); portion of fixed and movable fingers distal to fixed finger distal (FD) and movable finger medial (MM) teeth respectively, as measured from notch directly distal to FD or MM respectively, to terminal tooth (tip of finger). When FD and/or MM absent, approximate position where FD or MM would be located inferred from its position in related taxa (see section on Dentition). However, proximal margin of mucron often neither identifiable, nor deducible, rendering comparison among well delimited mucra impossible. Historical use: terminal fang (Pocock, 1895: 84; Purcell, 1899, 1902; Hewitt, 1919b: 30; Lamoral, 1972); "toothless terminal portion of the dorsal jaw" (Lawrence, 1927: 67); *Endteil*; *unbezahntes Ende des Fingers* (Birula, 1937a), measured from anterior end of median series to tip of finger, see fixed finger for *Endteil* vs. *Basalteil*; *mucrón* (in Spanish literature, e.g., Maury, 1970; Rocha, 2002); mucron (in English literature, e.g., González Reyes and Corronca, 2013); untoothed finger (Hrušková-Martišová et al., 2010a). References to fang, mucron and apex of finger commonly used but not explicitly defined, especially not in manner facilitating comparison among homologous structures across taxa. Rocha (2002: 446) defined mucron as "distal portion of cheliceral fingers where there are no teeth". Applying this definition to fixed finger with additional toothlike flanges and denticles anterior to FD and MM on one hand (e.g., Pls. 59D, 92C), and absence of any or all primary teeth on the other, results in term mucron referring to structures unlikely to be homologous in different taxa, e.g., the use of terminal fang by Purcell (1899: 394) to describe the finger distal to the fondal teeth in an eremobatid chelicera (Purcell, 1899: 389, fig. 2). It is less ambiguous to define the mucron of the fixed and movable fingers on the basis of position relative to FD and MM, respectively, but at the expense of being difficult or impossible to identify its proximal border when these teeth are absent. See also “fang”.

mucron organ (mo): Small, round structure, paler than surrounding cuticle, prolaterally on mucron, slightly distal to fixed (dorsal) finger distal (FD) tooth. In both sexes in Galeodidae (Pl. 60A) and Solpugidae (Fig. 24B, Pl. 27E); observed in females and juveniles in Mummuciidae (Botero-Trujillo, personal commun.). Often difficult to detect. Might be present across the order. Commonly on shallow or small prodistally directed toothlike structure; in male Solpugidae, often combined with distally directed, toothlike flagellar groove process (FGP) (Fig. 24B, insert). Function and distribution among species unknown. Reference to “tooth” in Solpugidae, but no reference to organ in Galeodidae or Solpugidae. Historical use (for toothlike elevation in Solpugidae): *Zahnhöcker* (absent in *Solpuga erythronota* Kraepelin, 1900, currently placed in *Solpugema*) (Kraepelin, 1900: 6); “inner tooth on termimal fang” (Purcell, 1899).

multidentate: Dental pattern in which all teeth approximately equal in size, regularly spaced, and situated in relatively straight row on fixed (dorsal) and/or movable (ventral) fingers, in lateral view (Pl. 24R, fixed finger). Differentiation between median row of teeth and retrofondal teeth often obscured. Additional secondary teeth, mostly similar in size, often present proximal (MSP) and distal (FST, MST) to primary teeth in some Karschiidae, e.g., *Barrussus pentheri* (Werner, 1905) (Pl. 52C, D), Eremobatidae, e.g., *Horribates bantai* Muma, 1989 (Pl. 78C, D) and Melanoblossiinae, e.g., *Lawrencega minuta* Wharton, 1981 and *L. procera* Wharton, 1981 (Pl. 158B, F). Subproximal and subterminal secondary teeth can be slightly raised relative to preceding teeth in Melanoblossiinae, e.g., *L. solaris* Wharton, 1981 (Wharton, 1981: 53, fig. 55) and usually readily identified due to comparatively smaller size, forming denticle-like, serrated cutting edge. Historical use: “vielzähnig mit eineinzelnen grösseren Zähnen” for *Eusimonia* (Kraepelin, 1901).

paturon: First segment of solifuge chelicera, i.e., manus and fixed finger (Fig. 1A; Dunlop, 2000). Historical use: penultimate segment (Pocock, 1893); upper jaw (Purcell, 1899; Hewitt, 1919b: 33); *l’article basilaire* (Sørensen, 1914); basal segment of chelicera (Muma, 1951); fixed ramus (Dunlop, 2000); principal segment of chelicera (Klann and Alberti, 2010).

