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The systematics of Mantodea revisited: an updated classification incorporating multiple data sources (Insecta: Dictyoptera)

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Summary. After a brief synopsis of the history of mantodean classification, a re-organized systematic arrangement of extant praying mantids is provided. To overcome past homoplasy problems, a phylogenetic framework based on male genital structure was used, supplemented by published morphological, chromosomal and molecular data. As already noticed by previous authors, external morphology is highly homoplastic and does not provide useful systematic tools above subfamily level. In contrast, the morphology of male external genitalia is largely congruent with the results of recent molecular phylogenies, but contradicts the most widely used past systems. Additionally, some genital structures widely used for taxonomic purposes could be shown to be not homologous, most notably the distal process. Evolutionary transitions of the distal process and the phalloid apophysis across the mantodean phylogenetic tree are identified and named. The phalloid apophysis of many derived mantodeans shows a tendency towards bifurcation into an anterior and a posterior lobe. This and other observed genital traits are hypothesized to be an adaptation of males towards a stable copulatory grasp in groups exhibiting increased sexual dimorphism, associated with an increased risk for the male to be cannibalized during copulation. Genital characters allowed most genera to be unambiguously assigned to the major clades (superfamilies) recovered by our genital and previous molecular data. The few exceptions concern genera with secondarily simplified genitalia lacking diagnostic structures. Taxonomic literature is very heterogeneous, and several subfamilies yet lacking any modern revisionary treatment will need further refinement. To account for phylogenetic constraints, i.e. correct for past polyphyletic groupings, the number of families was elevated to 29, and the number of subfamilies to 60. We establish the new family Leptomantellidae, the new subfamilies Brancsikiinae and Deiphobinae, the new tribes Leptomiopterygini, Hagiomantini, Gonypetellini, Bolbellini, Epsomantini, Neomantini, Amantini, Armenini, Danuriellini, Deiphobini, Cotigaonopsini, Didymocoryphini, Oxyelaeini, Heterochaetulini, Rhodomantini and Pseudoxyopsidini, and the new subtribes Amphecostephanina, Bolbina, Tricondylomimina, Gonypetyllina, Antistiina, Toxomantina and Tarachomantina. New morphological diagnoses are provided for the currently recognized families. Despite a few yet to be solved problems, this work offers the urgently needed working base for future studies in Mantodean systematics, life history and ecology.

Resumé. La systématique des Mantodea revisitée : une classification actualisée intégrant plusieurs sources de données (Insecta : Dictyoptera). Après un bref aperçu de l'historique de la classification des Mantes, un arrangement réorganisé de la systématique de leurs espèces actuelles est proposé sur la base d'une trame phylogénétique établie en tenant compte des genitalia mâles en plus des données morphologiques, chromosomiques et moléculaires. Ainsi que cela avait déjà été remarqué par le passé, la morphologie externe est hautement homoplastique et ne fournit pas à elle seule des critères utilisables en systématique au-delà du niveau sous-famille, contrairement aux genitalia mâles qui sont largement congruents avec les résultats obtenus lors des récentes phylogénies moléculaires, mais qui sont partiellement en contradiction avec les systèmes utilisés auparavant. Cependant, certaines structures génitales largement utilisées en taxonomie peuvent se révéler non homologues, spécialement le processus distal. Les transitions évolutives de ce processus et de l'apophyse phalloïde sont identifiées et nommées. En particulier il y a une tendance dans divers groupes dérivés à une bifurcation de l'apophyse phalloïde en deux lobes, antérieur et postérieur, sans doute en rapport avec une adaptation dans les groupes à fort dimorphisme sexuel. À considérer aussi que dans certains cas les genitalia mâles peuvent être secondairement simplifiés et ne plus présenter de structures diagnostiques. Toutefois la littérature taxonomique est très hétérogène et divers groupes nécessiteraient encore des révisions. En prenant en considération les contraintes phylogénétiques pour corriger les groupements polyphylétiques du passé, le nombre des familles a dû être porté à 29 et celui des sous-familles à 60. Sont proposées la nouvelle famille des Leptomantellidae, les nouvelles sous-familles des Brancsikiinae et des Deiphobinae, les nouvelles tribus des Leptomiopterygini, des Hagiomantini, des Gonypetellini, des Bolbellini, des Epsomantini, des Neomantini, des Amantini, des Armenini, des Danuriellini, des Deiphobini, des Cotigaonopsini, des Didymocoryphini, des Oxyelaeini, des Heterochaetulini, des Rhodomantini et des Pseudoxyopsidini, et les nouvelles sous-tribus des Amphecostephanina, des Bolbina, des Tricondylomimina, des Gonypetyllina, des Antistiina, des Toxomantina et des Tarachomantina. Les diagnoses des différentes familles sont enfin rappelées avant la conclusion. En dépit de quelques problèmes non encore résolus, ce

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nouveau système de classification, dont le besoin urgent se faisait sentir, doit constituer une nouvelle base de départ pour les prochaines recherches en systématique, biologie et écologie des Mantodea.

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Keywords: praying mantids; natural classification; comparative anatomy; phylogeny; family group names

This [...] *plays into a misperception that you are not doing real science unless you are doing it on computers* (Kelly 2008).

One, admittedly subjective, test of a phylogeny for a biologist is that it must make sense according to various ecological, biogeographic and behavioural criteria (Huys & Boxshall 1991)

Already Beier (1935c) pointed out the difficulties systematists are faced with when trying to find a natural classification for praying mantids (Mantodea). Diverse morphological specializations and convergent developments obscure natural relationships and make it difficult to separate homologous from homoplastic characters (Handlirsch 1925, 1930; Beier 1964; Klass & Ehrmann 2005). Most authors agree that we are still far from a satisfying systematic arrangement in this order (Beier 1964, 1968b; Roy 1987, 1999b; Ehrmann 1997, 2002; Grimaldi & Engel 2005; Otte & Spearman 2005; Wieland 2006, 2013; Rivera 2010b).

It is useful at this point to give a brief history of classification of praying mantids (see also Roy 2014). At first Linnaeus (1758) treated *Mantis* as a "group" or subgenus of *Gryllus*; later, he elevated *Mantis* to genus level (Linnaeus 1767). However, at that time the taxon did not only encompass mantids, but also phasmids (Phasmatodea) and mantispids (Neuroptera, Mantispidae). This situation persisted until 1796, when Lichtenstein erected the genus *Phasma*. Shortly after, Illiger (1798) created *Empusa*, in addition to *Phyllium* and *Mantispa*, so that the different insect taxa confused since Linnaeus under the name of *Mantis* were finally separated (Lichtenstein 1802). Latreille (1802) was the first to consider mantids as a family.

Thunberg (1815) added *Gongylus*, and it is only in 1831 that nine other genera were added by Audinet-Serville. During the next decades several other genera and species were created, so that the number of valid names of the genus group was 36 with more than 100 species at the end of 1842, distributed in four families (Mantidae, Empusidae, Harpagidae and Acanthopsidae), the three latter named by Burmeister (1838).

Saussure (1872a) to Saussure (1872b) improved the classification of mantids by introducing tribes and subtribes, distributed in the two main groups "Nudipèdes" and "Lobipèdes", according to whether the mid and hind legs were simple or lobate.

The years that followed saw important contributions by Stål (1877), who distinguished six subfamilies, Westwood (1889) with 16 groups, Brunner de Wattenwyl (1893) with six tribes, and Kirby (1904) with eight subfamilies, before Giglio-Tos established 32 subfamilies in 1919, which he reprised and detailed in his monograph of 1927. This work was published posthumously and classified mantids into a single orthopteran family, Mantidae, with 32 subfamilies and 110 groups with the value of tribes. It also provided identification keys for most of the 1461 species in 393 genera known at the time. Even though Giglio-Tos' systematic arrangement was heavily criticized by his colleagues (Hebard 1920; Werner 1923; Handlirsch 1930; Beier 1934a, 1935b, 1964), his monograph remained the most important reference on Mantodean systematics for decades.

Handlirsch (1930) was the first to consider Chaeteessidae as a separate family, distinct from Mantidae, which he parted into 16 subfamilies. Shortly after, Beier (1934a, 1934b, 1934c, 1935a, 1935b, 1935c) completed the series "*Genera Insectorum*" for mantids, with nine subfamilies added to the three previously treated by Rehn (1911) and Giglio-Tos (1913, 1921).

The classification was reorganized by Chopard (1949), now with 13 families, among them Mantidae with a dozen of subfamilies. This classification was not followed by Beier (1964), who classified Mantodea into eight families: Chaeteessidae, Metallyticidae, Mantoididae, Amorphoscelidae, Eremiaphilidae, Hymenopodidae, Mantidae and Empusidae. The speciose families were further subdivided into subfamilies and tribes, several newly named. This classification was reprised by the same author in 1968, and was universally followed during subsequent years.

Nonetheless, some authors progressively proposed adjustments to this classification: Vickery & Kevan (1983), Roy (1987), Terra (1995), Ehrmann (1997) and Roy (1999b). The last classification in use was that of Ehrmann & Roy (in Ehrmann 2002) with 15 families, retained by Otte & Spearman (2005) after addition of two extinct families. A comparative overview of the most commonly used systems is given in Table 1.

However, recent DNA-based phylogenies (Svenson & Whiting 2004, 2009; Yager & Svenson 2008; Legendre et al. 2015; Svenson et al. 2015, 2016a, 2016b; Rivera & Svenson 2016; Svenson & Rodrigues 2017) were largely incongruent with current systematic classification, as most classic families and subfamilies turned out to be polyphyletic, finally confirming Beier's opinion from 1935 (Berg et al. 2011; Wieland & Schütte 2012; Wieland 2013). Systematists were now left with no useful tool to work with, since the external morphological characters used exclusively until today as a basis for

Table 1. A comparison of the most relevant classification systems of Mantodea.

Giglio-Tos (1919)	Handlirsch (1930)	Chopard (1949)	Beier (1964)	Ehrmann & Roy (in Ehrmann 2002)
Fam. Mantidae	**Ord. Mantodea**	**sOrd. Mantodea**	**Ord. Mantodea**	**Ord. Mantodea**
sF. Perlamantinae	Fam. Chaeteessidae	Fam. Amorphoscelidae	Fam. Chaeteessidae	Fam. Mantoididae
Paraoxypili		sF. Perlamantinae		
Perlamantes				
Sphaeromantes		sF. Paraoxypilinae		
Compsothespes				
sF. Eremiaphilinae	Fam. Mantidae	Fam. Mantoididae	Fam. Metallyticidae	Fam. Chaeteessidae
Metallytici	sF. Mantoidinae			
Mantoidae				
Eremiaphilae				
Humbertiellae				
Tarachodes				
Episcopi				
Pyrgomantes				
Dysaules				
Oxyophthalmi				
Orthoderae				
sF. Iridopteriginae	sF. Metallyticinae	Fam. Eremiaphilidae	Fam. Mantoididae	Fam. Metallyticidae
Tarachinae				
Iridopteriges				
Tropidomantes				
Nanomantes				
Stenomantes				
sF. Amelinae	sF. Choeradodinae	Fam. Orthoderidae	Fam. Amorphoscelidae	Fam. Amorphoscelidae
Ameles			sF. Amorphoscelinae	sF. Amorphoscelinae
Gonypetae			sF. Paraoxypilinae	sF. Perlamantinae
Chroicopterae				sF. Paraoxypilinae
sF. Compsomantinae	sF. Orthoderinae	Fam. Choeradodidae	Fam. Eremiaphilidae	Fam. Eremiaphilidae
Compsomantes				
sF. Dystactinae	sF. Eremiaphilinae	Fam. Deroplatyidae	Fam. Hymenopodidae	Fam. Acanthopodidae
Distactae			sF. Acromantinae	sF. Acanthopinae
			Tribe Epaphroditini	
			Tribe Acontistini	sF. Acontiothespinae
			Tribe Acromantini	
				sF. Stenophyllinae
			sF. Hymenopodinae	
sF. Miopteriginae	sF. Mantinae	Fam. Thespidae		Fam. Hymenopodidae
Miopteriges	Humbertiellae		sF. Oxypilinae	sF. Epaphroditinae
	Tarachinae			
	Iridopteriges			sF. Acromantinae
	Tropidomantes			
	Nanomantes			sF. Oxypilinae
	Stenomantes			
	Ameles			sF. Hymenopodinae
	Gonypetae			
sF. Parathespinae	Chroicopterae	Fam. Mantidae	Fam. Mantidae	Fam. Liturgusidae
Musoniae	Compsomantes		sF. Orthoderinae	
Parathespes	Distactae		sF. Choeradodinae	
Hoplocoryphae	Miopteriges		sF. Tarachodinae	Fam. Tarachodidae
sF. Thespinae	Musoniae		sF. Liturgusinae	sF. Tarachodinae
Euchomenellae	Parathespes		sF. Caliridinae	sF. Caliridinae
Schizocephalae	Hoplocoryphae		sF. Thespinae	
Leptocolae	Euchomenellae		Tribe Pseudomiopterygini	
Thespes	Schizocephalae		Tribe Thespini	
sF. Pseudomiopteriginae	Leptocolae		Tribe Parathespini	
Pseudomiopteriges	Thespes		Tribe Hoplocoryphini	
sF. Oxypilinae	Pseudomiopteriges		sF. Oligonychinae	
Oxypili	Oxyothespes		Tribe Oligonychini	
			Tribe Pogonogasterini	
			sF. Haaniinae	

(*continued*)

Table 1. (*Continued*).

Giglio-Tos (1919)	Handlirsch (1930)	Chopard (1949)	Beier (1964)	Ehrmann & Roy (in Ehrmann 2002)
	Liturgusae			Fam. Thespidae
	Dactylopteriges		sF. Oxyothespinae	sF. Pseudomiopteriginae
sF. Oligonicinae	Gonatistellae		sF. Angelinae	sF. Miopteryginae
Oligonices	Calirides		sF. Schizocephalinae	sF. Thespinae
Haaniae	Deromantes		sF. Compsothespinae	Tribe Thespini
sF. Oxyothespinae	Leptomantes		sF. Iridopteryginae	Tribe Parathespini
Oxyothespes	Majangae		Tribe Hapalomantini	sF. Hoplocoryphinae
sF. Liturgusinae	Mellierae		Tribe Iridopterygini	sF. Oligonicinae
Liturgusae	Mellierellae		Tribe Tropidomantini	Tribe Oligonicini
Dactylopteriges	Coptopteriges		sF. Amelinae	Tribe Pogonogasterini
Gonatistellae	Photinae			sF. Haaninae
	Orthoderellae			
	Irides			
	Trachymantes			
sF. Sibyllinae	Sphodropodae			
Arriae	Parasphendales			
Sibyllae	Phyllomantes			
	Cilniae			
sF. Caliridinae	Callimantes		Tribe Dystactini	Fam. Iridopterygidae
Calirides	Stagmomantes		Tribe Amelini	sF. Hapalomantinae
Deromantes	Phasmomantes		sF. Mantinae	sF. Iridopteryginae
Leptomantes	Bisanthes		Tribe Mantini	sF. Nanomantinae
	Polyspilotae		Tribe Miomantini	Tribe Nanomantini
	Mantes		Tribe Archimantini	Tribe Fulcinini
	Tenoderae		sF. Vatinae	sF. Nilomantinae
	Hierodulae		Tribe Stagmatopterini	sF. Tropidomantinae
	Archimantes		Tribe Vatini	Fam. Mantidae
	Pseudomantes		Tribe Heterochaetini	sF. Orthoderinae
	Solygiae		Tribe Danuriini	
	Fischeriae			sF. Oxyothespinae
	Euchomenae			Tribe Paraseveriniini
	Ischnomantes			
	Pseudempusae			Tribe Oxyothespini
	Omomantes			sF. Angelinae
	Sphaeromantes			sF. Schizocephalinae
	Arriae			
				sF. Compsothespinae
				sF. Chroicopterinae
sF. Majanginae	sF. Sibyllinae	Fam. Metallyticidae	sF. Photininae	
Majangae			Tribe Photinini	
sF. Mellierinae			Tribe Coptopterygini	
Mellierae			sF. Deroplatinae	
Mellierellae			Tribe Deroplatini	
sF. Photininae			Tribe Parablepharini	
Coptopteriges			sF. Phyllotheliinae	
Photinae			sF. Sibyllinae	
Orthoderellae			sF. Toxoderinae	
Irides			Tribe Toxoderini	
			Tribe Stenophyllini	
	sF. Empusinae			sF. Dystactinae
	sF. Pyrgomentinae [sic]			sF. Amelinae
	Tarachodes			sF. Mantinae
	Episcopi			Tribe Polyspilotini
	Pyrgomantes			Tribe Paramantini
	Dysaules			Tribe Archimantini
	sF. Deroplatinae			Tribe Mantini

(*continued*)

Table 1. (*Continued*).

Giglio-Tos (1919)	Handlirsch (1930)	Chopard (1949)	Beier (1964)	Ehrmann & Roy (in Ehrmann 2002)
				sF. Miomantinae
				Tribe Miomantini
				Tribe Rivetinini
				sF. Stagmomantinae
				sF. Mellierinae
				sF. Stagmatopterinae
				sF. Vatinae
				Tribe Vatini
				Tribe Heterochaetini
				Tribe Danuriini
sF. Choeradodinae				
Choeradodes				
sF. Deroplatinae				
Deroplates				
sF. Mantinae	Fulcininae			
Trachymantes	sF. Oligonycinae			
Sphodropodae	Oligonyces			
Parasphendales	Haaniae			
Phyllomantes				
Cilniae				
Callimantes	sF. Compsothespinae			
Stagmomantes				
Phasmomantes				
Bisanthes				
Polypilotae				
Mantes				
Tenoderae				
Hierodulae				
sF. Archimantinae				
Archimantes				
Pseudomantes				
sF. Solygiinae				
Solygiae				
sF. Fischeriinae		Fam. Hymenopodidae		sF. Antemninae
Fischeriae				sF. Photininae
Euchomenae				Tribe Photinini
Ischnomantes				Tribe Coptopterygini
Pseudempusae				sF. Choeradodinae
Omomantes				sF. Deroplatyinae
sF. Acontistinae				sF. Phyllotheliinae
Acontistae				
Callibiae				
	sF. Amorphoscelinae			
	Paraoxypili			
	Perlamantes			
	sF. Hymenopodidae			
	Oxypili			
	Acontistae			
	Callibiae			
	Epaphroditae			
	Parablephares			
	Phyllocraniae			
	Anaxarchae			
	Acromantes			

(*continued*)

Table 1. (*Continued*).

Giglio-Tos (1919)	Handlirsch (1930)	Chopard (1949)	Beier (1964)	Ehrmann & Roy (in Ehrmann 2002)
	Ambiviae			
	Phyllothelides			
	Galinthiades			
sF. Epaphroditinae				Fam. Toxoderidae
Epaphroditae	Antissae			Tribe Toxoderopsini
Parablephares	Hestiasulae			Tribe Aethalochroaini
Phyllocraniae	Otomantes			Tribe Toxoderini
	Panurgicae			
	Hymenopoda			
	Pseudocreobotrae			
sF. Acromantinae				Fam. Sibyllidae
Anaxarchae				
Acromantes				
Ambiviae				
Phyllothelides				
Galinthiades				
sF. Hymenopodinae				
Antissae				
Hestiasulae				
Otomantes				
Panurgicae				
Hymenopoda				
Pseudocreobotrae				
sF. Toxoderinae		Fam. Toxoderidae		
Paradanuriae				
Toxoderae				
Loxomantes				
Calamothespes				
Stenophyllae				
sF. Vatinae				
Cardiopterae	sF. Vatinae	Fam. Vatidae		
Oxyopsides	Cardiopterae			
Stagmatopterae	Stagmatopterae			
Vates	Vatides			
Heterochaetae	Pseuempusae			
Ceratocraniae	Heterochaetae			
Aethalochroae	Popae			
Danuriae	Jallae			
Popae				
sF. Empusinae	sF. Toxoderinae	Fam. Empusidae	Fam. Empusidae	Fam. Empusidae
Empusae	Paradanuriae		sF. Empusinae	sF. Empusinae
Blepharodes	Toxoderae		sF. Blepharodinae	Tribe Idolomorphini
Idola	Loxomantes			Tribe Empusini
	Calamothespes			sF. Blepharodinae
	Stenophyllae			Tribe Blepharodini
	Aethalochroae			Tribe Idolomantini
Total number of genera 388	-	-	-	**434**
Total number of species 1364	-	**~1800**	**~1700**	**~2300**

classification in Mantodea were shown to be indeed highly homoplastic, a consequence of convergent evolution of unrelated mantid lineages into similar ecomorphs. Hughes-Schrader (1953) was one of the first to recognize the need for a multidisciplinary approach in mantodean systematics: "In several areas of mantid systematics an underlying basic relationship has become masked by striking morphological specializations; it is precisely here, in the evaluation of such characters, that evidence from allied fields can be most useful in the development of an evolutionarily significant classification". Molecular results, and recent advances in mantodean comparative morphology, physiology and behavior (e.g. Wieland 2006; Hill 2007; Holwell et al. 2007a; Yager & Svenson 2008; Faucheux 2009; Koehler & Predel 2010; Watanabe & Yano 2010; Prete et al. 2011, 2012, 2013, Wipfler et al. 2011; Allen et al. 2013), confirmed the unsatisfactory state of the current system, and underlined the necessity of a new approach in mantodean systematics.

We here present a new, updated classification for extant Mantodea compiled from morphological, chromosomal and molecular data.

Methods

Published data

We have consulted all available literature providing good morphological and cytogenetic data in a phylogenetic or taxonomic context, in addition to recent molecular-based phylogenies. We focused on unambiguous and unique characters, particularly for the basal dichotomies. The highly homoplastic nature of most external morphological characters rendered them generally useless above subfamily level, with some notable exceptions (e.g. the cyclopean ear). However, the morphology of the male genitalia turned out to be highly conserved and in concordance with most of the major clades obtained by recent molecular analyses. Genital traits do not only provide a taxonomic tool, as used so far, but allow valuable insights at a broader systematic-phylogenetic level as well. They also allowed us to fit into the system those genera which were omitted by molecular studies. However, not all groups have been equally well studied in this regard in the past; certain subfamilies or tribes await further refinement. In detail, we have considered the following publications (in addition to original descriptions):

Phylogeny: Klass (1997), Grimaldi (2003), Svenson (2007), Yager & Svenson (2008), Svenson & Whiting (2004, 2009), Wieland (2013), Misof et al. (2014), Legendre et al. (2015), Tong et al. (2015), Svenson et al. 2015, 2016a, 2016b, Agudelo (2015), Rivera & Svenson (2016), Svenson & Rodrigues (2017).

Chromosomes: King (1931), Asana (1934), Williams (1938), White (1940, 1941, 1951, 1965, 1975), Hughes-Schrader (1943a, 1943b, 1950, 1953), Matthey (1949), Gupta (1964, 1966, 1975), Singh & Kacker (1978), Orozco et al. (1980), Liebenberg et al. (1991), Orozco (1992).

External morphology: Westwood (1889), Wood-Mason (1889, 1891), Saussure & Zehntner (1894, 1895), Rehn (1911), Giglio-Tos (1913, 1921, 1927), Beier (1934a, 1934b, 1934c, 1935a, 1935b, 1935c), Terra (1982, 1995), Ehrmann (2002), Yager & Svenson (2008), Wieland (2006, 2013), Béthoux & Wieland (2009), Gorochov (2013), Svenson et al. (2015), Bai et al. (2016), Brannoch et al. (2017).

Genitalia: Chopard (1914, 1920), Hinton (1939), Beier (1950), Beier (1953a, 1953b), Beier (1954), La Greca (1954a, 1954b), Beier (1955), La Greca (1955a, 1955b, 1955c), La Greca (1956a, 1956b), Beier (1957a, 1957b), Paulian (1957, 1958), Heitzmann (1959, 1962), Roy (1962a, 1962b), Kaltenbach (1963), Roy (1963a, 1963b), Beier (1963), Mistshenko (1964), Roy (1964a, 1964b), Heitzmann-Fontenelle (1965), Roy (1965a, 1965b), Beier (1966), La Greca (1966), Roy (1966a, 1966b, 1966c, 1966d), Ragge & Roy (1967), Roy (1967a, 1967b, 1967c), Beier (1968a), Gillon & Roy (1968), Roy (1968a, 1968b), Beier (1969a, 1969b), Heitzmann-Fontenelle (1969), Roy (1969, 1970, 1971, 1972, 1973, 1975), Kis (1973), Roy & Leston (1975), La Greca (1977), Roy (1977a), Balderson (1978), Yamasaki (1981), Kaltenbach (1982), Kaltenbach (1983), La Greca & Lombardo (1983, 1984), Roy (1984), Lombardo (1986a, 1986c, 1986d), Prost & Roy (1986), La Greca & Lombardo (1987a, 1987b, 1988a, 1988b), Zhang (1988), Lombardo (1989), Milledge (1989), Roy (1989), Kaltenbach (1990), La Greca & Lombardo (1990), Lombardo (1990), Milledge (1990), Ramsay (1990), Kaltenbach (1991), Lombardo (1991), Roy (1991), Cerdà (1992), Jantsch (1992), Lombardo (1992a, 1992b), Cerdá (1993), La Greca & Lombardo (1993), Lombardo (1993a, 1993b), Roy (1993), Wang (1993), Kaltenbach (1994), Jantsch (1994a, 1994b, 1995), Lombardo (1995a, 1995b), Roy (1995), Kaltenbach (1996), Lombardo (1996), Roy (1996), Çiplak & Demirsoy (1997), Klass (1997), La Greca & Lombardo (1997), Lombardo (1997), Milledge (1997), Yang (1997), Anisyutkin (1998), Kaltenbach (1998), Lombardo (1998), Lombardo & Ayala (1999), Lombardo (1999), Roy (1999a), Yang & Wang (1999), Lombardo (2000a, 2000b), Soomro & Soomro (2000), Roy (2000), Lombardo & Agabiti (2001), Roy (2001, 2002a, 2002b, 2002c, 2002d, 2002e), Yang (2002), Agudelo & Chica (2003a, 2003b), Rivera (2003), Roy (2003a, 2003b, 2003c, 2003d), Ippolito & Lombardo (2004), Lombardo & Ippolito (2004), Lombardo & Marletta (2004), Lombardo & Perez-Gelabert (2004), Roy (2004a, 2004b, 2004c, 2004d), Stiewe (2004), Anisyutkin (2005), Anisyutkin & Gorochov (2005), Ariza & Salazar (2005), Battiston & Fontana (2005), Battiston et al. (2005), Mériguet (2005), Milledge (2005), Rivera (2005), Roy (2005a, 2005b, 2005c), Ghate et al. (2006), Mukherjee et al. (2006), Orofino et al. (2006), Roy (2006a), Holwell et al. (2007b), Ippolito (2007), Roy (2007a, 2007b), Roy & Svenson (2007), Stiewe (2007), Xu (2007), Anisyutkin (2008), Battiston & Picciau (2008a, 2008b), Bragg (2008), Roy (2008a, 2008b), Ehrmann & Roy (2009), Jensen et al. (2009), Roy (2009a, 2009b, 2009c), Roy & Ehrmann (2009), Roy & Stiewe (2009), Vyjayandi et al. (2009), Agabiti et al. (2010), Battiston et al. (2010), Bragg (2010), Mukherjee & Ghate (2010), Rivera (2010a), Roy (2011), Stiewe & Roy (2010), Berg et al. (2011), Lombardo & Umbriaco (2011), Medellín & Salazar (2011), Rivera et al. (2011), Roy & Schütte (2010), Roy & Stiewe (2011), Roy & Svenson (2011), Svenson & Roy (2011), Ippolito & Lombardo (2012), da Cruz Menezes & Bravo (2012), Roy (2012), Shcherbakov (2012), da Cruz Menezes & Bravo (2013), Lombardo et al. (2013), Mériguet (2013), Roy (2013a, 2013b, 2013d), Roy & Stiewe (2013), Svenson (2014), Lombardo et al. (2014), Holwell (2014), Milledge (2014),

Battiston et al. (2014), Roy & Stiewe (2014), Svenson & Vollmer (2014), Schwarz & Helmkampf (2014), Lombardo et al. (2014), Agudelo (2014), Scherrer (2014), Roy & Ehrmann (2014b), Agudelo & Rafael (2014), Roy & Schwarz (2014), da Cruz Menezes & Bravo (2015), Agudelo & Rivera (2015), Schwarz (2015), Shcherbakov & Savitsky (2015), Roy (2015), Maldaner et al. (2015), François & Roy (2015), Ippolito & Lombardo (2015), Agudelo (2015), Brannoch & Svenson (2016a, 2016b), Hashimoto et al. (2016), Rivera & Svenson (2016), Roy & Stiewe (2016), Shcherbakov et al. (2016), Roy & Schütte (2016), Roy (2016), Rodrigues & Cancello (2016), Chatterjee et al. (2016), Roy (2017), Wu & Liu (2017), Schwarz (2017), Stiewe & Shcherbakov (2017), Rodrigues et al. (2017), Schwarz & Shcherbakov (2017), Maldaner & Rafael (2017), Roy & Stiewe (2017), Shcherbakov (2017), Rodrigues & Svenson (2017), Battiston et al. (2018), Shcherbakov & Anisyutkin (2018), Vermeersch (2018), Schwarz et al. (2018), Mériguet (2018), Schwarz & Roy (2018).

Genitalia preparations

In addition to published genital data, we used own genitalia preparations, many of which are depicted here for the first time. Abdomen apices were macerated in cold KOH solution for 12–48 h, or gently boiled for a few minutes under constant supervision, then neutralized with acetic acid, washed in demineralized water, and dehydrated in 70% ethanol and 96% ethanol. Terminalia were separated into supra-anal and sub-genital parts, the phallomeres were spread without overlapping, then all parts were embedded in Euparal on a numbered slide provided with the data of the specimen. The genitalia are presented in figures, usually in ventral view, with some exceptions. Homologous structures are named consistently throughout the figures. For genital structures and definitions see Chopard (1920), Snodgrass (1937, 1957), La Greca (1955c), Klass (1997), and Brannoch et al. (2017) (but see below). Forewing nomenclature follows Béthoux & Wieland (2009).

Bringing the system together

We compiled our system using all available information provided by the four datasets. The published information on male genitalia in addition to our own genitalia preparations allowed us to carry out the most exhaustive comparative study of mantodean genitalia ever attempted, covering all families and subfamilies recognized by us. Published molecular, chromosomal and morphological data as well as our own morphological studies were used for further refinement. We favored a comparative and evolutionary approach, and the principles and argumentation scheme of phylogenetic systematics (Hennig 1965, 1966), over a character matrix and probability calculations. As long as shared derived characters (apomorphies) are used to designate relationships, a Hennigian approach is not inferior to algorithm-based methods (Slater 1984; Wägele & Wetzel 1994; Bechly 2000; Dayrat 2005; Wheeler & Valdecasas 2007; Klausnitzer 2010). Even though our aim was not to provide a full-resolution phylogeny, our phylogenetic frame is based on clear, polarized apomorphies, which are named and discussed, and as such provide a solid base for the proposed systematic classification.

Our holistic approach includes data from studies gained by both comparative and cladistic methods. We think that only complementary techniques may yield satisfying results in this group of insects where relationships are obscured by highly variable morphologies, and homoplasies are the rule rather than the exception (see Wheeler 2008). It turned out that the phylogenetic frame gained from the morphological and chromosomal characters used by us was largely congruent with the molecular phylogenetic trees depicted in Svenson & Whiting (2009), Svenson et al. (2015), Rivera & Svenson (2016), and, to lesser degrees, Yager & Svenson (2008), Legendre et al. (2015), and Svenson & Rodrigues (2017). This is, for instance, the case with basal nodes (in case of *Metallyticus* with the second alternative proposed by Svenson & Whiting 2009). In a few instances, particularly at more terminal nodes, morphological characters were in conflict with molecular data. Generally, we have given priority to our own comparative genital data, since they provide testable hypotheses in form of apomorphies supporting the respective systematic placement, and because in most of those cases molecular results were in conflict as well. When morphological and genital data provided no further refinement, however, but two or more molecular analyses congruently resolved the respective subgroup, we have incorporated the results into our system.

The system is hierarchically organized. Each clade above tribe level has been unambiguously assigned to a certain position in the proposed phylogeny. This position is coded in abbreviated form at the beginning of the line: for example, the family Amorphoscelidae is coded as "$2_4.1.2_2.1$." which corresponds to node 2.2.2.2.1.2.2.1 in the dichotomous phylogeny. However, we have not taken a purely cladistic approach to classification, so families and particularly subfamilies of speciose families are not always of the same phylogenetic rank. Although we are aware of the criticisms this may cause, our opinion is that a classification system has to facilitate taxonomic work in the first place, and at the same time provide enough resolution to allow an assessment of diversity and speciation patterns. Or, to cite D. Keith McE. Kevan (1961): "Classification should be based on phylogeny, not ruled by it". As long as the prerequisite of monophyla is met (as opposed to cladistic holophyla), it is more conceivable to assign all major clades of a highly diversified family to their respective subfamily, than to strictly stick to cladistic classification and lose resolution in derived groups due to collapsing clades and lack of available family group names (see Benton 2000; Mayr & Bock 2002; Brummitt 2006 for a thorough discussion of the matter). A similar approach has recently been taken by Svenson et al. (2015) and Rivera & Svenson (2016). Further, and against opinions frequently raised by phylogenetists, we have decided to name clades above the family group. We chose this approach to mark important dichotomies, particularly since we provide synapomorphies for most of the supra-familial clades. For any given group, this provides a more stable classification even if future studies may justify a different phylogenetic placement of one of its subgroups.

Explanations and apomorphies are given in the annotations. We have validated important monophyletic groups by naming synapomorphies, which was largely possible for genital traits, less so for external morphological characters. Polarization of

characters is provided by adding the plesiomorphic condition (in italics) in brackets just behind the respective apomorphy.

External morphology provided useful criteria only below family (species-poor groups) or subfamily (species-rich groups) level. Despite recent advances in morphologically based cladistic phylogeny (Wieland 2013), the obtained topology is plagued by homoplasies and not just incongruent with genital, molecular or chromosomal data, but even with classic systematic arrangements (Giglio-Tos 1927; Beier 1964; Ehrmann 2002), and as such not followed here. At sub-familial resolution, however, external morphological characters offered useful criteria equivalent to those provided by genitalia.

To provide a quick overview on distribution, geographic acronyms are given behind each genus.

Abbreviations

Morphology: We have retained and, where necessary, modified the Klass (1997) terminology for genital structures of interest to facilitate comparison: **afa** = phalloid apophysis; **aafa** = anterior lobe of phalloid apophysis of Cernomantodea; **paa** = apical process of left phallomere, titillator; **bl** = basal lobe of ventral phallomere; **dll** = dorsal lamina lobe of Thespidae; **fl** = flagellum; **loa** = membranous lobe; **pafa** = posterior lobe of phalloid apophysis of Cernomantodea; **pda** = primary distal process; **sdp** = secondary distal process of Schizomantodea; **sdpl** = lateral secondary distal process of Cernomantodea; **sdpm** = median secondary distal process of Cernomantodea; **tdp** = tertiary distal process of Tarachodina; **vla** = ventral lobe of ventral phallomere.

Distribution: **AN** = Antillean Region; **AT** = Afrotropics, excluding Madagascar; **AU** = Australasia; **MD** = Madagascar, including islands of the Western Indian Ocean; **NA** = Nearctic; **NT** = Neotropics, excluding the Antilles; **OR** = Oriental; **PL** = Palearctic.

Institutions and collections: **CS** = first author's personal collection; **MFN** = Museum für Naturkunde, Berlin, Germany; **MNHN** = Muséum national d'Histoire naturelle, Paris, France; **NHM** = The Natural History Museum, London, UK; **NMB** = Naturhistorisches Museum Basel, Switzerland; **NRM** = Naturhistoriska Riksmuseet Stockholm, Sweden; **PMN** = Pfalzmuseum Bad Dürkheim, Germany; **SMNK** = Staatliches Museum für Naturkunde Karlsruhe, Germany; **TS** = Tobias Schulze's collection; **ZMH** = Biozentrum Grindel und Zoologisches Museum, Hamburg, Germany.

Phylogeny: **MRCA** = Most recent common ancestor.

The system

Mantodea Latreille, 1802[1]
→ → fossil Mesozoic taxa
Eumantodea *sensu* Grimaldi, 2003, *nec* Wood-Mason, 1889[2]
1. Superfam. CHAETEESSOIDEA Handlirsch, 1925
Fam. Chaeteessidae Handlirsch, 1925[3]
Chaeteessa Burmeister, 1838[4] [NT]
2. Spinomantodea **nom. nov**.[5]
2.1. Superfam. MANTOIDOIDEA Giglio-Tos, 1919
Fam. Mantoididae Giglio-Tos, 1919[6]
Mantoida Newman, 1838[7] [NT, AN]
Paramantoida Agudelo, 2014[8] [NT]
2.2. Schizomantodea **nom. nov**.[9]
2.2.1. Superfam. METALLYTICOIDEA Giglio-Tos, 1917
Fam. Metallyticidae Giglio-Tos, 1917[10]
Metallyticus Westwood, 1835 [OR]
2_3. Artimantodea Svenson & Whiting, 2009[11]
2_3.1. Amerimantodea **nom. nov**.[12]
2_3.1.1. Superfam. THESPOIDEA Saussure, 1869
Fam. Thespidae Saussure, 1869[13]
$2_3.1_3$. Subfam. Pseudopogonogastrinae Rivera & Svenson, 2016
Pseudopogonogaster Beier, 1942 [NT]
2_3.1.1.2.1.1. Subfam. Pseudomiopteryginae Giglio-Tos, 1915
Pseudomiopteryx Saussure, 1870 [NT]
Promiopteryx Giglio-Tos, 1915 [NT, AN]
2_3.1.1.2.1.2. Subfam. Bantiinae Rivera & Svenson, 2016[14]
Bantia Stål, 1877 [NT]
Bantiella Giglio-Tos, 1915 [NT, AN]
Thrinaconyx Saussure, 1892 [NT]
Diabantia Giglio-Tos, 1915 [NT]
Mantillica Westwood, 1889[15] [NT]
Mantellias Westwood, 1889 [NT]
2_3.1.1.2.2.1. Subfam. Miobantiinae Roy, 2013[16]
Miobantia Giglio-Tos, 1917 [NT]
Eumiopteryx Giglio-Tos, 1915 [NT]

Anamiopteryx Giglio-Tos, 1915 [NT]
Chloromiopteryx Giglio-Tos, 1915[17] [NT]
Paradiabantia Piza, 1973[18] [NT]

2_3.1.1.2_3.1. Subfam. Musoniellinae Rivera & Svenson, 2016[19] stat. rev.

Tribe Leptomiopterygini **n. trib**.[20]
Leptomiopteryx Chopard, 1912 [NT]

Tribe Musoniellini Rivera & Svenson, 2016
Musoniella Giglio-Tos, 1916[21] [NT, AT?]
Eumusonia Giglio-Tos, 1916 [NT]
Pizaia Terra, 1982 [NT]

2_3.1.1.2_4. Subfam. Thespinae Saussure, 1869[19]

Tribe Thespini Saussure, 1869
Pseudomusonia Werner, 1909 [NT]
Musoniola Giglio-Tos, 1917 [NT]
Musonia Stål, 1877 [NT, AN]
Macromusonia Hebard, 1922 [NT]
Thespis Audinet-Serville, 1831 [NT, AN]
Paramusonia Rehn, 1904 [NT, AN]

Tribe Oligonychini Saussure, 1892

Subtribe Pogonogasterina Beier, 1935[22]
Thesprotiella Giglio-Tos, 1915 [NT]
Pogonogaster Rehn, 1918 [NT]
Carrikerella Hebard, 1920 [NT]

Subtribe Oligonychina Saussure, 1892
Thesprotia Stål, 1877 [NT, AN, NA]
Oligonyx Saussure, 1869 [NT, AN]
Oligonicella Giglio-Tos, 1915 [NT, NA]
Bistanta Anderson, 2018[23] [NT, NA]
Galapagia Scudder, 1893 [NT]
Piscomantis Rivera & Vergara-Cobián, 2017 [NT]
Liguanea Rehn & Hebard, 1938 [AN]

2_3.1.2. Superfam. ACANTHOPOIDEA Burmeister, 1838[24]

2_3.1.2.1. **Fam. Angelidae Beier, 1935**[25]
Angela Audinet-Serville, 1838[26] [NT, AN]

2_3.1.2_2.1. **Fam. Coptopterygidae Giglio-Tos, 1915**[27, 28]
Coptopteryx Saussure, 1869 [NT]
Brunneria Saussure, 1869 [NT, NA]

2_3.1.2_3.1. **Fam. Liturgusidae Giglio-Tos, 1915**[27, 29]

Tribe Liturgusini Giglio-Tos, 1915
Liturgusa Saussure, 1869 [NT, AN]
Fuga Svenson, 2014 [NT]
Velox Svenson, 2014 [NT]
Corticomantis Svenson, 2014 [NT]

Tribe Hagiomantini **n. trib**.[30]
Hagiomantis Saussure & Zehntner, 1894[31] [NT]

2_3.1.2_4.1. **Fam. Photinaidae Giglio-Tos, 1915**[27, 32]

2_3.1.2_4.1.1. Subfam. Macromantinae Brunner de Wattenwyl, 1893
Macromantis Saussure, 1871 [NT]

2_3.1.2_4.1.2.1. Subfam. Photiomantinae Rivera & Svenson, 2016
Photiomantis Piza, 1968[33] [NT]

2_3.1.2_4.1.2_2.1. Subfam. Cardiopterinae Rehn, 1911
Cardioptera Burmeister, 1838[34] [NT]

2_3.1.2_4.1.2_3. Subfam. Photinainae Giglio-Tos, 1915[35]

Tribe Microphotinaini Rivera & Svenson, 2016 **emend.**
Microphotina Beier, 1935[36] [NT]
Chromatophotina Rivera, 2010 [NT]

Tribe Photinaini Giglio-Tos, 1915
Subtribe Photinaina Giglio-Tos, 1915
Photina Burmeister, 1838 [NT]
Metriomantis Saussure & Zehntner, 1894 [NT]
Hicetia Saussure & Zehntner, 1894 [NT]
Photinella Giglio-Tos, 1915 [NT]
Subtribe Orthoderellina Giglio-Tos, 1919
Orthoderella Giglio-Tos, 1897 [NT]
Paraphotina Giglio-Tos, 1915 [NT]

$2_3.1.2_5$. **Fam. Acanthopidae Burmeister, 1838**[27, 37]

$2_3.1.2_5.1$. Subfam. Acanthopinae Burmeister, 1838
Acanthops Audinet-Serville, 1831[38] [NT, AN]
Pseudacanthops Saussure, 1870 [NT]
Plesiacanthops Chopard, 1930 [NT]
Miracanthops Roy, 2004 [NT]
Lagrecacanthops Roy, 2004 [NT]
Decimiana Uvarov, 1940 [NT]
Metilia Stål, 1877 [NT]
Metacanthops Agudelo & Maldaner, 2019 [NT]

$2_3.1.2_6$. Subfam. Stenophyllinae Saussure, 1869[39]
Tribe Stenophyllini Saussure, 1869[40]
Stenophylla Westwood, 1843 [NT]
Tribe Acontistini Giglio-Tos, 1915[41]
Subtribe Callibiina Giglio-Tos, 1919
Callibia Stål, 1877 [NT]
Subtribe Acontistina Giglio-Tos, 1915[42]
Ovalimantis Roy, 2015 [NT]
Acontista Saussure & Zehntner, 1894[43] [NT, AN]
Raptrix Terra, 1995 [NT]
Tithrone Stål, 1877 [NT, AN]
Paratithrone Lombardo, 1996 [NT]
[*Astollia* Kirby, 1904][44] [NT]

2_4. Cernomantodea Svenson & Whiting 2009[45]

$2_4.1$. Nanomantodea **nom. nov**.[46]

$2_4.1.1$. Superfam. CHROICOPTEROIDEA Giglio-Tos, 1915
Fam. Chroicopteridae Giglio-Tos, 1915[47]

$2_4.1.1.1$. Subfam. Tarachininae Giglio-Tos, 1915[48]
Tribe Gonypetellini **n. trib**.[49]
Gonypetella Giglio-Tos, 1915 [AT]
Telomantis Giglio-Tos, 1915 [AT, MD]
Tribe Tarachinini Giglio-Tos, 1915[50]
Tarachina Werner, 1907 [AT]

$2_4.1.1.2$. Subfam. Chroicopterinae Giglio-Tos, 1915
Tribe Bolbellini **n. trib**.[51]
Bolbella Giglio-Tos, 1915 [AT]
Dystactula Giglio-Tos, 1927 [AT]
Tribe Chroicopterini Giglio-Tos, 1915[52]
Subtribe Dystactina Giglio-Tos, 1915[53]
Dystacta Saussure, 1871 [AT]
Pseudodystacta Kaltenbach, 1996 [AT]
Achlaenella Giglio-Tos, 1915 [AT]
Achlaena Karsch, 1892 [AT]
Subtribe Amphecostephanina **n. subtrib.**
Amphecostephanus Rehn, 1912[54] [AT]
Subtribe Bisanthina Giglio-Tos, 1917
Bisanthe Stål, 1876[55] [AT]

Subtribe Chroicopterina Giglio-Tos, 1915[56]

Chroicoptera Stål, 1871 [AT]
Entelloptera Beier, 1942 [AT]
Carvilia Stål, 1876[55] [AT]
Congomantis Werner, 1929 [AT]
Rhachimantis Giglio-Tos, 1915 [AT]
Geothespis Giglio-Tos, 1916[55] [AT]
Namamantis Kaltenbach, 1996 [AT]
Chopardentella Kaltenbach, 1996 [AT]
Paraligaria Beier, 1969 [AT]
Macracanthopus Uvarov, 1940 [AT]
Ligaria Stål, 1877 [AT]
Ligariella Giglio-Tos, 1915 [AT]
Entella (*Entella*) Stål, 1877 [AT]
Entella (*Euentella*) Kaltenbach, 1996 [AT]
Ligentella Kaltenbach, 1996 [AT]
Parentella Giglio-Tos, 1915 [AT]
Betamantis Giglio-Tos, 1915 [AT]
Sphaeromantis Schulthess, 1898 [AT]

2_4.1.2. Superfam. NANOMANTOIDEA Brunner de Wattenwyl, 1893[57]

2_4.1.2.1. **Fam. Leptomantellidae n. fam**.[58]

Leptomantella Uvarov, 1940 [OR]
Aetaella Hebard, 1920 [OR]
Hebardiella Werner, 1924 [OR]
Hebardia Werner, 1921 [OR]

2_4.1.2_2.1. **Fam. Amorphoscelidae Stål**, 1877[59, 60]

2_4.1.2_2.1.1. Subfam. Perlamantinae Giglio-Tos, 1913

Paramorphoscelis Werner, 1907 [AT]
Perlamantis Guérin-Méneville, 1843 [PL]

2_4.1.2_2.1.2. Subfam. Amorphoscelinae Stål, 1877[61]

Amorphoscelis Stål, 1871 [AT, PL, OR]
Caudatoscelis Roy, 1973 [AT]
Bolivaroscelis Roy, 1973 [AT]
Gigliotoscelis Roy, 1973 [AT]
Maculatoscelis Roy, 1973 [AT]

2_4.1.2_3. **Fam. Nanomantidae Brunner de Wattenwyl**, 1893[59, 62]

2_4.1.2_3.1.1. Subfam. Hapalomantinae Beier, 1964

Tribe Hapalomantini Beier, 1964[63]

Hapalomantis (*Hapalomantis*) Stål, 1871 [AT]
Hapalomantis (*Bolbira*) Giglio-Tos, 1915 [AT]
Bolbena (*Bolbena*) Giglio-Tos, 1915 [AT]
Bolbena (*Bolboda*) Giglio-Tos, 1915 [AT]
Bolbula Giglio-Tos, 1915 [AT]
Hapalogymnes Kaltenbach, 1996 [AT]

Tribe Nilomantini Ehrmann & Roy, 2002[63]

Nilomantis Werner, 1907 [AT]
Ilomantis Giglio-Tos, 1915[64] [MD]
Negromantis Giglio-Tos, 1915[65] [AT, MD]
Melomantis Giglio-Tos, 1915 [AT]
Chloromantis Kaltenbach, 1998 [AT]
Hyalomantis Giglio-Tos, 1915 [MD]
Platycalymma Westwood, 1889 [MD]
Enicophlebia, Westwood, 1889 [MD]
Cornucollis Brannoch & Svenson, 2016 [MD]

$2_4.1.2_3.1.2.$ Subfam. Tropidomantinae Giglio-Tos, 1915[66]
Tribe Epsomantini **n. trib**.[67]
Epsomantis Giglio-Tos, 1915 [OR]
Tribe Tropidomantini Giglio-Tos, 1915
Tropidomantis Stål, 1877 [OR]
Eomantis Giglio-Tos, 1915 [OR]
Pliacanthopus (*Pliacanthopus*) Giglio-Tos, 1927 [OR]
Pliacanthopus (*Malayamantis*) Koçak & Kemal, 2008 [OR]
Oligocanthopus Beier, 1935 [OR]
Sinomantis Beier, 1933 [OR]
$2_4.1.2_4.1.$ Subfam. Nanomantinae Brunner de Wattenwyl, 1893[68]
Miromantis Giglio-Tos, 1915 [OR]
Ormomantis Giglio-Tos, 1915 [OR]
Oxymantis Werner, 1931 [OR]
Sceptuchus Hebard, 1920 [OR]
Nanomantis Saussure, 1871[69] [OR, AU]
Parananomantis Mukherjee, 1995 [OR]
$2_4.1.2_5.$ Subfam. Fulciniinae Ehrmann & Roy, 2002[70]
Tribe Fulciniini Ehrmann & Roy (2002)
Fulcinia Stål, 1877 [AU]
Calofulcinia Giglio-Tos, 1915 [AU]
Hedigerella Werner, 1933 [AU]
Tylomantis Giglio-Tos, 1915 [AU]
Fulciniella Giglio-Tos, 1915 [AU]
Pilomantis Giglio-Tos, 1915 [AU]
Ima Tindale, 1924[71] [AU]
Papugalepsus Werner, 1928 [AU]
Machairima Beier, 1965 [AU]
Nannofulcinia Beier, 1965 [AU]
Tribe Stenomantini Giglio-Tos, 1915[72]
Fulciniola Giglio-Tos, 1915 [AU]
Stenomantis Saussure, 1871 [AU]
Ciulfina Giglio-Tos, 1915 [AU]
Tribe Neomantini **n. trib**.[73]
Neomantis Giglio-Tos, 1915 [AU]
Kongobatha Hebard, 1920 [AU]
Tribe Paraoxypilini Saussure, 1872[74]
Subtribe Bolbina **n. subtrib.**
Bolbe Stål, 1877 [AU]
Papubolbe Beier, 1965 [AU]
Subtribe Paraoxypilina Saussure, 1872[75]
Paraoxypilus Saussure, 1870 [AU]
Cliomantis Giglio-Tos, 1913 [AU]
Exparoxypilus Beier, 1929 [AT]
Myrmecomantis Giglio-Tos, 1913 [AU]
Metoxypilus Giglio-Tos, 1913 [AU]
Gyromantis Giglio-Tos, 1913 [AU]
Phthersigena (*Phthersigena*) Stål, 1871 [AU]
Phthersigena (*Glabromantis*) Sjöstedt, 1918 [AU]
Nesoxypilus Beier, 1965 [AU]
$2_5.$ Metamantodea **nom. nov**.[76]
$2_5.1.$ Superfam. GONYPETOIDEA Westwood, 1889
Fam. Gonypetidae Westwood, 1889[77]
$2_5.1.1.$ Subfam. Iridopteryginae Giglio-Tos, 1915[78]
Tribe Iridopterygini Giglio-Tos, 1915[79]
Subtribe Tricondylomimina **n. subtrib.**

Tricondylomimus Chopard, 1930[80] [OR]
Subtribe Iridopterygina Giglio-Tos, 1915[81]
Spilomantis Giglio-Tos, 1915 [OR]
Hapalopeza Stål, 1877 [OR]
Hapalopezella Giglio-Tos, 1915 [OR]
Iridopteryx Saussure, 1869 [OR]
Micromantis Saussure, 1870 [OR]
Pezomantis Uvarov, 1927 [OR]
Muscimantis Henry, 1931 [OR]
Tribe Amantini **n. trib.**
Amantis Giglio-Tos, 1915 [OR]
2_5.1.2. Subfam. Gonypetinae Westwood, 1889
Tribe Armenini **n. trib**.[82]
Armene Stål, 1877 [PL]
Tribe Gonypetini Westwood, 1889[83]
Subtribe Gonypetina Westwood, 1889
Elaea Stål, 1877 [AT, PL]
Memantis Giglio-Tos, 1915 [OR]
Gonypeta Saussure, 1869 [OR]
Myrcinus Stål, 1877 [OR]
Bimantis Giglio-Tos, 1915 [OR]
Dimantis Giglio-Tos, 1915 [OR]
Gonypetoides Beier, 1942 [OR]
Gimantis Giglio-Tos, 1915 [OR]
Elmantis Giglio-Tos, 1915 [OR]
Subtribe Gonypetyllina **n. subtrib**.[84]
Armeniola Giglio-Tos, 1915 [OR]
Gonypetyllis Wood-Mason, 1891[85] [OR]
Holaptilon Beier, 1964 [PL]
Subtribe Compsomantina Giglio-Tos, 1915[86]
Compsomantis Saussure, 1872 [OR]
Subtribe Humbertiellina Brunner de Wattenwyl, 1893[87]
Humbertiella Saussure, 1869[88] [OR]
Paratheopompa Schwarz & Ehrmann, 2017 [OR]
Theopompa Stål, 1877 [OR]
2_6. Lobipedia Saussure, 1870 **sensu nov**.[89]
2_6.1. Superfam. EPAPHRODITOIDEA Brunner de Wattenwyl, 1893[90]
2_6.1.1. **Fam. Majangidae Giglio-Tos, 1915**
2_6.1.1.1. Subfam. Brancsikiinae **n. subfam**.[91]
Brancsikia Saussure & Zehntner, 1895 [MD]
2_6.1.1.2. Subfam. Majanginae Giglio-Tos, 1915[92]
Tribe Danuriellini **n. trib**.[93]
Danuriella Westwood, 1889 [MD]
Tribe Majangini Giglio-Tos, 1915[94]
Majanga Wood-Mason, 1891 [MD]
Liturgusella Giglio-Tos, 1915 [MD]
2_6.1.2. **Fam. Epaphroditidae Brunner de Wattenwyl, 1893[95]**
2_6.1.2.1. Subfam. Gonatistinae Saussure, 1869[96]
Gonatista Saussure, 1869 [AN, NA]
Gonatistella Giglio-Tos, 1915[97] [AU?]
2_6.1.2.2. Subfam. Epaphroditinae Brunner de Wattenwyl, 1893
Tribe Epaphroditini Brunner de Wattenwyl, 1893[98]
Epaphrodita Audinet-Serville, 1831 [AN]
Tribe Callimantini Giglio-Tos, 1919[99]

Callimantis Stål, 1877 [AN]

2_7. Mantimorpha **nom. nov**.[100]

2_7.1. Superfam. HAANIOIDEA Giglio-Tos, 1915

Fam. Haaniidae Giglio-Tos, 1915[101]

2_7.1.1. Subfam. Caliridinae Giglio-Tos, 1915[102]

Caliris Giglio-Tos, 1915[103] [OR]

Gildella Giglio-Tos, 1927 [OR]

2_7.1.2. Subfam. Haaniinae Giglio-Tos, 1915[104]

Tribe Arriini Giglio-Tos, 1919[105]

Arria Stål, 1877 [OR][106]

Sinomiopteryx Tinkham, 1937[107] [OR]

Tribe Haaniini Giglio-Tos, 1915[108]

Astape Stål, 1877[109] [OR]

Haania Saussure, 1871[110] [OR]

2_8. Heteromantodea **nom. nov**.[111]

2_8.1. Superfam. EREMIAPHILOIDEA Saussure, 1869[112]

2_8.1.1. **Fam. Rivetinidae Ehrmann & Roy, 2002**[113]

2_8.1.1.1. Subfam. Rivetininae Ehrmann & Roy, 2002[114]

Tribe Rivetinini Ehrmann & Roy (2002)

Teddia Burr, 1899 [AT]

Rivetina Berland & Chopard, 1922 [PL]

Rivetinula La Greca, 1977 [OR]

Pararivetina Beier, 1931 [OR]

Bolivaria Stål, 1877 [PL]

Geomantis Pantel, 1896 [PL]

Microthespis Werner, 1908 [AT, PL]

Tribe Ischnomantini Giglio-Tos, 1916[115]

Eremoplana Stål, 1877 [PL]

Ischnomantis Stål, 1877 [AT]

2_8.1.1.2. Subfam. Deiphobinae **n. subfam**.[116]

Tribe Deiphobini **n. trib**.[117]

Deiphobe Stål, 1877 [OR]

Deiphobella Giglio-Tos, 1916 [OR]

Indothespis Werner, 1935 [OR]

Tribe Cotigaonopsini **n. trib.**

Cotigaonopsis Vyjayandi, 2009[118] [OR]

2_8.1.2.1. **Fam. Amelidae Westwood, 1889**[119]

Tribe Amelini Westwood, 1889

Apteromantis Werner, 1931 [PL]

Ameles Burmeister, 1838 [PL]

Pseudoyersinia Kirby, 1904 [PL]

Tribe Litaneutriini Jantsch, 1999[120]

Yersiniops Hebard, 1931 [NA]

Yersinia Saussure, 1869 [NA]

Litaneutria Saussure, 1892 [NA]

2_8.1.2_2.1. **Fam. Eremiaphilidae Saussure, 1869**[121, 122]

2_8.1.2_2.1.1. Subfam. Parathespinae Giglio-Tos, 1916

Parathespis Saussure, 1869[123] [OR]

2_8.1.2_2.1.2.1. Subfam. Iridinae Westwood, 1889[124]

Tribe Schizocephalini Saussure, 1869

Schizocephala Audinet-Serville, 1831[125] [OR]

Tribe Didymocoryphini **n. trib.**

Didymocorypha Wood-Mason, 1877[126] [OR]

Tribe Dysaulini Giglio-Tos, 1919[127]

Dysaules Stål, 1877 [OR]

Oxyophthalma Saussure, 1861 [OR]
Dysaulophthalma Stiewe, 2009 [OR]
Tribe Iridini Westwood, 1889[127]
Paroxyophthalmus Wood-Mason, 1889 [AT]
Episcopomantis Uvarov, 1940 [AT]
Iris Saussure, 1869 [AT, PL, OR]
$2_8.1.2_2.1.2_2.1.$ Subfam. Eremiaphilinae Saussure, 1869[128]
Eremiaphila Lefebvre, 1835 [PL, AT]
Heteronutarsus Lefèbvre, 1835 [PL]
$2_8.1.2_2.1.2_3.$ Subfam. Tarachodinae Giglio-Tos, 1917[129]
Tribe Oxyelaeini **n. trib**.[130]
Oxyelaea Giglio-Tos, 1917 [AT]
Charieis Burr, 1900 [AT]
Tribe Tarachodini Giglio-Tos, 1917[131]
Subtribe Antistiina **n. subtrib**.[132]
Antistia Stål, 1876 [AT]
Ariusia Stål, 1877 [AT]
Subtribe Tarachodina Giglio-Tos, 1917[133]
Nothogalepsus Beier, 1969 [AT]
Tarachodes (*Tarachodes*) Burmeister, 1838 [AT]
Tarachodes (*Chiropacha*) Charpentier, 1841 [AT]
Tarachodes (*Chiropus*) Saussure, 1869 [AT]
Tarachodes (*Tarachodina*) Beier, 1957 [AT]
Tarachodes (*Barbachodes*) Beier, 1957 [AT]
Tarachodula Giglio-Tos, 1917 [AT]
Tarachodella Giglio-Tos, 1917 [AT]
Galepsus (*Galepsus*) Stål, 1877 [AT]
Galepsus (*Lygdamia*) Stål, 1877 [AT]
Galepsus (*Syngalepsus*) Beier, 1954 [AT]
Galepsus (*Onychogalepsus*) Beier, 1954 [AT, MD]
Paragalepsus Beier, 1930 [AT]
Plastogalepsus Beier, 1954 [AT]
Pseudogalepsus Beier, 1954 [AT]
Metagalepsus Roy, 1971 [AT]
Oxyophthalmellus Giglio-Tos, 1917 [AT]
Pyrgomantis Gerstaecker, 1869 [AT]
Nesogalepsus Beier, 1954 [MD]
Tuberculepsus Roy, 2008 [MD]
Paralygdamia Saussure & Zehntner, 1895 [MD]
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$2_8.1.2_3.1.$ Subfam. Heterochaetinae Brunner de Wattenwyl, 1893
Heterochaeta Westwood, 1843[135] [AT]
$2_8.1.2_4.1.$ Subfam. Compsothespinae Giglio-Tos, 1913
Compsothespis Saussure, 1872[136] [AT, AU?]
$2_8.1.2_5.1.$ Subfam. Oxyothespinae Giglio-Tos, 1916[137]
Tribe Oxyothespini Giglio-Tos, 1916[138]
Oxyothespis Saussure, 1870 [AT, PL]
Paraseverinia Lombardo, 1991 [PL]
Somalithespis Lombardo, 1991 [AT]
Sinaiella Uvarov, 1924[139] [AT, PL]
Severinia Finot, 1902 [AT, PL]
Acithespis Giglio-Tos, 1916 [AT]
Lobothespis La Greca & Lombardo, 1987 [PL]
Tribe Heterochaetulini **n. trib.**
Heterochaetula Wood-Mason, 1889[140] [OR]

2_8.1.2_6. Subfam. Toxoderinae Saussure, 1869[141]
Tribe Calamothespini Giglio-Tos, 1914[142]
Subtribe Toxomantina **n. subtrib.**
Toxomantis Giglio-Tos, 1914[143] [OR, PL]
Subtribe Calamothespina Giglio-Tos, 1914
Calamothespis Werner, 1907[144] [AT]
Belomantis Giglio-Tos, 1914 [AT]
Tribe Aethalochroini Giglio-Tos, 1914[145]
Pareuthyphlebs Werner, 1928 [AT, PL]
Aethalochroa Wood-Mason, 1877[146] [OR]
Oestomantis Giglio-Tos, 1914 [OR]
Tribe Toxoderopsini Ehrmann & Roy, 2002[147]
Toxodanuria Uvarov, 1940 [OR]
Euthyphleps Wood-Mason, 1889 [PL, OR]
Toxoderella Giglio-Tos, 1914 [AU?]
Toxoderopsis Wood-Mason, 1889 [OR]
Tribe Toxoderini Saussure, 1869[147]
Stenotoxodera Roy, 2009 [OR]
Paratoxodera Wood-Mason, 1889 [OR]
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Protoxodera Werner, 1930 [OR]
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2_9.1. Superfam. HOPLOCORYPHOIDEA Giglio-Tos, 1916
Fam. Hoplocoryphidae Giglio-Tos, 1916[149]
Hoplocorypha Stål, 1871 [AT]
Hoplocoryphella Giglio-Tos, 1916 [AT]
Apterocorypha Roy, 1966 [MD]
2_{10}. Calomantodea **nom. nov**.[150]
2_{10}.1. Superfam. MIOMANTOIDEA Westwood, 1889
Fam. Miomantidae Westwood, 1889[151]
Subfam. Solygiinae Giglio-Tos, 1919
Solygia Stål, 1877[152] [AT]
Subfam. Miomantinae Westwood, 1889[153]
Taumantis Giglio-Tos, 1917 [AT]
Parasphendale Schulthess, 1898 [AT]
Cilnia Stål, 1876 [AT]
Paracilnia Werner, 1909 [AT]
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2_{11}. Promantidea **nom. nov**.[154]
2_{11}.1. Superfam. GALINTHIADOIDEA Giglio-Tos, 1919
Fam. Galinthiadidae Giglio-Tos 1919[155]
Galinthias Stål, 1877[156] [AT, PL]
Congoharpax La Greca, 1954[157] [AT]
Pseudoharpax Saussure, 1870 [AT]
Harpagomantis Kirby, 1899 [AT]
2_{12}. Mantidea **sensu n**.[158]
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2_{12}.1_3. Subfam. Blepharodinae Giglio-Tos, 1919[161]
Blepharodes Bolívar, 1890 [AT]
Blepharopsis Rehn, 1902 [AT, PL, OR]
2_{12}.1.1.2. Subfam. Empusinae Burmeister, 1838

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Idolomantis Uvarov, 1940 [AT]
Tribe Empusini Burmeister, 1838[163]
Subtribe Empusina Burmeister, 1838
Gongylus Thunberg, 1815 [OR]
Empusa Illiger, 1798 [AT, PL, OR]
Dilatempusa Roy, 2004 [AT]
Hypsicorypha Krauss, 1892 [PL]
Subtribe Idolomorphina Ehrmann & Roy, 2002[164]
Idolomorpha Burmeister, 1838 [AT]
Hemiempusa Saussure & Zehntner, 1895 [AT]
Chopardempusa Paulian, 1958 [MD]

2_{12}.1.2. **Fam. Hymenopodidae Giglio-Tos, 1915**[165]

2_{12}.1.2.1.1. Subfam. Phyllocraniinae Brunner de Wattenwyl, 1893[166]
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2_{12}.1.2.1.2. Subfam. Sibyllinae Giglio-Tos, 1915[167]
Presibylla Bolívar, 1908 [AT]
Leptosibylla Roy, 1996 [AT]
Sibylla (*Sibylla*) Stål, 1877 [AT]
Sibylla (*Sibyllopsis*) Roy, 1996 [AT]

2_{12}.1.2.2.1. Subfam. Hymenopodinae Giglio-Tos, 1915[168]
Tribe Anaxarchini Giglio-Tos 1919[169]
Odontomantis Saussure, 1871 [OR]
Euantissa Giglio-Tos, 1927 [OR]
Nemotha Wood-Mason, 1884[170] [OR]
Heliomantis Giglio-Tos, 1915 [OR]
Anaxarcha Stål, 1877 [OR]
Werneriana Shcherbakov et al., 2016 [OR]
Tribe Hymenopodini Giglio-Tos, 1915[171]
Subtribe Hymenopodina Giglio-Tos, 1915[172]
Theopropus Saussure, 1898 [OR]
Helvia Stål, 1877[173] [OR]
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Chlidonoptera Karsch, 1892 [AT]
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Panurgica Karsch, 1896 [AT]

2_{12}.1.2$_3$.1. Subfam. Phyllothelyinae Brunner de Wattenwyl 1893[174]
Tribe Parablepharini Giglio-Tos, 1915[175]
Parablepharis Saussure, 1870 [OR]
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Ceratocrania Westwood, 1889 [OR]

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Ceratomantis Wood-Mason, 1876 [OR]
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[*Pseudoxypilus* Giglio-Tos, 1915][181] [OR]
Junodia Schulthess, 1899 [AT]
Oxypilus (*Oxypilus*) Audinet-Serville, 1831 [AT]
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Astyliasula Schwarz & Shcherbakov, 2017 [OR]
Pseudohestiasula Schwarz & Shcherbakov, 2017 [OR]

2_{12}.1.2_5. Subfam. Acromantinae Brunner de Wattenwyl, 1893[184]

Tribe Otomantini Giglio-Tos, 1915[185]
Otomantis Bolívar, 1890 [AT]
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Anasigerpes Giglio-Tos, 1915 [AT]

Tribe Acromantini Brunner de Wattenwyl, 1893[188]
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Ambivia Stål, 1877 [OR]
Psychomantis Giglio-Tos, 1915 [OR]
Parapsychomantis Shcherbakov, 2017 [OR]
Oligomantis Giglio-Tos, 1915 [OR]
Rhomantis Giglio-Tos, 1915 [OR]
Acromantis Saussure, 1870 [OR, AU]
Citharomantis Rehn, 1909 [OR]

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2_{13}.1. **Fam. Dactylopterygidae Giglio-Tos, 1915**[190]
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Dactylopteryx Karsch, 1892 [AT]
Theopompella Giglio-Tos, 1917 [AT]

2_{14}.1. **Fam. Deroplatyidae Westwood, 1889**[191]

2_{14}.1.1. Subfam. Popinae Brunner de Wattenwyl, 1893[192]

Tribe Popini Brunner de Wattenwyl, 1893[193]
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Macropopa Giglio-Tos, 1914 [AT]
Danuria (*Danuria*) Stål, 1856 [AT]
Danuria (*Danuriodes*) Giglio-Tos, 1907 [AT]
Macrodanuria Sjöstedt, 1900 [AT]
Neodanuria La Greca & Lombardo, 1987 [AT]

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Subtribe Euchomenina Giglio-Tos, 1916[195]
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Subtribe Leptocolina Giglio-Tos, 1916
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Stenopyga (*Stenopygella*) Giglio-Tos, 1916 [AT]
Stenopyga (*Agriomantis*) Giglio-Tos, 1916 [AT]
Agrionopsis Werner, 1908 [AT]
Leptocola Gerstaecker, 1883 [AT]

2_{14}.1.2. Subfam. Deroplatyinae Westwood, 1889[196]

Tribe Euchomenellini Giglio-Tos, 1916[197]
Tagalomantis Hebard, 1920 [OR]
Euchomenella Giglio-Tos, 1916 [OR]
Indomenella Roy, 2008 [OR]
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Tribe Deroplatyini Westwood, 1889[198]

Subtribe Pseudempusina Rehn, 1911[199]
Pseudempusa Brunner de Wattenwyl, 1893 [OR]

Mythomantis Giglio-Tos, 1916 [OR]
Subtribe Deroplatyina Westwood 1889[200]
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2_{15}. **Fam. Mantidae Latreille, 1802 sensu nov.**[201]

2_{15}.1. Subfam. Mellierinae Giglio-Tos, 1915[202]
Tribe Rhodomantini **n. trib.**
Rhodomantis Giglio-Tos, 1917[203] [AU]
Mellierella Giglio-Tos, 1915 [AU]
Scolodera Milledge, 1989 [AU]
Tribe Mellierini Giglio-Tos, 1915[204]
Melliera Saussure, 1892 [NT]
Xystropeltis Rehn, 1935 [NT]

2_{16}.1.1. Subfam. Orthoderinae Saussure, 1869[205]
Orthodera Burmeister, 1838 [AU]
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2_{16}.1.2. Subfam. Choeradodinae Saussure, 1869[205]
Asiadodis Roy, 2004 [OR]
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2_{17}.1. Subfam. Mantinae Latreille, 1802[206]
Mantis Linnaeus, 1758 [AT, PL, OR, AU]
Mantilia Roy, 1993 [AT]
Statilia Stål, 1877 [AT, OR, AU]

2_{18}.1. Subfam. Deromantinae Giglio-Tos, 1919[207]
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2_{20}.1. Subfam. Tenoderinae Brunner de Wattenwyl, 1893[209]
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Subtribe Polyspilotina Giglio-Tos, 1917[211]
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Plistospilota Giglio-Tos, 1911 [AT]
Prohierodula Bolívar, 1908 [AT]
Cataspilota Giglio-Tos, 1917 [AT]
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Tenodera Burmeister, 1838 [AT, PL, OR, AU]
Notomantis Tindale, 1923 [AU]
Mesopteryx Saussure, 1870 [OR]
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Subtribe Paramantina Roy, 1973[213]
Epitenodera Giglio-Tos, 1912 [AT]
Paramantis Roy, 1967 [AT, MD]
Alalomantis Giglio-Tos, 1917 [AT]
Sphodromantis Stål, 1871 [AT, PL]
Rhomboderella Giglio-Tos, 1912 [AT]
Subtribe Tarachomantina **n. subtrib.**
Nausicaamantis Mériguet, 2018 [MD]
Tarachomantis (*Tarachomantis*) Brancsik, 1893 [MD]
Tarachomantis (*Madamantis*) Mériguet, 2013 [MD]
Mantasoa Mériguet, 2005 [MD]
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2_{21}.1. Subfam. Hierodulinae Brunner de Wattenwyl, 1893[214]
Tribe Hierodulini Brunner de Wattenwyl, 1893[215]

Mekongomantis Schwarz et al., 2018 [OR]
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Hierodula Burmeister, 1838 [PL, OR, AU]
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Stictomantis Beier, 1942 [OR]
Rhombodera Burmeister, 1838 [OR, AU]
Tamolanica Werner, 1923 [OR, AU]
Pnigomantis Giglio-Tos, 1917 [AU]
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Tribe Antemnini Terra, 1995[221]
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Parastagmatoptera Saussure, 1871 [NT, AN]
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Pseudoxyops Saussure & Zehntner, 1894 [NT]
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Subtribe Vatina Stål, 1877[228]
Pseudovates Saussure, 1869[229] [NT, NA, AN]
Callivates Roy, 2003 [NT]
Alangularis Svenson et al., 2015 [NT]
Vates Burmeister, 1838 [NT, AN]
Zoolea Audinet-Serville, 1839 [NT]

Annotations

[1] **Mantodea**. Monophyly of Mantodea is not disputed here (for synapomorphies see Wieland 2013, p. 10; Bai et al. 2016). Which of the many Paleozoic or Mesozoic roachoids constitutes its immediate sister-group is still a matter of debate (Grimaldi 2003; Béthoux & Wieland 2009; Gorochov 2013; Dittmann et al. 2015; Bai et al. 2016; Guan et al. 2016; Hörnig et al. 2017). Several candidates from the blattodean–mantodean transition zone have recently been discovered (e.g. Dittmann et al. 2015; Bai et al. 2016; Poinar & Brown 2017).

One putative synapomorphy deserves special attention: the pseudovein. This is an oblique depression with sclerotized integument on the tegmen, along the line where the posterior margin of the anal field of the opposite tegmen is positioned when wings are closed (Gorochov 2006; Figure 1a, b). It is discernible in virtually every fossil wing attributable to Mantodea as well as in early Eumantodea (e.g. Nel & Roy 1996; Grimaldi 2003; Hörnig et al. 2013; Wieland 2013, p. 107), and has been presumed to be a putative synapomorphy of the order by Wieland (2013, p. 107). However, it is also present in some modern cockroaches, albeit on the lower tegmen only (Gorochov 2006). Its functions are not well understood, but it is conceivable to assume that it facilitates proper wing folding and positioning relative to each other when at rest. Whether it also helps to reduce shearing stress during flight (see Brackenbury 1991, 1999) has not been investigated so far. In Carboniferous, Permian, and Lower Cretaceous putative mantodeans, the pseudovein extends onto the anal field (Grimaldi 2003; Béthoux & Wieland 2009; Hörnig et al. 2013; but see Gorochov 2013 vs. Guan et al. 2016 for a re-interpretation of the Paleozoic fossils), while in more modern representatives it is restricted to the discoidal field. Since the tegmen is bent along the anal fold during upstroke, to reduce shearing stress and to restrict the wing fold to distal parts of the tegmen (Brackenbury 1991, 1999), it may be argued that a rigidification line across this fold would somehow affect wing kinematics. In any case, in Eumantodea there is a tendency to reduce the pseudovein to the anterior part of the tegmen. Ramsay (1990, p. 41ff) and Wieland (2013, p. 106f) discuss the structure and argue that it is probably homologous to the stigma of higher mantodeans. We follow this interpretation due to reasons discussed below.

[2] **Eumantodea**. Grimaldi (2003) coined the term Neomantodea for a clade comprising the Cretaceous fossil taxon †*Ambermantis* Grimaldi, 2003 + extant Mantodea (= Eumantodea). The putative apomorphies of this clade have been critically discussed by Wieland (2013, p. 29f). However, the phylogenetic relationships and classification of fossil taxa are beyond the scope of this article. The name Eumantodea was first proposed by Wood-Mason (1889) for a subset of modern mantodeans, but here the term is used for crown-group mantodeans as defined by Grimaldi (2003) and followed by Svenson & Whiting (2009). Synapomorphy of Eumantodea: two (vs. *lack of*) discoidal spines (Grimaldi 2003; Wieland 2013, p. 30). Hypothetical groundplan of eumantodean (possibly mantodean, but fossil genitalia not known) phallomeres: left complex not completely sclerotized, with ventral phallomere sclerotized along left and right margin, and sclerites of left phallomere small and simple; processes of left complex (**pda, paa**) connected (see also Bai et al. 2016); right phallomere short and broad, folded along right margin, with ventral sclerotized process (see Klass 1997, figures 28–52, and Figure 2a-c for details in Mantoididae and Chaeteessidae); membranous lobe present, but phalloid apophysis (**afa**) missing (this interpretation differs of that of Klass 1997, who regards the membranous lobe of *Chaeteessa* as its phalloid apophysis, see his figures 31, 32 and 34).

[3] **Chaeteessidae**. Apomorphies: curved (vs. *straight*) foretibia (besides its only extant representative *Chaeteessa*, this feature is also present in an undescribed Baltic amber chaeteessid investigated by us); foreleg spines elongate and inequal in size (vs. *not elongate and of similar size*); cerci longer (vs. *shorter*) than half of abdomen length. The spines on the walking legs have been interpreted as a plesiomorphic roachoid trait (Wieland 2013, 89ff, 125; Hörnig et al. 2017). Several fossil taxa described after wings have been assigned to this family (reviewed in Grimaldi 2003). Due to the variability observed in extant and fossil mantodean wing venation patterns (see, for instance, the discussion on individual variability in Nel & Roy 1996; Béthoux & Wieland 2009), we have largely avoided them here and only discuss key morphological characters available in extant or amber chaeteessids.

[4] ***Chaeteessa***. Autapomorphy: apical claw reduced to small tubercle (vs. *well-developed and curved*) (Roy 1999b; Wieland 2013, pp. 85, 157ff). Genitalia (Figure 2a): enlarged ventral process; distal process (**pda**) membraneous, tightly fused to titillator (**paa**), together functioning as one process the dorsal and ventral parts of which are formed by **paa** and **pda**, respectively. **Pda** is regarded as missing in Klass (1997, figures 28, 31, 32, 34).

[5] **Spinomantodea**. Synapomorphies: loss (vs. *presence*) of posteroventral spine on genicular lobe of forefemur (secondarily re-evolved in certain groups); three (vs. *two*) discoidal spines on forefemur; loss (vs. *presence*) of spines on the walking legs; distal process (**pda**) sclerotized (vs. *membraneous*); phalloid apophysis (**afa**) present (vs. *missing*) (**loa**, *nec* **afa** in Klass 1997, figures 44, 45; the structure named **afa** in those figures is not the phalloid apophysis).

[6] **Mantoididae**. The pseudovein in this family exhibits a particular configuration: the respective parts of RP + M and CuA follow its course, so that the initial pseudovein (largely

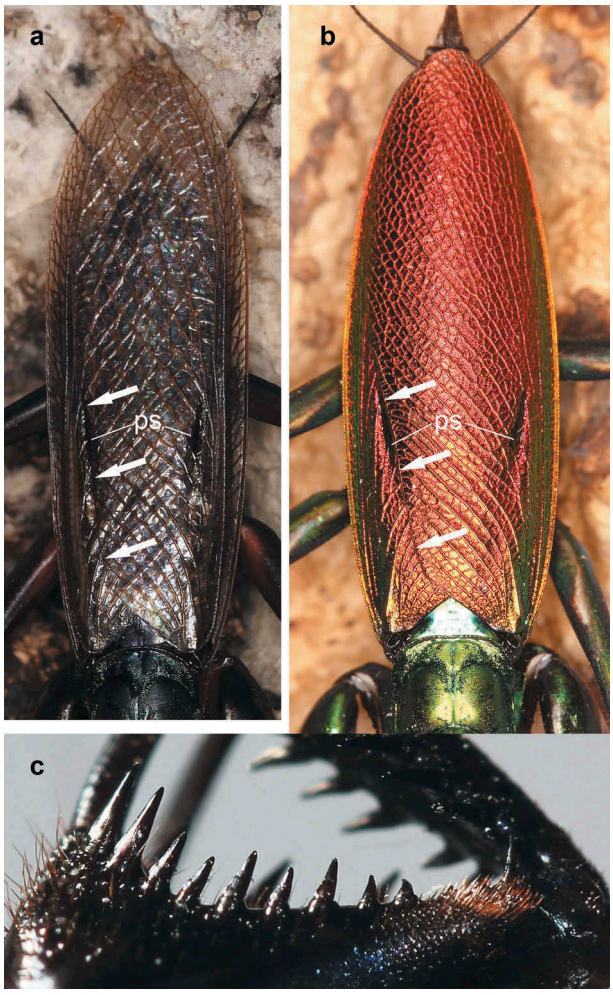

Figure 1. Genus *Metallyticus* Westwood, 1935. Tegmina of, **a**, male of *Metallyticus violaceus* (Burmeister, 1838), and, **b**, female of *Metallyticus splendidus* Westwood, 1935 in dorsal view, showing shape and position of pseudovein (**ps**) in living specimens; Note posterior margin of tegmen relative to pseudovein when wings are fully closed (white arrows); **c**, anteroventral margin of forefemur in female *Metallyticus violaceus* showing alternate sizes of spines. Not to scale.

composed of cross-veins) is replaced in most parts by longitudinal veins (most expressed in *Paramantoida*). Particularly RP + M departs from RA in this area, only to curve again towards RA distally and join it at about middle of tegmen. This distal part of the curvature follows the pseudovein depression for most of its length (see Béthoux & Wieland 2009; Wieland 2013, figure 335; Agudelo 2014). The spacing apart of RA and RP + M at the proximal third of the tegmen (vs. *RA and RP + M subparallel*) can be regarded as a synapomorphy of the family. Genitalia examples are depicted in Figure 2b, c.

[7] ***Mantoida***. Phalloid apophysis triangular, spiny (La Greca & Lombardo 1990; Klass 1997, figures 44, 45, "loa"; Figure 2b). The triangular or slightly bifurcate shape of the apophysis observed in some *Mantoida* species is interpreted here as the first instance of such a configuration and shows that the genetic disposition for a bifurcate apophysis has developed very early in eumantodean history. Despite subsequent reduction in early schizomantodeans, the re-emergence of a bilobed apophysis in various amerimantodeans and cernomantodeans (see below) could be interpreted as yet another exception from Dollo's law.

Mantoida may be paraphyletic with respect to *Paramantoida*, since both abdominal shape (subparallel *vs*. fusiform) and morphology of the genitalia observed in this genus (spiny *vs*. not spiny **paa-pda**, degree of sclerotization of left complex) are more variable than the difference between *Paramantoida* and a certain subset of *Mantoida* species (see La Greca & Lombardo 1990; Agudelo 2014; and Figure 2b, c).

[8] ***Paramantoida***. Autapomorphies: reduction of posteroventral spines on forefemur to one or two spinules (vs. *four distinct spines*); **afa** elongate (vs. *short*), sinuous, with spiny apex (Agudelo 2014; Figure 2c).

[9] **Schizomantodea**. Synapomorphies: foretibial spines increasing in length distally (vs. *irregular or subequal, but without tendency to increase in length*); anteroventral forefemoral spines alternating in length (vs. *of similar size*); phallomeres (Figures 2d-f, 3-26) fully (vs. *partially*) sclerotized; processes of left complex separated (vs. *fused*); **afa** long, acute and curved (vs. *broader, triangular or sinuous, spiny*); primary distal process (**pda**) translocated to left side (vs. *at apex*) of ventral phallomere; short secondary distal process (**sdp**) on **vla** (vs. *sdp missing, vla not widened*). This represents the genitalia groundplan for Schizomantodea, as expressed in *Metallyticus*. That the lobe on the left side is homologous to the distal process of *Mantoida* (**pda** in Klass 1997) is exemplified by the fact that, even though not connected to the titillator (**paa**) like in *Mantoida*, the two processes are still juxtaposed in this group (compare Figure 2d, and positions depicted in Klass 1997, figures 20, 23). As a consequence, a secondary distal process (**sdp**) is developed on the distal part of the widened opposite lobe of the ventral phallomere (**vla** in Klass 1997, figures 20, 23–27) in Schizomantodea. That is, **the distal process of Artimantodea is not homologous to the distal process of *Chaeteessa* and *Mantoida***. In *Metallyticus* both the primary and the secondary distal processes are present (Figure 2d–f). The non-homology of the distal processes was overlooked due to low mantodean taxon sampling in Klass (1997) study focusing more on blattodean genital characters. Actually, the remnants of the primary distal process are present in many

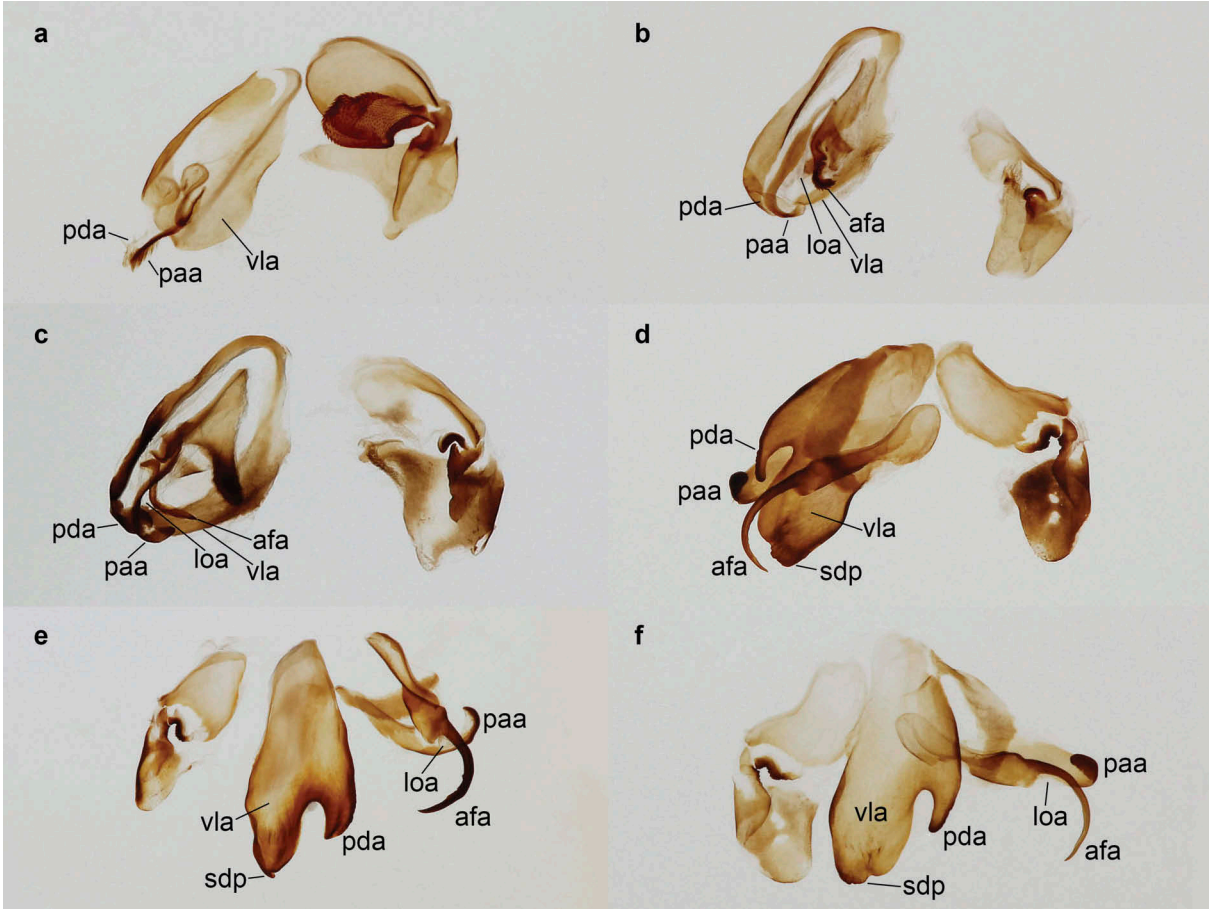

Figure 2. Genitalia of Chaeteessidae, Mantoididae and Metallyticidae. **a**, *Chaeteessa caudata* Saussure, 1871, from N Brazil, dorsal view (SMNK 01554, prep. Schwarz No. 179); **loa** not discernible in the figure, but present; **b**, *Mantoida* sp., from N Brazil, dorsal view (SMNK 05088, prep. Schwarz No. 176); **c**, *Paramantoida amazonica* Agudelo, 2014, from N Brazil, dorsal view (SMNK 05085, prep. Schwarz No. 292); **d**, *Metallyticus splendidus* Westwood, 1835, from the Malay Peninsula, dorsal view (CS, prep. Schwarz No. 253); **e**, *Metallyticus violaceus* (Burmeister, 1838), from Laos, ventral view (CS, prep. Schwarz No. 105); **f**, *Metallyticus splendidus* Westwood, 1835, from the Malay Peninsula, ventral view (CS, prep. Schwarz No. 29). Not to scale.

artimantodeans as a rounded lobe just distad of the joint with the left phallomere; particularly Thespidae possess a well-developed **pda**, often in combination with a long and curved phalloid apophysis, while at the same time also have a secondary and more strongly developed process on **vla** (e.g. *Miobantia, Pseudomiopteryx, Musoniella, Thesprotia, Thesprotiella*; see Cerdá 1993; Lombardo & Agabiti 2001; Agudelo & Chica 2003b; Battiston & Picciau 2008b; Scherrer 2014; Rivera & Svenson 2016; and Figure 3a–j). The plesiomorphic condition (with respect to *Metallyticus*) of the phalloid apophysis (long, acute and curved) is also present in some acanthopoids (*Brunneria, Cardioptera, Chromatophotina, Macromantis*; see Heitzmann-Fontenelle 1969; Roy 2002b; Agudelo & Chica 2003a; Rivera 2010a; Figure 4d), while in most artimantodeans it is secondarily altered in various ways and morphologically diverse.

[10] **Metallyticidae**. Autapomorphies: metallic (vs. *non-metallic, pigment-based*) coloration; proximal posteroventral spine on forefemur elongate (vs. *not elongate*); reduction (vs. *presence*) of two (of three) discoidal spines (see Wieland 2013, pp. 77, 154ff, and his figures 414–417 for details). As opposed to early instars, in the adult the remaining discoidal spine is found on the distal side of the femoral groove in one row with the anteroventral spines, due to an ontogenetic change of shape and location of the claw-groove. Anteroventral spines not alternating in length in adults of *M. splendidus* Westwood, 1835, but character present in its nymphs (Wieland 2013, figure 415), and in nymphs and adults of *M. violaceus* (Burmeister, 1838) (Figure 1c).

The distal part of the pseudovein (traversed by veins of CuA) has developed a certain degree of callosity in this group (Figure 1a, b). It may be homologous to the callosity on the stigma of Artimantodea, but due to the dorsoventrally flattened body in *Metallyticus*, the pseudovein is located posteriorly of RP + M, as is also the case for the posterior margin of the upper tegmen when folded over the lower tegmen. This

contrasts with the situation observed in most other extant mantodeans, where the entire posterior end of the discoidal field of the upper tegmen follows RP + M of the lower tegmen. In Artimantodea, the stigma is located between CuA and RP + M, encompassing some branches of the first, and is covered in the lower tegmen by the distalmost part of the anal field and the anal fold of the upper tegmen. We argue that the callosity at the posterior end of the pseudovein is a synapomorphy of Schizomantodea, with subsequent loss of the anterior part of the pseudovein in Artimantodea. This is accompanied by further rigidification of the stigma in Artimantodea, while in *Metallyticus* the flattening of body and tegmina caused a slight translocation of the pseudovein away from the anterior and towards the posterior margin of the tegmen. However, it is also possible that the callosity was evolved independently in *Metallyticus* and Artimantodea. Irrespective of the origin of the callosity in *Metallyticus*, and given the position of the pseudovein in relation to the anal fold of the opposite tegmen in Chaeteessidae, Mantoididae and Metallyticidae, there is no reason to assume a convergent origin of pseudovein and artimantodean stigma. Most Amerimantodea and early Cernomantodea exhibit an intermediate stage. The stigma of these taxa is oblique and narrow, and, particularly in Thespidae, much reminiscent of the pseudovein of Mantoididae.

[11] **Artimantodea**. Synapomorphies: well-marked (vs. *missing*) supracoxal dilatation; elongate (vs. *short and broad*) forefemur with the claw-groove moved distally (vs. *at base*); four (vs. *three*) discoidal spines (secondarily reduced to three in some groups); wings with elongate stigma (vs. *pseudovein*), becoming more or less ellipsoid in derived Cernomantodea; proximal lobe (**bl**) on right side of ventral phallomere (vs. *ventral phallomere without such lobe*). In contrast, an elongate prothorax is probably not a synapomorphy, but evolved independently in several artimantodean lineages. This is indicated by the fact that early lineages of both Amerimantodea (Pseudomiopteryginae + Bantiinae) and Cernomantodea (Tarachininae, Bolbellini, several groups among nanomantoids) have relatively short prothoraces, with a ratio of metazona to prozona comparable to *Metallyticus*.

[12] **Amerimantodea**. Synapomorphy: triangular supraanal plate (vs. *transverse with rounded or truncate apex*). While this work was in progress, Rivera & Svenson (2016) presented a molecular phylogeny of this group, circumscribed as "polymorphic earless praying mantises", and formally placed them under the superfamily Acanthopoidea. Resulting clades were characterized morphologically, but no explicit apomorphies were stated. Nevertheless, the classification scheme proposed by Rivera & Svenson (2016) is largely congruent with the morphological data presented here. We have basically followed their arrangement, except in a few cases discussed below, and where a change of rank seemingly better reflects phylogenetic relationships.

[13] **Thespidae**. Synapomorphies: distalmost anteroventral spine(s) of foretibiae translocated (vs. *not translocated*) to dorsal side of tibia (Rivera & Svenson 2016) (reversed in adults of some groups); females apterous (vs. *winged*); dorsal apical lobe of forecoxa elongate (vs. *not elongate*); dorsal lamina of left phallomere with (vs. *without*) a rounded lobe (**dll**) juxtaposed the primary distal process (**pda**) (Figure 3a–j). The wings of males are distinctly pilose (Rivera & Svenson 2016). The translocated distal anteroventral spine of the tibiae, frequently reversed in adults, is regarded as putatively homoplastic by Rivera & Svenson (2016). Given that it occurs in juveniles of Pseudomiopteryginae, Bantiinae, and Thespinae, we regard this character as a synapomorphy of Thespidae, with subsequent secondary losses in Pseudopogonogastrinae, Miobantiinae, and Musoniellinae. Morphological and genital data support the phylogenetic scenario of Rivera & Svenson (2016) and, to a lesser degree, Svenson & Whiting (2009). While Pseudopogonogastrinae is a morphologically highly derived group, it shares with Pseudomiopteryginae, Bantiinae, and Miobantiinae the plesiomorphic condition in the dorsal lamina with one lobe only (Lombardo & Ayala 1999; Figure 3a, b). In addition, the latter three are characterized by relatively short pronota and broad wings. Bantiinae have a highly modified left complex, with the ventral phallomere and left phallomere being fused anteriorly, rendering the whole structure Ω-shaped (Rivera & Svenson 2016; Figure 3b) but otherwise fitting well into this group. Musoniellinae and Thespinae, on the other hand, are united by narrow wings (with *Leptomiopteryx* exhibiting an intermediate stage) and, more importantly, by **dll** being forked, producing a second, more or less lobate process on the dorsal lamina, just anteriad the titillator (Figure 3c–j). There is also a tendency towards body elongation in this group. The oblique and narrow stigma is a plesiomorphic trait (see above).

[14] **Bantiinae**. Autapomorphy: ventral and left phallomere broadly fused (Figure 3b) (vs. *not fused*) anteriorly (Rivera & Svenson 2016).