peduncle: Stem section of leaf-like flagellum in Galeodidae (Pls. 30D, 31E). Not considered homologous to flagellar stalk. Historical use: stem (Pocock, 1900b); *stiel* [stem] (Kraepelin, 1901; Birula, 1905a; Roewer, 1934: 508); stalk (Hirst, 1912); *Stiel des Flagellums* (Birula, 1905a); *stalk* or *peduncle* (Birula, 1916); *Füßchen* or *Füsschen* [foot] (Birula, 1929b: 276, fig. 2; 1937a); stalk (Lawrence, 1956: 129; Turk, 1960).

plumose setae: Feathered setae with distinct shaft, finely branched distally (Fig. 10B; Lawrence, 1956). Restricted to prolateral cheliceral surface and lateral lips of rostrum in Solifugae. Broadly applied by other authors, e.g., “plumose bristles” reported to protect stigmata of Karschiidae (Muma, 1976: 2), and palpal papillae being “well feathered” (Hewit, 1919b: 12). Most dorsal retrolateral proximal cluster (*rlpc*) seta may be weakly plumose. Historical use: *gewimperte Borste* (Birula, 1913: 352, fig. 3); *gefiederte Wangenborstenreihe* (Birula, 1913); plumose setae (Wharton, 1981).

primary flagellum: Distinctly modified and well differentiated ventral flagellar seta (*vfs*); hypothesized to be derived from apicalmost seta in proventral distal (*pvd*) series of setae (Pl. 46). In Karschiidae (*Barrus*, *Barrussus*, and *Eusimonia*), usually dorsally curved, more or less cylindrical structure (Pls. 30D, 31B). In Rhagodidae, ventral structure in diploflagellar complex (Pls. 30F, 31D). See also flagellum, or male flagellum. Historical use: In *Karschia* (Karschiidae): flagellum (Kraepelin, 1901: 145). In *Barrus*, *Barrussus* and *Eusimonia* (Karschiidae): flagellum (Simon, 1879: 128,129, 131; Kraepelin, 1901: 140; Hirst, 1908, 1910); *Viertelkreishorn* or *Horn* (Roewer, 1934; Pieper 1977); *Haken* (Birula, 1935a). In Gylippinae: flagellum (Kraepelin, 1901: 185). In Rhagodidae: flagellum (referring to both structures in diploflagellar complex, e.g. Kraepelin, 1901: 30; Roewer: 1934, 264).

primary teeth: Generally most differentiated (largest, often more sclerotized) teeth on cheliceral fingers (Pls. 21, 22A–D); Pocock, 1895). Three teeth on fixed finger (FP, FM, FD), two (MP, MM) on movable finger in unmodified condition (Pl. 22B). Historical use: *canines* (Dufour, 1861); *dents principals* (Simon, 1879); chief denticles (Birula, 1926); large teeth (e.g., Turk, 1948; Wharton, 1981); main teeth (e.g., Lawrence, 1965b, 1968).

principal retrolateral finger (*principal rlf*) setae: Modified dorsal retrolateral finger (*rlf*) setae (Fig. 14, Pl. 16A). Most distinct in daesiid genus, *Blossia*; one, two or three long, curved, tapering, non-plumose setae situated on retrodorsal surface of chelicera, slightly ventral to its dorsal margin, dorsal and distal to flagellum, directed distally and approximately parallel to fixed finger (Fig. 14, Pl. 144). Here considered to also include modified *rlf* setae in other taxa, e.g., two distinctly elongated setae in Galeodidae (Pl. 16A; Lawrence, 1954: 118). Historical use (in *Blossia*; generally referring only to dorsalmost modified seta even in presence of second, more ventral modified seta): “differentiated distal bristle” (Purcell, 1903a); distal dorsal bristle (Hewitt, 1914a, 1919a; Lawrence, 1928); *spiculierter Borste* [spiculed bristle] (Roewer, 1934: 152); spiculated bristle (Lawrence, 1935); “enlarged bristle on dorsal jaw” (Lawrence, 1955); *Seta principali*s (Roewer, 1941); principal seta (Lawrence, 1965a; Lamoral, 1972; Wharton, 1981; Reddick et al., 2010). Lawrence (1935: 75) recognized similarity between a slightly modified, more ventrally situated *rlf* seta and two dorsal “spiculated setae”, but did not regard these as possible serial homologs (also see Lawrence, 1935: 80, fig. 7); nor was a distinction recognized between “spiculated setae” situated retrolaterally on the chelicera as part of *rlf* setae and “spiculated setae” situated prolaterally on the chelicera as possible modified prolateral setae (e.g., Lawrence, 1935: 75, 76, figs. 3, 4). Note: “Principal setae” also used to refer to the flagella of Melanoblossiinae (*Seta principalis des Flagellum-Komplexes*, Roewer, 1941) and *Karschia* (*Seta principalis flagella*, Roewer, 1934: 291), the spiniform setae of the flagellar complex (*fcs*) of Gylippinae (Wharton, 1981), and the retrolateral manus spiniform seta (*rlms*) of Gylippinae (*Spina principalis*, Roewer, 1934: 308; principle [sic] spine, Koç, 2011: 120, fig. 3).

prodorsal cluster of spiniform setae (*pdcs*): Small field of short spiniform setae prodistally on fixed (dorsal) finger next to callus in some *Chelypus* Purcell, 1902 species (Pls. 32C, 33E).

pro- and retrolateral interdigital sockets: Sockets on movable finger into which pro- and retrolateral interdigital condyles rotate (Pl. 2, stippled line). Historical use: *Gelenkpfannen* [joint sockets] (Roewer, 1934: 54, fig. 49).

prodorsal distal margin (pddm): Dorsal margin of asetose area of fixed finger situated directly dorsal to prodorsal distal (*pdd*) row of setae (Fig. 1C).

prodorsal distal (*pdd*) setae: Dorsal row of distal setae, situated directly ventral to prodorsal distal margin (pddm) of asetose area on fixed finger (Pls. 12A, 13). *pdd* and *pvd* series connect distally at an angle; distalmost seta of *pvd* series (i.e., ventral flagellar seta) directly adjacent to distalmost seta of *pdd* series (i.e., dorsal flagellar seta). Flagella and associated modified setae in flagellar complex hypothesized to be derived from ventral flagellar seta (*vfs*) as part of *pvd* series (including precursor to primary flagellum), dorsal flagellar setae as part of *pdd* setae (including precursor to secondary flagellum). Generally, *pdd* setae hypothesized to give rise to modified flagellar complex subspiniform to spiniform (*fcs*) setae (Pls. 30B–D, G, H, 31A, B, E, F, 32B, H, 33C, I), when present.

prodorsal granular tooth: Granular structure parallel to medial tooth (MM) prodorsally on movable finger in *Hexisopus* Karsch, 1879 (Hexisopodidae) (Pls. 127E, 128A). Historical use: mesal ridge or row of denticles (Wharton, 1981: 48), well-rounded tubercle (Wharton, 1981:5); “small but distinct tooth dorso-medially at distal edge of median patch of bristles” (Wharton, 1981: 51).

prodorsal proximal (*pdp*) setae: One row and, in some taxa, a possible second less developed row, of setae on manus, extending longitudinally along prodorsal surface of chelicera (Fig. 11, Pls. 12A, 13, 14), often with prominent, elevated sockets in Eremobatidae and Gylippinae. Historical use: *Langsreihe von Borsten* (*lr*, Birula, 1913: 331, fig. 9; *l*, Birula, 1938: 81, fig. 52).

prodorsal serrate carina: Short ridge distal to the median series of teeth on movable finger, offset prolaterally from cutting edge, in Hexisopodidae (*Chelypus*) (Pl. 130F). Historical use: “row of minute inner teeth” (Purcell, 1902: 225); “serrated keels”, inner row of … teeth confined to the distal end of the fang", "row of minute teeth forming serrated ridge" (Lamoral, 1973: 90); "distally placed mesal ridge or row of denticles" (Wharton, 1981: 45).

profondal proximal (PFP) and profondal medial (PFM) teeth: Two most differentiated teeth in profondal row (Pls. 21A, 22E). Usually largest fondal tooth. Typically tall and narrow, separated by either a diastema (e.g. Maury, 1976) or small profondal submedial (PFSM) tooth. Single, rarely two, profondal subproximal tooth/teeth (PFSP) may be present, situated proximal to PFP.

prolateral dental process (PLDP): Prominent, carinate process on prolateral side of cutting edge of cheliceral finger, at flagellar base in Hexisopodidae (Pls. 130A, D, 131). In some species, process hinders or prevents movement of flagellum past a certain point of rotation. Hypothesized to be fused with primary teeth in *Hexisopus*. Historical use: In *Chelypus*: "tubercle immediately adjacent to basal enlargement of flagellum" (Hewitt, 1919c: 214). In *Hexisopus*: "slight proximal protuberance … bearing three small round teeth" (Lamoral, 1972: 120), "one tooth near base of flagellum" (Wharton, 1981: 52) and "low ridge adjacent to base of flagellum" (Wharton, 1981: 51).

prolateral interdigital condyli (pic): Semi-circular articulation sclerites (condyli) situated prolaterally at base of fixed (dorsal) finger (Figs. 1, 2, Pl. 2). See interdigital condyli.

prolateral setae: Setae on prolateral side of paturon (Pls. 12A, 13, 14); comprises different series and setal fields, i.e., proventral distal (*pvd*) series, proventral subdistal (*pvsd*) series, prodorsal distal (*pdd*) series, prodorsal proximal (*pdp*) series, prodorsal ventral (*pdv*) series, promedial proximal cluster (*pmpc*) of setae, and promedial (*pm*) setal field.