[15] ***Mantillica***. The genus was recently shown to be monotypic: while *Mantillica beieri* Kaltenbach, 1957 was transferred to *Mantoida* by Agudelo (2014), as suggested previously by Terra (1995) and Rivera (2010b), *M. sialidea* Westwood, 1889 was shortly after transferred to *Thrinaconyx* (Agudelo & Rafael 2014).

[16] **Miobantiinae**. Distinguished from Pseudomiopteryginae by less broad and less tuberculate pronotum, from Bantiinae by left and ventral phallomere not being fused into a Ω-shaped structure, and from Pseudopogonogastrinae by the lack of pronotal protuberances, broader wings in males and lack of foliaceous lobes in females (Rivera & Svenson 2016; pers. obs.).

This tribe as understood previously (*sensu* Ehrmann 2002) was not monophyletic. The current arrangement is based on Rivera & Svenson (2016) and confirmed by own

genital data. *Leptomiopteryx*, for example, has a bilobed **dll** on the dorsal lamina (Figure 3c) and is therefore better placed among Musoniellinae.

[17] ***Chloromiopteryx***. *Emboicy* Terra, 1982 has recently been revealed to be a junior synonym (Agudelo & Rivera 2015).

[18] ***Paradiabantia***. This genus has recently been revalidated by Rivera & Svenson (2016).

[19] **Musoniellinae + Thespinae**. Both Svenson & Whiting (2009) and Rivera & Svenson (2016) found Thespini (*sensu* Beier 1935a, 1964; Ehrmann 2002) to be paraphyletic. Both studies, however, resolved *Musoniella* and *Eumusonia* outside Thespini, and the latter as more closely related to Oligonychini (*partim*). Rivera & Svenson (2016) refrained from further subdividing their Thespini (treated here as subfamily), and commented upon the scattered occurrence of a dorsal spine on the foretibiae among the group. They also noted that several taxa have been incorrectly assigned to particular genera in the past, reflected in their paraphyly in the resulting phylogenetic tree (Rivera & Svenson 2016, figure 4). However, their topology differentiates between a number of genera with largely unmodified forelegs and (usually) five posteroventral spines on the foretibiae in the adult stage (Thespini), and a sister-group consisting of species with reduced foreleg armature and the dorsolateral translocation of the apical anteroventral tibial spine more or less retained in adults (Oligonychini). Exceptions, like Thespini with dorsolateral tibial spines (*Pseudomusonia*) and oligonychinines without (*Liguanea, Galapagia, Piscomantis*) only underscore this character as a putative autapomorphy of the family, prone to various stages of reduction in adults. As noted by Rivera and Svenson (2016), additional genera will have to be created in the future to accommodate divergent species of currently polyphyletic genera.

Due to the forked (vs. *simple*) **dll** on the dorsal lamina common to Musoniellinae and Thespinae (Figure 3c–j) (the same structure being simple in Pseudopogonogastrinae, Pseudomiopteryginae, Bantiinae, and Miobantiinae) we concur with Svenson & Whiting (2009) and Rivera & Svenson (2016) in considering Musoniellinae and Thespinae as sister taxa, but have chosen a different rank to account for Thespinae diversity and thespid phylogenetic patterns.

[20] **Leptomiopterygini n. trib**. Distinguished from Musoniellini by broad tegmina with diverging anterior and posterior margins, and by the distal lobe of **dll** being partially fused with **paa** (Figure 3c vs. 3d, e).

[21] ***Musoniella***. *Congomantis* Werner, 1929 is a junior synonym (Schwarz & Roy 2018). Its only species, *Congomantis femoralis* Werner, 1929, is known from a single specimen labeled as "Luluaburg, Belg. Congo, 1926" (today Kananga, DRC). Examination of the type (NMB) revealed it to belong to *Musoniella*. Whether the specimen was wrongly labeled or really collected in Africa remains unknown (Schwarz & Roy 2018).

[22] **Pogonogasterina**. Synapomorphy: vertex with (vs. *without*) a bifid process above the ocelli. Oligonychina do not have such a process.

[23] ***Bistanta***. This replacement name has been introduced by Anderson (2018) to accommodate *Bactromantis mexicana* (Saussure & Zehntner, 1894) and related species previously assigned to *Bactromantis* Scudder, 1896. The type specimen of *Bactromantis virga* Scudder, 1896, the genotype, had been recognized to be a juvenile *Stagmomantis carolina* (Johansson, 1763) by Rehn & Hebard (1916), but this went unnoticed until being recently confirmed by Anderson (2018). Thus, *Bactromantis* Scudder, 1896 has to be regarded as a junior synonym of *Stagmomantis* Saussure, 1869.

[24] **Acanthopoidea**. Synapomorphies: **bl** elongate (vs. *not elongate*); right margin of ventral phallomere between **bl** and apex membraneous (vs. *sclerotized*) (Figures 4a–h, 5a–h). The systematic arrangement in this group is based on Agudelo (2015) and Rivera & Svenson (2016), with some exceptions. Contrary to the latter study, we use Acanthopoidea in a more restricted sense, excluding Thespidae. Also, ranks may differ from those proposed by Rivera & Svenson (2016).

[25] **Angelidae**. Autapomorphies: females brachypterous (vs. *macropterous*); alae colored (vs. *hyaline*), longer (vs. *not longer*) than tegmina; cerci flattened (vs. *cylindrical*). This systematic position among a clade of acanthopoids concurs with Yager & Svenson (2008), Agudelo (2015), and Rivera & Svenson (2016), and is supported by morphological and genital traits.

[26] ***Angela***. This is the only genus currently included in the family. *Thespoides bolivari* Chopard, 1916, until recently regarded as closely related to *Angela*, has been shown by Rivera (2014) to be a chimeric individual, consisting of pronotum, forelegs, and head of *Angela guianensis* Rehn, 1906 attached to a thespine hind body. The latter is now lost.

[27] **Coptopterygidae + (Liturgusidae + (Photinaidae + Acanthopidae))**. Synapomorphy: five (vs. *four*) posteroventral spines on forefemur.

[28] **Coptopterygidae**. Autapomorphies: tegmina of females brachypterous (vs. *meso- to macropterous*); alae totally reduced (vs. *present*); loss of one discoidal spine.

[29] **Liturgusidae**. *Liturgusa* and related genera are described by Beier (1931b), Ehrmann (2002, pp. 163, 206) and Svenson (2014) to possess four posteroventral spines on the forefemur, there is, however, an additional spine on the posterior side of the genicular lobe (La Greca 1939; Svenson 2014). It remains unclear if this spine was re-evolved from the condition seen in *Chaeteessa* or whether it is a spine of the posteroventral row moved distally. If the latter is not the case, the re-evolved genicular spine and one lost posteroventral

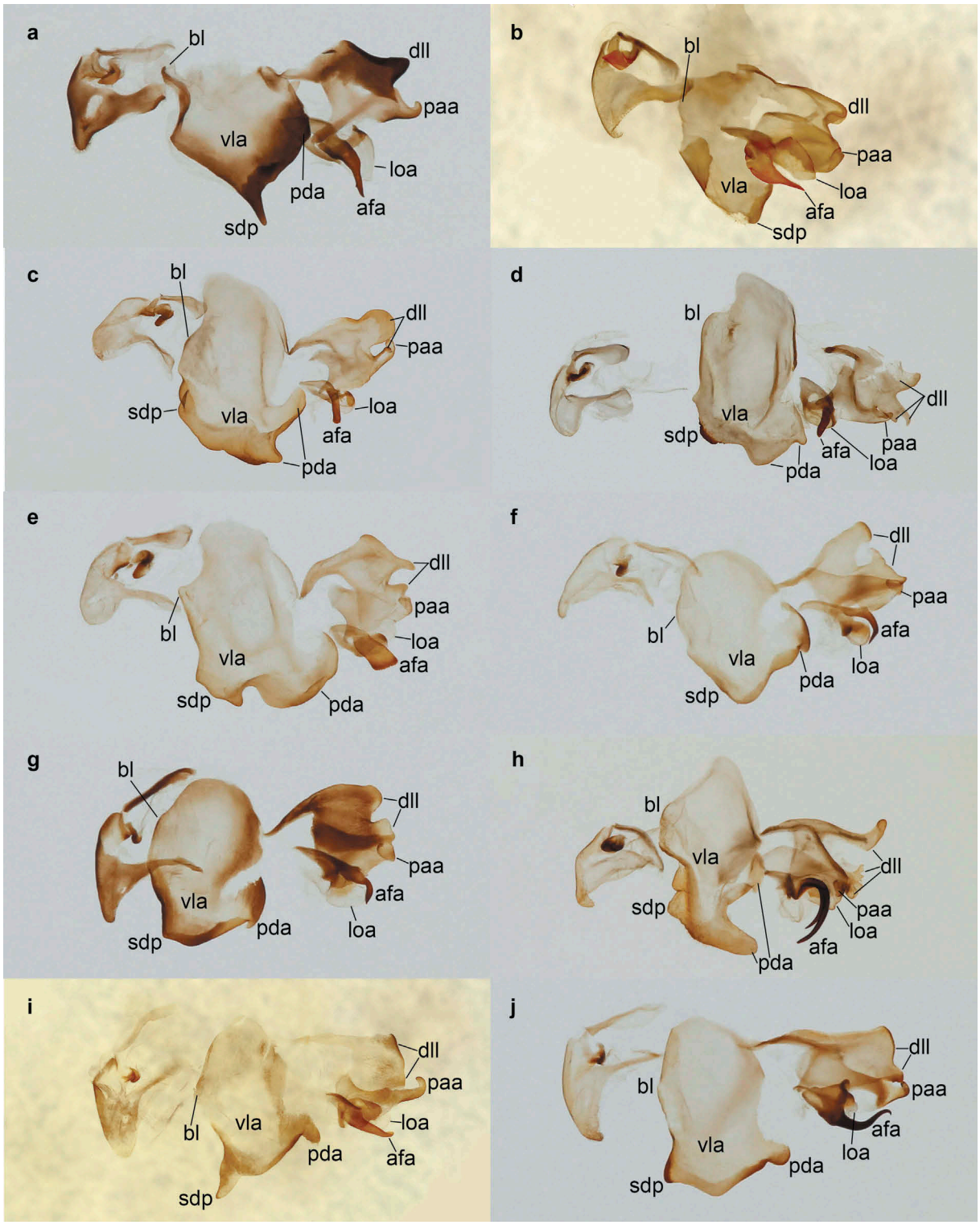

Figure 3. Genitalia of Thespidae, ventral view. **a**, *Pseudomiopteryx infuscata* Saussure & Zehntner, 1894, from Panama (CS, prep. Schwarz No. 154); **b**, *Bantia fusca* Chopard, 1912, from French Guyana (MNHN, prep. Roy No. 3508); **c**, *Leptomiopteryx dispar* Chopard, 1912, from French Guyana (CS, prep. Schwarz No. 155); **d**, *Eumusonia livida* (Audinet-Serville, 1839), from E Brazil (CS, prep. Schwarz No. 160); **e**, *Musoniella* sp., from E Brazil (CS, prep. Schwarz No. 173); **f**, *Musonia surinama* (Saussure, 1869), from Panama (CS, prep. Schwarz No. 169); **g**, *Pseudomusonia lineativentris* (Stål, 1877), from Panama (CS, prep. Schwarz No. 168); **h**, *Macromusonia major* (Saussure & Zehntner, 1894), from French Guyana (CS, prep. Schwarz No. 170); **i**, *Oligonyx insularis* Bonfils, 1967, from Guadeloupe (MNHN, prep. Roy No. 3404); **j**, *Thesprotia graminis* (Scudder, 1877), from USA (CS, prep. Schwarz No. 151). Not to scale.

spine would be synapomorphies of this family. Characteristic is also a second, irregular line of shorter spines located slightly mediad of the posteroventral spines. Genitalia simplified, with short **sdp** and short but pointed **afa** (Svenson 2014; Figure 4c).

[30] **Hagiomantini n. trib**. Distinguished from Liturgusini by tuberculate mid and hind legs (Svenson 2014).

[31] ***Hagiomantis***. *Liturgusa mesopoda* Westwood, 1889 was transferred by Svenson (2014) to the genus *Hagiomantis*, but it differs in pronotal and wing shape, and hind wing color, from the other species in this genus. It probably deserves a genus of its own.

[32] **Photinaidae**. Morphological characters characterizing subfamilies are given in Rivera & Svenson (2016). Here, only polarized and additional characters are given.

[33] ***Photiomantis***. *Margaromantis* Piza, 1982, *Rehniella* Lombardo, 1999, *Colombiella* Koçak & Kemal, 2008 and *Lombardoa* Özdikmen, 2008 were all recently shown to be synonyms of this genus (Agudelo & Rivera 2015).

[34] ***Cardioptera***. Autapomorphies: loss of one discoidal spine; subgenital plate with (vs. *without*) a black marking.

[35] **Photinaina**. In early photinaids (Macromantinae, Photiomantinae, Cardiopterinae) **bl** is more or less unmodified, and **afa** is acute and curved (Figure 4d, e). The latter is also the case in Microphotinaini (François & Roy 2015), but with regard to **bl** this group exhibits the photinaine condition: in these two tribes, this structure is more or less rigidified (Microphotinaini, Orthoderellina), while in Photinaina it is also distinctly curved (Figure 4f–h).

[36] ***Microphotina***. This genus is probably not monophyletic (François & Roy 2015).

[37] **Acanthopidae**. Synapomorphies: vertex with (vs. *without*) a short process (secondarily reduced in some taxa); anterior femora with six or more (vs. *five*) posteroventral spines; posteroventral spines of foretibiae decumbent (vs. *not decumbent, more or less like anteroventral spines*); last segment of cerci enlarged (vs. *not enlarged, conical*); **loa** strongly developed, more or less pilose, largely enclosing **afa** (Figure 5a–h) (vs. *not pilose and not enlarged*); **afa** with (vs. *without*) an anterior lobe in addition to the posterior lobe (anterior lobe secondarily reduced in some groups).

We differ in the arrangement of this group from Rivera & Svenson (2016) by treating it as one family. Also, the position of *Stenophylla* differs from that study because of morphological apomorphies which allow a more parsimonious placement as sister to Acontistini. Forcing *Stenophylla* to become sister of Acanthopinae + Acontistinae would require the discoidal spine to be lost twice (in *Stenophylla* and Acontistini), and the femoral lobes to be either independently acquired in *Stenophylla* and Acontistini or lost in Acanthopinae. While this is possible, a placement of *Stenophylla* as sister to Acontistini not only circumvents this additional step by assuming one origin for the lobes and one loss of the discoidal spine, it is also supported by the shape of pronotum and forelegs, and the remnants of the vertex processes in early Acontistinines (*Callibia, Ovalimantis*).

[38] ***Acanthops***. This genus as currently understood is probably paraphyletic with respect to some of the other genera. The genus *Plesiacanthops* Chopard, 1913 has been resurrected by Schwarz & Roy (2018). Other species have been recently moved from *Acanthops* to *Metacanthops* by Agudelo et al. (2019).

[39] **Stenophyllinae**. Synapomorphy: vertex with (vs. *without*) two lateral processes above eyes (reduced in derived Acontistina); loss of one discoidal spine; ventral carina of walking leg femora developed (vs. *not developed*) into lobes.

[40] **Stenophyllini**. Autapomorphies: last, enlarged segment of cerci elongate (vs. *not elongate*); genitalia (Figure 5f) strongly simplified, ventral phallomere without (vs. *with*) **bl, sdp** very indistinct (vs. *well-developed*), **afa** slender and acute (vs. *broader and serrate*).

[41] **Acontistini**. Synapomorphies: forefemur with five (vs. *six or more*) posteroventral spines; last segment of cerci not enlarged (vs. *enlarged*).

[42] **Acontistina**. Apomorphy: loss (vs. *presence*) of lobes on walking leg femora.

[43] ***Acontista***. As pointed out by Rivera & Svenson (2016), this genus is paraphyletic with respect to at least *Raptrix*, likely necessitating the future resurrection of *Metaphotina* Piza, 1964 to accommodate a southern group of species with brachypterous females. *A. gracilis* Chopard, 1912 and related species probably also deserve a genus of their own.

[44] ***Astollia***. For comments on this enigmatic genus, known only from Stoll's (1787, 1813) figure, see Roy (2006b).

[45] **Cernomantodea**. Synapomorphies: cyclopean ear (Yager & Svenson 2008; Svenson & Whiting 2009); ventral phallomere with two (vs. *one*) small, rounded secondary processes: one at its distal tip (**sdpm**), the second on the right distal side (**sdpl**); **afa** with an anterior (**aafa**) and posterior (**pafa**) lobe (vs. *not bifurcate, simple*), **aafa** indistinct and rounded, **pafa** short, more or less digitiform (see also comments under Chroicopteridae). This is the groundplan condition of cernomantodean genitalia. The plesiomorphic condition is retained by most nanomantoids, but even among groups with substantial changes the original components may be seen, except when completely reduced.

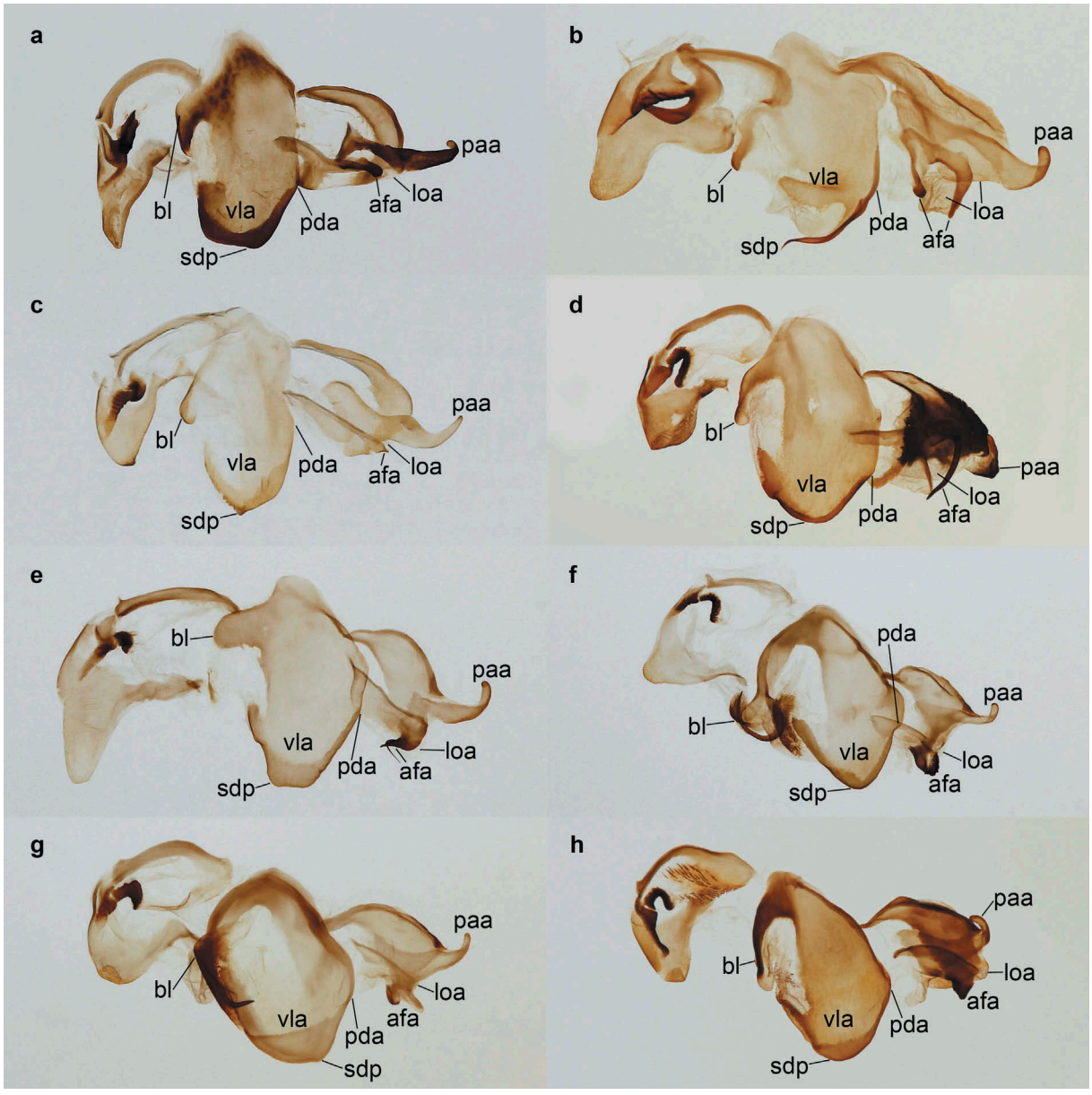

Figure 4. Genitalia of Angelidae, Liturgusidae and Photinaidae, ventral view. **a**, *Angela subhyalina* (Chopard, 1914), from Ecuador (CS, prep. Schwarz No. 110); **b**, *Coptopteryx argentina* (Burmeister, 1864), from N Argentina (CS, prep. Schwarz No. 212); **c**, *Liturgusa maroni* Svenson, 2014, from French Guyana (CS, prep. Schwarz No. 70); **d**, *Macromantis hyalina* (De Geer, 1773), from Peru (CS, prep. Schwarz No. 268); **e**, *Photiomantis planicephala* (Rehn, 1916), from Brazil (CS, prep. Schwarz No. 271); **f**, *Photina vitrea* (Burmeister, 1838), from Argentina (CS, prep. Schwarz No. 244); **g**, *Metriomantis pilosa* Chopard, 1912, from French Guyana (CS, prep. Schwarz No. 217); **h**, *Orthoderella major* (Piza, 1962), from E Brazil (CS, prep. Schwarz No. 162). Not to scale.

The various distal processes observed among cernomantodeans are not necessarily homologous: while both **sdpm** and **sdpl** may be retained and functional, as e.g. in several Chroicopteridae (Figure 6c, g), Leptomantellidae (Figure 6i), Nanomantidae (Figure 8f–h), Amorphoscelinae (Figure 7c, f), *Brancsikia* (Figure 10e), Amelidae (Figure 12c), *Schizocephala* (Figure 12f), *Galepsus* (Figure 13f), *Orthodera* (Figure 20c), *Choeradodis* (Figure 20d), *Deromantis* (Figure 20g), *Tisma* (Figure 22e), and most Hierodulinae (Figures 23b, d–g, 24e, f), usually one of the processes is reduced in favor of the other. More or less straight processes, as seen, e.g. in *Phyllocrania* (Figure 15e), *Afrothespis* (Figure 18e) and Mantinae (Figure 20e, f), originate from the median distal process (**sdpm**). Hook-like processes mostly develop through an emargination of the phallomere just proximad of the lateral distal process (**sdpl**), with subsequent rigidification of **sdpl** and loss of **sdpm**. Transitional stages with various degrees of emargination, or

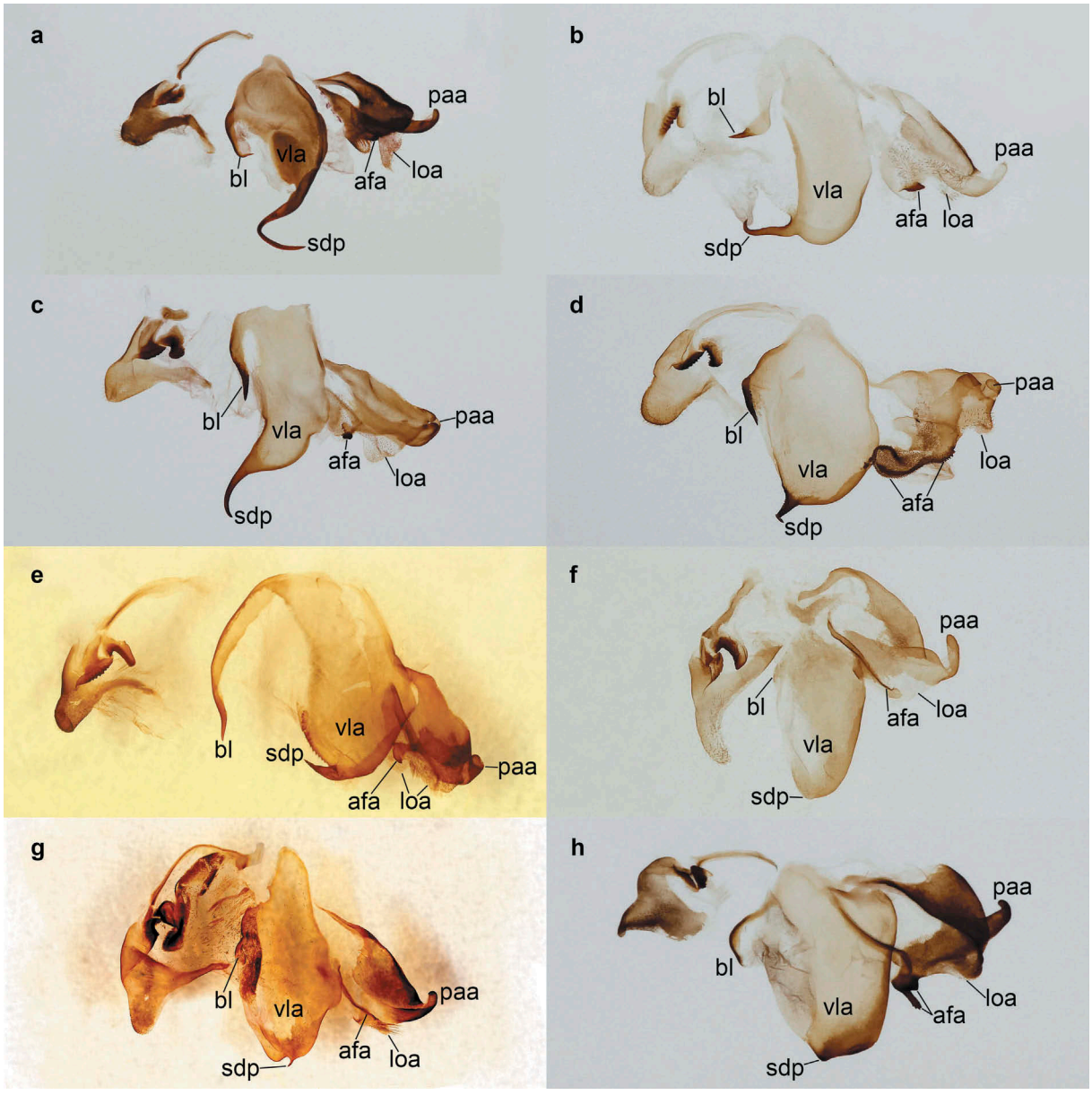

Figure 5. Genitalia of Acanthopidae, ventral view. **a**, *Acanthops erosula* Stål, 1877, from Peru (CS, prep. Schwarz No. 88); **b**, *Acanthops* sp., from Isla Margarita, Venezuela (CS, prep. Schwarz No. 28); **c**, *Pseudacanthops lobipes* La Greca & Lombardo, 1997, from Peru (CS, prep. Schwarz No. 265), genitalia slightly damaged anteriorly; **d**, *Decimiana hebardi* Lombardo, 2000, from Bolivia (CS, prep. Schwarz No. 269); **e**, *Lagrecacanthops guyanensis* Roy, 2004, holotype (MNHN, prep. Roy No. 3884); **f**, *Stenophylla cornigera* Westwood, 1843, from Venezuela (SMNK 10158, prep. Roy No. 3871); **g**, *Ovalimantis maculata* Roy, 2015, holotype (MNHN, prep. Roy No. 4563); **h**, *Raptrix perspicua* (Fabricius, 1787), from French Guyana (CS, prep. Schwarz No. 156). Not to scale.

with hook-like lateral process and median process still present as a distal lobe at the base of the hook can be observed, e.g. in Chroicopterinae (Figure 6f, h), *Humbertiella* (Figure 10a, b), some *Haania* (Figure 11e, f), *Parathespis* (Figure 12d), *Dysaules* (Figure 12i), most Tarachodinae (Figure 13a–c, e), *Heterochaeta* (Figure 14a), *Pseudempusa* (Figure 19c), *Deroplatys* (Figure 19e), Mellierinae (Figure 20a, b), some Tenoderinae (Figure 21b, c), *Tismomorpha* (Figure 22f), and *Sphodropoda* (Figure 24g).

Likewise, of the two distal processes of Madagascan Tarachodina, the right one is a novel structure (**tdp**) evolved alongside **sdpl**, with no homologs outside Tarachodina (Figure 13h).

Putatively synapomorphic for the group as a whole are also lobes on the abdomen, consisting of large lateral tergal and smaller sternal lobes in combination with median tergal and sternal lobes. They are frequently secondarily reduced (especially the median lobes, often lost in macropterous

species) or re-evolved. Such lobes are present, e.g. in *Achlaena, Geothespis, Platycalymma, Calofulcinia, Muscimantis, Elaea, Elmantis, Myrcinus, Theopompa, Danuriella, Majanga, Gonatista, Epaphrodita*, Haaninae, *Tarachodes*, Toxoderini, *Hoplocorypha, Harpagomantis*, many Hymenopoidea and Deroplatyidae, *Theopompella*, and Vatini.

[46] **Nanomantodea**. Heterogenous group of small-bodied to at most medium-sized mantids without clear morphological synapomorphies, characterized by some primitive characters like mostly short (rarely elongate as in *Leptomantella* or *Stenomantis*) pronota and ciliate tegmina, and with rather diverse genitalia which can be derived from the cernomantodean groundplan.

[47] **Chroicopteridae**. Synapomorphies: females brachypterous (vs. *macropterous*); phalloid apophysis with (vs. *without*) a flagellum (secondarily lost or modified in some species). The flagellum is inserted at a position near or on the anterior lobe (cf. Kaltenbach 1996; Figure 6h).

Most early (Tarachininae) and some derived chroicopterids (*Achlaena, Parentella*) have myrmecomorphic nymphs (retained until the adult stage in females of *Gonypetella* and *Tarachina*; Gillon & Roy 1968; Ehrmann 1991; Hevers & Liske 1991). We regard this trait as a putative synapomorphy of the family, but further studies on postembryonic development of the other genera (particularly of Bolbellini) are necessary to underscore this assumption.

The phylogenetic position of Chroicopteridae resolves rather unstable in molecular studies: sister of Iridopteryginae in Svenson (2007) and, with slight changes, in Yager & Svenson (2008) and Legendre et al. (2015), and of Nanomantidae in Svenson & Whiting (2009). Morphological traits concur with the latter hypothesis, and since the distinctive chroicopterid genitalia represent independent developments from the plesiomorphic (nanomantoid) condition unparalleled in other mantodeans, it is retained here.

[48] **Tarachininae**. Synapomorphy: females apterous (vs. *brachypterous*).

[49] **Gonypetellini n. trib**. Synapomorphies: **paa** T-shaped (vs. *simply curved*), reversed to normal in some of the species, as those depicted in Figure 6a, b; **afa** more or less simple (vs. *bilobate*). Some species have secondarily lost the flagellum on the phalloid apophysis (Kaltenbach 1990, 1996; Figure 6a, b).

[50] **Tarachinini**. Autapomorphies: loss of first discoidal spine; weakly (vs. *typically*) developed foreleg spination (see Roy 1969 for details); both **sdpm** and **sdpl** developed into a spine-like process (vs. *short and with rounded apices*); "flagellum" robust, long, fused (vs. *not fused*) to base of phalloid apophysis; **pafa** largely reduced (vs. *distinctly developed*) (Figure 6c).

[51] **Bolbellini n. trib**. Synapomorphies: basal lobe of ventral phallomere strongly developed, elongate (vs. *not elongate*) (secondarily reduced in some *Dystactula* species); **sdpl s**trongly elongate, toothed, pointing craniad (vs. *not toothed, pointing laterad*); **sdpm** usually present and acute (vs. *rounded*), but short (Beier 1953b; Kaltenbach 1996; Roy 2006a; Stiewe 2007). In most *Bolbella* species the flagellum is multi-cuspidate.

[52] **Chroicopterini. Pafa** more or less digitiform. Flagellum usually present.

[53] **Dystactina**. Characterized by less elaborate genitalia than the following subtribes, with weakly developed spination, reduced flagellum (except *Pseudodystacta*) and rather indistinct **sdpl** and **sdpm**. The heavily sclerotized, toothed phalloid apophysis (except *Dystacta*) is a plesiomorphic trait also present in many Tarachininae (Kaltenbach 1990, 1996). We left in this group only those genera with similar external morphology and genitalia like those described above, removing *Congomantis* (which is a junior synonym of *Musoniella*, see comments under that genus) and moving *Rhachimantis* (the type of which is in bad condition and lacks the abdomen apex, MFN) to Chroicopterina. Still, the group as currently conceived may not be monophyletic.

[54] ***Amphecostephanus***. The unusual morphology of this genus caused considerable discussion among taxonomists regarding its systematic affinities. Rehn (1912) regarded his new genus as a member of the section Pachymantides of the subfamily Creobotrinae, but noted its distinctiveness from the other genera of that group. Giglio-Tos (1919) placed it among his "Distactae" alongside *Gonypetella, Telomantis, Dystactella, Dystacta, Achlaena* and *Achlaenella*. Beier (1934a), however, criticized Giglio-Tos' placement as "ungrounded" and transferred the genus to Hymenopodinae Epaphroditini alongside *Phyllocrania* due to its process on the vertex and the five posteroventral spines on the forefemur. This position alongside *Phyllocrania* has been widely adopted since (Beier 1964, 1968b; Ehrmann 2002; Otte & Spearman 2005) but has not been without criticisms. Roy (1977b) commented on the peculiar morphology and genitalia of the genus and proposed a position among Acromantinae alongside *Oxypilus*, admitting that the two genera are not particularly closely related. Roy (1999b, 2008a) reprised the topic and expressed doubts whether *Amphecostephanus* is a member of Epaphroditinae. Morphological phylogeny (Wieland 2013, figures 394, 395) resolves *Amphecostephanus* as sister to a heterogenous assemblage of gonypetines, amelines, rivetinines, tarachodines and chroicopterines. This prompted Svenson et al. (2015) to exclude this genus from Hymenopodidae despite lack of molecular evidence due to unavailable specimens.

The genitalia of *Amphecostephanus*, depicted here for the first time (Figure 6e), in concordance with its external morphology, support the original placement of Giglio-Tos (1919) alongside Dystactina. Its autapomorphies (process on the vertex, five vs. *four* posteroventral spines, incised

vs. *conical* last segment of the cerci) are unique among chroicopterids and underscore its assignment to an own subtribe.

[55] ***Bisanthe, Carvilia* and *Geothespis***. The systematic placement of these three genera had to be revised. They have been classified before as a member of Mantidae among Miomantini (Beier 1964, including Rivetinini *sensu* Ehrmann 2002) or Rivetinini (Giglio-Tos 1927, as Eufischeriellae; Ehrmann 2002; Otte & Spearman 2005). However, several distinctive characters, like their X0 sex chromosome system (*Bisanthe*), male genitalia of the chroicopterine type, including a flagellum in *Carvilia* (see Kaltenbach 1996 for details), and digging devices on the females' valves (*Geothespis*), are not consistent with the previous systematic position among Mantidae, Miomantidae or Rivetinidae. The distinctive genitalia of *Bisanthe* (Figure 6f) share characters with both Chroicopterina and *Amphecostephanus*, but differ from those of Miomantidae and Mantidae. *Bisanthe* differs from Dystactina and Chroicopterina in the shape of the two lobes of **afa**; from *Amphecostephanus* by the lack of a vertex process, simple cerci, and by having just four posteroventral spines. *Geothespis* shares lobed tergites and the morphology of pronotum and forelegs with *Carvilia*, and valvular digging devices with the *Ligaria* group in general (Wieland 2013, pp. 114–117, figures 371–375).

[56] **Chroicopterina**. In this group, the apical part of ventral phallomere and the lateral part of left phallomere are more or less toothed. The ventral phallomere shows a considerable variability across genera: while the phallomere and its two distal processes are not much modified in *Chroicoptera* and *Entelloptera*, and in *Carvilia, Namamantis, Chopardentella* and *Paraligaria* an emargination on the right side has formed a more or less curved lobe, in *Macracanthopus* and some *Ligaria* and *Entella* species-groups a curvature tendency of the whole distal part of the phallomere can be observed, so that the two small but dentate distal processes face to the right (see e.g. Beier 1953b, 1954, 1955, 1969a, 1969b; Kaltenbach 1990, 1996; Figure 6g, h).

[57] **Nanomantoidea**. Genitalia in this group are rather simplified compared to previous clade (Figures 6i, j, 7a-e, 8a–f). Putative groundplan: weak sclerotization; both **sdpm** and **sdpl** present as small lobes; rather short **paa**; and a simple, weakly sclerotized **afa**. The more complex structures seen in some groups (Amorphoscelinae, Stenomantini; Figures 7c, 7f, 8g, h) are secondarily developed and can be homologized with the groundplan condition. The bifurcation of **afa** into an anterior and a posterior lobe is distinct in Hapalomantinae (see Kaltenbach 1996), *Eomantis* (Figure 8b) and some Fulcininiines (Figure 8g) but largely reduced in the other groups.

A putative synapomorphy of this group is the flattened and elongate last segment of the cercus; it can be observed to a varying degree in several not closely related genera (e.g. *Leptomantella*, Amorphoscelinae, *Pliacanthopus, Fulciniola*). It is possible that this feature was secondarily reduced in most genera, while being retained and even exaggerated (e.g. Amorphoscelinae) in others.

[58] **Leptomantellidae n. fam**. Distinguished from all other nanomantoids except *Epsomantis* by the presence of four discoidal spines. Distinguished from *Epsomantis* by the slender pronotum without distinct expansion, and the presence of four instead of five posteroventral spines on the forefemora.

[59] **Amorphoscelidae + Nanomantidae**. Synapomorphy: loss of one discoidal spine.

[60] **Amorphoscelidae**. Synapomorphies: loss (vs. *presence*) of foretibial spines; loss (vs. *presence*) of posteroventral spines on forefemur; anteroventral spines reduced to three; discoidal spines reduced to one (vs. *three*).

[61] **Amorphoscelinae**. Synapomorphies: loss (vs. *presence*) of anteroventral spines on forefemur; last segment of cerci greatly enlarged and flattened (vs. *possibly flattened but not greatly enlarged*). Also, the genitalia of most species have undergone significant modifications, with the basal lobe developed into simple to multicuspidate spines and hooks of various shapes, and **sdpm** and **sdpl** lost or juxtaposed to various degrees (for examples see Roy 1962b, 1963b, 1964a, 1965b, 1966a, 1966d, 1967a, 1984, 2007b, 2009c, 2011, among others; Figure 7c–f). The most plesiomorphic-looking genitals are found in the *Amorphoscelis philippina* species group (Figure 7d); whether this reflects a true plesiomorphic condition or a secondary structural simplification remains to be investigated.

[62] **Nanomantidae**. There are two larger clades in this group, also obtained by molecular results (Svenson & Whiting 2009): Hapalomantinae + Tropidomantinae vs. Nanomantinae + Fulciniinae. This arrangement largely reflects biogeographic patterns (Gondwanan origin, see Svenson & Whiting 2009 for details), but is also supported by morphological results. Hapalomantinae + Tropidomantinae are distinguished from Nanomantinae + Fulciniinae by their distinctly keeled pronotum (particularly the metazona) and a lamellar expansion of the pronotum. We regard these two characters as a synapomorphy of the group, even though the lamellar expansion may be secondarily reduced in Hapalomantini.

A putative synapomorphy of Nanomantinae + Fulciniinae has been described by Giglio-Tos (1927) for the tegmen venation. In members of this clade, RP + M and CuA abruptly diverge after the stigma, the resulting space being filled by a dense reticulation unlike that on other parts of the tegmen. This is the case in most fulciniines investigated by us and *Nanomantis australis* Saussure, 1871, but less expressed or reduced in Neomantini and Oriental members of

Nanomantinae. Given the unclear monophyly of *Nanomantis* (see below), it is well possible that this character is a synapomorphy of *Nanomantis* + Fulciniinae, necessitating nomenclatural changes in Oriental Nanomantinae in the future.

[63] **Hapalomantini & Nilomantini**. The two tribes are distinguished by both their external morphology and genital features (Kaltenbach 1996). Hapalomantini are of brownish body color, and their pronotal expansion is much reduced, though still visible. In their genitalia, **sdpm** and **sdpl** are fused to form a more or less truncate or spoon-like process, and the phalloid apophysis has both **aafa** and **pafa** expressed. Nilomantini, on the other hand, are all pale greenish or yellowish, with a distinct pronotal expansion, and often conical eyes. In this group, **sdpm** is conical or elongate, while **sdpl** is reduced (except *Hyalomantis*), and **afa** is usually tuberculate or dentate (Roy & Leston 1975; Kaltenbach 1996; Svenson & Roy 2011; Brannoch & Svenson 2016a, 2016b).

[64] ***Ilomantis***. The validity of this genus has been recently proven by Brannoch & Svenson (2016b).

[65] ***Negromantis.*** *Mimomantis* Giglio-Tos, 1915 and *Luteomantis* Sjöstedt (1924) were synonymized with *Negromantis* by Beier (1935, p. 55).

[66] **Tropidomantinae**. This group is distinguished from Nilomantinae, at least in the genera investigated by us, by their genitalia, which have **sdpl** distinctly developed at the expense of **sdpm** and with pointed apex (Figure 8a–e). The phalloid apophysis can be plesiomorphically bilobed in some genera (*Tropidomantis, Eomantis, Sinomantis*, Figure 8a, b, 8e), or secondarily simplified in others (*Pliacanthopus, Oligocanthopus*, Figure 8c, d).

[67] **Epsomantini n. trib**. Autapomorphies: five (vs. *four*) posteroventral spines on forefemur; four (vs. *three*) discoidal spines. We regard these unusual features to have (re-)evolved in conjunction from the typical nanomantid condition. All other features, like the distinct pronotal expansion, the carinate metazona, the setaceous forelegs, the configuration of foreleg spines, the enlarged costal field, and wing venation, are in concordance with features exhibited by Nilomantini and Tropidomantinae. We have not been able to investigate the male genitalia, though, so future rearrangements are possible when more data become available.

[68] **Nanomantinae**. The monophyly of this subfamily has yet to be proven. We could not investigate all genera, but *Miromantis* (Figure 8f) and *Sceptuchus* (Lombardo 1993b; pers. obs.) both have very simple genitalia, with **sdpm** and **sdpl** expressed as rounded lobes and **afa** simplified and rounded. We regard this configuration as genitalia groundplan for the group, as it corresponds very well to the nanomantoid condition.

[69] ***Nanomantis***. This genus, as currently conceived, is polyphyletic: the Oriental representatives probably belong to other genera of Nanomantinae.

[70] **Fulciniinae**. Very characteristic for the group is the forewing venation pattern described above, found outside the subfamily only in *Nanomantis australis*. Genitalia are relatively simple (very similar to Nanomantinae) in most genera (e.g. Milledge 1989; Figure 8h) but secondarily very elaborate in *Stenomantis* and *Ciulfina* (Holwell et al. 2007; Holwell 2014; Figure 8i). Also characteristic is the (putatively apomorphic) brownish body color.

[71] ***Ima***. Autapomorphy: XY sex chromosome system, so far unique among mantodeans (White 1975).

[72] **Stenomantini**. Apomorphies: body elongate, adapted to a bark-living lifestyle (vs. *not elongate and not particularly adapted to bark-living lifestyle*).

[73] **Neomantini n. trib**. Apomorphies: greenish (vs. *brownish*) body color, aiding in camouflage among leaves. The classification among Fulciniinae is supported by molecular data (Yager & Svenson 2008; Svenson & Whiting 2009; Legendre et al. 2015). Considered as a member of Tropidomantinae before (Giglio-Tos 1927; Beier 1935c; Ehrmann 2002).

[74] **Paraoxypilini**. A putative apomorphy is myrmecomorphy in nymphs (vs. *nymphs not engaged in ant mimicry*). Most genera also have adults resembling ants or other hymenopterans, though not all (*Gyromantis, Cliomantis*).

[75] **Paraoxypilina**. Synapomorphy: reduced (vs. *typical*) foreleg spination (for details see Beier 1929; Wieland 2013, p. 62ff, figures 180, 196–201, 217, 218, 245, 246).

[76] **Metamantodea**. Synapomorphies: distinct coloration of the hind wings: the discoidal field and adjacent parts of the anal field are yellowish-brown to reddish-brown, and feature an apical, dark, more or less eyespot-like marking, while the remaining posterior parts of the anal field are smoky with pale crossveins. This pattern is present at least in females of most early metamantodeans, e.g. Gonypetinae, Majanginae, Epaphroditinae, Rivetinidae, and even in derived genera such as *Astyliasula*. In the other groups, the pattern has been altered in various ways (up to the extent of total reduction) but can still be homologized when present, e.g. in Caliridinae, Miomantinae, Galinthiadidae, *Idolomantis*, Hymenopodinae, *Theopompella*, and Deroplatyidae. That is, **all hind wing color patterns in metamantodeans, including subapical eyespots, are homologous**.

Another putative metamantodean synapomorphy is their distinct pattern of pronotal markings or tubercles, consisting of two paramedian pairs on the prozona and four such pairs on the metazona. In addition, there are also 2–3 pairs of lateral whitish markings of triangular shape. In several lineages some or all of the markings develop into tubercles, while the whitish lateral markings become more or less dark. The large, toothlike

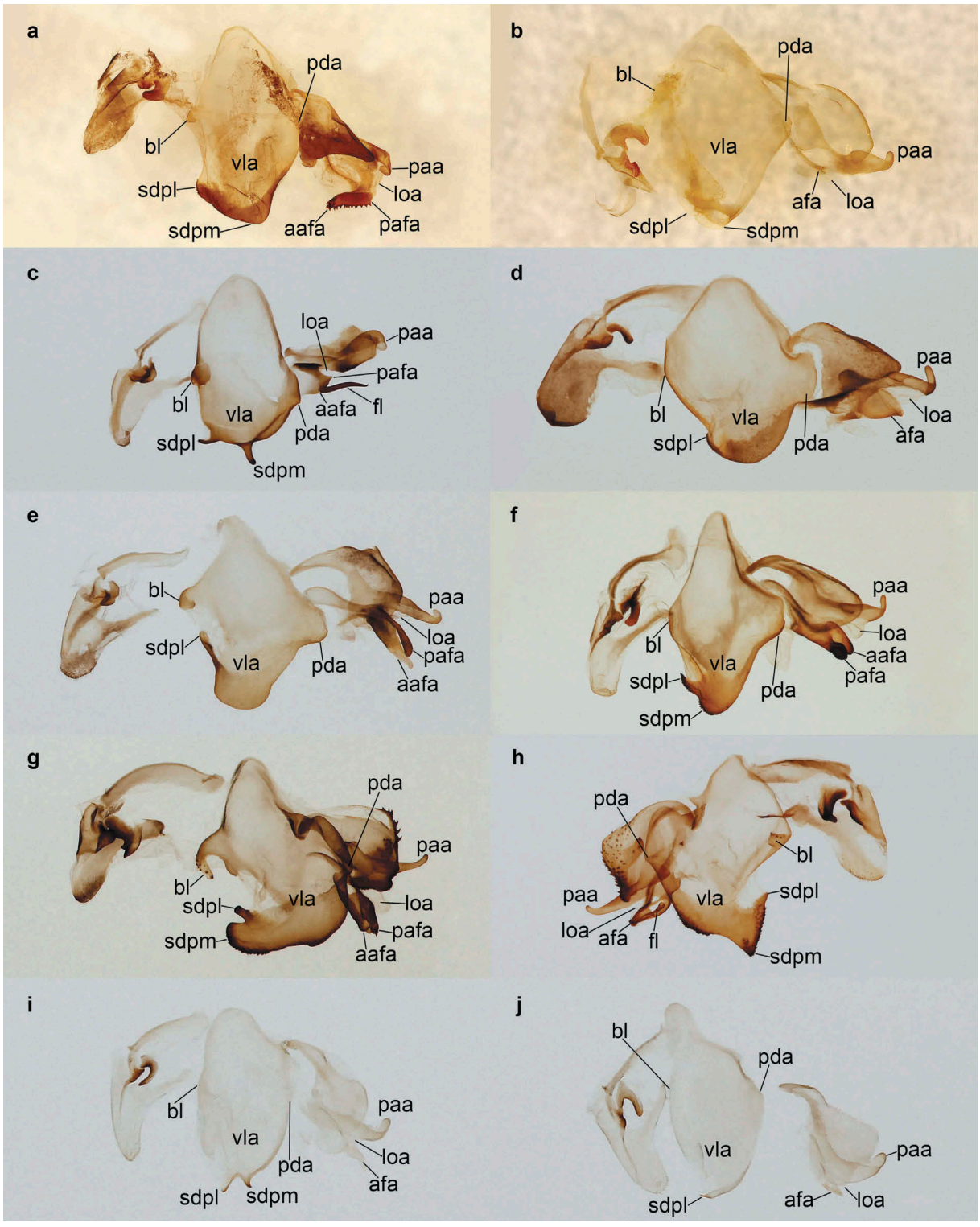

Figure 6. Genitalia of Chroicopteridae and Leptomantellidae, ventral view. **a**, *Gonypetella punctata* Giglio-Tos, 1915, from the Central African Republic (MNHN, prep. Roy No. 2786); **b**, *Telomantis lamperti* (Werner, 1906), from Kenya (MNHN, prep. Roy No. 4021); **c**, *Tarachina occidentalis* Giglio-Tos, 1915, from N Ivory Coast (CS, prep. Schwarz No. 264); **d**, *Dystacta alticeps* (Schaum, 1853), from Namibia (SMNK 02335, prep. Schwarz No. 177); **e**, *Amphecostephanus rex* Rehn, 1912, from Tanzania (MFN, prep. Schwarz No. 203); **f**, *Bisanthe lagrecai* Kaltenbach, 1996, from N South Africa (CS, prep. Schwarz No. 153); **g**, *Entella transvaalica* Beier, 1955, from N South Africa (SMNK 02727, prep. Schwarz No. 206); **h**, *Ligaria* cf. *inexpectata* Kaltenbach, 1996 with chirally mirrored genitalia, from Natal, South Africa (SMNK 04904, prep. Schwarz No. 178); **i**, *Aetaella bakeri* Hebard, 1920, from Panay, Philippines (CS, prep. Schwarz No. 125); **j**, *Leptomantella lactea* (Saussure, 1870), from Panay, Philippines (CS, prep. Schwarz No. 123). Not to scale.

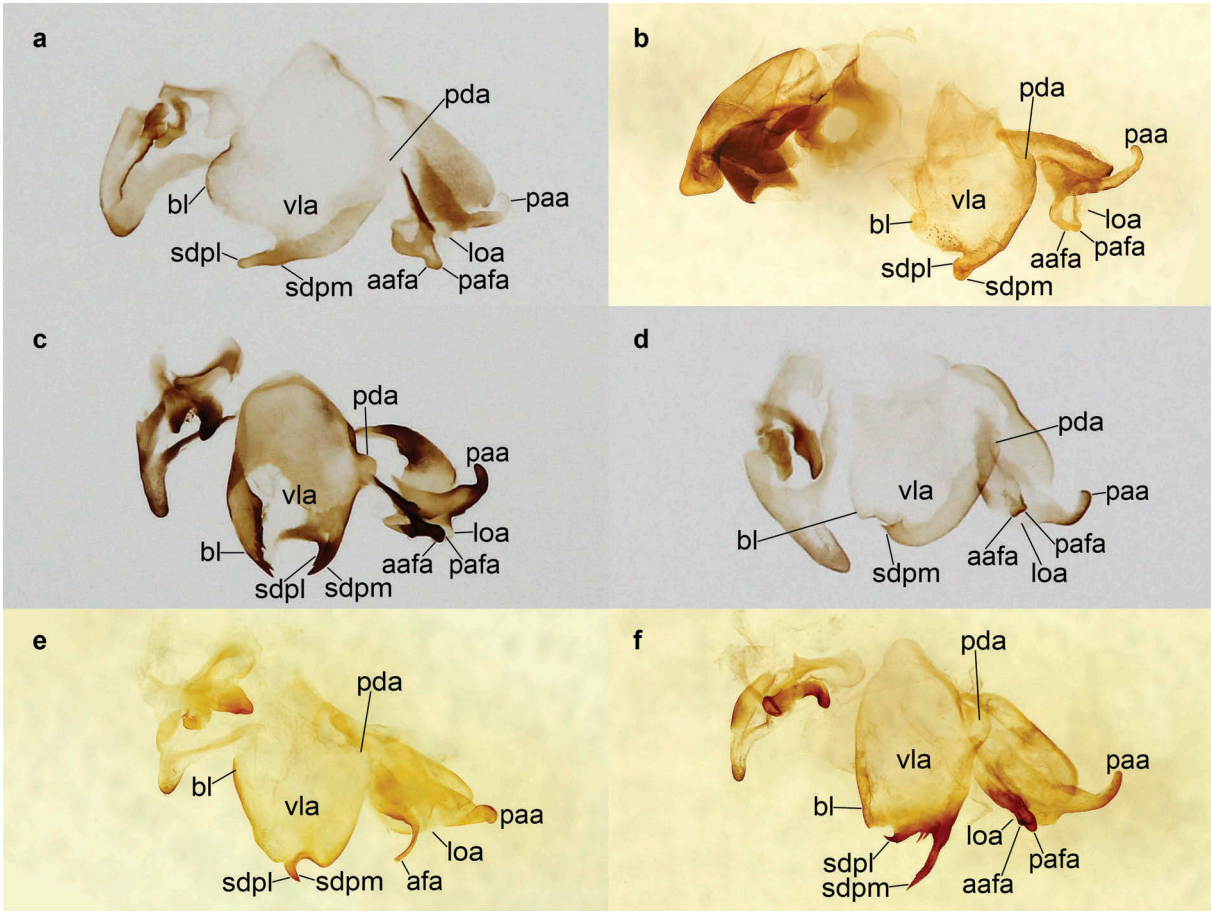

Figure 7. Genitalia of Amorphoscelidae, ventral view. **a**, *Perlamantis allibertii* Guérin-Méneville, 1843, from S France (CS, prep. Schwarz No. 26); **b**, *Paramorphoscelis gondokorensis* Werner, 1907, from Congo (MNHN, prep. Roy No. 2314); **c**, *Amorphoscelis subnigra* Werner, 1933, from Sabah, Borneo (CS, prep. Schwarz No. 235); **d**, *Amorphoscelis* sp., from Sabah, Borneo (CS, prep. Schwarz No. 38); **e**, *Bolivaroscelis carinata* (Bolivar, 1908), from the Central African Republic (MNHN, prep. Roy No. 1464); **f**, *Caudatoscelis annulipes* (Karsch, 1892), from Cameroon (MNHN, prep. Roy No. 2588).

tubercles on the metazona of metamantodeans posteriad the supracoxal sulcus usually derive from the second or third pair of metazonal markings, with some exceptions (*Theopompa*), while the first pair, situated on the lateral margins of the supra-coxal dilatation, is most likely to disappear. Lateral markings and/or paramedian tubercles are seen in Gonypetinae (e.g. *Compsomantis, Myrcinus, Humbertiella* and *Theopompa*), Majangidae, Epaphroditidae, Haaniinae (Figure 27), Tarachodini, Aethalochroini, Toxoderini, Oxypilini, *Majangella, Oxypiloidea*, Dactylopterygidae, *Popa*, Deroplatyinae (*Deroplatys, Pseudempusa, Mythomantis, Tagalomantis*), Mellierinae, and *Heterovates*. Despite different pronotal shapes, the markings or respective tubercles can be easily homologized when present. They are frequently reduced and re-evolved to various degrees in metamantodeans.

A common occurrence in metamantodeans is the presence of abdominal lobes (described under Cernomantodea). Even though putatively synapomorphic for the whole Cernomantodea clade, it is this clade which they are characteristic for.

[77] **Gonypetidae**. Apomorphies of this family are hard to define: in most taxa **sdpl** builds up the distal process at the expense of **sdpm**, and the cernomantodean bifurcation of **afa** is reduced (Figures 9a, b, 9d–j, 10a–d), but *Armene* exhibits a bifurcate **afa** with rounded anterior and posterior lobes. Its distal process is straight (Figure 9c), but nevertheless derived from **sdpl**, as revealed by comparison with *Amantis* and other Gonypetinae. A putative synapomorphy are the sexually dimorphic forefemora, those of males being usually much

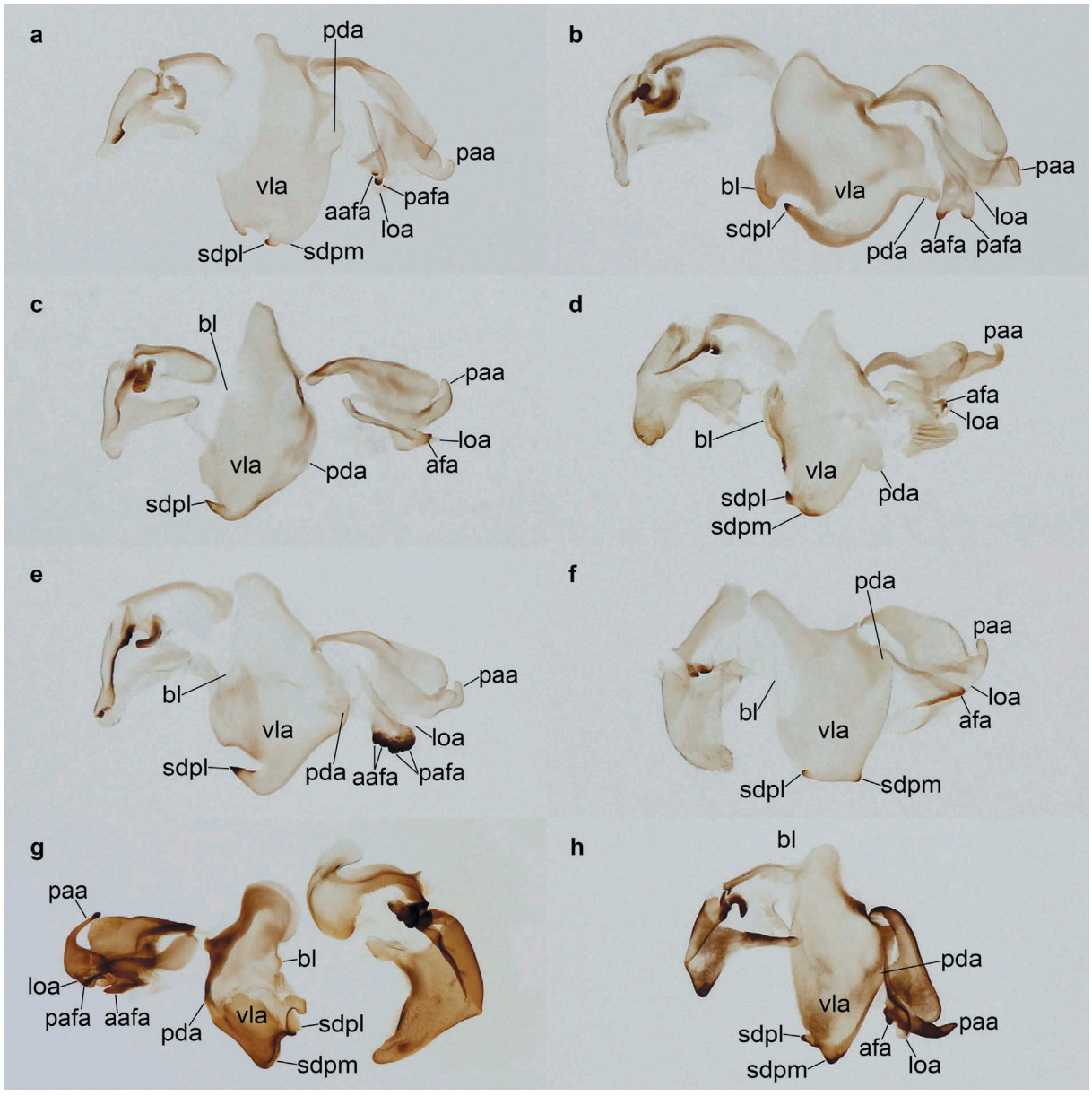

Figure 8. Genitalia of Nanomantidae, ventral view. **a**, *Tropidomantis tenera* (Stål, 1860), from N Borneo (CS, prep. Schwarz No. 259); **b**, *Eomantis* cf. *guttatipennis* Stål, 1877, from Thailand (CS, prep. Schwarz No. 196); **c**, *Pliacanthopus* (Malayamantis) *flavus* (Giglio-Tos, 1915), from Sabah, Borneo (SMNK 11480, prep. Schwarz No. 136); **d**, *Oligocanthopus ornatus* (Beier, 1935), from Sabah, Borneo (CS, prep. Schwarz No. 124); **e**, *Sinomantis denticulata* Beier, 1933, from Thailand (CS, prep. Schwarz No. 226); **f**, *Miromantis mirandula* (Westwood, 1889), from Sarawak, Borneo (CS, prep. Schwarz No. 147); **g**, *Stenomantis novaeguineae* (De Haan, 1842) with chirally mirrored genitalia, from Papua New Guinea (SMNK 10156, prep. Schwarz No. 205); **h**, *Phthersigena* (*Glabromantis*) *unicornis* Tindale, 1923, from SW Australia (SMNK 07168, prep. Schwarz No. 208). Not to scale.

darker than those of females. This trait is very obvious in *Amantis, Spilomantis*, some *Hapalopeza, Gimantis* and *Compsomantis*, less so in other genera, particularly when both sexes are very dark (*Myrcinus*) or engaged in particular types of camouflage (*Tricondylomimus*, Humbertiellina).

[78] **Iridopteryginae**. Synapomorphies: myrmecomorphic (vs. *non-myrmecomorphic*) nymphs; characteristic forefemoral spine armament. This subfamily exhibits a very distinct forefemoral spination, with the second and third discoidal spine being close to each other and very similar in length, while the first large anteroventral spine is much larger than the remaining and situated just opposite the third discoidal spine (described in detail in Stiewe & Shcherbakov 2017). A close relationship of *Amantis* with Iridopterygini (instead of the classical arrangement as part of the genera here united under Gonypetinae) was

also found by molecular studies (Svenson & Whiting 2009; Legendre et al. 2015).

[79] **Iridopterygini**. Distinguished from Amantini by a more distinctly defined supracoxal dilatation, and, consequently, prozona and metazona having parallel margins. The metazona widens at base into a distinct collar. In *Amantis*, the pronotum is more diamond-shaped, and the lateral margins of prozona and metazona converge towards anterior and posterior margin, respectively.

[80] ***Tricondylomimus***. Stiewe & Shcherbakov (2017) could show that this genus is not synonymous with *Nemotha*, as suggested by Beier (1935c). Morphological characters, like the spination pattern of the forelegs, particularly of the foretibiae, wing venation, and head morphology, differ considerably from *Nemotha* but are consistent with iridopterygines. *Pseudogousa* Tinkham, 1937 is a junior synonym (Stiewe & Shcherbakov 2017).

[81] **Iridopterygina**. Synapomorphy: reduction of first (proximal) discoidal spine (vs. *proximal discoidal spine exhibiting typical size for the group*). In *Spilomantis*, the first discoidal spine is still present as a tubercle or very small spine, while it is totally lost in the remaining genera.

[82] **Armenini n. trib**. Apomorphy: loss of first discoidal spine. A plesiomorphic trait are the macropterous females.

[83] **Gonypetini**. Synapomorphy: females mesopterous to brachypterous. Female macroptery in *Paratheopompa* and *Theopompa* is secondary.

[84] **Gonypetyllina n. subtrib**. Synapomorphies: females apterous (vs. *brachypterous*); pronotum shortened and squat (metazona at most 1.5 times as long as prozona) (vs. *diamond-shaped and with well-marked supracoxal dilatation, metazona about 2 times as long as prozona*). The pronotal expansion obscuring the supracoxal dilatation is an apomorphy shared with Compsomantina and Humbertiellina.

[85] ***Gonypetyllis***. *Haldwania* Beier, 1930 and *Paula* Liana, 2009 are regarded by Mukherjee et al. (2014) to be junior synonyms. There remains some doubt as to this interpretation; a revision of the complex is needed.

[86] **Compsomantina**. Apomorphies: reduced (vs. *distinct*) tuberculation, particularly on pronotum; pronotum with a pair of very distinct paramedian dark markings at its posterior fourth (vs. *without such markings*). A new genus belonging to this group is currently under description by the first author.

[87] **Humbertiellina**. Synapomorphies: adaptation to the bark-living lifestyle, with dorsoventrally flattened body, elongate antennae and styli, mottled coloration, and dorsal contour of forefemora neatly fitting along pronotal margin (between head and base of wings) when at rest (Wieland 2013, pp. 57–58; Schwarz & Ehrmann 2017) (vs. *no such adaptations*).

[88] ***Humbertiella***. The status of its two synonyms, *Theopompula* Giglio-Tos, 1917 and *Mintis* Yang & Wang, 1999, needs to be re-evaluated.

[89] **Lobipedia**. Synapomorphies (secondarily reduced in several groups): foliaceous expansion around supracoxal dilatation (vs. *no such expansion*) (independently evolved in Humbertiellina); walking leg femora with (vs. *without*) ventral lobes. The lobes on the abdomen are a plesiomorphic character.

[90] **Epaphroditoidea**. The lobe on the supra-anal plate present in *Epaphrodita* and *Brancsikia* is a putative synapomorphy of the group, even though it is lacking in the other genera here included. We argue in favor of a form of leaf resemblance to be ancestral for the group, and the lobe to have undergone secondary reductions in derived members due to their divergent ecological adaptations. Epaphroditoid genitalia exhibit a weakly developed **bl**, and the widening of **afa** into an anterior and a posterior lobe is likewise weakly expressed, visible in certain genera (e.g. *Brancsikia, Gonatista, Epaphrodita*; Lombardo & Perez-Gelabert 2004; Rodrigues & Svenson 2017; Figure 10c, h–i), but totally reduced in others. **Paa** is shaped normally, with the apex curved upwards.

A recent review of the genus *Brancsikia* (Roy & Schütte 2016) grouped this genus together with *Epaphrodita* in a family Epaphroditidae, due to morphological and genital characters. However, the Madagascan genus *Danuriella* was acknowledged as being closely related to *Brancsikia*, even though it lacks most of the respective morphological characters uniting *Brancsikia* with *Epaphrodita. Callimantis* and *Gonatista* are assigned here to Epaphroditidae due to genital characters (Figure 10h–j), a relationship recently confirmed by independent analyses (Rodrigues & Svenson 2017; Svenson & Rodrigues 2017). *Callimantis* and *Gonatista*, and the Madagascan bark mantids *Majanga* and *Liturgusella* also included here (Figure 10f, g), are not commented upon by Roy & Schütte (2016). While we assume monophyly of the lineage (and thus extinction of previously existent African members, see also Svenson & Rodrigues 2017), we chose to classify the Caribbean and Madagascan taxa in into two different families because of their slightly different genitalia (**sdpm** prominent in most Majangidae while absent in Epaphroditidae; see Rodrigues & Svenson 2017 for additional distinguishing characters) and their disjunct, relictual distribution.

[91] **Brancsikiinae n. subfam**. Autapomorphies: eyes conical, with a tubercle (vs. *rounded*); juxta-ocular bulges

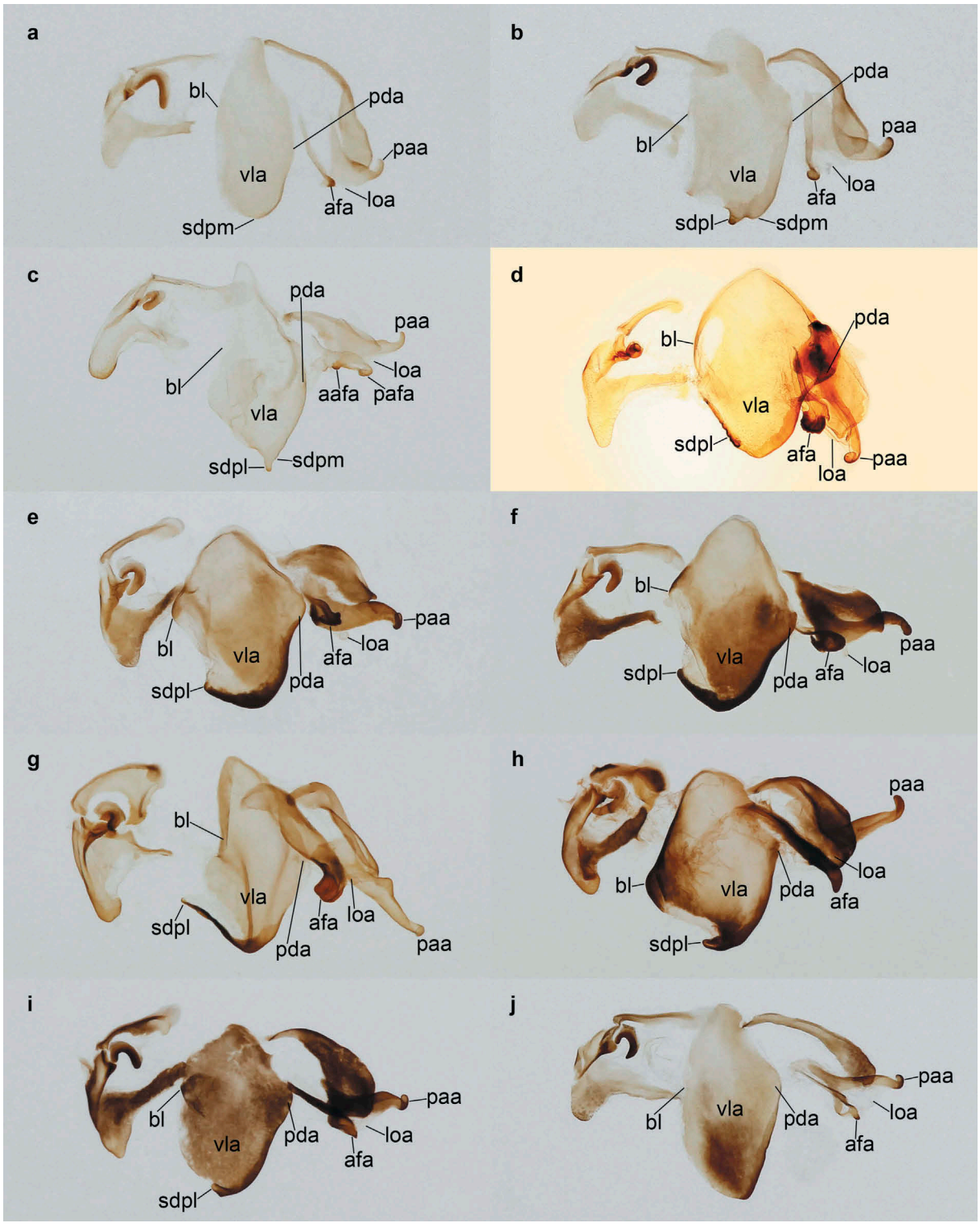

Figure 9. Genitalia of Gonypetidae, ventral view. **a**, *Hapalopeza tigrina* Westwood, 1889, from Sabah, Borneo (CS, prep. Schwarz No. 236); **b**, *Amantis reticulata* (De Haan, 1842), from Sabah, Borneo (CS, prep. Schwarz No. 250); **c**, *Armene* sp., from Afghanistan (CS, prep. Schwarz No. 133); **d**, *Elaea* cf. *marchali* (Reiche & Farmaire, 1847), from Kenya (SMNK 02370, prep. Schwarz No. 79); **e**, *Gimantis* sp., from W India (CS, prep. Schwarz No. 65); **f**, *Gimantis* sp., from the Malay Peninsula (CS, prep. Schwarz No. 131); **g**, *Gonypeta brigittae* Kaltenbach, 1994, from C Thailand (CS, prep. Schwarz No. 99); **h**, *Gonypeta borneana* Giglio-Tos, 1915, from Sabah, Borneo (ZMUH, prep. Schwarz No. 95); **i**, *Myrcinus tuberosus* Stål, 1877, from Brunei, Borneo (CS, prep. Schwarz No. 84); **j**, *Compsomantis* sp., from Sabah, Borneo (CS, prep. Schwarz No. 60). Not to scale.

flattened (vs. *protruding*); alae elongate, widely exceeding tegmina in females (vs. *tegmina and alae of about the same length*).

[92] **Majanginae**. Members of this subfamily are distinguished from Brancsikiinae by the distinctly rounded to conical juxta-ocular bulges, their strongly tuberculate pronotum with serrate margins, and with the metazona being strongly constricted after the supra-coxal dilatation, then gradually widening towards the base.

[93] **Danuriellini n. trib**. Autapomorphies: lobes on walking leg tibiae (vs. *walking leg tibiae without lobes*); adaptation to stick resemblance (vs. *leaf resemblance*).

[94] **Majangini**. Synapomorphies: adaptation to bark-living lifestyle, including elongation of antennae and walking legs, reduction of pronotal expansion, cryptic mottling pattern, and dorsoventrally flattened bodies (vs. *leaf resemblance involving other morphological adaptations*).

[95] **Epaphroditidae**. The phylogenetic position of this group has recently been resolved by Svenson & Rodrigues (2017). No member of the Madagascan Majangidae has been tested though, so the sister-group relationship of the two families proposed here on genital and morphological grounds has not yet been corroborated by molecular data. The cytology of *Callimantis*, the only genus of the group studied so far, shows some peculiarities: it shares a low chromosome number ($2n$ = 17 in the male) and achiasmatic meiosis (Hughes-Schrader 1943a) with many Amerimantodea, but the presence of a cyclopean ear of the DO type (see Yager & Svenson 2008 for definitions) as well as morphological, genital, and molecular data clearly indicate a placement among Cernomantodea.

Previously, *Epaphrodita* has been included in Svenson et al. (2015, figure 6) but resolved as sister to acanthopids or *Deroplatys* in the morphological analysis due to the homoplastic nature of the external characters used. Their molecular phylogeny (Svenson et al. 2015, figure 5) positioned *Epaphrodita* alongside eremiaphiloids, which is not supported by any morphological and genital synapomorphies. The arrangement used here is largely in concordance with a recent revision of Epaphroditidae by Rodrigues & Svenson (2017), who, however, did not comment upon *Gonatistella*.

[96] **Gonatistinae**. Synapomorphy: adaptation to bark-living lifestyle, including elongation of antennae, walking legs, and styli, contour of forefemora fitting to pronotal margin, widening of wings in males, cryptic mottling pattern, and dorsoventrally flattened bodies (vs. *leaf resemblance involving other morphological adaptations*).

[97] ***Gonatistella***. Enigmatic monotypic genus, erected for *Theopompa nigropicta* Westwood, 1889, described from Australia and never found since. Morphological features present in the type, like shape of wings, prosternal coloration, configuration of posteroventral spines on the foretibiae, and shape of supra-anal plate, among others, support a classification among Epaphroditinae Gonatistini alongside *Gonatista*, leaving its putative Australian locality with a question mark. The specimen may have been mislabeled. In fact, it is so similar to *Gonatista* in all respects that it may well turn out to be a synonym of the latter.

[98] **Epaphroditini**. This group has retained the most plesiomorphic characters compared to the other two genera, like the leaf resemblance, the lobe on the supra-anal plate, and a well-developed **sdpl** on the ventral phallomere (Figure 10i).

[99] **Callimantini**. Morphological apomorphies are related to this group's adaptation to a generalist lifestyle, that is reduction of lobes on pronotum, legs, and abdomen, and the emergence of green/brown polyphenism. For chromosomal autapomorphies see above.

[100] **Mantimorpha**. The anterior process on the phalloid apophysis is already present in earlier cernomantodean lineages as a weakly developed rounded lobe. Even though the bifurcation might have already developed as early as in *Mantoida* (see above), its re-emergence in Cernomantodea after being absent in early schizomantodeans qualifies this character as a synapomorphy of the group. However, despite an early origin, it is the clade here named Mantimorpha which is largely defined by this character. In mantimorphs, the morphology of the anterior lobe of the phalloid apophysis exhibits its highest diversity among mantodeans. In its most simple form, the phalloid apophysis is incised at apex (*Sinomiopteryx*, some *Hestiasula, Choeradodis*; Figures 11b, 17g, 20d). In *Haania* (Anisyutkin 2005; Anisyutkin & Gorochov 2005; Figure 11d–f), some *Hoplocorypha* (Beier 1954; Figure 14e), *Ceratocrania* (Figure 16j), and *Theopompella* (Roy 1963a; La Greca & Lombardo 1993; Figure 18b) the bifurcation is deeper and the two apices spaced apart. In most derived mantimorphs, the base of the apophysis widens more or less, spacing the two processes apart, and turns to the right. While the left (= posterior) process retains its place, the right (= anterior) process moves towards the base of the left phallomere (eremiaphiloids, most Mantidae, e.g. Figures 12a–c, 13h, 14b, d, 20h, 21a–h, 22a–c, 23a–d, g, h, 24a, b, d–g, 25a–j). The most extreme form is found in Toxoderinae, where the two processes of the phalloid apophysis span almost the entire length of the left phallomere (Roy 2009b; Wu & Liu 2017; Figure 14d). On the other hand, the bifurcation is frequently reduced to various degrees, either by a secondary fusion of **aafa** and **pafa**, as in miomantids, galinthiadids, hymenopoids, and early Mantidae (Figures 14e–h, 15a–f, 16a–i, 17a–h, 20a, e–g), or by reduction of **aafa** as in some eremiaphilids,

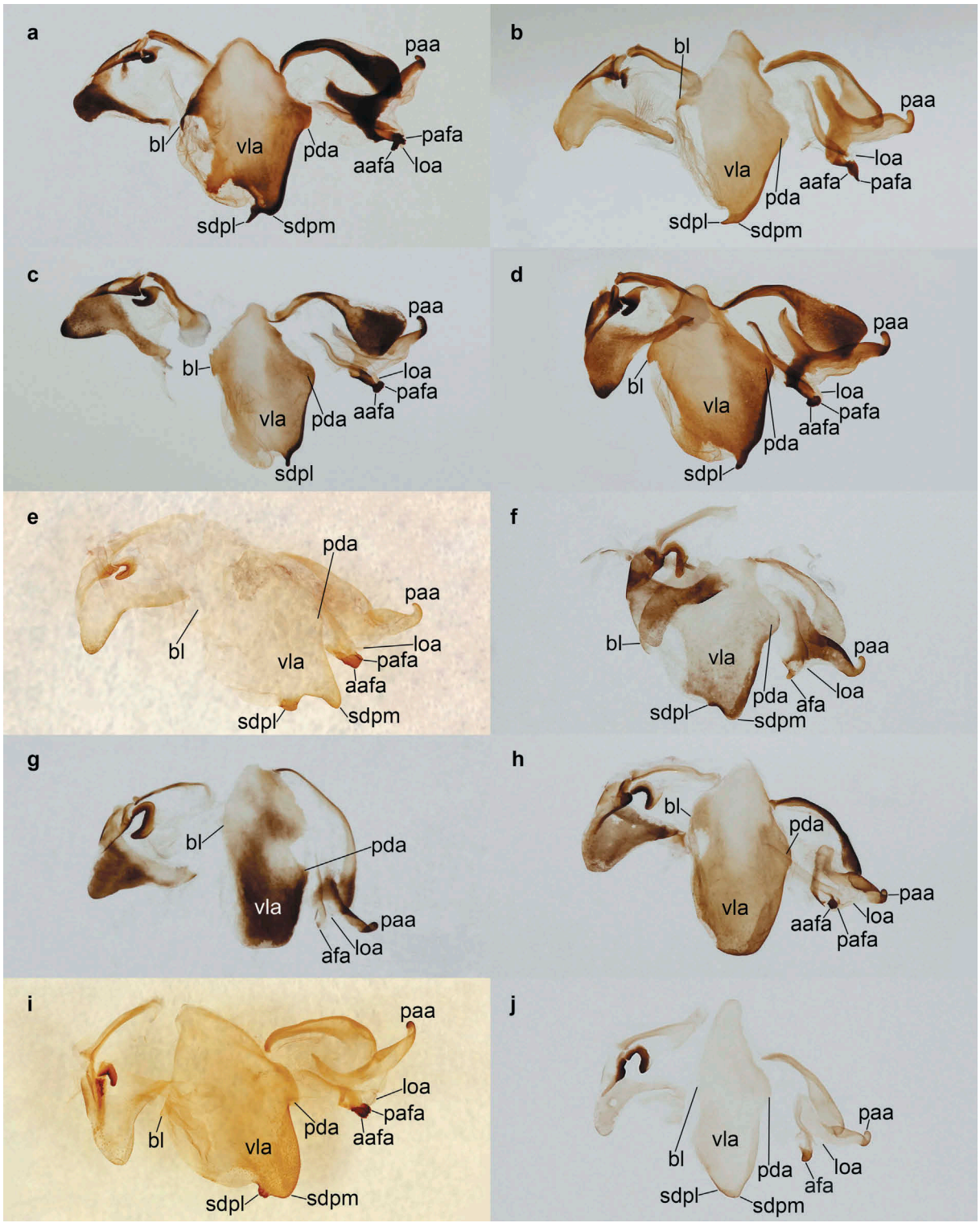

Figure 10. Genitalia of Gonypetidae, Majangidae, and Epaphroditidae, ventral view. **a**, *Humbertiella ceylonica* Saussure, 1869, from W India (CS, prep. Schwarz No. 64); **b**, *Humbertiella ocularis* Saussure, 1872, from Brunei, Borneo (CS, prep. Schwarz No. 54); **c**, *Theopompa servillei* (De Haan, 1842), from Java, Indonesia (CS, prep. Schwarz No. 109); **d**, *Theopompa* "tosta", from Sabah, Borneo (CS, prep. Schwarz No. 55); the name tosta Stål, 1877 should only be applied to Philippine specimens fitting to the types in the NRM; **e**, *Brancsikia freyi* (Brancsik, 1893), from E Madagascar (MNHN, prep. Roy No. 3799); **f**, *Majanga basilaris* (Westwood, 1889), from CE Madagascar (SMNK 11818, prep. Roy No. 4016); **g**, *Liturgusella malagassa* (Saussure & Zehntner, 1895), from Madagascar (CS, prep. Schwarz No. 67); **h**, *Gonatista grisea* (Fabricius, 1793), from USA (CS, prep. Schwarz No. 274); **i**, *Epaphrodita musarum* (Palisot de Beauvois, 1805), from Haiti (MNHN, prep. Roy No. 3409); **j**, *Callimantis antillarum* (Saussure, 1859), from the Dominican Republic (SMNK 01392, prep. Schwarz No. 83). Not to scale.

deroplatyines, and vatinines (Figures 12d–j, 13a–h, 14a, c, 18e, 26a–f).

While an anterior lobe on **afa** is here interpreted to be homologous in all cernomantodeans, it certainly (re-) evolved independently in Acanthopidae and certain Photinaidae through a bifurcation of the apex like in Cernomantodea (Figures 4b, e, g, 5a, d, h). It is remarkable that a similar structure has (re-)evolved independently in both Amerimantodea and Cernomantodea, suggesting considerable selective pressure. The interaction of the different parts of the phallomeres during copulation are not well understood yet in Mantodea, but recent studies could throw some light on copulatory interactions of male and female phallomeres via micro CT techniques (Holwell et al. 2015, Hashimoto et al. 2016). Thus, the right phallomere is a clasping device used to lift the female ovipositor, while the ventral phallomere and the apical process splay apart the subgenital plate.

Interestingly, Holwell et al. (2015) made no reference to the function of the phalloid apophysis, probably because the studied genus, *Ciulfina*, has a rather short and simple **afa** (Holwell et al. 2007b; Holwell 2014). In genera with a deeply bilobed **afa**, in natural position **aafa** is in close proximity to the ventral plate and its corresponding ventral process of the right phallomere (Figure 28). Notable in this context are the apices of **paa** and **sdp** pointing to opposing directions (explained by their functional purpose outlined above), and the close association of **pafa** with **sdpl** (see also Figure 2d). Since these resting positions will be altered during copulation, it would be interesting to apply the micro CT imaging to genera with different degrees of **sdpl/sdpm** and **afa** complexity.

The lineages with a strongly developed **aafa** exhibit a comparatively high degree of sexual dimorphism and sexually cannibalistic behavior (Schwarz unpublished). As a consequence, we postulate that the bilobed **afa** enhances the hold onto the female genitalia exercised by the right and ventral phallomeres and **paa**, assuring sperm transfer and prolonged copulation even in case the anterior parts of the male end up cannibalized.

The same effect can be assumed for the sexually very dimorphic chroicopterids, which, however, are presumed to have developed a yet different alternative by means of very elaborate shapes of ventral and left phallomeres and their processes, including strong spination on the strategically important parts (see above). That even slight intraspecific differences in genital shape already affect sperm transfer success and copulation duration could be shown by Holwell et al. (2010), so the observed different solutions for the same problem – to ensure successful sperm transfer in case of cannibalism – may be indeed explained by considerable selective pressure towards a stable copulatory grasp.

[101] **Haaniidae**. Autapomorphy: **bl** elongate (vs. *not elongate*).

[102] **Caliridinae**. Synapomorphies: alae with a unique eye-spot-like pattern (Westwood 1889; Giglio-Tos 1927; Beier 1935c) (vs. *alae with metamantodean color pattern, including apical darkening of discoidal field, but no distinct eye-spot*); **sdpm** serrate (vs. *not serrate, simple*); bifurcation of **afa** reduced (vs. *present*) (Figure 11a).

[103] ***Caliris***. *Beesonula* Uvarov, 1939 is a junior synonym (Schwarz & Roy 2018).

[104] **Haaniinae**. Apomorphies: subgenital plate incised (vs. *not incised*) between styli; wings (when present) infumate to hyaline (vs. *of metamantodean color type*).

[105] **Arrini**. Synapomorphy: females apterous (vs. *winged*).

[106] ***Arria***. *Palaeothespis* Tinkham, 1937 and *Pseudothespis*; Mukherjee, 1995 are junior synonyms (Schwarz & Roy 2018).

[107] ***Sinomiopteryx***. In at least one member of this genus, the proximal lobe of the ventral phallomere is fused to **vla**, protruding as a truncate lobe ventrad of **sdpm** and **sdpl** (Figure 11b). Males of other Arriini were not available for study, so it remains unknown how widespread this character is among this tribe.

[108] **Haaniini**. Synapomorphies: head and pronotum with process-like tubercles (vs. *smooth or only with small tubercles*), pronotum with (vs. *without*) a dentate to lamellate keel (Figure 27); apical anteroventral spine of foretibia moved dorsally (vs. *tibial armature not modified*).

[109] ***Astape***. Autapomorphy: loss of proximal posteroventral spine on foretibia; mid and hind legs toothed (vs. *not toothed*).

[110] ***Haania***. Autapomorphies: head with two pairs of more or less elongate juxta-ocular lobes (vs. *head more or less tuberculate but not with elongate juxta-ocular lobes*); supra-anal plate heart-shaped (vs. *triangular*); subapical anteroventral spine of foretibia moved dorsally (vs. *only apical anteroventral spine of foretibia moved dorsally*).

[111] **Heteromantodea**. Synapomorphy: proximal lobe of ventral phallomere reduced (vs. *present*).

[112] **Eremiaphiloidea**. Synapomorphies: females mesopterous to brachypterous (vs. *macropterous*); "tarachodid type" genitalia (Figures 12a–j, 13a–h, 14a–d): right phallomere with 3 fields of pronounced pilosity (vs. *no or indistinct pilosity*); ventral ridge of right phallomere long (vs. *not elongate*), irregularly dentate; **loa** pilose (vs. *not pilose*); **aafa** displaced anteriorly, bird-head-like, tuberculate (vs. *not displaced from **pafa**, rounded*). **Aafa** may change shape in derived groups to become spiny or hairy, or is altogether reduced, while

pafa has the shape of a strong spine with acute apex. In this group, the apex of the ventral phallomere developed into a curved and robust distal process, originated from the plesiomorphic cernomantodean condition through an emargination just proximad of the **sdpl**. Remnants of **sdpm** are plesiomorphically present, and may develop into a functional process at the expense of **sdpl** in some groups, e.g. *Parathespis, Schizocephala* (Figure 12d, f).

[113] **Rivetinidae**. Synapomorphies: apical marking on alae developed into a subapical eye-spot on alae (vs. *with marking but no clear eye-spot*).

[114] **Rivetininae**. Synapomorphy: **aafa** weakly sclerotized to membraneous, pilose (vs. *heavily sclerotized and toothed, but not pilose*) (Figure 12a).

[115] **Ischnomantini**. Autapomorphy: supra-anal plate strongly elongate (vs. *triangular and slightly longer than wide but not distinctly elongate*).

[116] **Deiphobinae n. subfam**. Distinguished from Rivetininae by their sclerotized, toothed **aafa** (a plesiomorphic character) (Figure 12b).

[117] **Deiphobini n. trib**. Apomorphy: large, beak-like **sdpl** (vs. *sdpl smaller, with remnants of sdpm present*) (Figure 12b).

[118] ***Cotigaonopsis***. Autapomorphy: males brachypterous (vs. *macropterous*).

[119] **Amelidae**. Former Amelinae as used by Beier (1964) turned out to be a taxonomic waste basket for small old world mantodeans with short prothoraces and brachypterous females. Most former Paleotropical members have genitalia of a fundamentally different type than eremiaphiloids and have been united here into the phylogenetically more ancient group Gonypetinae. True Amelinae, treated here as a family, is a homogenous group characterized, among other things, by conical eyes (secondarily reduced in adults of northern species

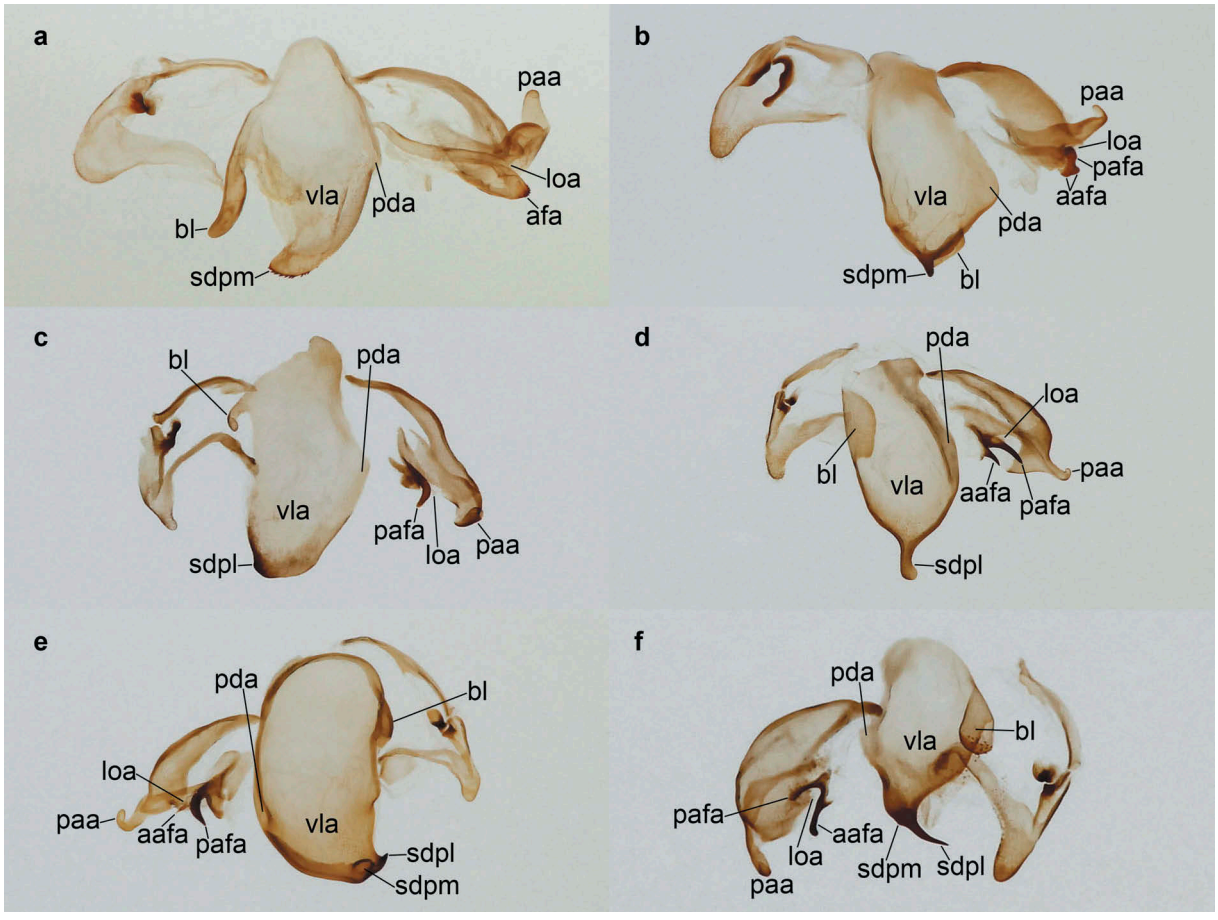

Figure 11. Genitalia of Haaniidae, ventral view. **a**, *Caliris elegans* Giglio-Tos, 1915, from the Malay Peninsula (TS, prep. Schwarz No. 166); **b**, *Sinomiopteryx* sp., from N Thailand (TS, prep. Schwarz No. 167); **c**, *Astape denticollis* Stål, 1877, from W Java (SMNK 03532, prep. Schwarz No. 142); **d**, *Haania* sp., from Panay, Philippines (CS, prep. Schwarz No. 106); **e**, *Haania confusa* Saussure, 1871 with chirally mirrored genitalia, from Brunei, Borneo (CS, prep. Schwarz No. 98); **f**, *Haania doroshenkoi* Anisyutkin & Gorochov, 2005 with chirally mirrored genitalia, from C Vietnam (TS, prep. Schwarz No. 144). Not to scale.

groups), relatively short prothoraces with well-marked supra-coxal dilatation, colored alae in females and short-winged males, more or less elongate and enlarged hind femora ("jumping legs"), and genitalia of the eremiaphiloid type: ventral phallomere with both **sdpm** and **sdpl** present, both processes short, acute and turned to the right; **aafa** plesiomorphically present in Palearctic Amelini, tuberculate, rounded; **pafa** subacute to acute and curved (secondarily shortened in some *Ameles* and *Pseudoyersinia* species); **loa** with pilosity field (Kaltenbach 1963; Lombardo 1986a, 1986c, 1986d; Agabiti et al. 2010; Battiston & Fontana 2005; Battiston et al. 2005, 2014; Figure 12c).

[120] **Litaneutriini**. Synapomorphy: loss (vs. *presence*) of **aafa** (Jantsch 1995; Battiston et al. 2005; pers. obs.).

[121] **Eremiaphilidae & Toxoderidae**. We regard the distinct hind wing coloration pattern, consisting of a concentric tessellation on a yellowish background, which merges to form a black patch in the anal field, as synapomorphic for the group, even though it is secondarily reduced in Parathespinae, early Iridinae, *Oxyophthalma, Dysaulophthalma*, and most Tarachodinae.

[122] **Eremiaphilidae**. This name has priority over Tarachodidae Handlirsch, 1930. Early groups (Parathespinae, Iridinae) have a concave vertex at least in juveniles, a feature shared with Amelidae and early Toxoderidae (*Heterochaeta*), while the most derived groups (Eremiaphilinae and Tarachodini) have straight to convex vertexes, a character state which is here interpreted to be a reversal. Eremiaphilidae is distinguished from other eremiaphiloid groups by an apomorphic reduction of **aafa**. In most taxa it is totally lost (Figures 12d–h, j, 13a–g), but very small remnants are visible, e.g. in *Dysaules* (Figure 12i) and *Paralygdamia* (Figure 13h).