promedial proximal cluster (*pmpc*) of setae: Dense cluster of fine, hairlike, short setae at base of paturon directly dorsoproximal to stridulatory plate (Fig. 11C, D, Pls. 12A, 14B).

promedial (*pm*) setal field: Field of setae between stridulatory area and proventral subdistal (*pvsd*) setal comb (Pls. 12A, 13, 14); contains regularly-spaced stridulatory setae, when present, interspersed with less developed setae (Pls. 10, 11). Historical use: *Querreihe* [transverse row] (*qr*, Birula, 1913: 331, fig. 9); *Das Mittelfeld der Innerseite der mandibeln* (Birula, 1929a).

proventral distal margin (pvdm): Ventral margin of asetose area of fixed (dorsal) finger directly ventral to the proventral distal (*pvd*) row of setae (Fig. 1C).

proventral distal (*pvd*) setae: One to three, approximately regular rows of usually plumose setae lining ventral margin of fixed finger, from base to apex thereof (Pls. 12A, 13, 14); distalmost seta in series (ventral flagellar seta, *vfs*) hypothesized to be homologous to flagellum. Historical use: *gefiederte Wangenborstenreihe* [row of plumose cheek bristles] (Birula 1913: 331, fig. 9); *soies ramifiées* [plumose setae] (Sørensen, 1914: 177); feathered bristles (Hewitt, 1919b); dental row (Lawrence, 1960); feathered bristles, plumose setae (e.g., Wharton, 1981). References to modified (highly elongated) *pvd* setae ventral to flagellum of *Karschia* (Pls. 1A, 46A, 47B): *säbelborsten* [saber bristles] (Kraepelin, 1901: 147); *grand soies ramifiées serrées* [large plumose setae] (Sørensen, 1914: 174); *spinae zygomaticae* (Roewer, 1934: 291).

proventral (*pv*) setae: Narrow, longitudinal field of setae, usually sparsely arranged, along proventral surface of chelicerae, ventral to stridulatory plate (Pls. 12A, 14A).

proventral subdistal (*pvsd*) setae: Series of non-plumose, acuminate setae situated proximal and parallel to proventral distal (*pvd*) setae (Pls. 12A, 13, 14). Includes comb at base of series. Historical use: thickened smooth setae parallel to dental row (Lawrence, 1960).

proventral subdistal (*pvsd*) setal comb: Markedly differentiated, straight, apically pointed, rigid, and regularly spaced setae (Pls. 12A, 13, 14); part of proventral subdistal (*pvsd*) row of setae, situated proximally in *pvsd* row.

retrodorsal process (RDP): Retrodorsal process at base of fixed finger in Eremobatidae, specifically *palpisetulosus* group of *Eremobates* (Muma, 1951) (Fig. 7B). Varies from shallow peaked ridge (Pls. 68D, 69D) to pronounced, flange-like process (Pls. 68J, 69F). Historical use: dorsal process (Muma and Brookhart, 1988); ectodorsal process (Muma, 1951).

retrolateral convexity: Retrolateral curved elevation of cuticle adjacent to bulbous base of flagellum; in Solpugidae (Fig. 25A, as visible through transparent base).

retrofondal apical (RFA) tooth/teeth: One or more teeth in retrofondal row situated proximal to the fixed finger primary (FP) tooth and distal to the retrofondal medial (RFM) tooth (Pls. 21B, 22F).

retrofondal proximal (RFP) and retrofondal medial (RFM) teeth: Two usually most differentiated teeth in retrofondal row (Pls. 21B, 22E, F). Retrofondal proximal (RFP) tooth situated proximal or subproximal in retrofondal row; typically equilateral triangle and usually largest tooth in retrofondal row. Retrofondal medial tooth (RFM) distalmost tooth in retrofondal row. Homology of teeth distal to RFM and proximal to fixewd finger proximal (FP) tooth, e.g., in Rhagodidae, and of denticles in fondal notch in Eremobatidae, remains unclear.

retrolateral finger (*rlf*) setae: Series of elongated, distally directed setae, often extending beyond tips of cheliceral fingers, situated close to margin of asetose area on fixed finger (Fig. 14, Pls. 12, 16). In all species and lifestages of the order. Historical use: “oblique row of simple bristles, bases of which are in a line more or less parallel with the dental series” (Hewit, 1919b: 58: fig. 10); “irregular row of simple bristles, more or less parallel to dental series” (Lawrence, 1935: 75).

retrolateral interdigital condyli (ric): Semi-circular articulation sclerites (condyli) situated retrolaterally at base of fixed (dorsal) finger (Figs. 1, 2, Pl. 2). See interdigital condyli.