[123] ***Parathespis***. Autapomorphies: back of head with (vs. *without*) a conical lobe on each side; total loss (vs. *presence*) of cyclopean ear (Yager & Svenson 2008); loss (vs. *presence*) of hind wing coloration pattern. Further characterized by the missing **aafa** (Figure 12d).

[124] **Iridinae**. Synapomorphies: vertex deeply excavated, strongly concave (vs. *slightly concave*), sometimes reduced in adults (*Iris*) but present in juveniles; five (vs. *four*) posteroventral spines on forefemur (secondarily reduced to four in some taxa); cerci elongate, thick (vs. *not thickened*).

[125] ***Schizocephala***. Apomorphies: loss of one discoidal spine; loss (vs. *presence*) of hind wing coloration pattern.

[126] ***Didymocorypha***. Autapomorphies: juxtaocular tubercles very long, adjacent, forming a "false" cone (vs. *head without false cone*); loss (vs. *presence*) of hind wing coloration pattern; **pafa** spiny (vs. *smooth*) (Figure 12e). Also characterized by the missing **aafa**.

[127] **Dysaulini & Iridini**. These two tribes are distinguished from Schizocephalini and Didymocoryphini by the second posteroventral spine of the forefemur being distinctly longer than the remaining spines (in *Dysaulophthalma* it is the first spine, since the basalmost spine is lost). The two groups are distinguished by an elongate lobe (dilatation) present on the forefemora of Iridini but lacking in Dysaulini (Giglio-Tos 1927). Also, the presence of a small **aafa** in *Dysaules* (Figure 12i) may be a valid distinguishing character, but we were not able to investigate males of *Oxyophthalma*, and those of *Dysaulophthalma* are unknown.

[128] **Eremiaphilinae**. Autapomorphies: adaptation to deserticolous, cursorial lifestyle: body short and stout, both sexes brachypterous, mid and hind legs elongate, penultimate sternite of female with two strong spines (digging devices, Wieland 2013, p. 114f, figure 276); genitalia simplified, processes short and stout (Figure 12j).

[129] **Tarachodinae**. Synapomorphic for the group is the twig-living lifestyle and the adaptations which come with it, like dorsoventrally flattened bodies, hypognathous heads, shortened walking legs, and disruptive coloration. Some genera (*Pyrgomantis, Galepsus, Paragalepsus*) have secondarily colonized grass blades, a convergently evolved trait shared with *Didymocorypha*.

[130] **Oxyelaeini n. trib**. Distinguished from Tarachodini by their conical, mammilate eyes (a plesiomorphic eremiaphiloid trait), flattened heads, and their short, inverted trapezoid and deeply sculpted pronota with rounded anterior and posterior margins.

[131] **Tarachodini**. Synapomorphies: vertex straight to convex (vs. *concave*); eyes rounded (vs. *conical*).

[132] **Antistiina n. subtrib**. Less specialized than Tarachodina, distinguished from the latter by their less flattened heads with rounded instead of ovoid eyes, well-pronounced supracoxal dilatation, constricted metazona, and rather simple right phallomere without the apical outgrowths present in Tarachodina except *Nothogalepsus* (Beier 1953a; Kaltenbach 1996; Roy 2003c).

[133] **Tarachodina**. In this group, the distal part of the right phallomere is highly diversified, often knob-, hook- or pincer-like, a unique trait in mantodeans (e.g. Beier 1954, 1957a, 1957b; Kaltenbach 1982, 1996, 1998; Figure 13a–h). The only exception is *Nothogalepsus* (Beier 1953a; Roy 2003c), which for this reason we place at the base of the clade. The most derived genera *Tuberculepsus, Nesogalepsus* and *Paralygdamia*, all endemic on Madagascar, have developed a tertiary distal process (**tdp**) alongside **sdpl** on the dextro-apical lobe of the ventral phallomere anteriad of the excavation that gave rise to **sdpl** (Roy & Schütte 2010; Roy 2016, 2017; Figure 13h). This structure is non-homologous to the right process of the ventral phallomere of certain

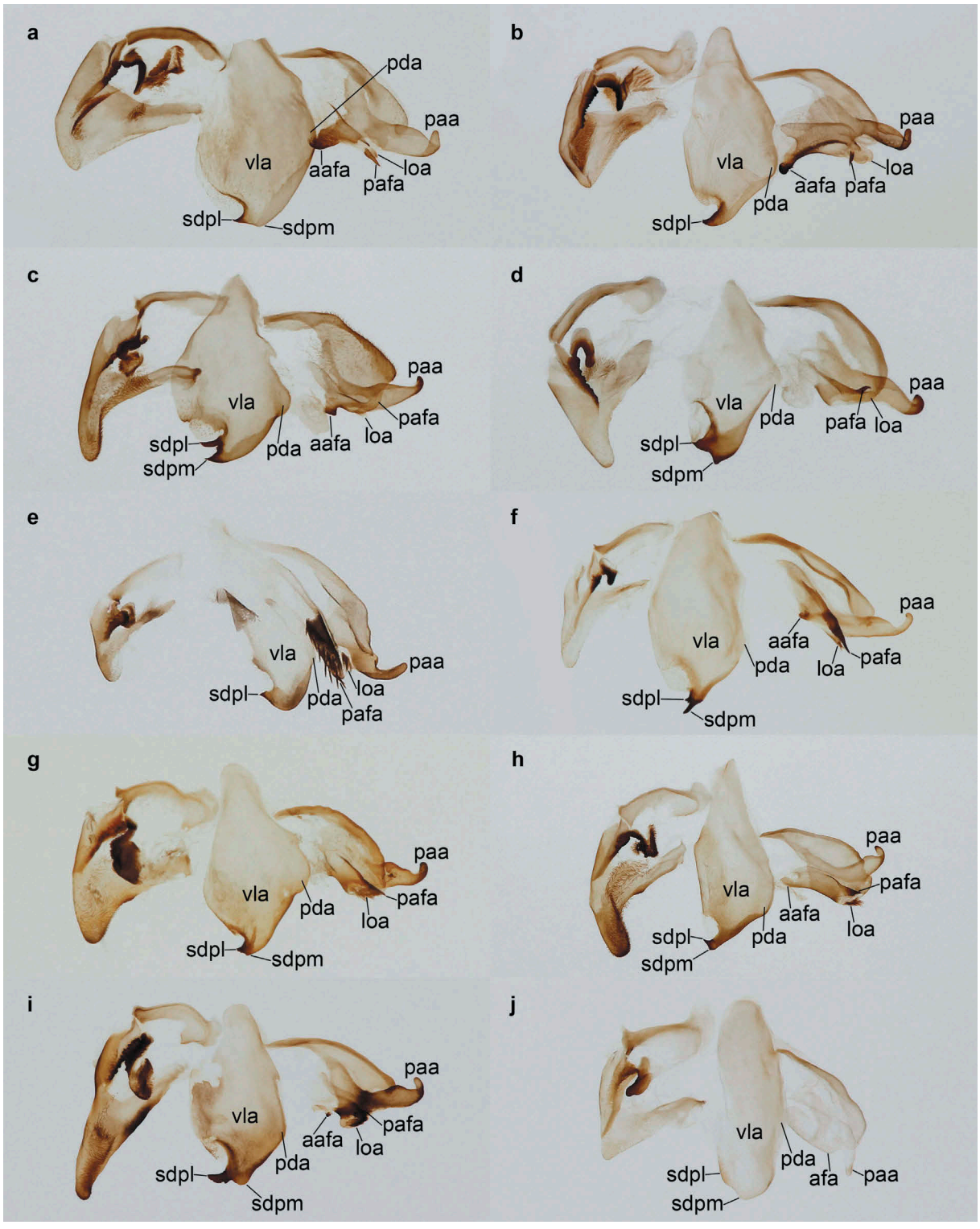

Figure 12. Genitalia of Rivetinidae, Amelidae, and Eremiaphilidae, ventral view. **a**, *Rivetina syriaca syriaca* (Saussure, 1869), from S Turkey (SMNK 08330, prep. Schwarz No. 182); **b**, *Deiphobe mesomelas* (Olivier, 1792), from N India (SMNK 02232, prep. Schwarz No. 181); **c**, *Ameles spallanzania* (Rossi, 1792), from S France (CS, prep. Schwarz No. 252); **d**, *Parathespis humbertiana* Saussure, 1869, from W India (CS, prep. Schwarz No. 73); **e**, *Didymocorypha lanceolata* (Fabricius, 1798), from W India (CS, prep. Schwarz No. 140); **f**, *Schizocephala bicornis* (Linnaeus, 1758), from W India (CS, prep. Schwarz No. 139); **g**, *Iris oratoria* (Linnaeus, 1758), from S Spain (CS, prep. Schwarz No. 159); **h**, *Episcopomantis chalybea* (Burmeister, 1838), from Namibia (CS, prep. Schwarz No. 243); **i**, *Dysaules longicollis* Stål, 1877, from W India (CS, prep. Schwarz No. 186); **j**, *Eremiaphila* sp., from Pakistan (CS, prep. Schwarz No. 174). Not to scale.

Amorphoscelinae, which is derived from a distally shifted **bl** (see comments under Amorphoscelinae).

[134] **Toxoderidae**. Characterized by elongate bodies, eyes with a spine or tubercle (secondarily reduced in some taxa), hind wings with concentric coloration pattern, and flattened (vs. *cylindrical*) cerci. Currently available molecular data suggest that Toxoderidae are only a subclade of Eremiaphilidae (Yager & Svenson 2008; Svenson & Whiting 2009, Legendre et al. 2015), but taxon sampling was rather low and outgroup taxa inconsistently resolved. Based on synapomorphic traits in their external morphology (tendency towards elongation of body and foretibiae, more or less flattened cerci, etc.) and plesiomorphic (with respect to Eremiaphilidae) characters of the external (mammilate eyes, hind wing color) and genital morphology (rivetinid type, e.g. the presence of a well-developed, bird-head-like **aafa** in most groups; La Greca & Lombardo 1984; Lombardo 1992a; Roy 2009b; Figure 14b, d; indistinct but present in *Heterochaeta*, Figure 14a) we here treat Toxoderidae as a distinct family, sister to Eremiaphilidae.

[135] ***Heterochaeta***. Synapomorphies: forecoxae with (vs. *without*) a dentate lobe at base; **aafa** indistinct or reduced (vs. *distinctly developed*).

[136] ***Compsothespis***. Synapomorphies: loss of one discoidal spine; foretibia shortened, claw-groove at apical third (vs. *at about middle*) of femur; X_1X_2Y (vs. *X0*) sex chromosome system of a type different from Mantidae. In contrast to the sex chromosome trivalent of the latter, in *Compsothespis* both ends of the X_2 chromosome are attached to the same arm of the Y chromosome (see White 1965 for details).

[137] **Oxyothespinae**. Distinguished from Compsothespinae by four (instead of three) discoidal spines and typical tibial spination; from Heterochaetinae and Toxoderinae by four instead of five posteroventral spines on forefemur; from Heterochaetinae also by a well-developed **aafa**; from Toxoderinae also by four instead of three discoidal spines and non-elongate tibiae (claw groove at middle of femur vs. at base in Toxoderinae).

[138] **Oxyothespini**. Distinguished from Heterochaetulini by their simple vertex and the X0 sex chromosome system.

[139] ***Sinaiella***. Apomorphies: loss of one discoidal spine; loss (vs. *presence*) of ocular spines.

[140] ***Heterochaetula***. *Cheddikulama* Henry, 1932 is a junior synonym (Mukherjee et al. 2014). Autapomorphies: vertex produced into a median and two paramedian lobes separated by sulci (vs. *vertex convex but not with three lobes*); X_1X_2Y (vs. *X0*) sex chromosome system of unclear type (Gupta 1966).

[141] **Toxoderinae**. Synapomorphies: loss of first (proximal) discoidal spine; foretibia elongate, claw-groove at base (vs. *at about middle*) of femur; shortened (vs. *not shortened*) walking leg femora; five (vs. *four*) posteroventral spines on forefemur; the latter character could be homologous with the condition in *Heterochaeta*.

[142] **Calamothespini**. Synapomorphies: adaptation to graminicolous (vs. *arbusticolous*) lifestyle: width and posterior contour of head fitting neatly to that of pronotum (vs. *head width larger than pronotum, contours not fitting*). This character has convergently evolved in *Compsothespis*.

[143] ***Toxomantis***. Synapomorphy: apical dorsal lobe on forefemora extremely elongate. Further distinguished from Calamothespina by the juxta-ocular bulges being not elongate, the margins of the prozona converging cephalad, shorter metazona (less than 1.5 times as long as forecoxae), and the asymmetrical, acute last segment of the cercus.

[144] ***Calamothespis***. *Dorymantis* Giglio-Tos, 1914 has recently been shown to be a junior synonym (Roy & Stiewe 2016).

[145] **Aethalochroini**. Synapomorphies: vertex separated from juxta-ocular region by a prominent sulcus (vs. *without or just a weakly expressed sulcus*); carinae on walking leg tibiae developed into lobes (vs. *walking leg tibiae with carinae but without lobes*).

[146] ***Aethalochroa***. *Loxomantis* Giglio-Tos, 1914 is a junior synonym (Mukherjee et al. 2014; Roy & Ehrmann 2014a).

[147] **Toxoderopsini & Toxoderini**. Synapomorphy: apical spine on walking leg femora extremely elongate. A synapomorphy of Toxoderopsini are the distally enlarged anterior coxae accommodating the head during cryptic position (vs. *anterior coxae not enlarged*). Toxoderopsini are further distinguished from Toxoderini by smaller dorsal and ventral lobes on the walking leg femora which are not developed into foliaceous expansions.

[148] **Pareumantodea**. Synapomorphy: supra-anal plate distinctly triangular or parabolic, at least as long as wide (vs. *wider than long*).

[149] **Hoplocoryphidae**. Synapomorphies: juxta-ocular bulges enlarged, vertex concave (vs. *straight*); loss of one discoidal spine; females apterous (vs. *mesopterous to macropterous*); in the genitalia, **sdpl** is developed into a slightly curved process, **sdpm** is reduced; **afa** tuberculate, more so posteriorly, slightly to deeply bifurcate (Beier 1954; Figure 14e). This group is homogenous and morphologically well-defined (for details see Beier 1935a; Roy 1966b; Lombardo 1986b; Ehrmann 2002), but its phylogenetic position remains unstable in molecular analyses (compare respective nodes in Svenson 2007; Yager & Svenson 2008; Svenson & Whiting 2009). Genital characters define this family as a mantimorph group outside the eremiaphiloid clade. The transition to calomantodeans with regard to the shape and structure of apophysis and distal process is clearly evident (see Beier 1954, Roy 1966b; and cf. Figure 14e with Figure 14f–h).

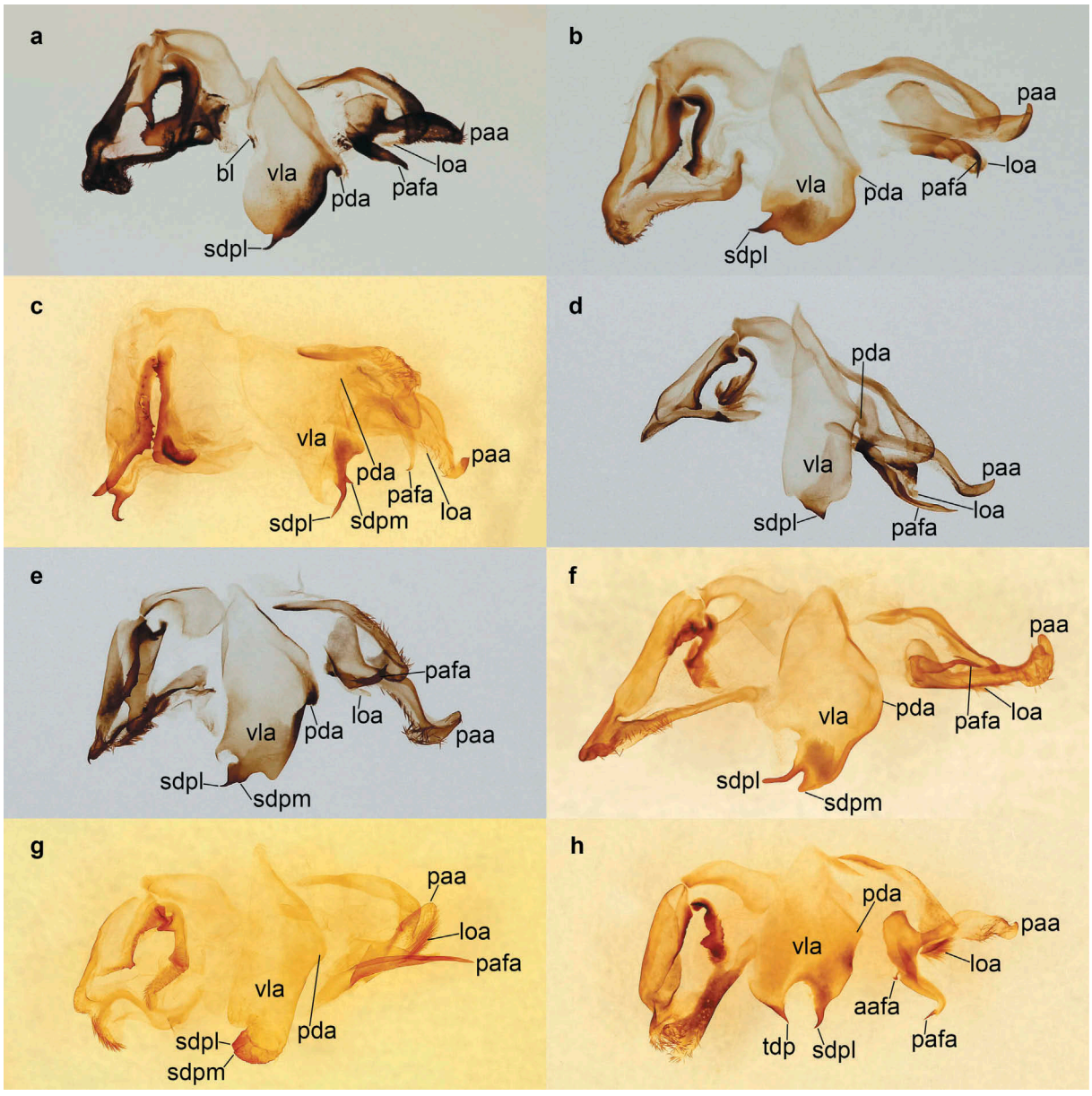

Figure 13. Genitalia of Eremiaphilidae, ventral view. **a**, *Tarachodes* (Tarachodes) karschii Werner, 1907, of unknown origin (CS, prep. Schwarz No. 157); **b**, *Tarachodes* sp., from the E Congo (CS, prep. Schwarz No. 158); **c**, *Tarachodella monticola* Giglio-Tos, 1917, from Cameroon (MNHN, prep. Roy No. 2762); **d**, *Pyrgomantis pallida* Giglio-Tos, 1917, from the Ivory Coast (CS, prep. Schwarz No. 233); **e**, *Galepsus* (*Onychogalepsus*) sp., from N South Africa (CS, prep. Schwarz No. 245); **f**, *Galepsus* (*Galepsus*) *globiceps* Beier, 1942, from Cameroon (MNHN, prep. Roy No. 2201); **g**, *Metagalepsus stramineus* (Sjöstedt, 1930), from Mali (MNHN, prep. Roy No. 1741); **h**, *Paralygdamia ifatyensis* Roy, 2016, paratype (MNHN, prep. Roy No. 3688).

[150] **Calomantodea**. Synapomorphies: denticulate (vs. *smooth*) posteroventral margins of the forefemora.

In the early families of this clade (Miomantidae, Galinthiadidae, Empusidae, most Hymenopodidae, some Dactylopterygidae), the bifurcation of the phalloid apophysis is largely reduced (Figures 14f–h, 15a–f, 16a–i, 17a–h, 18a), while becoming prominent again in some Deroplatyidae and most Mantidae (Figures 18d–h, 19f, 20b, d, h, 21a–h, 22a–c, 23a–d, f–h, 24a–h, 25a–j). The most parsimonious explanation is that this reduction is a synapomorphy of calomantodeans, with a secondary re-evolution in derived clades.

However, given the various cases of clearly incised apex even in relatively simple apophyses (see above), it cannot be ruled out that the core calomantodean stock retained the bifurcation, while it was independently reduced in the early off-shoots. Incidentally, in the groups where **afa** is simplified, **sdpl/sdpm** usually is as well, possibly indicating a decreased selective pressure towards a firm copulatory grasp during the time of early calomantodean radiation, through either decreased sexual selection or less female aggression towards males. Decreased sexual selection is to be expected when the genera are species-poor and with low levels of sympatricity, as is the case in most Miomantidae (except *Miomantis*), Galinthiadidae, and Hymenopodidae, or when successful fertilization relies largely on other factors like sperm competition or female choice (see e.g. Holwell et al. 2010 for a review and further references).

As Holwell et al. (2015, and references therein) point out, genital structures assuring a firm grip to the female genitalia are evolving through sexual conflict. In mantodeans, this explains the varying shapes of the mechanically anchoring **sdpl** or **sdpm**, while the clasping apparatus of the right phallomere is rather uniform. Obviously, there is no selective pressure on the functionally rather simple ovipositor clasp in most mantodeans. Putative exceptions are the sclerotized lobe on the left arm of the right phallomere of Tenoderinae and Hierodulinae (see below), and the species-specific right phallomeres of Tarachodinae. Incidentally, the latter are a very diverse group with high levels of sympatricity and very violent copulations. Investigation of female genitalia in this group may prove useful. In most other mantodeans, particularly the calomantodeans referred to here, only the ventral phallomere and those parts of the left phallomere which are directly involved in sperm transfer (that is **afa** and, to a lesser degree, **paa** which is inserted ventrad the ovipositor), are prone to strong sexual selection, and thus species-specificity.

Decreased aggression towards males may be dependent on ecological (food availability, see Berg et al. 2011 for a review), morphological (levels of sexual dimorphism), and behavioral factors (courtship of males). Food availability in a given habitat is expected to affect all sympatric generalist species in a similar way, whether dimorphic/aggressive or not. However, sexual dimorphism can lessen predation pressure on males either if largely decreased (i.e. the sexes are very similar in size), as in empusids, sibyllines, and some deroplatyids, or if extremely increased (i.e. the males are much smaller than females), as in miomantids, Hymenopodina, and *Deroplatys*. The former decreases the likelihood of a female to attack a conspecific almost as large as itself due to risk of injury. The latter brings the male out of reach of the female's forelegs when mounted onto its back.

Finally, courtship display is very common in calomantodeans, increasing conspecific recognition and lessening predation pressure on males (see Prete et al. 1999 and Berg et al. 2011 for a review and examples). The interaction between genital complexity, dimorphism, and sexual behavior is a promising field of research, which has only recently been explored (e.g. Holwell et al. 2010, 2015; Hashimoto et al. 2016).

[151] **Miomantidae**. Synapomorphies: vertex distinctly convex (vs. *straight*); surface of phalloid apophysis regularly serrate (vs. *tuberculate, only posteriorly serrate*), phalloid apophysis without bifurcation (vs. *distinctly bifurcate*). Large-scale molecular studies (Svenson 2007; Yager & Svenson 2008; Svenson & Whiting 2009; Legendre et al. 2015; Svenson & Rodrigues 2017) constantly resolve the phylogenetic position of this group as sister to a clade we here named Mantidea.

[152] ***Solygia***. This genus does not belong to Rivetinidae, as suggested by Beier (1935c) and Roy & Ehrmann (*in*: Ehrmann 2002). On the other hand, Giglio-Tos (1919, 1927) recognized it as distinct enough to deserve its own subfamily. Its genitalia (Figure 14f) clearly differ from those of Rivetinidae, particularly from those of *Ischnomantis* (see Chopard 1920), but share apomorphies with Miomantinae, e.g. a serrate **afa** with reduced bifurcation, and the rounded and serrate **sdpl** (Kaltenbach 1996; Figure 14g, h).

Solygia differs from *Ischnomantis* and Rivetinidae in general, in addition to the genital characters discussed above, by lacking the enlarged and blackened jugal fields on the wings. Further, male hind wings are largely hyaline, and both sexes lack an eye-spot. The supra-anal plate shows an elongate dorsal lobe in *Solygia*, while it is keeled but without lobe in *Ischnomantis*. The pronotal margins are more or less smooth in *Solygia*, while they are armed by blackish teeth in *Ischnomantis* and other Rivetinidae (compare shapes of pronotum and supra-anal plate in Kaltenbach 1998).

[153] **Miomantinae**. Autapomorphy: **paa** with (vs. *without*) an apical lobe.

[154] **Promantidea**. Synapomorphies: clypeus strongly keeled (vs. *not keeled*); re-evolution of **bl** on ventral phallomere; posteroventral spines of foretibiae decumbent (vs. *not decumbent*). Wieland (2013, p. 87f) distinguishes four different states of this character among mantodeans, aside from the normal condition. All spines decumbent and overlapping, corresponding to his state 3, are here interpreted to be an autapomorphy of Promantidea (independently evolved in Acanthopidae), but this condition is secondarily reduced or altered in some groups, so that four of the five character states distinguished by that author are all found in this clade.

[155] **Galinthiadidae**. Synapomorphies: ocellar tubercles long and subacute to acute (vs. *not elongate*); eyes with (vs.

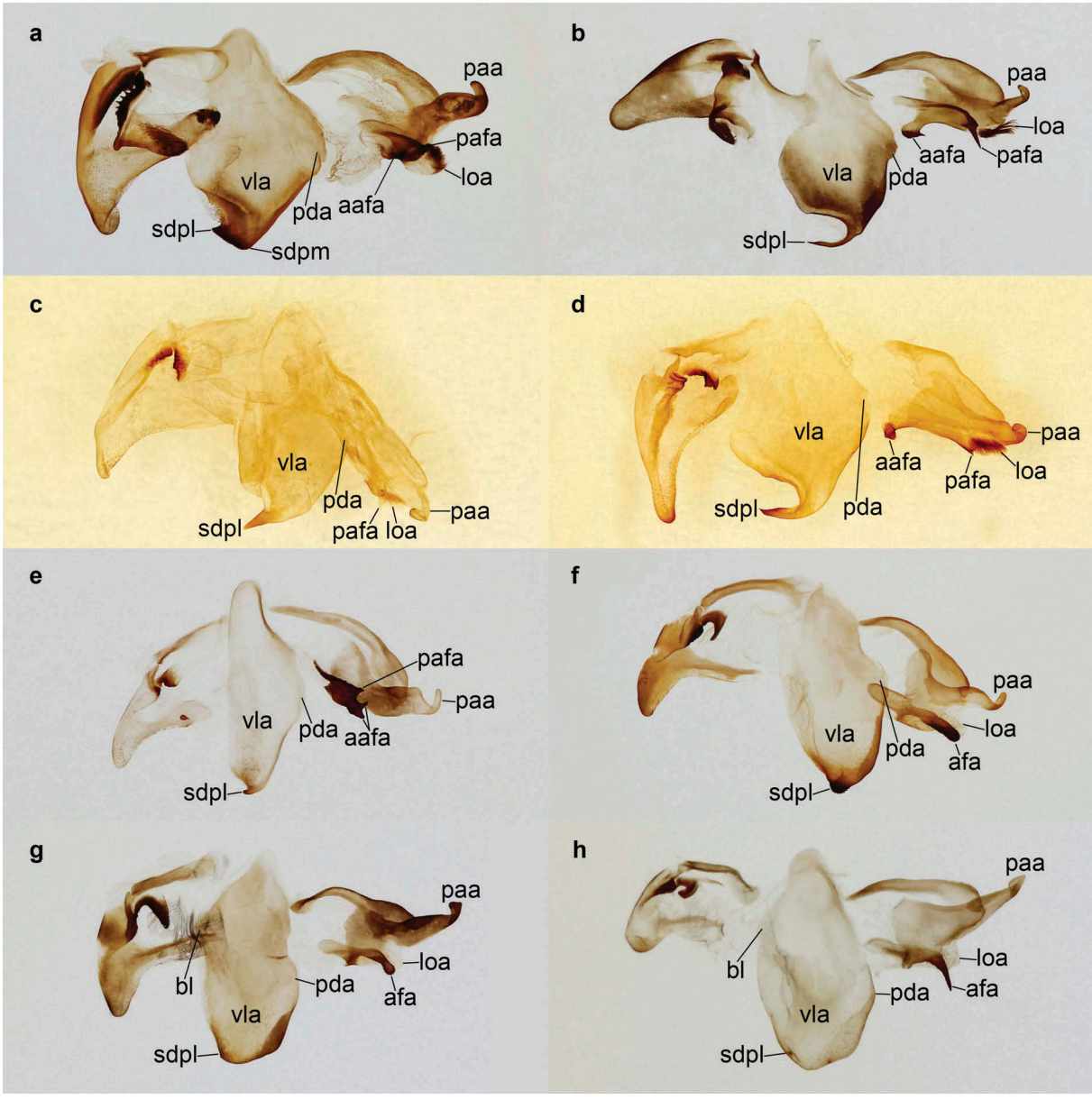

Figure 14. Genitalia of Toxoderidae, Hoplocoryphidae, and Miomantidae, ventral view. **a**, *Heterochaeta occidentalis* Beier, 1963, from Namibia (CS, prep. Schwarz No. 113); **b**, *Oxyothespis maroccana* Bolívar, 1908, from S Morocco (CS, prep. Schwarz No. 66); **c**, *Calamothespis prosti* Roy & Stiewe, 2016, holotype (MNHN, prep. Roy No. 2152); **d**, *Stenotoxodera porioni* Roy, 2009, paratype (MNHN, prep. Roy No. 3603); **e**, *Hoplocorypha nigerica* Beier, 1930, from N Ivory Coast (CS, prep. Schwarz No. 258); **f**, *Solygia sulcatifrons* (Audinet-Serville, 1838), from Gambia (CS, prep. Schwarz No. 194); **g**, *Parasphendale agrionina* (Gerstaecker, 1869), from Tanzania (CS, prep. Schwarz No. 152); **h**, *Miomantis paykullii* Stål, 1871, of unknown origin (CS, prep. Schwarz No. 171). Not to scale.

without) white spots in life; ventral side of forefemora with (vs. *without*) dense setae (Svenson et al. 2015). Molecular data indicate a systematic position outside Hymenopoidea, but could not provide a stable sister-group relationship so far: adelphotaxon of Dactylopteriginae in Svenson (2007), of Mantidae + (Deroplatyidae [*partim*] + (Dactylopteriginae + Hymenopoidea)) in Yager & Svenson (2008), of the group here named Mantidea in Svenson & Whiting (2009), and of Hoplocoryphidae in Svenson et al. (2015, figure 5). The total evidence tree in Svenson et al. (2015, figure 7) places Galinthiadidae as sister to Mantidea as defined here. Genital traits (see La Greca 1954b; Roy & Stiewe 2014; and Figure 15a, b), particularly the slender **paa**, support a position outside Hymenopoidea.

[156] ***Galinthias***. *Attalia* Uvarov, 1936 and *Arabistania* Koçak & Kemal, 2008 are junior synonyms (Roy & Stiewe 2014).

[157] ***Congoharpax***. This genus has five posteroventral spines on forefemur.

[158] **Mantidea**. Groundplan of mantidean genitalia: right phallomere simple; **bl** present; **sdpm** straight, triangular, with rounded apex; **sdpl** indistinct, but present; **aafa** and **pafa** more or less rounded (bifurcation reduced in some groups).

[159] **Hymenopoidea**. Synapomorphies (secondarily reduced in some groups): vertex with (vs. *without*) bifid process; eye-spot on abdomen in nymphs (vs. *abdomen without eye-spot*); **paa** short and broad (vs. *slender and with subacute apex*). In most hymenopoideans the genitalia are rather simplified, with **sdpm** and **sdpl** reduced or missing, and with a simple and rounded **afa** (Figures 16a–d, f, h, 17h). However, Empusidae and some Hymenopodidae (Phyllocraniinae, Phyllothelyini, Hestiasulini, Otomantini) exhibit the plesiomorphic mantidean condition in terms of a more or less truncate to bilobate **afa** (Figures 15c–e, 16i–j, 17e–j). The short and broad **paa** is exhibited by most early lineages (Empusidae, Phyllocraniinae, Sibyllinae, Hymenopodinae) and some Hestiasulini (Figures 15c–f, 16b–g, 17d–e), while in the more derived clades (Phyllothelyinae, most Oxypilinae, Acromantinae) **paa** is less broad and digitiform (Figures 16h, j, 17a, g–j). Some genera have secondarily developed rather derived genitals (e.g. Oxypilinae, *Otomantis, Oxypiloidea*; Roy 1966c, 1970, 1977b, 2013b; Stiewe & Roy 2010; Roy & Stiewe 2013; Lombardo et al. 2014; Figure 17b, c, j).

While this work was in progress, Svenson et al. (2015, 2016b) published phylogenies of this group. Their results are largely congruent with ours, with a few exceptions (see below). We encourage the reader to consult Svenson et al. (2015) for additional morphological synapomorphies of family groups.

[160] **Empusidae**. Autapomorphies: antennae of male bilobate (Wieland 2013, p. 48, figures 87–98; Svenson et al. 2015) (vs. *filiform or moniliform*); anteroventral spine formula consisting of one long spine alternating with three short ones (vs. *one long spine alternating with one short one*). The five posteroventral spines on the forefemur are an ambiguous character.

[161] **Blepharodini**. Distinguished from Empusidae by rounded apical lobes on forecoxae (Wieland 2013, p. 139–140; see below). We regard the lack of lobes on the walking femora in *Blepharodes* as a secondary reduction, lobed femora being the ancestral state in Hymenopoidea.

[162] **Idolomantini**. While traditionally classified alongside *Blepharopsis* + *Blepharodes* among Blepharodinae, a position not challenged by recent molecular (Svenson & Whiting 2009) and "total evidence" analyses (Svenson et al. 2015, figure 7), morphological data support a sister-group relationship to Empusini (Wieland 2013, p. 139ff, figures 395, 401; see also Svenson et al. 2016b, figure S1b).

Blepharodinae *sensu* Svenson et al. (2015) is united by plesiomorphic characters. The authors do not comment on the acute tip of the ventral apical lobe on the forecoxa in *Idolomantis* but encode this structure as "rounded" for Blepharodinae (including *Idolomantis*). Actually, the pointed tip of the ventral lobe is clearly visible in *Idolomantis* despite both apical lobes being included for their most part into the coxal lobes. In concordance with Wieland (2013, p. 140) we regard the acute tip of the (elongate) ventral apical lobe, and the elongation of the prothorax in *Idolomantis* as an autapomorphy of Idolomantini + Empusini, and for that reason do not follow the systematic arrangement in Svenson et al. (2015).

[163] **Empusini**. Synapomorphies: antennae bipectinate (vs. *bilobate*; Wieland 2013, p. 140, figures 87–90); foliaceous expansion of pronotum reduced to the area around supracoxal dilatation (vs. *encompassing most of pronotum except base*).

[164] **Idolomorphina**. Synapomorphy: antennae of male monopectinate (vs. *bipectinate*) (Roy 2004a; Wieland 2013, p. 140, figure 401).

[165] **Hymenopodidae**. Contrary to Hymenopoidea, the boundaries of this family are not well-defined morphologically (Roy 1999b; Svenson et al. 2015). It is basically characterized by plesiomorphic hymenopoid characters.

[166] **Phyllocraniinae**. The five posteroventral spines on the forefemur are an ambiguous character, as it is not clear whether they are an autapomorphy of this subfamily or a synplesiomorphy shared with Empusidae. In the latter case, the loss of one posteroventral spine would be a synapomorphy of remaining hymenopodids. However, the elongate head shape in *Phyllocrania* also resembles the empusid condition. Its genitalia are rather distinct (Roy 1963a; Figure 15e), differing from those of other hymenopodid subfamilies by the strongly developed ventral process of the right phallomere and the long **sdpm** (the other subfamilies usually exhibit **sdpl** while **sdpm** is reduced). In contrast, the left phallomere exhibits the typical early hymenopodid condition due to its broad **paa**.

In the morphological tree of Svenson et al. (2015) Phyllocraniinae also includes *Parablepharis* at the exclusion of *Amphecostephanus* (Svenson et al. 2015, figure 6b), which has not been tested but is considered to not belong to Hymenopodidae. However, the external morphological characters used by that study to unite *Phyllocrania* and *Parablepharis* are highly variable among hymenopodids, negative (= missing), or homoplastic (e.g. the foliaceous expansions; Svenson et al. 2015, Table S2). Other characters, like overall shape of head and of the process on the vertex, the armature of the forelegs, and the genitalia (Roy 1963a, 2008a; cf. Figures 15e, 16h) do not support the two genera having a

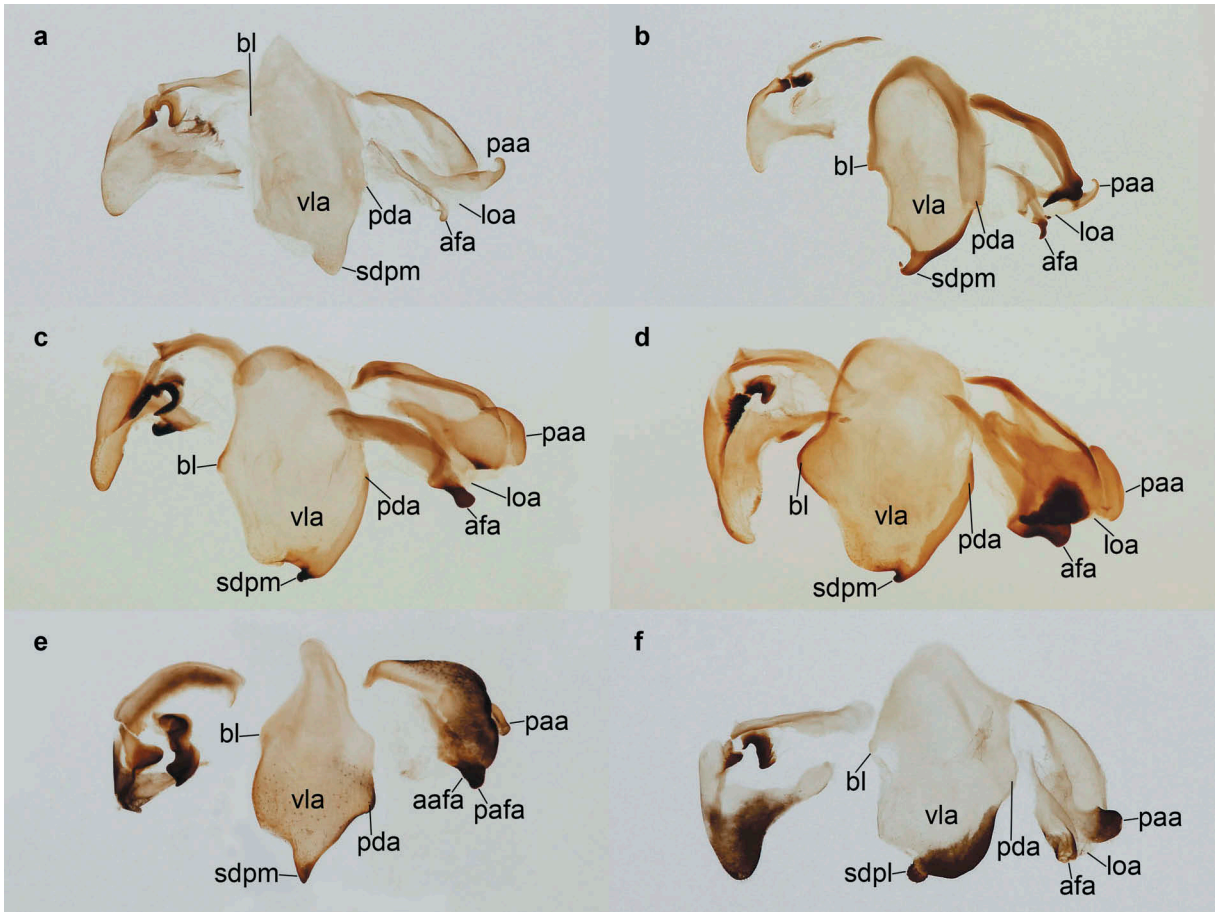

Figure 15. Genitalia of Galinthiadidae, Empusidae and Hymenopodidae, ventral view. **a**, *Pseudoharpax.* sp, from Gambia (CS, prep. Schwarz No. 161); **b**, *Harpagomantis tricolor* (Linnaeus, 1758), from South Africa (CS, prep. Schwarz No. 230); **c**, *Blepharopsis mendica* (Fabricius, 1775), from Djerba, Tunisia (CS, prep. Schwarz No. 201); **d**, *Idolomantis diabolica* Saussure, 1869, from Tanzania (CS, prep. Schwarz No. 36); **e**, *Phyllocrania paradoxa* Burmeister, 1838, from SE Kenya (CS, prep. Schwarz No. 199); **f**, *Sibylla* (*Sibyllopsis*) *pannulata* Karsch, 1894, from Cameroon (CS, prep. Schwarz No. 190). Not to scale.

common ancestor. The close relationship between *Parablepharis* and Phyllothelyinae, on the other hand, caused Phyllocraniinae and Phyllothelyinae to group together in the total evidence trees of Svenson et al. (2015, figure 7) and Svenson et al. (2016b, figure S1).

[167] **Sibyllinae**. Morphologically homogenous and well defined (see Roy 1996 for details). Molecular data suggest a classification among Hymenopodidae as sister-group of *Phyllocrania*, but the actual sister-group of *Phyllocrania* + Sibyllidae was not constantly resolved: Phyllothelyinae in Svenson (2007), Hymenopodinae in Yager & Svenson (2008), and remaining Hymenopodidae in Svenson & Whiting (2009) and Svenson et al. (2015) (molecular results only, Svenson et al. 2015, figure 5). In the total evidence tree of Svenson et al. (2015) Sibyllinae form a polytomy with Phyllocraniinae + Phyllothelyinae and remaining Hymenopodidae, while the subfamily resolves as sister to remaining Hymenopodidae in Svenson et al. (2016b, figure S1). Morphological and genital features (e.g. the broad **paa**; Figure 15f) support a phylogenetic position among early Hymenopodidae. An interesting developmental trait shared with Empusidae is the late (up to several days) color change of the newly developed wings from brownish to green after the molt to adulthood (cf. Schwarz et al. 2006).

[168] **Hymenopodinae**. No clear synapomorphies for this group could be found. The characters given by Svenson et al. (2015, p. 21–22) are also rather weak. For example, the bright coloration pattern of the hind wings is actually a plesiomorphic character of metamantodean origin and mantidean alteration, shown for example by Galinthiadidae. Largely reduced and faded patterns which can putatively be derived from the red and black mantidean pattern can be seen in *Idolomantis* and several derived hymenopodid genera (e.g. *Theopropus*).

[169] **Anaxarchini**. Synapomorphies: loss (vs. *presence*) of process on the vertex; reduction of lobes on walking leg femora (vs. *distinct lobes on walking leg femora*); certain type of ant mimicry in early nymphs (vs. *non-myrmecomorphic early nymphs*). Ant

mimicry is also found in other hymenopodids, e.g. Acromantinae and Oxypilinae, but the type employed by anaxarchinines is unique to the tribe and qualifies as a synapomorphy.

Shcherbakov et al. (2016) discuss some morphological characters of *Heliomantis* linking this genus with Giglio-Tos (1927) "Acromantes" (largely corresponding to the group here named Acromantini), e.g. the subapical lobes on the walking leg femora, and the subapical black band on the forecoxae (see Shcherbakov et al. 2016 for details). However, morphological characters of taxa interpreted here to be at the base of both Otomantini and Acromantini (*Otomantis* and *Metacromantis* Beier, 1930, respectively), i.e. mammilate eyes, well-developed juxtaocular bulges, a more or less distinct process on the vertex, hyaline, more or less truncate hind wings, and, not the least, another type of body coloration (dark brownish, with only the wings sometimes of greenish color) are expanding the definition of Acromantini and contrast with the expression of these characters in Anaxarchini. The walking leg lobes are here interpreted to be reduced in this group, with *Heliomantis* exhibiting an intermediate stage. The elongate pronotum of *Anaxarcha*, *Werneriana* and *Heliomantis* is likely a derived feature, as *Odontomantis* and *Euantissa* have shorter pronota comparable to Hymenopodini, with some species of the former closing the gap to *Werneriana* (e.g. "*Odontomantis*" *rhyssa* Werner, 1930; see Shcherbakov et al. 2016, figures 5, 6G). A sister-group relationship of Hymenopodini and Anaxarchini has consistently been found by molecular studies (Svenson & Whiting 2009; Legendre et al. 2015; Svenson et al. 2015, 2016b; Svenson & Rodrigues 2017). Current morphological data do not provide strong counterevidence for such a relationship, so it is retained here.

[170] ***Nemotha***. This genus does not belong to Iridopteryginae as suggested by Beier (1935c); already Wood-Mason (1884) pointed out its close affinities with *Odontomantis* and *Euantissa*, exemplified, for instance, by its numerous, decumbent posteroventral spines on the foretibiae. The genus is monotypic, since *Nemotha mirabilis* Beier, 1933 belongs to *Tricondylomimus* (Stiewe & Shcherbakov 2017).

[171] **Hymenopodini**. Synapomorphy: white markings on tegmina, the central mark ("eye-spot") being partially enclosed by black (see Wieland 2013, p. 144ff, figures 405, 406 for a discussion of putative eye-spot transitions in this group); bug mimicry in early nymphs (vs. *ant-mimicking early nymphs*). Bug mimicry was first described for *Hymenopus* (Shelford 1902) and later confirmed for *Helvia* and *Theopropus* (Schwarz 2015 and references therein). However, it also occurs in *Creobroter, Chlidonoptera*, and *Pseudocreobotra* (pers. obs.). Edmunds (1976) and Neumann (2006) regard the morphology of the first instars of *Pseudocreobotra* as instances of ant mimicry, but the enlarged first antennomere of the flagellum (described by Roy 1962a; Wieland 2013, p. 162, figures 426, 427), the curled abdomen, the foliaceous carinae on the walking leg femora, and the walking gait more closely match the appearance of nymphs of coreid and reduviid bugs.

[172] **Hymenopodina**. Synapomorphies: exaggerated sexual dimorphism ("giant" females, Schwarz 2015; Svenson et al. 2016b) (vs. *typical hymenopodid size difference*); distinct black band on prosternum (vs. *no black band on prosternum*) (secondarily reduced to a brownish median spot in *Hymenopus*).

[173] ***Helvia***. *Parymenopus* Wood-Mason, 1890 is a junior synonym (Schwarz 2015).

[174] **Phyllothelyinae**. Synapomorphy: area around spines on anterior coxae suffused (vs. *not suffused*) by black. Phyllothelyinae can be distinguished from Hymenopodinae by a very large lobe at the base of the walking leg femora, almost merging with the subapical lobe, and by the brownish body coloration. The configuration of the femoral lobes also distinguishes the group from Oxypilinae and Acromantinae, which may possess small but never merging lobes.

[175] **Parablepharini**: Apomorphies: anterior coxa with strong teeth emerging from a foliaceous expansion along dorsal side (vs. *small teeth not connected by foliaceous expansion*); anterior tibia dilated (vs. *not dilated*) dorsally. We regard the foliaceous expansion along the pronotum as such to be a plesiomorphic character already present in Empusidae, Phyllocraniinae, Hymenopodinae, and largely reduced but still present in Sibyllinae. The size and shape of the dilatation, however, may be apomorphic for *Parablepharis*.

[176] **Phyllothelyini**. Synapomorphies: pronotum elongate (vs. *not elongate*); foliaceous expansion along pronotum largely reduced (vs. *present*); proximal part of walking leg tibiae inflated (vs. *not inflated*).