retrolateral manus (*rlm*) setae: Randomly situated setae on retrolateral to dorsal surface of cheliceral manus (Pls. 12B, 16). Less developed and homogeneous in females; various setiform and spiniform setae in males. In dorsal view, spiniform mactosetae usually arranged in row curving along proximal (“oblique row of 6–8 spine-like setae posteriorly [on chelicera]”, according to Wharton, 1981: 29) and retrolateral margins of chelicera (Pl. 17). Spiniform setae typically increasing in length and robustness proximally to distally. Historical use for spiniform setae in Gylippinae: *Nebendornen* (Birula, 1913: 332); *spina accessoriae* [accessory spines] (Roewer, 1934: 308); spiniform setae (Gromov, 1998).

retrolateral manus spiniform (*rlms*) seta: Robust, strongly spiniform and differentiated seta, situated dorsomedially on retrolateral surface of manus in some male Gylippinae; distally directed (usually prolaterally, seldom retrolaterally), apically blunt or comb-like, notched or spirally coiled (Pls. 33I, 85B, 86B; Roewer, 1934: 120, fig. 101e, f). Thickened seta reported in some females, in same position as seta in males (Pl. 36D; Birula, 1913: 324, fig. 1, plate VIII). Historical use: *auffallend starkem Dornenpaar auf der dorsalen Fläche der Mdb*. (Kraepelin, 1901: 184); *Mandibulardorn* (Birula, 1907b; *md* in Birula, 1913: 331, fig. 9); *Spina principales* [principal spines] (Roewer, 1934: 308); principle [sic] spine (Koç, 2011: 120, fig. 3); posterior main spine (as "true spines", Lawrence, 1953); mandibular spine (Gromov, 1998).

retrolateral proximal cluster (*rlpc*) of setae: Clump of setae on small setose area situated proximally on retrolateral surface of movable finger, at or near base of granular row extending along finger (Pls. 12B, 18, 19). Typically comprising cluster of setae aligned with granulation, and single seta situated dorsal to cluster. Historical use: ectal cheliceral cluster setae (ECCS) (Muma, 1985); cheliceral setae (Punzo, 1998a: 228, figs. 7–13).

retrolateral setae: Setae on retrolateral surface of paturon and movable (ventral) finger (Pls. 12B, 16). On paturon, may be divided into largely homogeneous, anteriorly projecting setae on finger (retrolateral finger setae, *rlf*), and various setae on manus (retrolateral manus setae, *rlm*). Retrolateral proximal cluster (*rlpc*) of setae on movable finger. No distinct difference in structure or position among setae situated dorsally to slightly prodorsally versus setae situated retrolaterally on chelicera, hence collectively grouped with respective retrolateral setae (Pl. 17).

scapus: Broad, laminate section of leaf-like flagellum in Galeodidae (e.g., Birula, 1916) (Pls. 30G, 31E). Historical use: blade (Pocock, 1900b; Hirst, 1912); *Plättchen*

(Kraepelin, 1901); *Lanzette* (Birula, 1905a; 1937a); *Löffel* [spoon] (Birula, 1929b: fig. 2); *Endlanzette* (Roewer, 1934: 508); expanded portion (Lawrence, 1956: 129); head (Turk, 1960: 114).

secondary flagellum: Modified dorsal flagellar seta (*dfs*) (Pls. 30D, F, 31B, D), cf. primary flagellum. In Karschiidae (*Barrussus* and *Eusimonia*): usually fan-like membranous structure. In Rhagodidae: dorsal structure in diploflagellar complex. Historical use: In *Barrussus* and *Eusimonia* (Karschiidae): *Lamelle* (Simon, 1879: 131); *das Plättchen* (Kraepelin, 1901: 140; 1908a); vertical lamina (Hirst, 1908: 247); “thin, hairy, wing-shaped plate” (Hirst, 1910: 368); *Flagellum* or *Flagellumplättchen* (Birula, 1935a); *Bläschenflagellum* (Roewer, 1934); *Bläschen-Flagellum* (Pieper, 1977). In Rhagodidae: flagellum, referring to both structures in diploflagellar complex (e.g. Kraepelin, 1901).

secondary teeth: Teeth smaller and less differentiated than primary teeth, situated proximal, intermediate, and distal to primary teeth (Pls. 21, 22). Historical use: incisors (Dufour, 1861); minor teeth (Pocock, 1900b: 142, fig. 49; Hirst, 1908); *Zwischenzähne* [intermediate teeth] (Kraepelin, 1899, 1901; Roewer, 1934: 53); intermediate teeth (Whittick, 1939; Muma, 1951; Turk, 1960; Lawrence, 1962a; El-Hennawy, 1998, Botero-Trujillo, 2014); *dent intermédiaire* (*DI*) [intermediate teeth] (Panouse 1960b); *intermedio* (*I*) (Maury, 1984); minor teeth (Pocock, 1900b). Many authors (e.g., Kraepelin, 1901; Roewer, 1934; Maury, 1982; El-Hennawy, 1998; Rocha and Carvalho, 2006; Carvalho et. al., 2010) restricted use of “intermediate teeth” to submedial teeth on fixed and movable fingers, and subsumed subdistal tooth under anterior teeth.

setae: Multicellular, hollow, often slender processes produced by epidermal cells, situated movably in membraneous sockets (Gorb, 2001; Gordh and Headrick, 2001), e.g., Fig. 10.

setiform flagellar complex (*sfc*): Type of flagellar complex observed in Eremobatidae (Pls. 37–39), Lipophaginae (Pl. 36A–F) and Melanoblossiinae (Pl. 36G–I). Comprises distinctly differentiated apical cluster of modified setae; all setae in complex, including flagellum (if present) setiform in appearance. If present, flagellum weakly differentiated from, and/or obscured by other setae in cluster. Flagellum present in some Melanoblossiinae and Eremobatidae; absent in Lipophaginae. Setiform flagellar complex (i.e., variously modified cluster of setae which may include flagellum) not to be equated with flagellum itself (i.e., single most differentiated seta derived from ventral flagellar seta, or *vfs*). Historical use: In Melanoblossiinae: *Flagellaren Borstengruppe* (Roewer, 1934: 139); *Flagellum-Komplex* (Roewer, 1941: 127) flagellum (Lawrence, 1972; Wharton, 1981; Gromov, 2003b). In Eremobatidae: “flagellum composed of one or more modified setae” (El-Hennawy, 1990: 26); flagellar complex (Muma, 1970a: 3; Brookhart and Cushing, 2004). In Lipophaginae: “(f)lagellum …consisting of modified plumose setae” (Wharton, 1981: 39); without flagellum (Hewitt, 1919b: 23); flagellum not distinguishable (Purcell, 1903a).

setiform flagellar complex, type A: Setiform flagellar complex comprising setae belonging to proventral distal (*pvd*) and prodorsal distal (*pdd*) series of setae; in Eremobatidae (Pls. 37–39; table 13). Flagellum, if present, setiform. Never composed of only modified *pvd* setae as in type B and type C *sfc*; may be composed of *pdd* setae only (Pl. 37D). In *Eremobates*, *Eremochelis* and, to a lesser extent, *Eremothera*, comprising dorsal series (modified *pdd* setae), ventral series (*pvd* setae) and, usually, setiform flagellum (modified ventral flagellar seta). Flagellar groove may be present. In other genera, e.g., *Chanbria*, *Eremocosta* Roewer, 1934, and *Eremorhax*, comprising similarly or differently modified setae originating from *pdd* setal series, with or without flagellum. Setae may be striated; if plumose, very weakly so. Historical use: *Pinsel* or *Borstenbüschels* (Roewer, 1934: 163); *Flagelo ... representado po un "complejo de pelos" modificados* (Maury, 1984: 74); flagellum complex of setae (Muma, 1951); "flagellum-complex" (Muma, 1970a: 3; Brookhart and Cushing, 2002: 85, 2008: 49); male flagellar setae (Gromov, 2003b). Occasionally simply referred to as "male cheliceral flagellum" (e.g., El-Hennawy, 1990: 24).

setiform flagellar complex, type B: Setiform flagellar complex, comprising similarly modified (but see *Bdellophaga angulata* Wharton, 1981, Pl. 36C–F), often plumose setae apparently originating from proventral distal (*pvd*) series; in Lipophaginae (Pl. 36A–F).

setiform flagellar complex, type C: Setiform flagellar complex comprising modified proventral distal (*pvd*) setae arranged into unit with distinct, genus-specific shapes (e.g., cf. PL. 36G, H, I; Wharton, 1981: 53), situated in broad, shallow depression, termed flagellar complex depression; in Melanoblossiinae. Flagellum appears to be present but identity of primary flagellar homolog uncertain (Pl. 36G–I).

setiform flagellar complex, dorsal series: Dorsal row or group of setae within setiform flagellar complex of Eremobatidae (Pl. 38A, B). Simple, tubular (e.g., *Eremobates*) to robust (e.g., *Hemerotrecha* Banks, 1903) setae, usually projecting distally and/or curving dorsally. Hypothesized to be homologous to prodorsal distal setae (*pdd*).

setiform flagellar complex, ventral series: Ventral row or group of setae within setiform flagellar complex of Eremobatidae (Pl. 38A, B). Setae usually plumose, and bent apically to cover ventral part of flagellar groove. Hypothesized to be homologous to proventral distal setae (*pvd*).