[177] ***Phyllothelys***. Svenson et al. (2015) have resurrected *Kishinouyeum* Ôuchi, 1938 from synonymy with *Phyllothelys*, but as Ehrmann & Roy (2009) have pointed out, variability in *Phyllothelys* is considerable. This variability has not been sufficiently covered by the four species used in the study (e.g. the type species of *Kishinouyeum* has been omitted). Until *Phyllothelys* (*sensu* Ehrmann & Roy 2009) is revised with respect to *Ceratocrania*, we treat *Kishinouyeum* as a synonym.

[178] **Oxypilinae**. A recent study by Schwarz & Shcherbakov (2017) independently obtained the phylogenetic scheme recovered by the total evidence tree in Svenson et al. (2015), so we have largely followed these arrangements. Synapomorphies: lobe along dorsal margin of forefemora (vs. *dorsal lobe not extending along the total length of the femur*); very short, V-shaped metazona

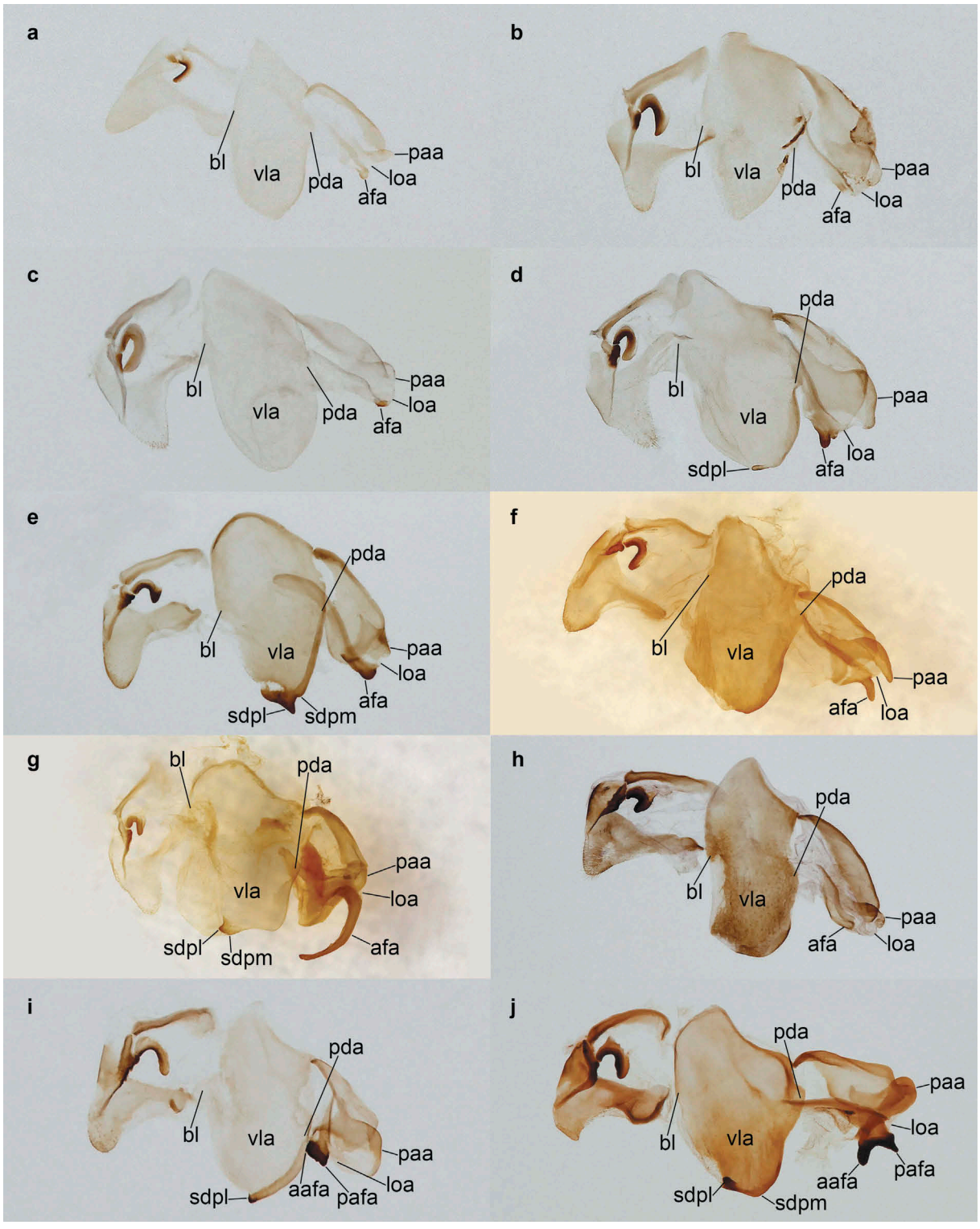

Figure 16. Genitalia of Hymenopodidae, ventral view. **a**, *Odontomantis* cf. *planiceps* (De Haan, 1842), from Thailand (CS, prep. Schwarz No. 234); **b**, *Theopropus elegans* (Westwood, 1832), from the Malay Peninsula (CS, prep. Schwarz No. 229); **c**, *Helvia cardinalis* Stål, 1877, from the Malay Peninsula (CS, prep. Schwarz No. 150); **d**, *Creobroter granulicollis* Saussure, 1870, from Brunei, Borneo (CS, prep. Schwarz No. 53); **e**, *Chlidonoptera vexillum* Karsch, 1892, from W Kenya (CS, prep. Schwarz No. 39); **f**, *Panurgica rehni* La Greca, 1954, from Congo (MNHN, prep. Roy No. 3012); **g**, *Chloroharpax modesta* (Gerstaecker, 1883), from Guinea (MNHN, prep. Roy No. 4480); **h**, *Parablepharis kuhlii asiatica* Roy, 2008, paratype from NW Laos (SMNK 06675, prep. Schwarz No. 207); **i**, *Phyllothelys* cf. *breve* (Wang, 1993), from Myanmar (CS, prep. Schwarz No. 200); **j**, *Ceratocrania macra* Westwood, 1889, from Sarawak, Borneo (CS, prep. Schwarz No. 197). Not to scale.

(vs. *metazona at least 1.5 times as long as prozona, sinuate or subparallel*); abdomen covered in dense setae (vs. *abdomen sparsely setose*) (Svenson et al. 2015; Schwarz & Shcherbakov 2017).

[179] **Oxypilini**. Synapomorphy: loss (vs. *presence*) of crenulation at the medioventral base of the posteroventral spines (Schwarz & Shcherbakov 2017). Further distinguished from Hestiasulini by four pairs of strong processes on the pronotum (see comments under Metamantodea).

[180] ***Pachymantis***. *Triaenocorypha dohertii* Wood-Mason, 1890 is the nymph of *Pachymantis bicingulata* (De Haan, 1842).

[181] ***Pseudoxypilus***. Enigmatic genus erected by Giglio-Tos (1915) for *Mantis hemerobius* Olivier, 1792 = *Mantis fenestrata* Stoll, 1813, known only from the figure in Stoll's publication. As already noted by Giglio-Tos, the figured specimen, if genuine at all, raises some doubt as to whether it is a mantodean.

[182] **Hestiasulini**. Synapomorphy: lobe on dorsal margin of forefemur about as wide as non-dilated part (vs. *about half as wide as non-dilated part*). Further distinguished from Oxypilini by the lack of ocellar spines, the lack of the lateral teeth on the vertex process, the lack of enlarged conical tubercles on the pronotum, and the presence of the denticulation at the base of the posteroventral spines (Schwarz & Shcherbakov 2017).

This tribe has recently been revised by Schwarz & Shcherbakov (2017). Genital (Figure 17f, g) and morphological features of several SE Asian species groups differ significantly from the type species *Hestiasula brunneriana* Saussure, 1871 (Figure 17d), having necessitated the resurrection of *Catestiasula* and the description of two new genera.

[183] ***Ephestiasula***. *Parahestiasula* Lombardo, 1995 has been synonymized with *Ephestiasula* (Ehrmann & Borer 2015).

[184] **Acromantinae**. This group can be distinguished from Oxypilinae by the dorsal lobe on forefemur never reaching the distal end, and by a ratio metazona/prozona above 1.5; from Phyllothelyini by the lack of black suffusion along forecoxal spines, shorter and more robust pronota, and lack of inflation of walking leg tibiae; from Parablepharini by the lack of dorsal subapical lobes on walking leg femora, by lacking a dorsal lobe on the tibia, and by the lack of a leaf-like expansion along the prothorax; from Hymenopodini by a brownish base color, the lack of white markings on the tegmina, and the lack of an eye-spot on abdomen in nymphs; from Anaxarchini by a brownish base color, the presence of a short process on the vertex (rarely reduced) and of distinctly triangular ventral lobes on the walking leg femora; from Sibyllinae by the shape of the pronotum, wings, and ventral phallomere; and from Phyllocraniinae by the lack of dorsal subapical lobes on the walking leg femora, the lack of a foliaceous process on the head (while a simple process may be present), and by four instead of five posteroventral spines on the foretibiae.

[185] **Otomantini**. This group can be distinguished from Acromantini by the smooth ventral margin of the forecoxae (Svenson et al. 2015). Other characters given by those authors are ambiguous. For example, truncate wing apexes are also present in *Metacromantis nigrofemorata* Ghate & Roy, 2006.

[186] ***Chrysomantis***. *Anoplosigerpes* Werner, 1928 and *Uvaromantis* Beier, 1930 are junior synonyms (Roy 2013c).

[187] ***Catasigerpes***. This former genus was recently downgraded to subgeneric level (Roy 2013b).

[188] **Acromantini**. Distinguished from Otomantini by the tuberculate ventral margins of the forecoxae (Svenson et al. 2015).

[189] **Mantoidea**. A tuberculate (vs. *smooth*) prozona, and a certain degree of brachyptery (vs. *macroptery*) in females are putative synapomorphies of this group. Early lineages also possess a pair of metazonal processes. They are found in *Theopompella, Zouza, Tagalomantis, Mellierella, Scolodera, Melliera, Xystropeltis*, and among derived taxa in *Heterovates*, and seem to derive in all genera from the anteriormost paramedian pair of pronotal markings, situated just posteriad the supra-coxal dilatation (IV in Figure 27). As explained above, these markings or corresponding tubercles are actually plesiomorphic characters of metamantodean origin which are interpreted here to have been re-evolved in Mantoidea, with subsequent secondary reductions in some subfamilies (most Popinae and Mantidae). However, it still remains to be shown if the tubercles seen in this group are homologous (i.e. if all evolved from the same metamantodean pair of tubercles) and as such qualify as a synapomorphy of the superfamily. Groundplan of mantoidean genitalia: right phallomere simple; **bl** present; **sdpm** straight, triangular, with rounded apex; **sdpl** well developed, with acute or subacute apex; **aafa** and **pafa** more or less digitiform (bifurcation reduced in some groups).

[190] **Dactylopterygidae**. Synapomorphies: adaptation to the bark-living lifestyle, with dorsoventrally flattened body, pronounced juxtaocular bulges, elongate antennae and styli, mottled coloration, widened costal field of wings, and dorsal contour of forefemora fitting along pronotal margin (between head and base of wings) when at rest (vs. *no such adaptations*).

Molecular studies differ considerably regarding the phylogenetic position of this group: while resolved as sister-group of Galinthiadidae in Svenson (2007), and as sister-group of Hymenopoidea in Yager & Svenson (2008), it found its latest position as adelphotaxon of Popinae among a monophyletic Deroplatyidae in Svenson & Whiting (2009), and of Popinae among a polyphyletic Deroplatyidae in Svenson et al. (2015) and Svenson & Rodrigues (2017). Consistent monophyly contrasting with the unstable phylogenetic position across studies strongly indicate that this

group represents a well-differentiated clade, corresponding to a family rank. Due to head (e.g. lack of vertex process, well-developed juxta-ocular bulges), pronotal (tubercles, foliaceous expansion), and genital characters (Figure 18a, b) we retained a classification among Mantoidea as sister to Deroplatyidae + Mantidae.

[191] **Deroplatyidae**. A lineage of predominantly stick-resembling genera united by genital morphology; largely underrepresented in Svenson & Whiting (2009). We hypothesize that brachyptery (but not necessarily stick resemblance) evolved independently in Popinae and Deroplatyinae. *Popa*, for instance, has fully macropterous males and mesopterous females, in contrast to other Popini, which have mesopterous males and brachypterous to micropterous females. Likewise, *Euchomena* is macropterous, while its sister-group Leptocolina have mesopterous males and micropterous females. Deroplatyinae all have macropterous males, while females are mesopterous to macropterous in Deroplatyini and brachypterous to micropterous in Euchomenellini (Schwarz 2017; Vermeersch 2018).

Genitalia groundplan: **bl** well developed; **sdpm** and **sdpl** present but short; **aafa** present, but less developed than **pafa**, rounded; **pafa** more or less acute (Figures 18c–h, 19a–f).

[192] **Popinae**. Genitalia groundplan: **sdpm** and **sdpl** rounded, merged into a digitiform **sdp; aafa** rounded (lost in some taxa, e.g. *Popa*, Figure 18c); **pafa** digitiform, subacute (Figure 18c–h).

[193] **Popini**. Synapomorphies: anterior coxae enlarged distally to accommodate head during cryptic position (vs. *anterior coxae not enlarged*) (independently evolved in Toxoderopsina); juxtaocular bulges large and conical, so that vertex neatly fits the anterior margin of pronotum.

[194] **Leptocolini**. Distinguished from Popinae by the lack on dorsal lobes on forecoxae, and the loss of apical lobes on the walking leg femora (except in females of *Stenopyga*).

[195] **Euchomenina**. Distinguished from Leptocolina by both sexes being macropterous.

[196] **Deroplatyinae**. Genitalia groundplan: **sdpm** largely reduced, forming a rounded lobe; **sdpl** acute; **aafa** reduced (re-evolved in certain *Deroplatys* species, Figure 19f); posterior lobe with more or less acute apex (Figure 19a–e).

[197] **Euchomenellini**. Synapomorphies: females strongly brachypterous; loss of **sdpm; sdpl** evolved into a curved, hook-like process (simplified in *Euchomenella* and *Phasmomantella*; Roy 2001, 2008b; Schwarz 2017; Vermeersch 2018; Figure 19a, b). Further distinguished from Deroplatyini by the lack of a pale subapical band on the alae (Schwarz & Helmkampf 2014; Schwarz 2017).

[198] **Deroplatyini**. This tribe has recently been rearranged by Schwarz & Helmkampf (2014), treated there as Deroplatyinae (see also Schwarz 2017).

[199] **Pseudempusina**. Autapomorphy: base of **sdpl** developed into a rounded lobe dextro-proximad of hook (**sdpl'**). The ventral phallomere of *Pseudempusa* thus has three processes: **sdpm** as a barely visible and almost reduced lobe at the median apex of the phallomere, **sdpl** as a curved hook pointing to the right, and **sdpl'** dextro-proximad of it (Figure 19c). **Sdpm** is totally reduced in *Mythomantis* (Schwarz & Helmkampf 2014; Figure 19d).

[200] **Deroplatyina**. Autapomorphies: adaptation to leaf resemblance, with foliaceous expansion along lateral pronotal margins, and costal field of female enlarged in proximal and distal half, with an excavation in between. The lobes on the lateral margins of the abdomen and on the walking leg femora are here interpreted to be a plesiomorphic trait, reduced in males of some *Deroplatys* species and in other Deroplatyidae.

[201] **Mantidae**. Synapomorphy: X_1X_2Y sex chromosome system, with each of the two X chromosomes attaching one of their arms to the corresponding arm of the Y chromosome at meiosis, thus building an M-shaped trivalent (White 1941, 1951, 1965; Hughes-Schrader 1950, 1953).

[202] **Mellierinae**. In this small but biogeographically interesting subfamily, the shape of the genitalia and the size of the Y chromosome show a transition paralleling those seen in remaining Mantidae: while some *Rhodomantis* species exhibit more or less the mantidean ground-plan condition (**sdpm** and **sdpl** present, **afa** short and more or less truncate), other species exhibit a tendency for curvature of the distal process, either retaining both processes or with one of them being reduced. The phalloid apophysis may be truncate, subacute or claw-like (Milledge 2014). In *Melliera* and *Mellierella* the curved distal process evolved from **sdpl**, since remnants of **sdpm** are visible distally (Figure 20a, b). The situation in *Xystropeltis* and *Scolodera* is ambiguous: both have curved distal processes with a subapical constriction, which may have evolved from the situation seen in *Melliera* and *Mellierella*, respectively, or represent independent developments. The phalloid apophysis of *Xystropeltis* and *Mellierella* is more or less rounded, while it is bilobed in *Melliera* and curved and acute in *Scolodera* (Milledge 1989; Lombardo 2000b; Medellín & Salazar 2011; Figure 20a, b). Both developments represent a convergently evolved analogue of the variation observed in Hierodulinae, Stagmomantinae and Vatinae.

The Y chromosome may be either normal-sized or small in the two *Rhodomantis* species studied so far, while it is small in *Melliera* (Hughes-Schrader 1950; White 1965).

Mellierinae are further characterized by their distinctly shaped prothorax with two very prominent protuberances in the metazona (see above, secondarily

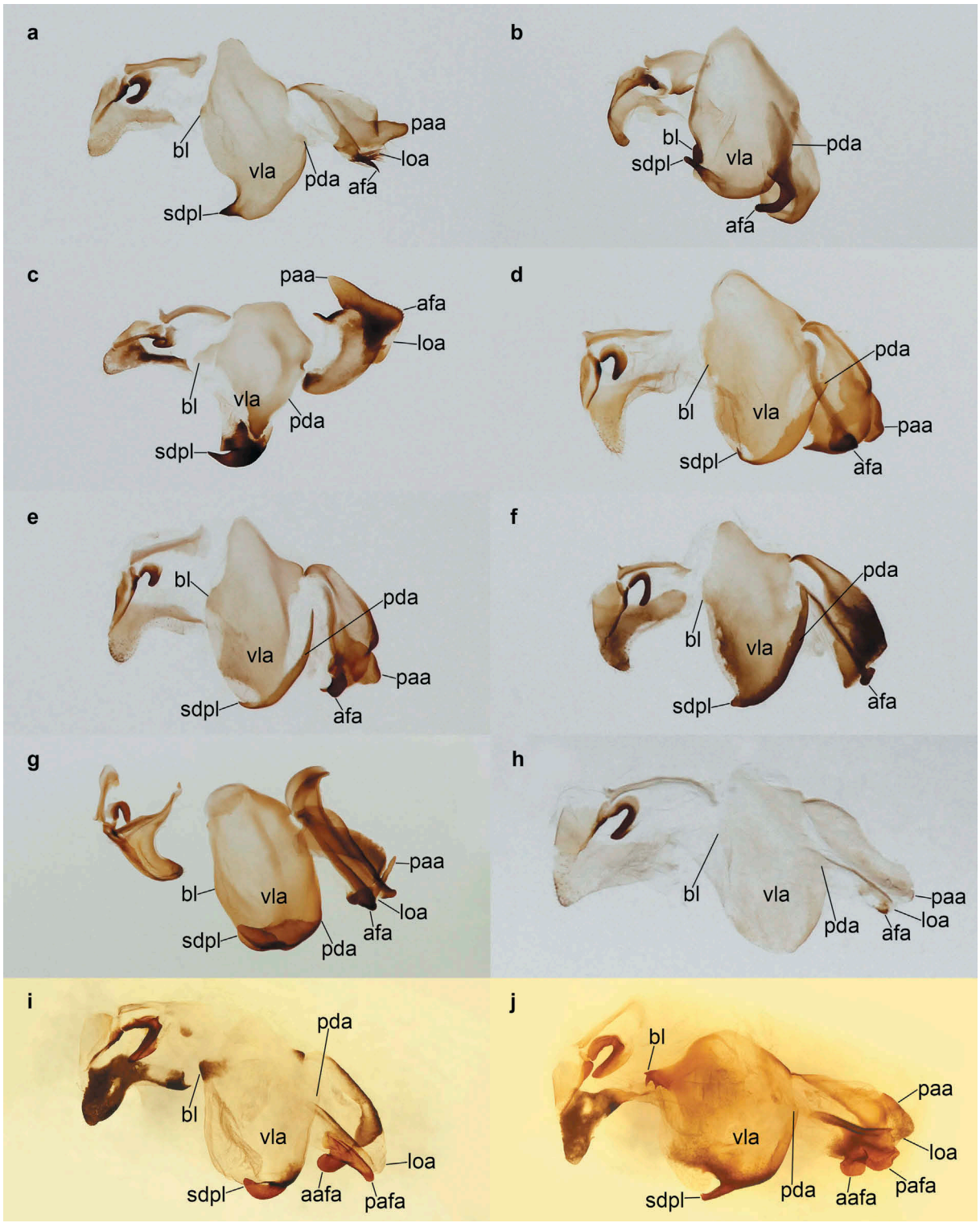

Figure 17. Genitalia of Hymenopodidae, ventral view. **a**, *Ceratomantis kimberlae* Svenson, 2007, from Sarawak, Borneo (CS, prep. Schwarz No. 241); **b**, *Junodia maternaschulzei* Stiewe & Roy, 2010, from Kenya (CS, prep. Schwarz No. 255); **c**, *Oxypilus* (*Oxypilus*) *gillonae* Roy, 1966, from N Ivory Coast (CS, prep. Schwarz No. 256); **d**, *Hestiasula brunneriana* Saussure, 1871, from W India (CS, prep. Schwarz No. 47); **e**, *Ephestiasula pictipes* (Wood-Mason, 1879), from W India (CS, prep. Schwarz No. 187); **f**, *Catestiasula moultoni* Giglio-Tos, 1915, from Sabah, Borneo (CS, prep. Schwarz No. 189); **g**, *Astyliasula phyllopus* (De Haan, 1842), from Sabah, Borneo (CS, prep. Schwarz No. 46); **h**, *Acromantis* sp., from S Thailand (CS, prep. Schwarz No. 69); **i**, *Chrysomantis speciosa* Giglio-Tos, 1915, from the Central African Republic (MNHN, prep. Roy No. 358); **j**, *Oxypiloidea* (Catasigerpes) *margarethae* Werner, 1912, from Cameroon (MNHN, prep. Roy No. 2126). Not to scale.

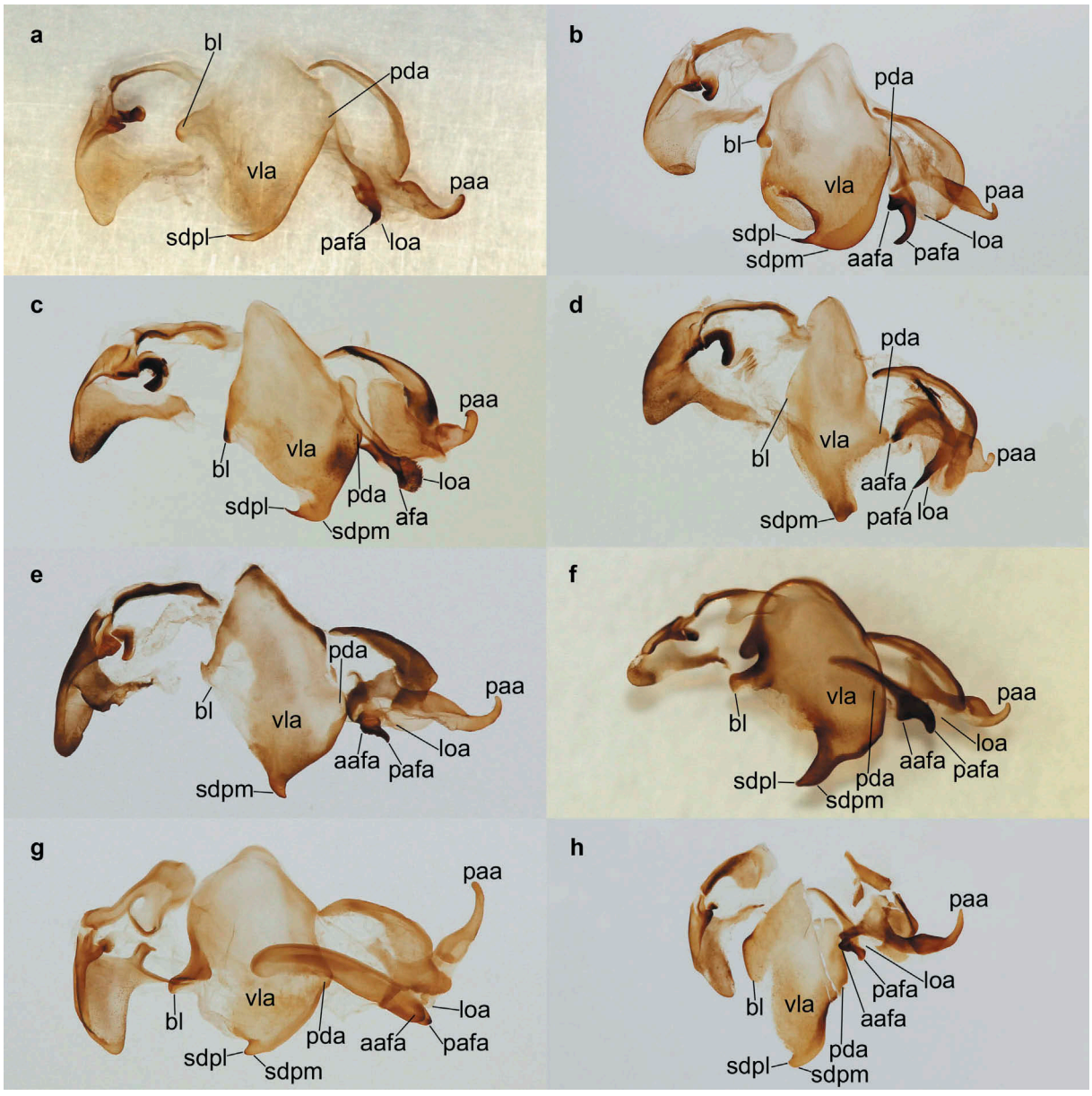

Figure 18. Genitalia of Dactylopterygidae and Deroplatyidae, ventral view. **a**, *Dactylopteryx orientalis* (Werner, 1906), from E Kenya (TS, prep. Schwarz No. 68); **b**, *Theopompella aurivillii* (Sjöstedt, 1900), from DRC (SMNK 11131, prep. Schwarz No. 288); **c**, *Popa spurca* Stål, 1856, from N Ivory Coast (CS, prep. Schwarz No. 165); **d**, *Neodanuria bolauana* (Saussure, 1869), from SE Kenya (CS, prep. Schwarz No. 114); **e**, *Afrothespis kenyana* Roy & Schwarz, 2014, paratype (MFN, prep. Schwarz No. 72); **f**, *Stenopyga* sp., from SE Kenya (TS, prep. Schwarz No. 49); **g**, *Agrionopsis distanti* (Kirby, 1899), from Tanzania (SMNK 00241, prep. Schwarz No. 180); **h**, *Leptocola stanleyana* (Westwood, 1889), damaged specimen from Cameroon (CS, prep. Schwarz No. 33). Not to scale.

reduced in *Rhodomantis*), an eye-spot-like pattern on the alae (secondarily reduced in some *Rhodomantis*, in *Scolodera* and in Mellierinae but subapical darkening still visible), and the brachypterous females. Other groups with brachypterous females (*Cataspilota*, Archimantina, Stagmomantini) have differently shaped genitalia (see below).

[203] ***Rhodomantis***. The sex chromosome trivalent of *Rhodomantis* differs from the structure as seen in remaining Mantidae by both X chromosomes being attached to the same Y chromosome arm, but available data allow for this autapomorphy, so far only known in this genus, to have evolved from the typical Mantidae condition (see White 1965 for details). In Svenson & Whiting (2009)

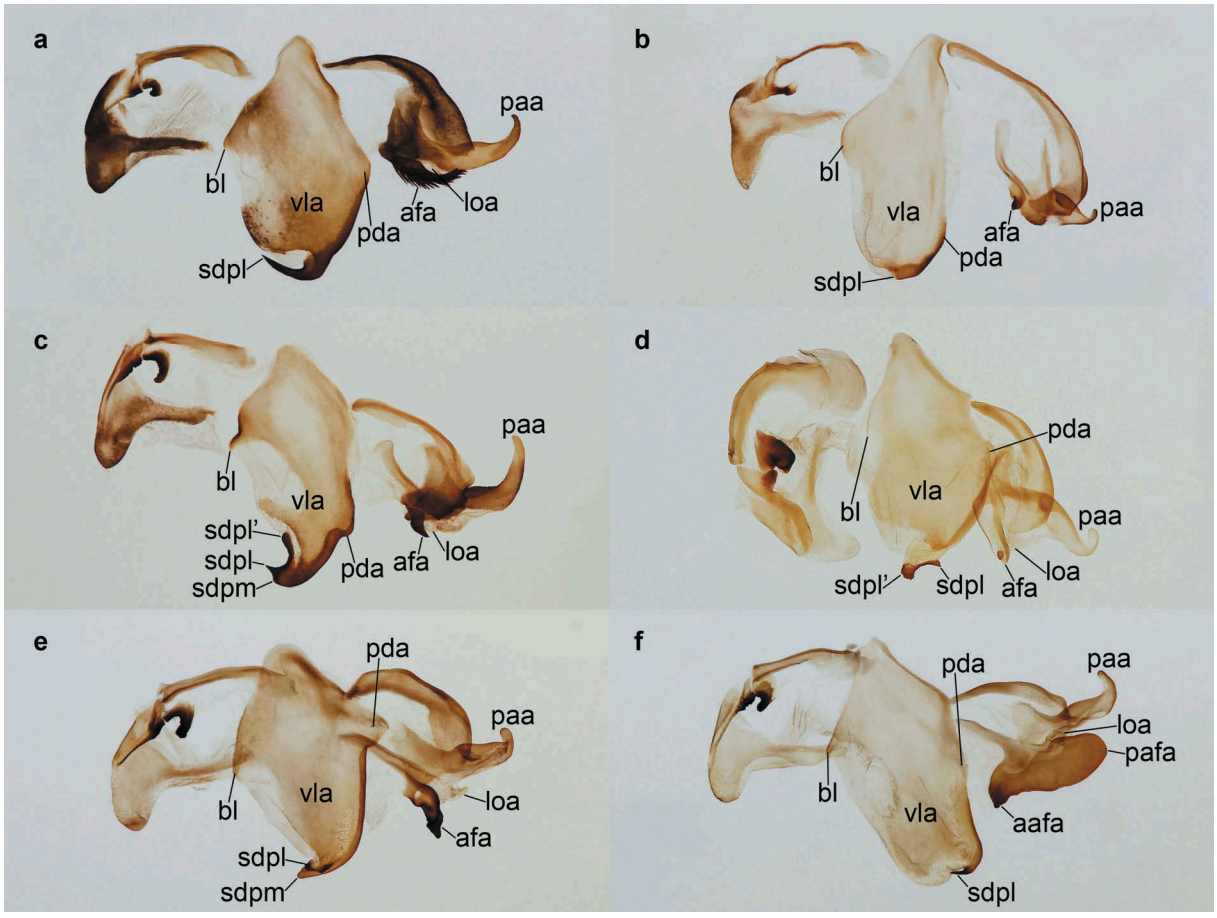

Figure 19. Genitalia of Deroplatyidae, ventral view. **a**, *Tagalomantis manillensis* Hebard, 1920, from Panay, Philippines (CS, prep. Schwarz No. 104); **b**, *Euchomenella matilei* Roy, 2001, from Brunei, Borneo (CS, prep. Schwarz No. 93); **c**, *Pseudempusa pinnapavonis* Brunner d. Wattenwyl, 1893, from Thailand (CS, prep. Schwarz No. 188); **d**, *Mythomantis serrata* Schwarz & Helmkampf, 2014, holotype (NHM, prep. Schwarz No. 42); **e**, *Deroplatys desiccata* Westwood, 1839, from Sabah, Borneo (CS, prep. Schwarz No. 90); **f**, *Deroplatys trigonodera* Westwood, 1889, from Sarawak, Borneo (CS, prep. Schwarz No. 87). Not to scale.

this genus is listed alongside *Mellierella* as "unknown Danuriini 1" and "unknown Danuriini 2", respectively (node 269) (see Milledge 2014).

[204] **Mellierini**. Distinguished from Rhodomantini by their more deeply bilobed phalloid apophysis (Lombardo 2000b; Medellín & Salazar 2011; Figure 20b).

[205] **Orthoderinae + Choeradodinae**. In early branches of Mantidae (Orthoderinae, Choeradodinae, Mantinae, Deromantinae) the distal process of the ventral phallomere retains the plesiomorphic condition (**sdpm** more or less straight with rounded apex, **sdpl** present), and **aafa** and **pafa** are more or less fused (Figure 20c–g). Conversely, in derived groups (Omomantinae, Tenoderinae, Hierodulinae, Stagmomantinae and Vatinae) the distal process is strongly curved, often bifid, and both lobes of **afa** are well developed (Figures 20h, 21a–h, 22a–f, 23a–h, 24a–g, 25a–j). **Aafa** is secondarily reduced in some further derived groups, e.g. some Archimantina, Vatini (Figures 24h, 26b, 26d–f).

Similarly, there is a tendency in the male Y chromosome, which is about the same size as the X chromosomes in *Mantis, Orthodera* and *Choeradodis*, to become progressively smaller in derived Mantidae clades, possibly due to translocations to X chromosomes (see White 1940, 1941, 1965; Hughes-Schrader 1943b, 1950 for details).

The sex chromosomes and male chromosome numbers of Orthoderinae ($2n$ = 25) and Choeradodinae ($2n$ = 31, but see Williams 1938) differ slightly from remaining Mantidae ($2n$ = 27 in the male). This underscores their evolutionary status as side branches of the initial radiation of X_1X_2Y mantids. Since they are lacking pronotal tubercles and both external and genital morphology shares many characteristic features with the following clades, the classification adopted here concurs largely with the position of these two groups found in Svenson & Whiting (2009) and Svenson & Rodrigues (2017), but differs slightly from the results of Yager &

Svenson (2008). However, in contrast to the above-mentioned studies we do not regard Mantinae as closely related to Mellierinae. Genital morphology strongly supports a sister-group relationship of Choeradodinae + Orthoderinae to Mantinae + remaining Mantidae (see below). A close relationship between Choeradodinae and Mantinae had been previously suggested by Roy (2004b).

A synapomorphy of the two subfamilies is their dilated pronotum which enfolds the head anteriorly. In Orthoderinae, the pronotal margins are more or less subparallel, while in Choeradodinae they are further expanded to form a penta- or hexagonal shield.

All Mantidae except Mellierinae exhibit an apomorphic loss of the denticulation at the base of the posteroventral spines. A trend towards reduction of this denticulation is already seen in Dactylopterygidae, Deroplatyidae and Mellierinae, but in the clade (Orthoderinae + Choeradodinae) + remaining Mantidae this trait is totally lost.

[206] **Mantinae**. Synapomorphies: lack (vs. *presence*) of an apical spine on the walking legs; presence (vs. *lack of*) microscopic teeth on dorsal side of anal field veins of alae and on abdominal pleura which aid in stridulation (Hill 2007).

[207] **Deromantinae**. Distinguished from the previous subfamilies by their very slender, elongate prothorax (more than six times as long as wide) with well-marked supracoxal dilatation, metazona with concave margins, elongate spines on forelegs, a groove between the proximal and the second posteroventral spine of the forefemur to accommodate the distalmost posteroventral spine of the foretibia, and hyaline or infumate, macropterous wings without patterns in males. Distinguished from the following subfamilies by their distinctive genitalia of the early Mantidae type (Roy 1973; Figure 20g).

[208] **Omomantinae**. Autapomorphy: loss (vs. *presence*) of proximal discoidal spine. Further distinguished from previous subfamilies by their genitalia of derived Mantidae type (Figure 20h).

[209] **Tenoderinae**. We regard the more or less sclerotized lobe on the left arm of the right dorsal phallomere (Figures 21a–h, 22b, c, 23a–c, 23g, h, 24c–e, 25c–i) as a putative synapomorphy of Tenoderinae + (Hierodulinae + (Stagmomantinae +Vatinae)). However, it is missing in some taxa (Figures 22a, 22d–f, 23d–f, 24a, b, 24f–h, 25a, b, 26a–f). Even though a subsequent reduction is likely, the possibility of a homoplastic character cannot be ruled out at the moment. The genitalia of many species of this diverse clade have not been studied yet.

Mesopteryx has somewhat unusual genitalia, due to a distinctly shaped phalloid apophysis (Figure 21h), but the other genital traits as well as its morphology fits best among Tenoderini. As outlined above, the bifid distal process observed in several Tenoderinae, Hierodulinae, and Stagmomantinae can be regarded as homologous to the character as expressed in early cernomantodeans, and a simple process is a derived character. In derived Mantidae it is **sdpl** that is retained, while **sdpm** is successively reduced (for transitional examples see Beier 1952; La Greca 1956b; Roy 1965a, 1965c, 1995, 2005a, 2012; Milledge 1997, 2005; Figures 21e, 22f, 23d, g, 24g).

Tenoderinae are distinguished from the subsequent subfamilies by their combination of **afa** being deeply forked (**aafa** and **pafa** widely spaced apart, even if apex of **aafa** is reduced), an elongate **loa**, and **sdpm** being mostly reduced (except *Tisma*, which exhibits a very elongate metazona with concave margins as distinguishing character) (Figures 21a–h, 22a–e).

[210] **Tenoderini**. Distinguished from Paramantini by their very elongate **sdpl** with a subapical constriction (Figure 21a–h). We regard the characteristic pattern of blackish transverse stripes in the costal and discoidal field of the alae as a synapomorphy of the group, even though it is reduced to chessboard-like patterns in *Tenodera* and *Notomantis* and totally lost in *Mesopteryx*.

[211] **Polyspilotina & Tenoderina**. In Polyspilotina remnants of **sdpm** are often visible, while the base of the distal process is unmodified (Figure 21a–d). In Tenoderina there are no traces of **sdpm** left, and the base of the distal process is translocated apicad (Figure 21e–h).

[212] **Paramantini**. Distinguished from Tenoderini by the lack of black stripes on the alae, and by the lack of the subapical constriction of **sdpl**.

[213] **Paramantina**. Synapomorphy: **pafa** and **loa** fused (Figure 22a-c). In Paramantina, **aafa** is well developed and hook-like, while it is reduced or absent in Tarachomantina except *Nausicaamantis* (Roy 2005a; Mériguet 2005, 2013; Figure 22d, e). The latter, however, exhibits a very robust, straight **aafa** (Mériguet 2018).

[214] **Hierodulinae**. Distinguished from Tenoderinae, Stagmomantinae, and Vatinae by their simple, not elongate **loa**, and their more compact **afa**, the two lobes being less spaced apart and more variable with regard to shape, orientation, and sclerotization than what is exhibited by other Mantidae subfamilies. Also, both **sdpm** and **sdpl** are often retained (Figures 22f, 23a–h, 24a–f).

[215] **Hierodulini**. *Hierodula* seems to be paraphyletic with respect to the other genera, a revision of the whole complex is urgently needed. *Rhombodera* as currently understood is not monophyletic.

[216] ***Ephierodula***. This genus has been recently revalidated (Schwarz & Roy 2018). It has frequently been confused by Chinese authors with *Hierodulella* (Zhang & Zou 1991; Wang 1993; Zhu et al. 2012; but see Yang & Wang 1999), a genus endemic to Wallacea.

[217] **Archimantini**. The group in its present constellation was found by molecular analyses (Yager & Svenson

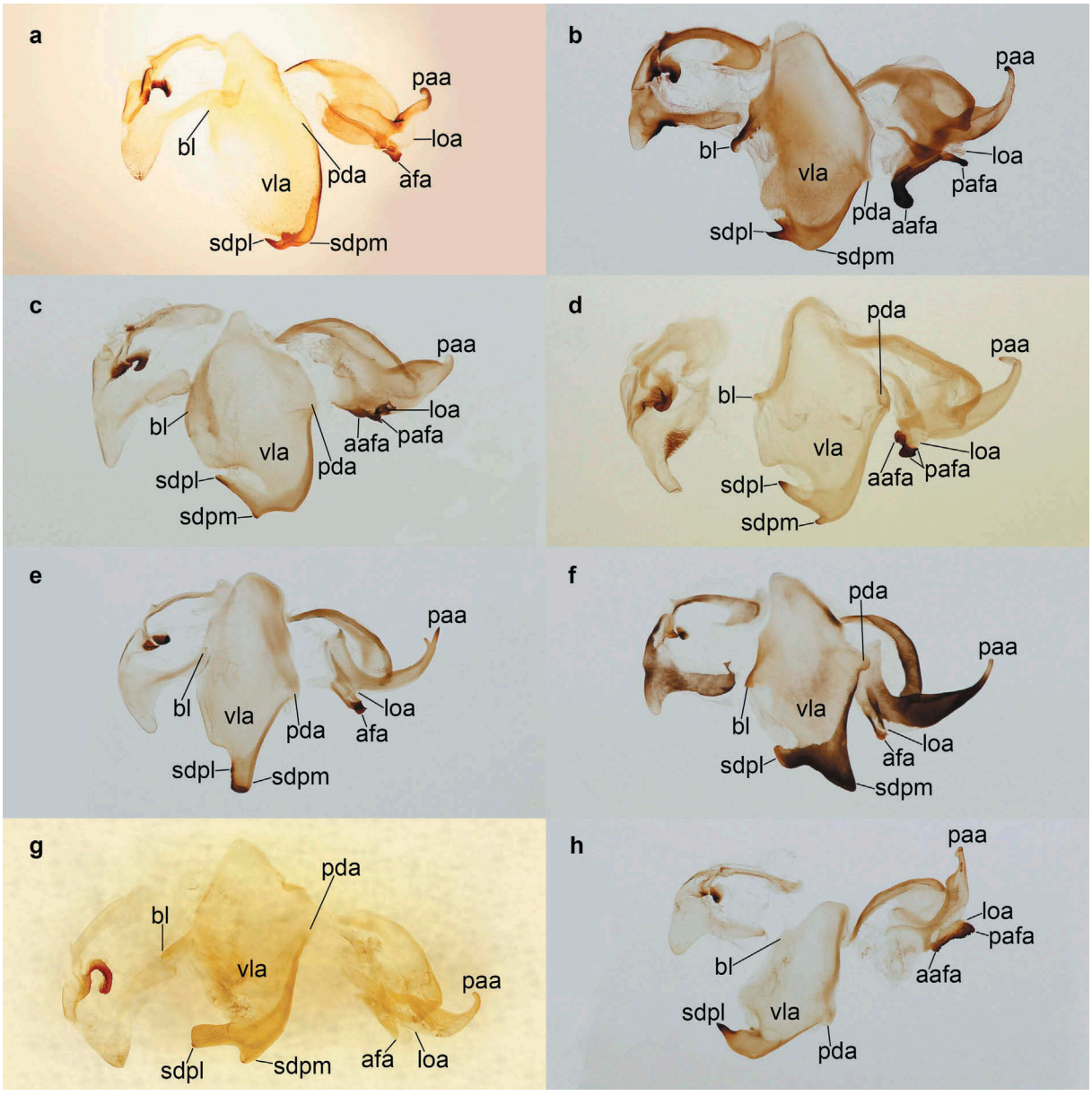

Figure 20. Genitalia of Mantidae, ventral view. **a**, *Mellierella biroi* Giglio-Tos, 1915, from Irian Jaya (SMNK 05667, prep. Schwarz No. 56); **b**, *Melliera major* (Saussure, 1872), from SE Mexico (SMNK 05663, prep. Schwarz No. 290); **c**, *Orthodera novaezealandiae* (Colenso, 1882), from New Zealand (CS, prep. Schwarz No. 127); **d**, *Choeradodis stalii* Wood-Mason, 1880, from Ecuador (CS, prep. Schwarz No. 202); **e**, *Mantis religiosa sinica* × *siedleckii*, from N Laos (CS, prep. Schwarz No. 116); **f**, *Statilia pallida* Werner, 1922, from Panay, Philippines (CS, prep. Schwarz No. 76); **g**, *Pseudostagmatoptera infuscata* (Roy, 1973), holotype (MNHN, prep. Roy No. 878); **h**, *Omomantis sigma* Rehn, 1949, from Cameroon (CS, prep. Schwarz No. 81). Not to scale.

2008; Svenson & Whiting 2009; Legendre et al. 2015; Svenson & Rodrigues 2017), but is also supported by genital and morphological data. The genitalia (Milledge 1997, 2005; Figure 24g, h) are clearly of the hieroduline type, with robust and often bifid distal process, and forked **afa**. A synapomorphy of Archimantini is the proximal two discoidal spines being about the same length, instead of the first to be distinctly shorter as in other Mantidae.

[218] **Trachymantina**. Synapomorphy: posteroventral margin of forefemora tuberculate (vs. *smooth*) (Milledge 2005).

[219] **Archimantina**. Synapomorphy: proximal discoidal spine longer than (vs. *equally long as*) second (Beier 1935c; Milledge 1997). This trait is also present in the hieroduline genus *Gretella* Werner, 1923, but we regard its occurrence in that poorly characterized genus to be independently evolved.

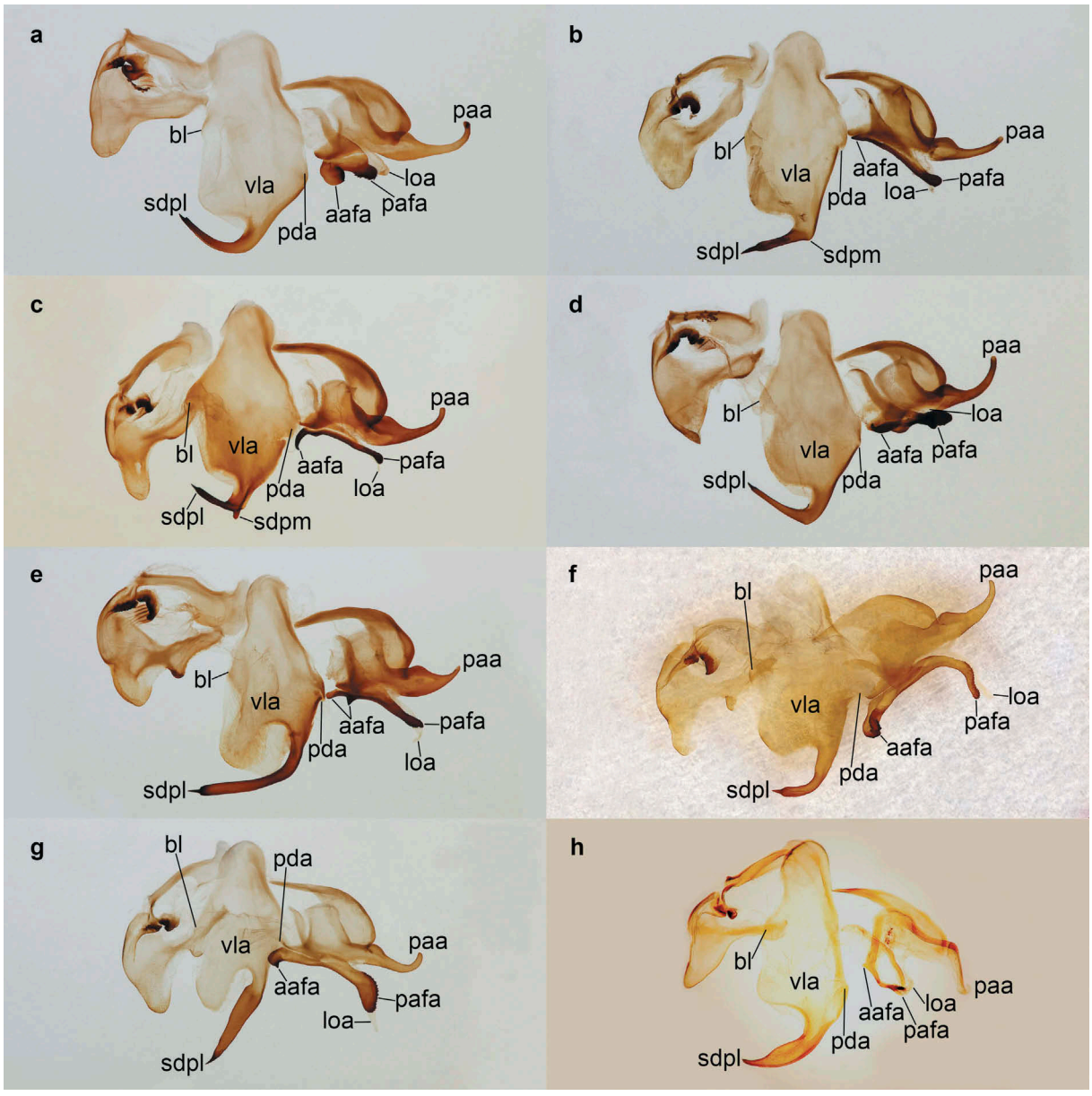

Figure 21. Genitalia of Mantidae, ventral view. **a**, *Polyspilota aeruginosa* (Goeze, 1778), from Ivory Coast (CS, prep. Schwarz No. 266); **b**, *Cataspilota misana* (Giglio-Tos, 1911), from SW Ivory Coast (CS, prep. Schwarz No. 117); **c**, *Plistospilota guineensis* Roy, 1965, from Ghana (CS, prep. Schwarz No. 115); **d**, *Prohierodula picta* (Gerstaecker, 1883), from Cameroon (CS, prep. Schwarz No. 219); **e**, *Tenospilota nova* (Beier, 1930), from the Malay Peninsula (CS, prep. Schwarz No. 242); **f**, *Notomantis brunneriana* (Saussure, 1871), from New Caledonia (MNHN, prep. Roy No. 4532); **g**, *Tenodera aridifolia* (Stoll, 1813), from Panay, Philippines (CS, prep. Schwarz No. 75); **h**, *Mesopteryx platycephala* (Stål, 1877), from Nepal (SMNK 05723, prep. Schwarz No. 57). Not to scale.

[220] **Stagmomantinae + Vatinae**. Synapomorphy: carinate (vs. *non-carinate*) mid and hind leg tibiae. Another putative apomorphy is the distinctive tessellation of the alae (reduced in Antemnini).

Two competing phylogenetic hypotheses regarding the position of this group have been presented so far by molecular studies: Tenoderinae + (Hierodulinae + (Stagmomantinae +Vatinae)) in Svenson & Whiting (2009) vs. Hierodulinae + (Tenoderinae + (Stagmomantinae + Vatinae)) in Yager & Svenson (2008) and Svenson & Rodrigues (2017). Genital data are inconclusive, allowing for both possibilities. The shape of **afa** in Stagmomantinae, Stagmatopterini, Oxyopsidini, and Pseudoxyopsidini (Figure 25a–j) is interpreted here as a synplesiomorphy shared with Tenoderinae, and as such do not provide an answer to

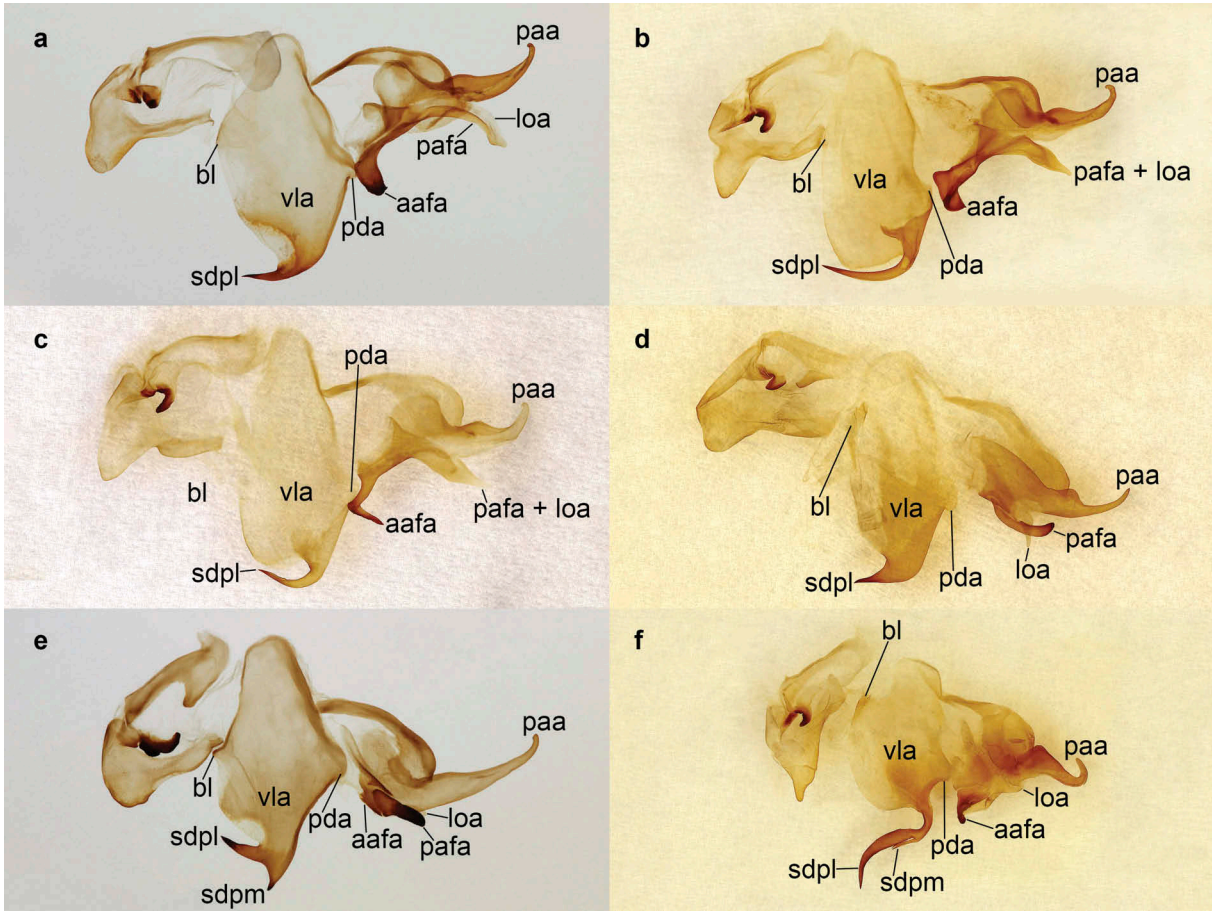

Figure 22. Genitalia of Mantidae, ventral view. **a**, *Sphodromantis* cf. *viridis* (Forskål, 1775), from Burkina Faso (CS, prep. Schwarz No. 126); **b**, *Paramantis togana* (Giglio-Tos, 1912), from Gabon (MNHN, prep. Roy No. 3235); **c**, *Alalomantis coxalis* (Saussure & Zehntner, 1895), from the Central African Republic (MNHN, prep. Roy No. 4287); **d**, *Tarachomantis* (*Madamantis*) *analamazoatra* Mériguet, 2013, paratype (MNHN, prep. Roy No. 3462); **e**, *Tisma pauliani* Roy, 2005, from Madagascar (CS, prep. Schwarz No. 225); **f**, *Tismomorpha vitripennis* (Bolívar, 1908), from Gabon (MNHN, prep. Roy No. 3273). Not to scale.

the problem. In Stagmomantinae + Vatinae there is a tendency towards elongation of **pda**. Vatini, in contrast, while being the morphologically most derived members of the clade, exhibit a trend towards simplification of genital structures, in terms of reduction of **pda** and of **aafa** (e.g. Cerdá 1993; Lombardo 2000b; Lombardo & Agabiti 2001; Roy 2003b; Battiston & Picciau 2008a; Roy & Ehrmann 2009; Medellín & Salazar 2011; Lombardo et al. 2014; Figure 26a–f).

[221] **Antemnini**. Distinguished from Stagmomantini by the fully macropterous females with enlarged costal field and acute apex, hyaline hindwings in both sexes, a process on the vertex (reduced in adult females), lateral and medioventral lobes on the abdomen, and the ventral carina of the walking leg femora being developed into lobes.

[222] ***Stagmomantis***. Some of the genera synonymized by Terra (1995) with *Stagmomantis*, like *Isomantis* Giglio-Tos, 1917 (Figure 25b), will probably have to be revalidated.

[223] **Vatinae**. Synapomorphy: antennomeres of males asymmetrical, antennae serrate to pectinate (vs. *antennomeres more or less symmetrical, antennae filiform*).

[224] **Stagmatopterini**. Distinguished from Oxyopsidini by the frontal shield being bicarinate and the antennae distinctly pectinate instead of just serrulate, from Pseudoxyopsidini by the less enlarged costal field of females (less than remaining parts of tegmen) and the pectinate antennae, from Heterovatina by the lack of pronotal tubercles, and from Vatina by the lack of ocellar processes.

[225] ***Lobocneme***. *Paroxyopsis* Rehn, 1911 has been recently synonymized with *Lobocneme* (Ippolito & Lombardo 2015).

[226] **Pseudoxyopsidini n. trib. and Vatini**. Vatini have been recently revised by Svenson et al. (2016a), treated

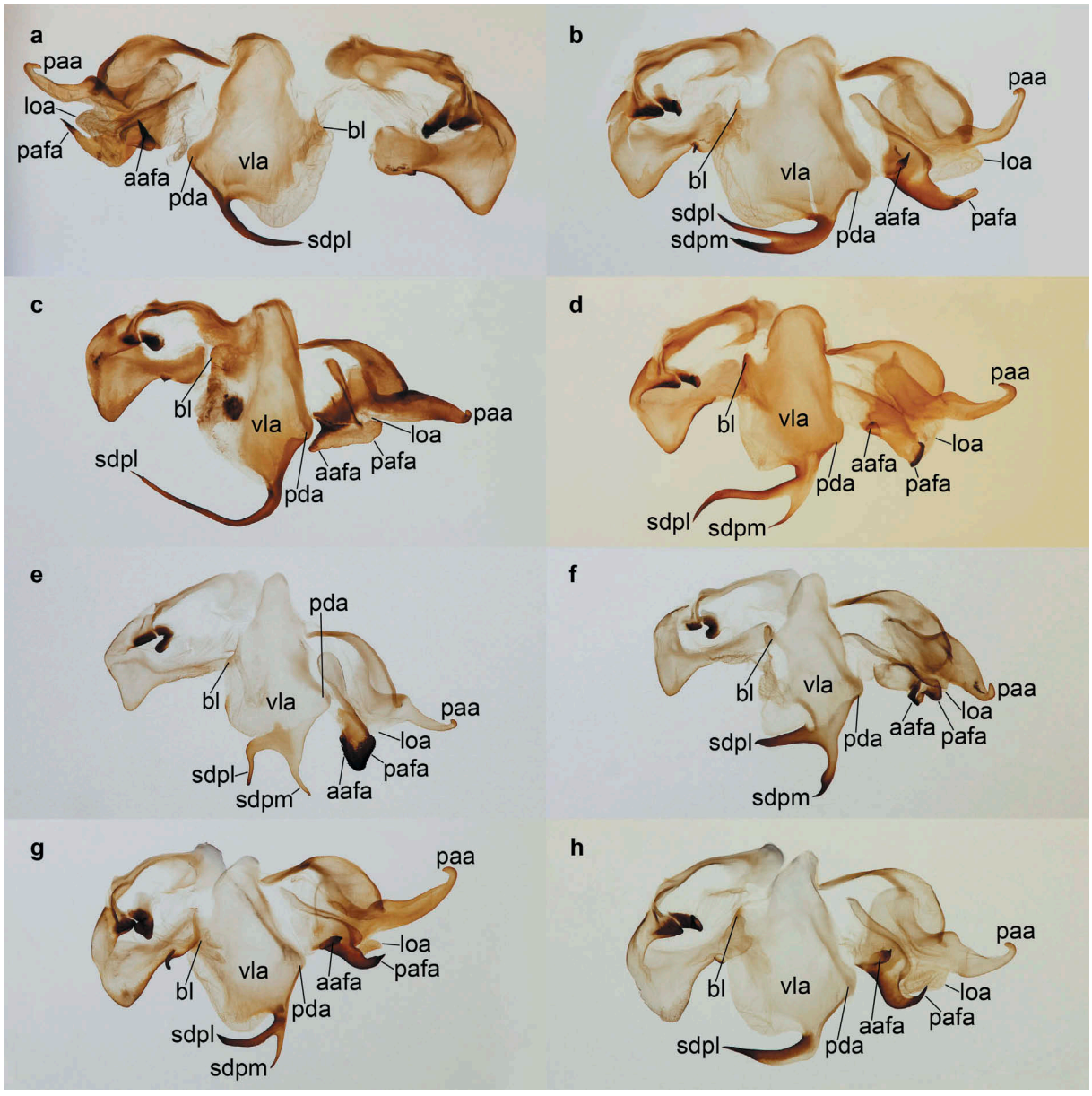

Figure 23. Genitalia of Mantidae, **a,** dorsal view, all others ventral view. **a**, *Rhombodera valida* Burmeister, 1838, from the Malay Peninsula (CS, prep. Schwarz No. 175); **b**, *Rhombodera* cf. *megaera* Rehn, 1903, from S Thailand (CS, prep. Schwarz No. 238); **c**, *Pnigomantis medioconstricta* (Westwood, 1889), from Flores (CS, prep. Schwarz No. 251); **d**, *Tamolanica tamolana* (Brancsik, 1897), from Papua New Guinea (CS, prep. Schwarz No. 183); **e**, *Camelomantis* cf. *penangica* Giglio-Tos, 1917, from Sarawak, Borneo (CS, prep. Schwarz No. 222); **f**, *Hierodula gracilicollis* Stål, 1877, from Brunei, Borneo (CS, prep. Schwarz No. 101); **g**, *Hierodula* cf. *venosa* (Olivier, 1792) from Sabah, Borneo (CS, prep. Schwarz No. 134); *H. venosa* was described from "Tranquebar" (= Tharangambadi) in India, it remains to be proven if this widespread SE Asian species, ascribed by Giglio-Tos to *venosa*, really belongs to this taxon; **h**, *Hierodula vitrea* (Stoll, 1813), from Sarawak, Borneo (CS, prep. Schwarz No. 120). Not to scale.

there as subfamily. We largely follow their arrangement, with two exceptions: first, in their total evidence tree (Svenson et al. 2016a, figure 3), *Chopardiella* is united with *Heterovates* by Svenson et al. (2016a) only on the base of plesiomorphic characters (lack of ocellar lobes and of a projection on the frontal shield), which are also shared with Oxyopsidini. While we agree with placing *Heterovates* into its own subtribe (the change of rank used here better reflects phylogenetic relationships), we follow the morphological analysis in Svenson et al. (2016a, figure 2) in placing *Chopardiella* (and related genera not sampled by Svenson et al. 2016a, see Agudelo & Rivera 2015) as sister to Vatini rather than to *Heterovates*, because of lack of clear apomorphies

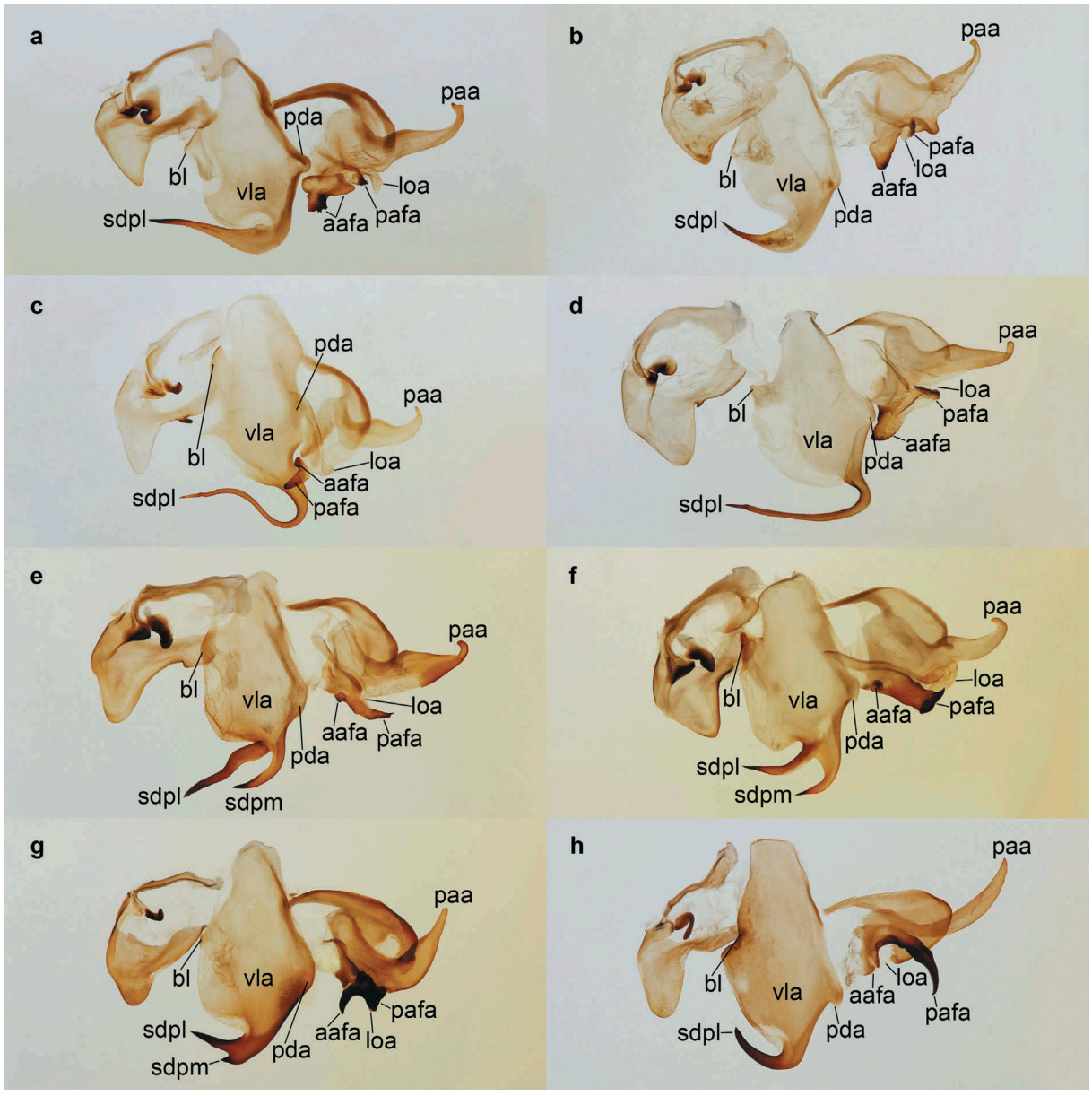

Figure 24. Genitalia of Mantidae, ventral view. **a**, *Hierodula dyaka* Westwood, 1889, from Brunei, Borneo (CS, prep. Schwarz No. 102); **b**, *Hierodula malaya* Stål, 1877, from Sabah, Borneo (CS, prep. Schwarz No. 92); **c**, *Hierodula membranacea* Burmeister, 1838, from W India (CS, prep. Schwarz No. 21); **d**, *Hierodula patellifera* Giglio-Tos, 1912, from Panay, Philippines (CS, prep. Schwarz No. 77); **e**, *Hierodula fuscescens* (Blanchard, 1853), from Ceram, Indonesia (CS, prep. Schwarz No. 132); **f**, *Hierodula majuscula* (Tindale, 1923), from NE Australia (CS, prep. Schwarz No. 164); **g**, *Sphodropoda quinquedens* (Macleay, 1826), from Queensland, Australia (CS, prep. Schwarz No. 128); **h**, *Archimantis gracilis* Milledge, 1997, from N Australia (CS, prep. Schwarz No. 184). Not to scale.

uniting the two genera concerned. In contrast, several external and genital morphological characters are shared by *Chopardiella* and other Pseudoxyopsidini with Oxyopsidini and Stagmatopterini (Figure 25f–j). They are interpreted here to be plesiomorphies with respect to Vatini. The lack of ocellar processes is an ancient plesiomorphic trait of Mantidae. The subapical posteroventral lobes on the walking legs are shared with oxyopsidinine genera like *Lobocneme*. On the other hand, the strongly enlarged but not abruptly tapering costal field of the tegmina of the female (at least as wide as remaining parts of tegmen) is not seen in any Vatini genus, and also differs from Oxyopsidini which have narrower costal fields. This character is regarded here as an autapomorphy of Pseudoxyopsidini (convergently evolved in Antemnini).

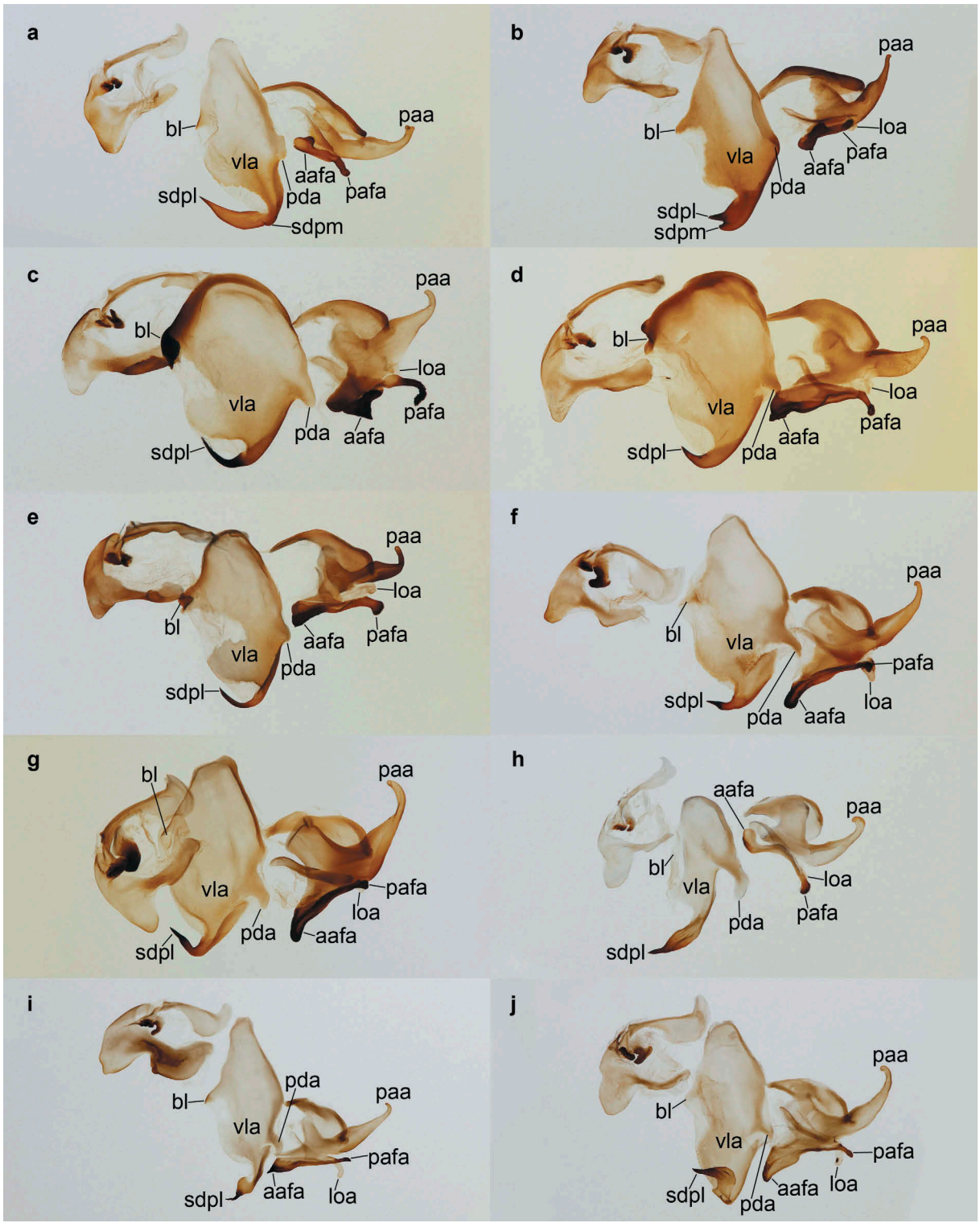

Figure 25. Genitalia of Mantidae, ventral view. **a**, *Antemna rapax* Stål, 1877, from C Panama (CS, prep. Schwarz No. 108); **b**, *Stagmomantis* (*Isomantis*) *domingensis* (Palisot de Beauvois, 1805), from the Dominican Republic (CS, prep. Schwarz No. 198); **c**, *Stagmomantis* sp., from C Panama (CS, prep. Schwarz No. 146); **d**, *Tauromantis championi* (Saussure & Zehntner, 1894), from C Costa Rica (SMNK 07135, prep. Schwarz No. 135); **e**, *Phasmomantis sumichrasti* (Saussure, 1861), from Yucatan, Mexico (SMNK 07138, prep. Schwarz No. 141); **f**, *Stagmatoptera hyaloptera* (Perty, 1832), from Uruguay (CS, prep. Schwarz No. 267); **g**, *Stagmatoptera septentrionalis* Saussure & Zehntner, 1894, from C Panama (CS, prep. Schwarz No. 145); **h**, *Parastagmatoptera immaculata* Chopard, 1911, from French Guyana (CS, prep. Schwarz No. 148); **i**, *Oxyopsis media* (Stål, 1877), from Paraguay (CS, prep. Schwarz No. 273); **j**, *Chopardiella latipennis* (Chopard, 1911), from French Guyana (CS, prep. Schwarz No. 231). Not to scale.

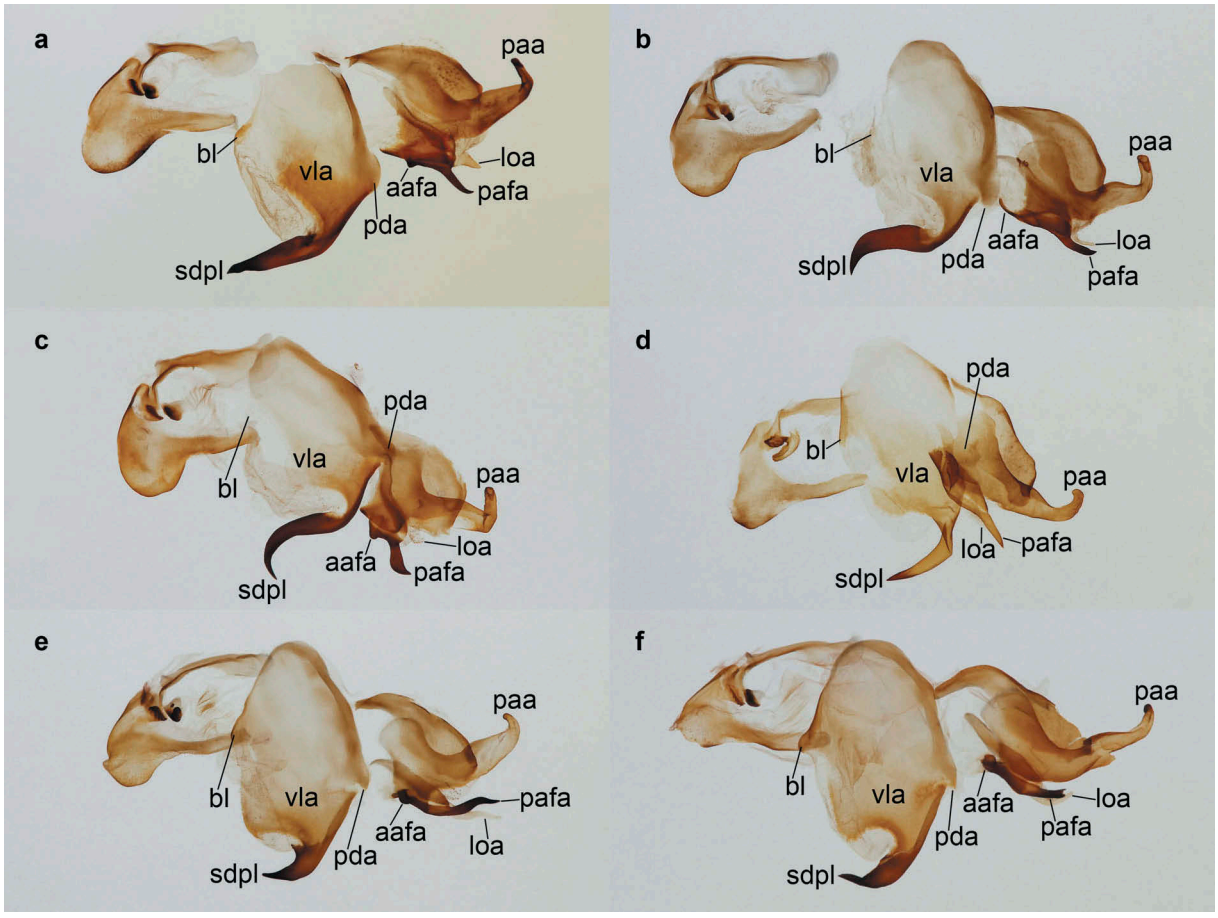

Figure 26. Genitalia of Mantidae, ventral view. **a**, *Pseudovates* (*Phyllovates*) sp., from French Guyana (CS, prep. Schwarz No. 118), ventral phallomere slightly damaged anteriorly; **b**, *Pseudovates* (*Phyllovates*) *chlorophaea* (Blanchard, 1836), from Texas, USA (CS, prep. Schwarz No. 221); **c**, *Pseudovates* (*Pseudovates*) *arizonae* Hebard, 1935, from Arizona, USA (CS, prep. Schwarz No. 246); **d**, *Zoolea major* Giglio-Tos, 1914, from Paraguay (CS, prep. Schwarz No. 8); **e**, *Vates pectinata* Saussure, 1871, from Mexico (CS, prep. Schwarz No. 247); **f**, *Vates lobata* (Fabricius, 1798), slightly damaged specimen from French Guyana (CS, prep. Schwarz No. 215). Not to scale.

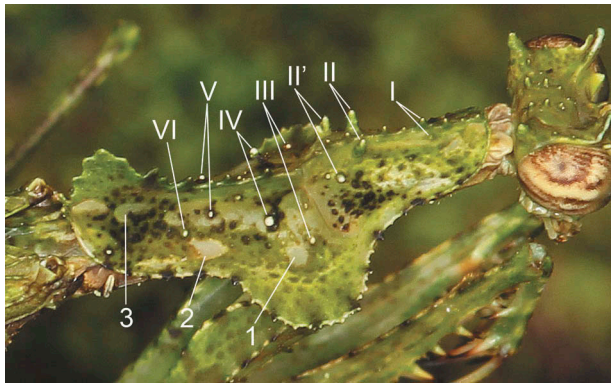

Figure 27. Pronotum of *Haania* sp., showing full set of pronotal tubercles (Roman numbers) and markings (Arabic numbers) of Metamantodea. Some additional tubercle pairs are typical for *Haania* and not part of the homologized set.

The yellow color pattern accompanying the veinules on the alae is also a plesiomorphic trait, exhibited by many Stagmomantini, Stagmatopterini, Oxyopsidini, and Pseudoxyopsidini. It is also found in *Heterovates* but not in other Vatini, thus confirming the "basal" position of *Heterovates* among Vatini.

Secondly, due to morphological data (see also Svenson et al. 2016a, figure 2), we regard *Callivates* as sister group of *Alangularis* + (*Vates* + *Zoolea*) rather than vice versa (Svenson et al. 2016a, figure 3). This is evidenced by an overall less specialized morphology, e.g. short ocellar processes, smaller lobes on mid and hind tibiae, the conspicuous black patterns on the female tegmen (shared with *Heterovates* and *Pseudovates*), and the peculiar shape of the subgenital plate (Roy 2003b). The latter is a trait shared with some

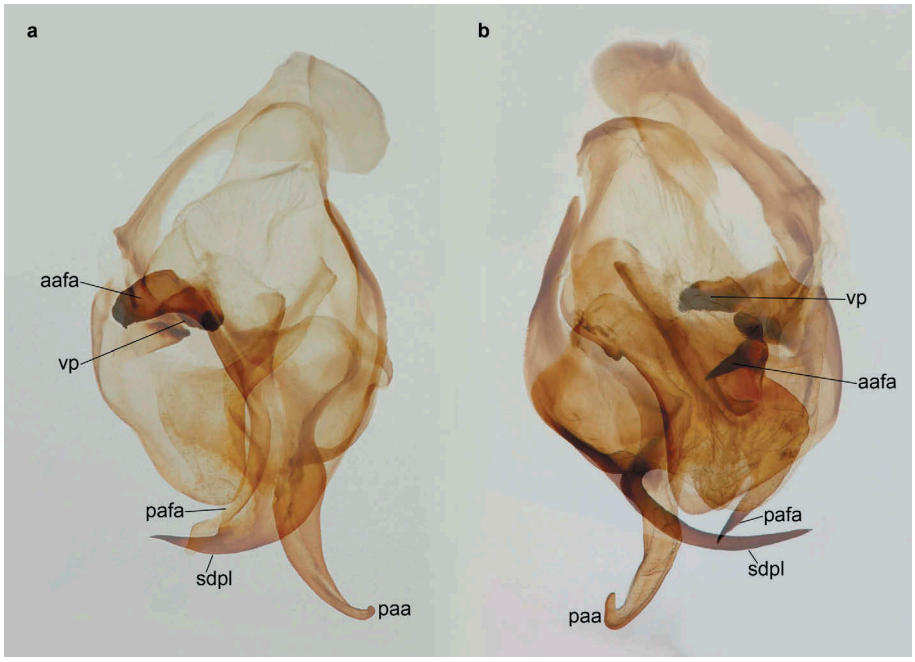

Figure 28. Genitalia of Mantidae in natural position, showing position of **aafa** relative to ventral process (**vp**) of right phallomere. **a**, *Sphodromantis* cf. *viridis*, ventral view; **b**, *Rhombodera valida*, dorsal view; upper layers semi-transparent for better visualization. Note opposing directions of **paa** and **sdpl**, and position of **pafa** relative to **sdpl.**

Pseudovates species (pers. obs.). The tegminal pattern is lost in the more derived genera *Alangularis, Vates* and *Zoolea*, which, on the other hand, have developed more elaborate lobes on legs and abdomen (see Svenson et al. 2016a for details).

[227] **Heterovatina**. Distinguished from Vatina by the lack of ocellar processes, the presence of two tubercles on the metazona just behind supracoxal sulcus, and tessellated alae.

[228] **Vatina**. Synapomorphy: presence (vs. *lack of*) two processes between the upper ocelli. The distinct tessellation is lost in this group, but the alae can nevertheless be infumate or partly yellowish.

[229] ***Pseudovates***. *Phyllovates* Kirby, 1905 and *Hagiotata* Saussure & Zehntner, 1894 have been dropped into synonymy of *Pseudovates* by Svenson et al. (2016a).

The main phylogenetic points may be summarized as follows:

(1) The distal process of Chaeteessidae and Mantoididae (**pda**) is not homologous to the similarly named structure (e.g. Klass 1997) of Schizomantodea.
(2) In Schizomantodea, a secondary distal process (**sdp**) is developed at the distal tip of the widened right lobe of the ventral phallomere (**vla**), while **pda** moves to the left.
(3) In *Metallyticus*, both **pda** and **sdp** are present, while in Artimantodea **pda** is reduced to a rounded lobe.
(4) In Artimantodea, a basal lobe (**bl**) develops on the right side of the ventral phallomere.
(5) In Cernomantodea, a second, lateral distal process (**sdpl**) develops alongside a median one (**sdpm**).
(6) In Cernomantodea, straight distal processes usually derive from **sdpm**, while curved hook-like processes originate through an emargination of the phallomere just proximad of **sdpl**.
(7) A bilobed phalloid apophysis (**afa**) is present in certain *Mantoida* species and may be synapomorphic for Spinomantodea.
(8) The schizomantodean phalloid apophysis (**afa**) is long, curved and with acute apex. It changes shape frequently in Artimantodea. A bifurcation is (re-)developed in certain Photinaidae, Acanthopidae and in Cernomantodea. In the latter two groups, secondary fusions of the lobes or reductions of the anterior lobe are common (Figure 29).
(9) The bilobed phalloid apophysis, as well as the dentition on the phallomeres in Chroicopteridae, correlate with a high degree of sexual dimorphism in the artimantodean clades exhibiting

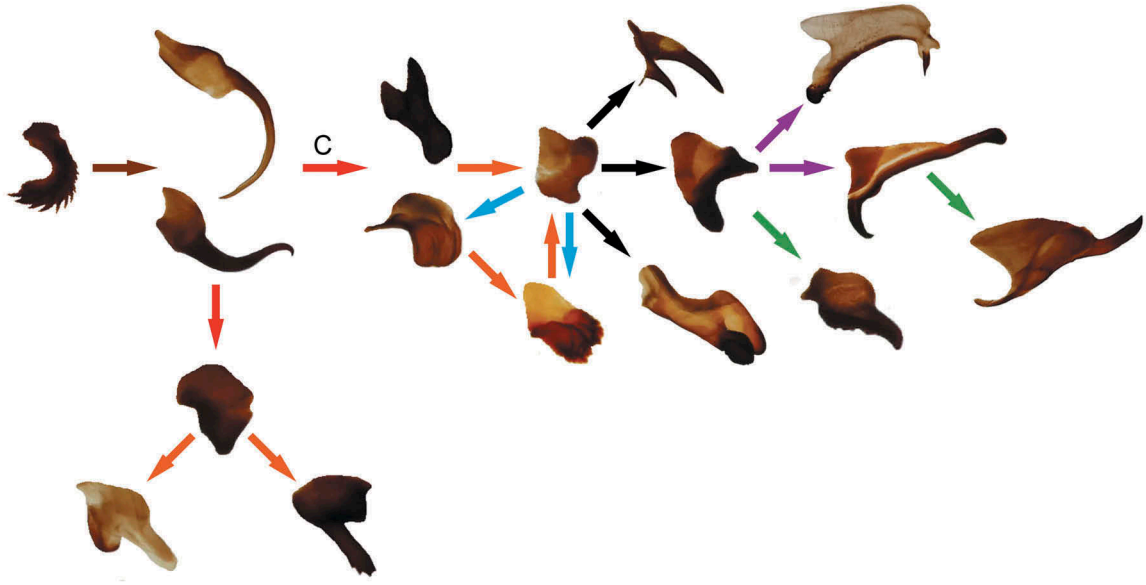

Figure 29. Schematic evolution of the mantodean phalloid apophysis. Color codes: **brown** = loss of spines, elongation; **red** = transition from long and slender to short and broad; **orange** = bifurcation; **blue** = loss of bifurcation; **black** = elongation of **aafa** and **pafa; purple** = spacing apart of **aafa** and **pafa; green** = reduction of **aafa**. C = Cernomantodea. Not to scale.

them, and are hypothesized to provide a mechanically stable grasp of the female valves, assuring sperm transfer in case the male is partially cannibalized.

(10) Most Mantodea are X0. The X_1X_2Y sex chromosome system has developed at least four times in Mantodea, the most common type (including two subtypes) is an autapomorphy of Mantidae. XY is found in *Ima*.

Diagnoses of families

Family Chaeteessidae Handlirsch, 1925

Type genus. *Chaeteessa* Burmeister, 1838

Diagnosis. Chaeteessids can be distinguished from all other mantodeans by the following combination of characters: pronotum sub-quadrate; foretibia curved posteriad; foreleg spines irregular in size; apical lobes of forefemur with long spine; two discoidal spines; claw-groove at base; walking legs with spines; tegmen with pseudovein; cyclopean ear missing; cerci longer than half of abdomen length; ventral phallomere sclerotized along left margin; pda membraneous; pda and paa fused; phalloid apophysis missing; right phallomere folded along right margin, with large serrate ventral process.

Phylogenetic definition. Currently monotypic, but with fossil representatives (see Otte & Spearman 2005); would include any newly discovered species more closely related to *Chaeteessa filata* Burmeister, 1838 than to any other species.

Remarks. The reduced tibial claw of *Chaeteessa* is not typical for the family and represents a secondary reduction.

Family Mantoididae Giglio-Tos, 1919

Type genus. *Mantoida* Newman, 1838.

Diagnosis. Mantoidids can be distinguished from all other mantodeans by the following combination of characters: pronotum sub-quadrate; foretibia straight; foreleg spines short; apical lobes of forefemur without spines; three discoidal spines; claw-groove at base; walking legs without spines; tegmen with pseudovein; cyclopean ear missing; cerci shorter than half of abdomen length; ventral phallomere sclerotized along left margin; pda sclerotized; pda and paa fused; phalloid apophysis present, simple, with spiny apex; right phallomere folded along right margin.

Phylogenetic definition. Includes the MRCA of *Mantoida* and *Paramantoida*, and all descendants thereof, and all species more closely related to *Mantoida nitida* Newman, 1838 than to *Chaeteessa filata, Metallyticus splendidus*

Westwood, 1835, *Thespis parva* Drury, 1773, *Photina brevis* Rehn, 1907, and Cernomantodea.

Remarks. The phalloid apophysis of this group has been incorrectly homologized by Klass (1997).

Family Metallyticidae Giglio-Tos, 1917

Type genus. *Metallyticus* Westwood, 1835.

Diagnosis. Metallyticids can be distinguished from all other mantodeans by the following combination of characters: metallic coloration; pronotum rectangular, slightly longer than wide; foretibia straight; foretibial spines increasing in length distally; apical lobes of forefemur without spines; proximal posteroventral spine of forefemur elongate; discoidal spines reduced to one, found in a row with anteroventral spines in adults (Wieland 2013); claw-groove at base; walking legs without spines; tegmen with pseudovein; cyclopean ear missing; cerci shorter than half of abdomen length; phallomeres fully sclerotized; processes of left complex separated; pda translocated to left side of ventral phallomere; short sdp on vla; phalloid apophysis long, acute and curved.

Phylogenetic definition. Currently monotypic; would include any newly discovered species more closely related to *Metallyticus splendidus* Westwood, 1835 than to *Chaeteessa filata, Mantoida nitida, Thespis parva, Photina brevis*, and Cernomantodea.

Family Thespidae Saussure, 1869

Type genus. *Thespis* Audinet-Serville, 1831.

Diagnosis. Thespids can be distinguished from all other mantodeans by the following combination of characters: pronotum rhomboidal or elongate; supracoxal dilatation well marked; dorsal apical lobe of forecoxa elongate; foretibia straight; apical lobes of forefemur without spines; three to four discoidal spines; elongate forefemur (claw-groove moved distally); walking legs without spines; wings of male pilose, tegmen with elongate stigma; females apterous; cyclopean ear missing; supra-anal plate triangular; cerci shorter than half of abdomen length; phallomeres fully sclerotized; processes of left complex separated; pda translocated to left side of ventral phallomere; sdp on vla; dorsal lamina of left phallomere with a rounded lobe.

Phylogenetic definition. Includes the MRCA of Pseudopogonogastrinae, Pseudomiopteryginae, Bantiinae, Miobantiinae, Musoniellinae, and Thespinae, and all descendants thereof, and all species more closely related to *Thespis parva* than to *Chaeteessa filata, Mantoida nitida, Metallyticus splendidus, Photina brevis*, and Cernomantodea.

Family Angelidae Beier, 1935

Type genus. *Angela* Audinet-Serville, 1839.

Diagnosis. Angelids can be distinguished from all other mantodeans by the following combination of characters: body, including pronotum, strongly elongate; supracoxal dilatation well marked; dorsal apical lobe of forecoxa not elongate; foretibia straight, with 5–6 posteroventral spines; apical lobes of forefemur with spines; four discoidal spines, with third spine the longest and the first longer than the second; claw-groove in apical half of femur; walking legs without spines; tegmen with elongate stigma; females brachypterous; alae colored in both sexes; cyclopean ear missing; supra-anal plate triangular; cerci shorter than half of abdomen length, flattened; phallomeres fully sclerotized; processes of left complex separated; ventral phallomere with a basal lobe on right side; pda translocated to left side of ventral phallomere, reduced; sdp mostly reduced; dorsal lamina of left phallomere without a rounded lobe; phalloid apophysis short and rounded.

Phylogenetic definition. Currently monotypic; would include any newly discovered species more closely related to *Angela quinquemaculata* (Olivier, 1792) than to *Chaeteessa filata, Mantoida nitida, Metallyticus splendidus, Thespis parva, Photina brevis*, and Cernomantodea.

Family Coptopterygidae Giglio-Tos, 1915

Type genus. *Coptopteryx* Saussure, 1869.

Diagnosis. Coptopterygids can be distinguished from all other mantodeans by the following combination of characters: supracoxal dilatation well marked; three discoidal spines; forefemora with 5 posteroventral spines; walking legs without spines; tegmen with elongate stigma; alae of female missing; cyclopean ear missing; supra-anal plate triangular; cerci shorter than half of abdomen length, not flattened; phallomeres fully sclerotized; processes of left complex separated; ventral phallomere with a basal lobe on right side; pda translocated to left side of ventral phallomere, reduced; sdp present, pointing to the right; phalloid apophysis with an anterior lobe; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of *Coptopteryx* and *Brunneria* and all descendants thereof, and all species more closely related to *Coptopteryx argentina* (Burmeister, 1864) than to *Chaeteessa filata,*

Mantoida nitida, Metallyticus splendidus, Thespis parva, Angela quinquemaculata, Liturgusa annulipes (Audinet-Serville, 1839), *Photina brevis, Acanthops fuscifolia* (Olivier, 1792), and Cernomantodea.

Family Liturgusidae Giglio-Tos, 1915

Type genus. *Liturgusa* Saussure, 1869.

Diagnosis. Liturgusids can be distinguished from all other mantodeans by the following combination of characters: body dorsoventrally flattened, adapted to bark-living lifestyle; supracoxal dilatation well marked; apical lobes of forefemur with long spines; four discoidal spines, the first never longer than the second; forefemora with 4 posteroventral spines, and with a row of smaller spine-like tubercles medioventrad of posteroventral spines; walking legs without spines; tegmen with elongate stigma; cyclopean ear missing; supra-anal plate triangular; cerci shorter than half of abdomen length, not flattened; phallomeres fully sclerotized, but simplified; processes of left complex separated; ventral phallomere with a basal lobe on right side; pda translocated to left side of ventral phallomere, reduced; sdp small and triangular or missing; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of Liturgusini and Hagiomantini, and all descendants thereof, and all species more closely related to *Liturgusa annulipes* than to *Chaeteessa filata, Mantoida nitida, Metallyticus splendidus, Thespis parva, Angela quinquemaculata, Coptopteryx argentina, Photina brevis, Acanthops fuscifolia*, and Cernomantodea.

Family Photinaidae Giglio-Tos, 1915

Type genus. *Photina*; Burmeister, 1838.

Diagnosis. Photinaids can be distinguished from all other mantodeans by the following combination of characters: supracoxal dilatation well marked; dorsal apical lobe of forecoxa slightly elongate; foretibia straight, with numerous posteroventral spines (about as much as or more than anteroventral spines); apical lobes of forefemur with short spines; three to four discoidal spines, when four, then the first never longer than the second; forefemora with 5 posteroventral spines; walking legs without spines; tegmen with elongate stigma; cyclopean ear missing; supra-anal plate triangular; cerci shorter than half of abdomen length; phallomeres fully sclerotized; processes of left complex separated; ventral phallomere with a basal lobe on right side; pda translocated to left side of ventral phallomere, reduced; sdp usually present; phalloid apophysis with an anterior lobe; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. includes the MRCA of Macromantinae, Photiomantinae, Cardiopterinae, and Photinainae, and all descendants thereof, and all species more closely related to *Photina brevis* than to *Chaeteessa filata, Mantoida nitida, Metallyticus splendidus, Thespis parva, Angela quinquemaculata, Coptopteryx argentina, Liturgusa annulipes, Acanthops fuscifolia*, and Cernomantodea.

Family Acanthopidae Burmeister, 1838

Type genus. *Acanthops* Audinet-Serville, 1831.