spine: Stiff, sharp, pointed and tapered unsocketed process without differentiation of cells, fixed immovably to body surface (Gorb, 2001; Gordh and Headrick, 2001). Type of cuticular protuberance (other examples include flanges, etc.). True spines rare in Solifugae, and on chelicera form hornlike or toothlike processes, e.g., in Karschiidae (Pl. 30D) and some Daesiidae, and tubercles on callus of Hexisopodidae (Fig. 6A, Pls. 129, 130B).

stylet-like finger: Apically tapering distal part of fixed finger. Dentition on stylet-shaped part usually absent, at most vestigial; common in male Eremobatidae (Pl. 65B, F, H, J) and Gylippinae (Pl. 85B).

stridulatory apparatus: All components putatively involved in stridulation, i.e., stridulatory plate, stridulatory ridges and stridulatory setae (Fig. 1C, Pl. 10; Hansen, 1893: 185). Historical use: stridulatory organ, including stridulatory setae (Hrušková-Martišová et al., 2008b); stridulatory organ, excluding stridulatory setae (Birula, 1913; Bayram et al., 2011).

stridulatory plate: Smooth, well defined area, devoid of setae, at base of chelicera on prolateral surface; stridulatory ridges may or may not be present (Figs. 1C, 24A, D, Pls. 8–10). Historical use: “plaque glabre de la face interne" (Dufour, 1861: 393); *Fläche* (Kraepelin, 1901); large, smooth area (Hewitt, 1913); stridulatory area (e.g., Hewitt, 1931); *Spiegelfläche* (Roewer, 1934: 52, fig. 47); stridulatory plate (Turk, 1960: 121).

stridulatory ridges: Approximately parallel, long, short, sometimes anastomosing ridges on stridulatory plate, aligned anteriorly with margin of plate (Figs. 1C, 24A, D, Pls. 8–10). Historical use: sharp keels (Hansen, 1893); horny ridges (Pocock, 1898); stridulatory ridges (Pocock, 1900b: 133); stridulatory ribs (Purcell, 1902); *Stridulationsriefen* [stridulatory ridges] (Kraepelin, 1901; Birula, 1913); fine furrows (Hewitt, 1912); stridulatory lamellae (Lawrence, 1966: 7); stridulatory organ/ridges (Wharton, 1981), stridulatory apparatus [refers to stridulatory ridges only] (Botero-Trujillo, 2014).

stridulatory setae: Regularly arranged setae within promedial setal field (Fig. 9, Pls. 10, 11; Turk, 1960), distinctly modified in Eremobatidae, Galeodidae and Rhagodidae. Modification typically comprises swollen base inserted almost parallel to cheliceral surface and long, thin, acuminate tips. Turk (1960) identified different types, i.e., galeodid type I (*arabs* type) (Fig. 9A, Pl. 11I), galeodid type II (*araneoides* type) (Fig. 9B, Pl.11G, H), galeodid type III (*medusae* type) (Fig. 9C), to which may be added an eremobatid type (Fig. 9E, Pl. 11E) and, similar to galeodid type II form, a rhagodid type (Fig. 9D, Pls. 10, 11F). Historical use: spiniform setae (Birula, 1925); *soies flagellées* (Benoit, 1964); spiny bristles (Dumortier, 1964); stridulatory hairs (Cloudsley-Thompson and Constantinou, 1984); stridulatory setae (Turk, 1960); stridulatory bristles (Hrušková-Martišová et al., 2008b).

subterminal flange (STF): Toothlike flange on cutting edge of dorsal finger between terminal tooth and distal tooth (FD) in Solpugidae (P. 109E, F) and Daesiidae

(Pls. 144B–F, 145B–F). Historical use: “zahnartig vorspringendem Eck” (for *Solpugema erythronota* (Kraepelin, 1900), *vide* Kraepelin, 1901).

supernumerary teeth: Obsolete term in solifuge dentition terminology. Historical use: supernumerary teeth described various teeth/denticles (see text), but most teeth to which previously applied may be assigned to one of dentition categories defined here.

ventral digital plagula (vdp): Asetose margin at base of movable finger, flanking ventral interdigital articular membrane (viam) distally (Pl. 2C, 6A).

ventral flagellar seta (v*fs*): Apicalmost seta of proventral distal (*pvd*) series; hypothesized precursor to primary male flagellum (Pls. 12A, 13, 46, 47).

ventral interdigital articular membrane (viam): see interdigital articular membrane (iam).

ventral manus plagula (vmp): Asetose, U-shaped excrescence on manus lining interdigital foramen ventrally, and flanking ventral interdigital articular membrane proximally (Fig. 1B, C, Pls. 2C, 6A). Connects pro- and retrolateral condyli. Historical use: *Chitinwulst* (Roewer, 1934: 55).

ventral notch (VN): Point where ventral side of movable (ventral) finger abruptly narrows towards apex, in Eremobatidae (Fig. 7B; Muma and Brookhart, 1988).

ventrodistal concavity: Oval, ventral to retrolateroventral hollow on asetose area of fixed finger of some male Eremobatidae, e.g., *Eremocosta titania* (Pls. 37C, 73B), *Hemerotrecha banksi* Brookhart and Cushing, 2008 (Brookhart and Cushing, 2008: 50, fig. 3). Historical use: groove (Muma, 1951), mesal ventral groove (Brookhart and Cushing, 2008: 50, fig. 3).

APPENDIX 3

CRITERIA FOR PRIMARY HOMOLOGY ASSESSMENT OF DENTITION IN MEDIAN SERIES

1. Structural; size and level of darkness: Primary teeth more differentiated (larger and darker) than secondary teeth.

   Corollary 1: Secondary teeth lost or reduced before primary teeth.

   Corollary 2: Primary teeth are lost distal to proximal.

   Corollary 3: Within-category of secondary teeth are lost in order of subordinate to principal (small to large).
2. Positional; relative to other primary teeth on finger: Movable finger: MP = proximalmost; MM = distalmost. Fixed finger: FP = proximalmost, first tooth after fondal teeth; FD = distalmost
3. Positional; relative to homolog on opposing finger: FP closes directly distal to MP, and FM to MM.
4. Corroboration between taxa and sexes; similarities in dental pattern and structures (e.g., flanges) between sexes and putatively related species.

LIST OF ABBREVIATIONS

Abbreviations referring to dentition or related terms are in capitals, those referring to setation in lowercase italics, and all other terms in lowercase.

BF, basifondal teeth

cgns, coxal gland nozzle setae

cgn, coxal gland nozzle

cgs, coxal gland setae

cpam, cheliceropeltidial articular membrane

cpc, cheliceropeltidial condyle

dfs, dorsal flagellar seta

ecpca, external cheliceropeltidial condylar attachment

fcp, flagellar complex plumose seta(e)

fcs, flagellar complex subspiniform or spiniform setae

FD, fixed finger, distal tooth

fg, flagellar groove

FG, flagellar groove process

fiam, fondal interdigital articular membrane

FM, fixed finger, medial tooth

FN, fondal notch

FP, fixed finger, proximal tooth

FSD, fixed finger, subdistal tooth/teeth

FSM, fixed finger, submedial tooth/teeth

FST, fixed finger, subterminal tooth/teeth

FT, fixed finger, terminal tooth

iam, interdigital articular membrane

lo, lyriform organ

mff, movable finger, fondal setae

MM, movable finger, medial tooth

MN, medial notch

MP, movable finger, proximal tooth

mpd, movable finger, prodorsal setae

MPL, movable finger, prolateral tooth

mpm, movable finger, promedial setae

mpv, movable finger, proventral setae

MSM, movable finger, submedial tooth/teeth

MSP, movable finger subproximal tooth/teeth

MST, movable finger subterminal teeth

MT, movable finger, terminal tooth

MVE, medioventral excrescence

mo, mucron organ

pdcs, prodorsal cluster of spiniform setae

pdd, prodorsal distal setae

pddm, prodorsal distal margin

pdp, prodorsal proximal setae

PF, profondal teeth

PFM, profondal medial tooth

PFP, profondal proximal tooth

PFSM, profondal submedial tooth

PFSP, profondal subproximal tooth

pic, prolateral interdigital condyle

PLDP, prolateral dental process

pm, promedial setae

principal rlf, principal retrolateral finger setae

pmpc, promedial proximal cluster of setae

pv, proventral setae

pvd, proventral distal setae

pvdm, proventral distal margin

pvsd, proventral subdistal setae

pvsd (comb), proventral subdistal setal comb

RDP, retrodorsal process

RFA, retrofondal apical tooth/teeth

RF, retrofondal teeth

RFM, retrofondal medial tooth

RFP, retrofondal proximal tooth

RFSM, retrofondal submedial tooth/teeth

RFSP, retrofondal subproximal tooth/teeth

ric, retrolateral interdigital condyle

rlf, retrolateral finger setae

rlm, retrolateral manus setae

rlms, retrolateral manus spiniform seta

rlpc, retrolateral proximal cluster of setae

sfc: setiform flagellar complex

STF, subterminal flange

vdp, ventral digital plagula

vfs, ventral flagellar seta

viam, ventral interdigital articular membrane

vmp, ventral manus plagula

VN, ventral notch on movable finger