Diagnosis. Acanthopids can be distinguished from all other mantodeans by the following combination of characters: body dead-leaf-like or very colorful; supracoxal dilatation well marked; foretibia straight, with numerous posteroventral spines (about as much as or more than anteroventral spines); posteroventral spines more or less decumbent; apical lobes of forefemur with short spines; three to four discoidal spines, when four, then the first never longer than the second; forefemora with at least 5 posteroventral spines; walking legs without spines; tegmen with elongate stigma; cyclopean ear missing; supra-anal plate triangular; cerci shorter than half of abdomen length. Last segment sometimes enlarged and incised; phallomeres fully sclerotized; processes of left complex separated; ventral phallomere with an elongate and usually acute basal lobe on right side; pda translocated to left side of ventral phallomere, reduced; sdp present; phalloid apophysis with an anterior lobe; membranous lobe strongly developed, more or less pilose; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of Acanthopinae and Stenophyllinae, and all descendants thereof, and all species more closely related to *Acanthops fuscifolia* than to *Chaeteessa filata, Mantoida nitida, Metallyticus splendidus, Thespis parva, Angela quinquemaculata, Coptopteryx argentina, Liturgusa annulipes, Photina brevis*, and Cernomantodea.

Family Chroicopteridae Giglio-Tos, 1915

Type genus. *Chroicoptera* Stål, 1871.

Diagnosis. Chroicopterids can be distinguished from all other mantodeans by the following combination of characters: small to medium-sized, usually brownish,

rarely green; supracoxal dilatation well marked; apical lobes of forefemur with short spines; three to four discoidal spines, when three, then the first longer than the second and all forefemoral spines very small, or phalloid apophysis with a bi- to multicuspidate flagellum; forefemora with 4–5 posteroventral spines, when with five then head with a foliaceous process; walking legs without lobes and without spines; females more or less brachypterous or apterous, when apterous then ant-like; cyclopean ear present; cerci shorter than half of abdomen length, cylindrical; females often with digging devices at abdominal end; phallomeres fully sclerotized, sometimes chirally mirrored; processes of left complex separated; ventral phallomere with a well-developed and usually sclerotized basal lobe on right side; pda translocated to left side of ventral phallomere, reduced; sdpm and sdpl present; apical portion of ventral phallomere and dorsal lamina of left phallomere covered in spinules, if not with spinules then females apterous and apical process T-shaped or sdpm and sdpl developed into strong spines; dorsal lamina without rounded lobe; phalloid apophysis with an anterior lobe and usually with a flagellum.

Phylogenetic definition. Includes the MRCA of Tarachininae and Chroicopterinae, and all descendants thereof, and all species more closely related to *Chroicoptera vidua* (Stål, 1856) than to *Chaeteessa filata, Mantoida nitida, Metallyticus splendidus, Nanomantis australis* Saussure, 1871, *Gonypeta punctata* (De Haan, 1842), *Majanga basilaris* (Westwood, 1889), *Epaphrodita musarum* (Palisot de Beauvois, 1805), *Haania lobiceps* (De Haan, 1842), *Mantis religiosa* Linneaus, 1758, and Amerimantodea.

Remarks. The genitalia of this family are very diverse, actually the most diverse observed in any mantodean family. This is in concordance with its putative old age and a phylogenetic position at the base of Cernomantodea. Nevertheless, both external and genital morphology can be derived from a hypothetical MRCA, and justify the systematic arrangement proposed here.

Family Leptomantellidae n. fam.

Type genus. *Leptomantella* Uvarov, 1940.

Diagnosis. Leptomantellids can be distinguished from all other mantodeans by the following combination of characters: small and always greenish; head without process; juxta-ocular bulges distinct, rounded; supracoxal dilatation well marked; apical lobes of forefemur with rather long spines; all foreleg spines very elongate; four discoidal spines; forefemora with 4 posteroventral spines; posteroventral spines of foretibiae inequal in length; walking legs without lobes but sometimes with spinules; both sexes macropterous, wings mostly hyaline or subhyaline; cyclopean ear present; cerci shorter than half of abdomen length, cylindrical; phallomeres weakly sclerotized, simplified; processes of left complex separated; ventral phallomere without basal lobe on right side; pda translocated to left side of ventral phallomere, reduced; sdpm usually present, sdpl mostly reduced; phalloid apophysis not bifurcate, simple; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of *Leptomantella, Aetaella, Hebardiella*, and *Hebardia*, and all descendants thereof; would include any newly discovered species more closely related to *Leptomantella albella* (Burmeister, 1838) than to *Chaeteessa filata, Mantoida nitida, Metallyticus splendidus, Chroicoptera vidua, Amorphoscelis annulicornis* Stål, 1871, *Nanomantis australis, Gonypeta punctata, Majanga basilaris, Epaphrodita musarum, Haania lobiceps, Mantis religiosa*, and Amerimantodea.

Family Amorphoscelidae Stål, 1877

Type genus. *Amorphoscelis* Stål, 1871.

Diagnosis. Amorphoscelids can be distinguished from all other mantodeans by the following combination of characters: small, dorsoventrally flattened, adapted to a bark-living lifestyle; head without process; juxta-ocular bulges very prominent; supracoxal dilatation indistinct, pronotum short, trapezoid; apical lobes of forefemur without spines; one discoidal spine; forefemora without posteroventral spines and with 0–4 anteroventral spines; spines on foretibiae completely reduced; walking legs without lobes and without spines; both sexes macropterous; cyclopean ear present; cerci shorter than half of abdomen length, cylindrical, sometimes with enlarged and flattened last cercomere; phallomeres moderately sclerotized; processes of left complex separated; ventral phallomere with basal lobe on right side, this lobe translocated to distal right margin of phallomere; pda translocated to left side of ventral phallomere; sdpm always present, sdpl sometimes reduced, both processes juxtaposed at left side of phallomere; anterior lobe of phalloid apophysis usually present, but indistinct; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of Perlamantinae and Amorphoscelinae, and all descendants thereof, and all species more closely related to *Amorphoscelis annulicornis* than to *Chaeteessa filata, Mantoida nitida, Metallyticus splendidus, Chroicoptera*

vidua, Leptomantella albella, Nanomantis australis, Gonypeta punctata, Majanga basilaris, Epaphrodita musarum, Haania lobiceps, Mantis religiosa, and Amerimantodea.

Family Nanomantidae Brunner de Wattenwyl, 1893

Type genus. *Nanomantis* Saussure, 1871.

Diagnosis. Nanomantids can be distinguished from all other mantodeans by the following combination of characters: small, greenish or brownish; vertex without process; juxta-ocular bulges distinct, often protruding; supracoxal dilatation moderately to well marked; metazona often with a keel; apical lobes of forefemur with rather long spines; forefemora with 2–3 discoidal and 4 posteroventral spines (rarely with 4 discoidal spines, and then in combination with 5 posteroventral spines, keeled metazona, and very wide costal field); walking legs without lobes and without spines; males macropterous, females macropterous to apterous; cyclopean ear present; cerci shorter than half of abdomen length, cylindrical or with flattened last cercomere; phallomeres weakly sclerotized, usually simplified, rarely elaborate, chirally mirrored in some taxa; processes of left complex separated; ventral phallomere with or without basal lobe on right side; pda translocated to left side of ventral phallomere; sdpm and sdpl usually present, rarely one or both reduced; phalloid apophysis bifid or with anterior lobe reduced; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of Hapalomantinae, Tropidomantinae, Nanomantinae, and Fulciniinae, and all descendants thereof, and all species more closely related to *Nanomantis australis* than to *Chaeteessa filata, Mantoida nitida, Metallyticus splendidus, Chroicoptera vidua, Leptomantella albella, Amorphoscelis annulicornis, Gonypeta punctata, Majanga basilaris, Epaphrodita musarum, Haania lobiceps, Mantis religiosa*, and Amerimantodea.

Family Gonypetidae Westwood, 1889

Type genus. *Gonypeta* Saussure, 1869.

Diagnosis. Gonypetids can be distinguished from all other mantodeans by the following combination of characters: small, greenish or brownish; vertex without process but sometimes with tubercles; juxta-ocular bulges distinct, often protruding; supracoxal dilatation moderately to well marked, but a slim foliaceous expansion may be present along pronotal margin obscuring the dilatation; pronotum often more or less tuberculate; metazona about two times as long as prozona; apical lobes of forefemur with a spine; forefemora with 3–4 discoidal and 4 posteroventral spines, and with distinct crenulation medioventrad posteroventral spines; walking legs without lobes and without spines; macropterous to apterous; anterior margin of tegmen distinctly ciliate; cyclopean ear present; cerci shorter than half of abdomen length, cylindrical; phallomeres well sclerotized, moderately to strongly pigmented but rather simplified; processes of left complex separated; ventral phallomere with or without basal lobe on right side; pda translocated to left side of ventral phallomere; sdpl present or reduced, short; sdpm usually missing, may be still present as a rounded lobe at base of sdpl; phalloid apophysis simple or slightly, rarely distinctly, bifurcate; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of Iridopteryginae and Gonypetinae, and all descendants thereof, and all species more closely related to *Gonypeta punctata* than to *Chaeteessa filata, Mantoida nitida, Metallyticus splendidus, Chroicoptera vidua, Leptomantella albella, Amorphoscelis annulicornis, Nanomantis australis, Majanga basilaris, Epaphrodita musarum, Haania lobiceps, Mantis religiosa*, and Amerimantodea.

Family Majangidae Giglio-Tos, 1915

Type genus. *Majanga* Wood-Mason, 1891.

Diagnosis. Majangids can be distinguished from all other mantodeans by the following combination of characters: coloration brownish, external morphology resembling dead plant matter or adapted to bark-living lifestyle; vertex without process; eyes rounded, then juxta-ocular bulges large to conical and two ocellar spines occasionally present, or conical, then pronotum with foliaceous expansion; supracoxal dilatation well marked, but may be obscured by foliaceous expansion; metazona at least 2 times as long as prozona; apical lobes of forefemur with a spine; forefemora with one or more dorsal lobes, with 4 discoidal and 4–5 posteroventral spines, and with distinct crenulation medioventrad posteroventral spines; claw-groove at proximal half of femur; posteroventral spines of foretibiae slightly decumbent; walking legs with lobes; if not with lobes then body very slender, walking legs very long, juxta-ocular bulges rounded, and ventral phallomere without basal lobe and without processes; males macropterous, females mesopterous, hind wings colored at least in females, with anterior part usually yellowish to brownish and with traces of an apical eye-spot, and posterior part smoky with light veins; hind wings

projecting beyond tegmina; cyclopean ear present; supra-anal plate trapezoid to triangular, with a keel that may be produced into a lobe; cerci shorter than half of abdomen length, cylindrical or slightly flattened; phallomeres sclerotized; processes of left complex separated; ventral phallomere usually with a small basal lobe on right side; pda translocated to left side of ventral phallomere; if sdpl and sdpm present, then short, with rounded or truncate apex; phalloid apophysis simple to slightly bifurcate; membraneous lobe not pilose; apical process without subapical lobe; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of Brancsikiinae and Majanginae, and all descendants thereof, and all species more closely related to *Majanga basilaris* than to *Chaeteessa filata, Mantoida nitida, Metallyticus splendidus, Gonypeta punctata, Epaphrodita musarum, Haania lobiceps, Eremiaphila audouini* Lefèbvre, 1835, *Hoplocorypha macra* Stål, 1856, *Mantis religiosa*, Amerimantodea, and Nanomantodea.

Family Epaphroditidae Brunner de Wattenwyl, 1893

Type genus. *Epaphrodita* Audinet-Serville, 1831.

Diagnosis. Epaphroditids can be distinguished from all other mantodeans by the following combination of characters: vertex with or without a short process; eyes rounded to slightly conical; juxta-ocular bulges indistinct to protruding; pronotum more or less tuberculate, supracoxal dilatation moderately to well marked; metazona at least 2 times as long as prozona; apical lobes of forefemur with a very short spine; forefemora with a dorsal lobe in the proximal half, with 4 discoidal and 4 posteroventral spines, and with distinct crenulation medioventrad posteroventral spines; claw-groove at proximal half of femur; walking leg femora with or without ventral lobes; males macropterous, females mesopterous; hind wings colored at least in females, with anterior part usually yellowish to brownish and with traces of an eye-spot at apex, and posterior part smoky with light veins; hind wings projecting beyond tegmina; cyclopean ear present; supra-anal plate triangular, with a keel that may be produced into a lobe; cerci shorter than half of abdomen length, cylindrical; phallomeres sclerotized; processes of left complex separated; ventral phallomere without basal lobe on right side; pda translocated to left side of ventral phallomere; sdpl may be present but small, tuberculate, sdpm missing; phalloid apophysis slightly bifurcate, more or less tuberculate; membraneous lobe not pilose; apical process without subapical lobe; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of Gonatistinae and Epaphroditinae, and all descendants thereof, and all species more closely related to *Epaphrodita musarum* than to *Chaeteessa filata, Mantoida nitida, Metallyticus splendidus, Gonypeta punctata, Majanga basilaris, Haania lobiceps, Eremiaphila audouini, Hoplocorypha macra, Mantis religiosa*, Amerimantodea, and Nanomantodea.

Family Haaniidae Westwood, 1889

Type genus. *Haania* Saussure, 1871.

Diagnosis. Haaniids can be distinguished from all other mantodeans by the following combination of characters: small, either greenish, then head and pronotum without tubercles, posteroventral spines of forefemur with a posterior black stripe, alae with an eye-spot, and phalloid apophysis not bifid, or brownish and more or less mottled with green and dark, then head and pronotum tuberculate and abdomen with lobes; juxta-ocular bulges distinct, protruding; supracoxal dilatation well marked; metazona about 2–3 times as long as prozona; apical lobes of forefemur with a spine; forefemora with 4 discoidal and 3–4 posteroventral spines; walking legs without lobes, occasionally with spines; males macropterous, females macropterous to apterous; cyclopean ear present; cerci shorter than half of abdomen length, cylindrical; phallomeres well sclerotized, sometimes chirally mirrored; processes of left complex separated; ventral phallomere with a very elongate basal lobe on right side, this lobe occasionally partially fused to distal part of phallomere; pda translocated to left side of ventral phallomere; either sdpl or sdpm present, rarely both; phalloid apophysis usually bifurcate; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of Caliridinae and Haaniinae, and all descendants thereof, and all species more closely related to *Haania lobiceps* than to *Chaeteessa filata, Mantoida nitida, Metallyticus splendidus, Chroicoptera vidua, Leptomantella albella, Amorphoscelis annulicornis, Nanomantis australis, Gonypeta punctata, Majanga basilaris, Epaphrodita musarum, Rivetina baetica* (Rambur, 1838), *Ameles picteti* (Saussure, 1869), *Eremiaphila audouini, Toxodera denticulata* Audinet-Serville, 1837, *Hoplocorypha macra*, *Mantis religiosa*, and Amerimantodea.

Remarks. The morphologically very different subfamilies Caliridinae and Haaniinae are united by the elongate basal lobe of the ventral phallomere.

Family Rivetinidae Ehrmann & Roy, 2002

Type genus. *Rivetina* Berland & Chopard, 1922.

Diagnosis. Rivetinids can be distinguished from all other mantodeans by the following combination of characters: medium to large, brownish; vertex without process, distinctly convex; juxta-ocular bulges indistinct; supracoxal dilatation well marked; metazona at least 2 times as long as prozona; apical lobes of forefemur with a spine; forefemora with 4 discoidal and 4–5 posteroventral spines; walking legs without lobes and without spines; males mesopterous to macropterous, females micropterous to brachypterous, rarely both sexes apterous; tegmina with enlarged, black anal field; alae smoky, with an apical eye-spot; cyclopean ear present; supra-anal plate elongate, triangular or truncate; cerci shorter than half of abdomen length, cylindrical; phallomeres well sclerotized; right phallomere ventrally with three pilosity fields, ventral ridge very elongate; processes of left complex separated; ventral phallomere without basal lobe on right side; pda translocated to left side of ventral phallomere; sdpl present, sdpm reduced to rounded lobe at base of sdpl; phalloid apophysis bifurcate, anterior lobe widely separated from posterior lobe, bird-head like and tuberculate or pilose, posterior lobe has the shape of a strong spine; membraneous lobe more or less pilose; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of Rivetininae and Deiphobinae, and all descendants thereof, and all species more closely related to *Rivetina baetica* than to *Chaeteessa filata*, *Mantoida nitida*, *Metallyticus splendidus*, *Chroicoptera vidua*, *Leptomantella albella*, *Amorphoscelis annulicornis*, *Nanomantis australis*, *Gonypeta punctata*, *Majanga basilaris*, *Epaphrodita musarum*, *Haania lobiceps*, *Ameles picteti*, *Eremiaphila audouini*, *Toxodera denticulata*, *Hoplocorypha macra*, *Mantis religiosa*, and Amerimantodea.

Family Amelidae Westwood, 1889

Type genus. *Ameles* Burmeister, 1838.

Diagnosis. Amelids can be distinguished from all other mantodeans by the following combination of characters: small, brownish; vertex without process; eyes rounded to conical; juxta-ocular bulges indistinct; supracoxal dilatation well marked; metazona at most 2 times as long as prozona; apical lobes of forefemur with a spine; forefemora with 4 discoidal and 4 posteroventral spines; walking legs without lobes and without spines, hind legs elongate; males brachypterous to macropterous, females micropterous; alae without apical eye-spot; cyclopean ear present; supra-anal plate triangular; cerci shorter than half of abdomen length, cylindrical; phallomeres well sclerotized; right phallomere ventrally with two pilosity fields, ventral ridge very elongate; processes of left complex separated; ventral phallomere without basal lobe on right side; pda translocated to left side of ventral phallomere; both sdpl and sdpm present; phalloid apophysis usually bifurcate, anterior lobe tuberculate, posterior lobe fused to membranous lobe along most of its length, only apex free in form of a small tooth; membraneous lobe more or less pilose; dorsal lamina of left phallomere without a rounded lobe, setose.

Phylogenetic definition. Includes the MRCA of Amelini and Litaneutrini, and all descendants thereof, and all species more closely related to *Ameles picteti* than to *Chaeteessa filata*, *Mantoida nitida*, *Metallyticus splendidus*, *Chroicoptera vidua*, *Leptomantella albella*, *Amorphoscelis annulicornis*, *Nanomantis australis*, *Gonypeta punctata*, *Majanga basilaris*, *Epaphrodita musarum*, *Haania lobiceps*, *Rivetina baetica*, *Eremiaphila audouini*, *Toxodera denticulata*, *Hoplocorypha macra*, *Mantis religiosa*, and Amerimantodea.

Family Eremiaphilidae Saussure, 1869

Type genus. *Eremiaphila* Lefèbvre, 1835.

Diagnosis. Eremiaphilids can be distinguished from all other mantodeans by the following combination of characters: vertex without process; eyes more or less ellipsoid; juxta-ocular bulges indistinct to slightly protruding; supracoxal dilatation indistinctly to moderately marked, pronotum often more or less rectangular; metazona at least 2 times as long as prozona; apical lobes of forefemur with a short spine; forefemora with 4 discoidal and 4–5 posteroventral spines; walking legs without lobes and without spines; males brachypterous to macropterous, females micropterous to brachypterous; alae without apical eye-spot; cyclopean ear usually present; supra-anal plate transverse to triangular; cerci shorter than half of abdomen length, cylindrical or slightly compressed laterally; phallomeres well sclerotized; right phallomere ventrally more or less pilose, apically sometimes with accessory lobes or with a strong spine, ventral ridge very elongate, often heavily serrate and with spines; processes of left complex separated; ventral phallomere without basal lobe on right side; pda translocated to left side of ventral phallomere; sdpl usually present, sdpm present at least as a lobe or tooth at base of sdpl, rarely both missing; anterior lobe of phalloid apophysis more or less reduced and membraneous, posterior lobe has the

shape of a strong spine, rarely totally missing; membraneous lobe more or less pilose; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of Parathespinae, Iridinae, Eremiaphilinae and Tarachodinae, and all descendants thereof, and all species more closely related to *Eremiaphila audouini* than to *Chaeteessa filata*, *Mantoida nitida*, *Metallyticus splendidus*, *Chroicoptera vidua*, *Leptomantella albella*, *Amorphoscelis annulicornis*, *Nanomantis australis*, *Gonypeta punctata*, *Majanga basilaris*, *Epaphrodita musarum*, *Haania lobiceps*, *Rivetina baetica*, *Ameles picteti*, *Toxodera denticulata*, *Hoplocorypha macra*, *Mantis religiosa*, and Amerimantodea.

Remarks. Morphologically very heterogeneous, but united by typical eremiaphiloid genitalia. Only the ventral and left phallomere of name-giving Eremiaphilinae are very simplified, indicating very recent and still ongoing speciation events.

Family Toxoderidae Saussure, 1869

Type genus. *Toxodera* Audinet-Serville, 1837.

Diagnosis. Toxoderids can be distinguished from all other mantodeans by the following combination of characters: body elongate, medium to large, brownish; vertex sometimes with a short process; eyes rounded to conical, mostly with a lateral tubercle or spine; juxta-ocular bulges indistinct to protruding; supracoxal dilatation well marked; metazona at least 2½ times as long as prozona, keeled, more or less triangular in cross-section; apical lobes of forefemur with a spine; forefemora with 3–4 discoidal and 4–8 posteroventral spines, if with more than 4 posteroventral spines then tibia very elongate and claw-groove near base of femur; walking legs with or without lobes, genicular lobes and spines may be elongate; males mesopterous, females micropterous to mesopterous; cyclopean ear present; supra-anal plate triangular; cerci shorter than half of abdomen length, flattened; phallomeres well sclerotized; right phallomere ventrally with two pilosity fields, ventral ridge elongate; processes of left complex separated; ventral phallomere without basal lobe on right side; pda translocated to left side of ventral phallomere; sdpl present, sdpm reduced to at most a rounded lobe at base of sdpl; phalloid apophysis bifurcate, anterior lobe widely separated from posterior lobe, bird-head-like and tuberculate, rarely membraneous, posterior lobe has the shape of a strong spine; membraneous lobe pilose; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of Heterochaetinae, Compsothespinae, Oxyothespinae, and Toxoderinae, and all descendants thereof, and all species more closely related to *Toxodera denticulata* than to *Chaeteessa filata*, *Mantoida nitida*, *Metallyticus splendidus*, *Chroicoptera vidua*, *Leptomantella albella*, *Amorphoscelis annulicornis*, *Nanomantis australis*, *Gonypeta punctata*, *Majanga basilaris*, *Epaphrodita musarum*, *Haania lobiceps*, *Rivetina baetica*, *Ameles picteti*, *Eremiaphila audouini*, *Hoplocorypha macra*, *Mantis religiosa*, and Amerimantodea.

Family Hoplocoryphidae Giglio-Tos, 1916

Type genus. *Hoplocorypha* Stål, 1871.

Diagnosis. Hoplocoryphids can be distinguished from all other mantodeans by the following combination of characters: body elongate, brownish; vertex without process; eyes rounded; juxta-ocular bulges large, conical; supracoxal dilatation distinct; metazona at least 2 times as long as prozona, more or less triangular in cross-section, with a median and one or more paramedian keels; apical lobes of forefemur with a short spine; forefemora with 3 discoidal and 4 posteroventral spines, claw-groove at apical third; walking legs without lobes; males mesopterous to apterous, females apterous; cyclopean ear present; tergites with small median lobes at posterior margin in females; supra-anal plate triangular, elongate; cerci shorter than half of abdomen length, flattened; phallomeres moderately sclerotized; processes of left complex separated; ventral phallomere without basal lobe on right side; pda translocated to left side of ventral phallomere; sdpl present or missing, sdpm always missing; phalloid apophysis slightly to distinctly bifurcate, tuberculate, strongly sclerotized, with elaborate sculptures; membraneous lobe not pilose; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of *Hoplocorypha*, *Hoplocoryphella* and *Apterocorypha*, and all descendants thereof; would include any newly discovered species more closely related to *Hoplocorypha macra* than to *Chaeteessa filata*, *Mantoida nitida*, *Metallyticus splendidus*, *Chroicoptera vidua*, *Leptomantella albella*, *Nanomantis australis*, *Gonypeta punctata*, *Majanga basilaris*, *Epaphrodita musarum*, *Haania lobiceps*, *Rivetina baetica*, *Ameles picteti*, *Eremiaphila audouini*, *Miomantis monacha* (Fabricius, 1787), *Galinthias amoena* (Saussure, 1871), *Mantis religiosa*, and Amerimantodea.

Family Miomantidae Westwood, 1889

Type genus. *Miomantis* Saussure, 1870.

Diagnosis. Miomantids can be distinguished from all other mantodeans by the following combination of characters:

vertex without process, distinctly convex; eyes rounded to slightly conical; juxta-ocular bulges indistinct; supracoxal dilatation well marked; metazona at least 2 times as long as prozona, with a median keel; apical lobes of forefemur with a very short spine; forefemora with 4 discoidal and 4 posteroventral spines, and with distinct crenulation medioventrad posteroventral spines; claw-groove at about middle of femur or slightly proximad of it; walking legs without lobes; males mesopterous to macropterous, females brachypterous to mesopterous; cyclopean ear present; supra-anal plate triangular, elongate; cerci shorter than half of abdomen length, cylindrical; phallomeres sclerotized; processes of left complex separated; ventral phallomere without basal lobe on right side; pda translocated to left side of ventral phallomere; sdpl present but small, tuberculate, sdpm always missing; phalloid apophysis simple, serrate; membraneous lobe not pilose; apical process sometimes with subapical lobe; dorsal lamina of left phallomere without a rounded lobe.

Phylogenetic definition. Includes the MRCA of Solygiinae and Miomantinae, and all descendants thereof, and all species more closely related to *Miomantis monacha* than to *Chaeteessa filata, Mantoida nitida, Metallyticus splendidus, Gonypeta punctata, Majanga basilaris, Epaphrodita musarum, Haania lobiceps, Rivetina baetica, Ameles picteti, Eremiaphila audouini, Hoplocorypha macra, Galinthias amoena, Hymenopus coronatus* (Olivier, 1792), *Mantis religiosa*, Amerimantodea, and Nanomantodea.

Family Galinthiadidae Giglio-Tos, 1919

Type genus. *Galinthias* Stål, 1877.

Diagnosis. Galinthiadids can be distinguished from all other mantodeans by the following combination of characters: color green, or green and white, with colored alae; vertex without process, concave; eyes conical, with a dorsal tubercle; ocellar spines fused at base to form a short process carrying the ocelli; pronotum with more or less wide foliaceous expansion; supracoxal dilatation well marked, but may be obscured by foliaceous expansion; metazona at least 1½ times as long as prozona; apical lobes of forefemur without or with a very short spine; forefemora with 4 discoidal and 4–5 posteroventral spines, and with distinct crenulation medioventrad posteroventral spines, area between the anteroventral and posteroventral spines setose; claw-groove at proximal half of femur; posteroventral spines of foretibiae slightly decumbent; walking leg femora with ventral lobes, tibiae thickened or with dorsal and ventral lobes; both sexes macropterous; alae red and black, with more or less hyaline apex; cyclopean ear present; supra-anal plate triangular; cerci shorter than half of abdomen length, cylindrical; phallomeres moderately sclerotized; processes of left complex separated; ventral phallomere without, rarely with small basal lobe on right side; pda translocated to left side of ventral phallomere, indistinct; sdpm usually present, acute to subtriangular, sdpl reduced to at most a round lobe; phalloid apophysis simple, knob-like, rarely with a subacute process; membraneous lobe not pilose; apical process without subapical lobe; dorsal lamina of left phallomere without a rounded lobe along left margin, but sometimes with a ventral lobe around base of apical process.

Phylogenetic definition. Includes the MRCA of *Galinthias*, *Congoharpax*, *Pseudoharpax*, and *Harpagomantis*, and all descendants thereof; would include any newly discovered species more closely related to *Galinthias amoena* than to *Chaeteessa filata*, *Mantoida nitida*, *Metallyticus splendidus*, *Gonypeta punctata*, *Majanga basilaris*, *Epaphrodita musarum*, *Haania lobiceps*, *Hoplocorypha macra*, *Miomantis monacha*, *Empusa pauperata* (Fabricius, 1781), *Hymenopus coronatus*, *Mantis religiosa*, Amerimantodea, Nanomantodea, and Eremiaphiloidea.

Family Empusidae Burmeister, 1838

Type genus. *Empusa* Illiger, 1798.

Diagnosis. Empusids can be distinguished from all other mantodeans by the following combination of characters: vertex with a more or less elongate process; eyes ellipsoid, without tubercle; clypeus and frontal shield with a strong median keel produced dorsally into a process; ocellar spines missing; antennae of male pectinate; pronotum with more or less wide foliaceous expansion at least around supracoxal dilatation; supracoxal dilatation well marked, but may be obscured by foliaceous expansion; metazona at least 2 times as long as prozona; forecoxae with red and blue color pattern anteriorly; apical lobes of forefemur with a short spine; forefemora with 4 discoidal and 5–6 posteroventral spines, and with distinct crenulation medioventrad posteroventral spines; anteroventral spines with an arrangement consisting of three short spines between two large ones; foretibiae dorsally tuberculate; walking leg coxae and femora with ventral lobes, sometimes without, dorsal lobes may also be present on femora; tibiae simple; both sexes macropterous, rarely female micropterous; alae hyaline or yellowish subopaque with hyaline apex; cyclopean ear present; supra-anal plate rounded; cerci shorter than half of abdomen length, cylindrical; subgenital plate with a dorsal submarginal ridge on right side; phallomeres sclerotized; processes of left complex separated; ventral phallomere with a small basal lobe on right side; pda translocated to left side of

ventral phallomere, indistinct; sdpm present, more or less subtriangular, sdpl reduced; phalloid apophysis simple to slightly bifurcate; membraneous lobe not pilose; apical process very broad, truncate at apex; dorsal lamina of left phallomere without a rounded lobe along left margin.

Phylogenetic definition. Includes the MRCA of Blepharodinae and Empusinae, and all descendants thereof, and any species more closely related to *Empusa pauperata* than to *Chaeteessa filata*, *Mantoida nitida*, *Metallyticus splendidus*, *Gonypeta punctata*, *Majanga basilaris*, *Epaphrodita musarum*, *Haania lobiceps*, *Hoplocorypha macra*, *Miomantis monacha*, *Galinthias amoena*, *Hymenopus coronatus*, *Dactylopteryx flexuosa* Karsch, 1892, *Deroplatys desiccata* Westwood, 1839, *Mantis religiosa*, Amerimantodea, Nanomantodea, and Eremiaphiloidea.

Family Hymenopodidae Giglio-Tos, 1915

Type genus. *Hymenopus* Audinet-Serville, 1831.

Diagnosis. Hymenopodids can be distinguished from all other mantodeans by the following combination of characters: vertex with a process of various shapes, from a conical tubercle to a quadricuspidate or foliaceous process, if without process then forefemora dilated or posteroventral spines of foretibiae decumbent; eyes ellipsoid to conical, with or without tubercle; clypeus more or less keeled; frontal shield either with a strong median or two weaker paramedian keels; ocellar spines absent, if present then pronotum with 4–6 spine-like processes; pronotum with more or less wide foliaceous expansion at least around supracoxal dilatation; supracoxal dilatation well marked, but may be obscured by foliaceous expansion; metazona about as long as to much longer than prozona; apical lobes of forefemur usually with a short spine; forefemora with 4 discoidal and 4 posteroventral spines, if with 5 posteroventral spines then vertex with large, irregular process; forefemur with distinct crenulation medioventrad posteroventral spines, if without then pronotum with 2–3 pairs of long processes; posteroventral spines of foretibiae decumbent, if not decumbent then vertex with a process; walking leg femora with at least apical ventral lobes, if without lobes then forefemora dilated and/or posteroventral spines of foretibiae decumbent; males macropterous, females macropterous to apterous; cyclopean ear present; supra-anal plate more or less rounded; cerci shorter than half of abdomen length, cylindrical; subgenital plate may lack styli, then with two dorsal submarginal ridges on right side; phallomeres sclerotized; processes of left complex separated; ventral phallomere without or with only a small basal lobe on right side; pda translocated to left side of ventral phallomere, indistinct; sdpm or sdpl present, very rarely both, then one reduced to a small lobe only, existing process small, rounded or triangular; phalloid apophysis short, simple and knob-like to more or less bifid; apical process short, broad to very broad, truncate or rounded at apex, sometimes missing, if longer and digitiform then subgenital plate without styli; dorsal lamina of left phallomere without a rounded lobe along left margin but often entire left phallomere with significant modifications (folds, fusions).

Phylogenetic definition. Includes the MRCA of Phyllocraniinae, Sibyllinae, Hymenopodinae, Phyllothelyinae, Oxypilinae and Acromantinae, and all descendants thereof, and any species more closely related to *Hymenopus coronatus* than to *Chaeteessa filata*, *Mantoida nitida*, *Metallyticus splendidus*, *Gonypeta punctata*, *Majanga basilaris*, *Epaphrodita musarum*, *Haania lobiceps*, *Hoplocorypha macra*, *Miomantis monacha*, *Galinthias amoena*, *Empusa pauperata*, *Dactylopteryx flexuosa*, *Deroplatys desiccata*, *Mantis religiosa*, Amerimantodea, Nanomantodea, and Eremiaphiloidea.

Family Dactylopterygidae Giglio-Tos, 1915

Type genus. *Dactylopteryx* Karsch, 1892.

Diagnosis. Dactylopterygids can be distinguished from all other mantodeans by the following combination of characters: dorsoventrally flattened, gray or brown, mottled with pale and dark as an adaptation to a bark-living lifestyle; vertex without process, but sometimes with tubercles; eyes rounded, exophthalmic; juxta-ocular bulges protruding, conical; pronotum tuberculate, with a more or less wide foliaceous expansion at least around supracoxal dilatation; supracoxal dilatation well marked, but may be obscured by foliaceous expansion; metazona at least 2 times as long as prozona; apical lobes of forefemur with a rather long spine; forefemora with 4 discoidal and 4 posteroventral spines, and with more or less distinct crenulation medioventrad posteroventral spines; claw-groove at proximal half of femur; posteroventral spines of foretibiae not decumbent; walking legs without lobes; males macropterous, females macropterous to mesopterous; cyclopean ear present; supra-anal plate rounded; cerci shorter than half of abdomen length, cylindrical; phallomeres sclerotized; processes of left complex separated; ventral phallomere with a basal lobe on right side; pda translocated to left side of ventral phallomere; sdpm missing; sdpl present, acute, pointed to the right; phalloid apophysis short, simple to bifid; apical

process shaped normally; dorsal lamina of left phallomere without a rounded lobe along left margin.

Phylogenetic definition. Includes the MRCA of *Dactylopteryx*, *Theopompella*, and *Zouza*, and all descendants thereof; would include any newly discovered species more closely related to *Dactylopteryx flexuosa* than to *Chaeteessa filata*, *Mantoida nitida*, *Metallyticus splendidus*, *Gonypeta punctata*, *Majanga basilaris*, *Epaphrodita musarum*, *Haania lobiceps*, *Hoplocorypha macra*, *Miomantis monacha*, *Galinthias amoena*, *Empusa pauperata*, *Hymenopus coronatus*, *Deroplatys desiccata*, *Mantis religiosa*, Amerimantodea, Nanomantodea, and Eremiaphiloidea.

Family Deroplatyidae Westwood, 1889

Type genus. *Deroplatys* Westwood, 1839.

Diagnosis. Deroplatyids can be distinguished from all other mantodeans by the following combination of characters: brownish, rather elongate, stick- or leaf-resembling; vertex without process; eyes rounded or slightly conical; juxta-ocular bulges indistinct; frontal shield not keeled; pronotum either very elongate, at least 5.5 times as long as wide, or with large foliaceous expansion along entire margin; supracoxal dilatation well marked, but may be obscured by foliaceous expansion; metazona at least 3 times as long as prozona; apical lobes of forefemur at most with a very short spine; forefemora with 4 discoidal and 4 posteroventral spines, without distinct crenulation medioventrad posteroventral spines; posteroventral spines of foretibiae not decumbent; walking legs sometimes with subapical ventral lobes; males mesopterous to macropterous, females macropterous to brachypterous; cyclopean ear present; supra-anal plate rounded or incised, with sinuate margins; cerci shorter than half of abdomen length, cylindrical; phallomeres sclerotized; processes of left complex separated; ventral phallomere usually with a basal lobe on right side, rarely without; pda translocated to left side of ventral phallomere; sdpm or sdpl present, often both; phalloid apophysis short, bifurcate or with reduced anterior lobe; apical process shaped normally; dorsal lamina of left phallomere without a rounded lobe along left margin.

Phylogenetic definition. includes the MRCA of Popinae and Deroplatyinae, and all descendants thereof, and any species more closely related to *Deroplatys desiccata* than to *Chaeteessa filata*, *Mantoida nitida*, *Metallyticus splendidus*, *Gonypeta punctata*, *Majanga basilaris*, *Epaphrodita musarum*, *Haania lobiceps*, *Hoplocorypha macra*, *Miomantis monacha*, *Galinthias amoena*, *Empusa pauperata*, *Hymenopus coronatus*, *Dactylopteryx flexuosa*, *Mantis religiosa*, Amerimantodea, Nanomantodea, and Eremiaphiloidea.

Family Mantidae Latreille, 1802

Type genus. *Mantis* Linnaeus, 1758.

Diagnosis. Mantidae can be distinguished from all other mantodeans by the following combination of characters: vertex without process, if with small process than anterior femora with dorsal lobe and walking leg femora with very large ventral lobes; eyes rounded or slightly conical; juxta-ocular bulges indistinct; frontal shield not keeled medially; ocellar tubercles usually missing, if present then legs with several sets of lobes or female tegmina with two large oblique markings; pronotum simple, sometimes with a foliaceous expansion; supracoxal dilatation well marked, but may be obscured by foliaceous expansion; metazona at least 2 times as long as prozona; apical lobes of forefemur at most with a very short spine; forefemora with 3–4 discoidal and 4 posteroventral spines, without distinct crenulation medioventrad posteroventral spines; posteroventral spines of foretibiae not decumbent; walking legs sometimes with subapical ventral lobes; males mesopterous to macropterous, females macropterous to brachypterous; cyclopean ear present; supra-anal plate wider than long, more or less triangular; cerci shorter than half of abdomen length, mostly cylindrical, rarely flattened; phallomeres sclerotized; processes of left complex separated; ventral phallomere with or without a basal lobe on right side; pda translocated to left side of ventral phallomere; sdpm or sdpl present, often both; if sdpm is the main process then phalloid apophysis usually short and simple, if sdpl is the main process then phalloid apophysis strongly bifid; apical process sometimes with subapical tooth; dorsal lamina of left phallomere without a rounded lobe along left margin.

Phylogenetic definition. Includes the MRCA of Mellierinae, Orthoderinae, Choeradodinae, Mantinae, Deromantinae, Omomantinae, Tenoderinae, Hierodulinae, Stagmomantinae, and Vatinae, and all descendants thereof, and any species more closely related to *Mantis religiosa* than to *Chaeteessa filata*, *Mantoida nitida*, *Metallyticus splendidus*, *Gonypeta punctata*, *Majanga basilaris*, *Epaphrodita musarum*, *Haania lobiceps*, *Hoplocorypha macra*, *Miomantis monacha*, *Galinthias amoena*, *Empusa pauperata*, *Hymenopus coronatus*, *Dactylopteryx flexuosa*, *Deroplatys desiccata*, Amerimantodea, Nanomantodea, and Eremiaphiloidea.

Conclusion

The classification presented here is the first totally new approach since Beier's system of 1964. It is the first and

Table 2. Phylogeny and higher-level classification of Mantodea used in this paper.

Systematic arrangement							No. of genera
-				Chaeteessoidea	Chaeteessidae	-	1
Spinomantodea	-			Mantoidoidea	Mantoididae	-	2
	Schizomantodea	-		Metallyticoidea	Metallyticidae	-	1
		Artimantodea	Amerimantodea	Thespoidea	Thespidae	Pseudopogonogastrinae	1
						Pseudomiopteryginae	2
						Bantiinae	6
						Miobantiinae	5
						Musoniellinae	4
						Thespinae	16
				Acanthopoidea	Angelidae	-	1
					Coptopterygidae	-	2
					Liturgusidae	-	5
					Photinaidae	Macromantinae	1
						Photiomantinae	1
						Cardiopterinae	1
						Photinainae	8
					Acanthopidae	Acanthopinae	8
						Stenophyllinae	8
			Cernomantodea	Chroicopteroidea	Chroicopteridae	Tarachininae	3
						Chroicopterinae	25
				Nanomantoidea	Leptomantellidae	-	4
					Amorphoscelidae	Perlamantinae	2
						Amorphoscelinae	5
					Nanomantidae	Hapalomantinae	13
						Tropidomantinae	6
						Nanomantinae	6
						Fulciniinae	25
				Gonypetoidea	Gonypetidae	Iridopteryginae	9
						Gonypetinae	17
				Epaphroditoidea	Majangidae	Brancsikiinae	1
						Majanginae	3
					Epaphroditidae	Gonatistinae	2
						Epaphroditinae	2
				Haanioidea	Haaniidae	Caliridinae	2
						Haaninae	4
				Eremiaphiloidea	Rivetinidae	Rivetininae	9
						Deiphobinae	4
					Amelidae	-	6
					Eremiaphilidae	Parathespinae	1
						Iridinae	8
						Eremiaphilinae	2
						Tarachodinae	18
					Toxoderidae	Heterochaetinae	1

(*continued*)

Table 2. (*Continued*).

Systematic arrangement				No. of genera
			Compsothespinae	1
			Oxyothespinae	8
			Toxoderinae	15
	Hoplocoryphoidea	Hoplocoryphidae	-	3
	Miomantoidea	Miomantidae	Solygiinae	1
			Miomantinae	6
	Galinthiadoidea	Galinthiadidae	-	4
	Hymenopoidea	Empusidae	Blepharodinae	2
			Empusinae	8
		Hymenopodidae	Phyllocraniinae	1
			Sibyllinae	3
			Hymenopodinae	14
			Phyllothelyinae	3
			Oxypilinae	10
			Acromantinae	13
	Mantoidea	Dactylopterygidae	-	3
		Deroplatyidae	Popinae	10
			Deroplatyinae	7
		Mantidae	Mellierinae	5
			Orthoderinae	2
			Choeradodinae	2
			Mantinae	3
			Deromantinae	2
			Omomantinae	1
			Tenoderinae	17
			Hierodulinae	23
			Stagmomantinae	5
			Vatinae	13
Total	**16**	**29**	**60**	**436**

only one for Mantodea based on a phylogenetic framework compiled from chromosomal, molecular and morphological data, with an emphasis on male genitalia. As such, it better reflects natural relationships than any previous system in use. A synopsis of the classification is presented in Table 2. We are aware that our system is still open to improvements, with much work to do, particularly on a generic level, until we reach a satisfactory systemic classification for Mantodea. Particularly promising is a deeper understanding of the hitherto overlooked evolutionary transitions of male genital structures, which provide a more exhaustive set of potentially important characters than the processes used here. We hope that our tentative efforts will stimulate new and fruitful morphological work on these intriguing insects.

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Appendix. A checklist of the family-group names and their type genera used in this paper

Type genus	Original name	Present names
Acanthops Audinet-Serville, 1831	Acanthopsidae Burmeister, 1838	Acanthopoidea, -idae, -inae
Acontista Saussure & Zehntner, 1894	Acontistinae Giglio-Tos, 1915	Acontistini, -ina
Acromantis Saussure, 1870	Acromantes Brunner de Wattenwyl, 1893	Acromantinae, -ini
Aethalochroa Wood-Mason, 1877	Aethalochroae Giglio-Tos, 1914	Aethalochroini
Ameles Burmeister, 1838	Amelides Westwood, 1889	Amelidae, -inae, -ini, -ina
Amantis Giglio-Tos, 1915	-	Amantini
Amorphoscelis Stål, 1871	Amorphoscelidae Stål, 1877	Amorphoscelidae, -inae
Amphecostephanus Rehn, 1912	-	Amphecostephanina
Anaxarcha Stål, 1877	Anaxarchae Giglio-Tos, 1919	Anaxarchini
Angela Audinet-Serville, 1838	Angelini Beier, 1935	Angelidae
Antemna Stål, 1877	Antemninae Terra, 1995	Antemnini
Antistia Stål, 1876	-	Antistiina
Archimantis Saussure, 1869	Archimantinae Giglio-Tos, 1917	Archimantini, -ina
Armene Stål, 1877	-	Armenina
Arria Stål, 1877	Arriae Giglio-Tos, 1919	Arriini
Bantia Stål, 1877	-	Bantiinae
Bisanthe Stål, 1876	Bisanthes Giglio-Tos, 1917	Bisanthina
Blepharodes Bolívar, 1890	Blepharodes Giglio-Tos, 1919	Blepharodinae
Brancsikia Saussure & Zehntner, 1895	-	Brancsikiinae
Calamothespis Werner, 1907	Calamothespes Giglio-Tos, 1914	Calamothespini
Callibia Stål, 1877	Callibiae Giglio-Tos, 1919	Callibiina
Caliris Giglio-Tos, 1915	Calirides Giglio-Tos, 1915	Caliridinae
Callimantis Stål, 1877	Callimantes Giglio-Tos, 1919	Callimantini
Cardioptera Burmeister, 1838	Cardiopterae Rehn, 1911	Cardiopterinae
Chaeteessa Burmeister, 1838	Chaeteessinae Handlirsch, 1925	Chaeteessoidea, -idae
Choeradodis Audinet-Serville, 1831	Choeradodites Saussure, 1869	Choeradodinae
Chroicoptera Stål, 1871	Chroicopterae Giglio-Tos, 1915	Chroicopteroidea, -idae, -inae, -ini, -ina
Compsomantis Saussure, 1872	Compsomantes Giglio-Tos, 1915	Compsomantina
Compsothespis Saussure, 1872	Compsothespes Giglio-Tos, 1913	Compsothespinae
Coptopteryx Saussure, 1869	Coptopteriges Giglio-Tos, 1915	Coptopterygidae
Cotigaonopsis Vyjayandi et al. 2009	-	Cotigaonopsini
Dactylopteryx Karsch, 1892	Dactylopteriges Giglio-Tos, 1915	Dactylopterygidae
Danuriella Westwood, 1889	-	Danuriellini
Deiphobe Stål, 1877	-	Deiphobinae, -ini
Deromantis Giglio-Tos, 1916	Deromantes Giglio-Tos, 1919	Deromantinae
Deroplatys Westwood, 1839	Deroplatides Westwood, 1889	Deroplatyidae, -inae, -ini, -ina
Didymocorypha Wood-Mason, 1877	-	Didymocoryphini
Dysaules Stål, 1877	Dysaules Giglio-Tos, 1919	Dysaulini
Dystacta Saussure, 1871	Dystactinae Giglio-Tos, 1915	Dystactina
Empusa Illiger, 1798	Empusidae Burmeister, 1838	Empusidae, -inae, -ini, -ina
Epaphrodita Audinet-Serville, 1831	Epaphroditae Brunner de Wattenwyl, 1893	Epaphroditoidea, -idae, -inae, -ini
Epsomantis Giglio-Tos, 1915	-	Epsomantini
Eremiaphila Lefebvre, 1835	Eremiaphilini Saussure, 1869	Eremiaphiloidea, -idae, -inae
Euchomena Saussure, 1870	Euchomenae Giglio-Tos, 1916	Euchomenina
Euchomenella Giglio-Tos, 1916	Euchomenellae Giglio-Tos, 1916	Euchomenellini

(*continued*)

(*Continued*).

Type genus	Original name	Present names
Fulcinia Stål, 1877	Fulcinini Ehrmann & Roy, 2002	Fulciniinae, -ini
Galinthias Stål, 1877	Galinthiades Giglio-Tos, 1919	Galinthiadoidea, -idae
Gonatista Saussure, 1869	Gonatistites Saussure, 1869	Gonatistinae
Gonypeta Saussure, 1869	Gonypetides Westwood, 1889	Gonypetoidea, -idae, -inae, -ini, -ina
Gonypetella Giglio-Tos, 1915	-	Gonypetellini
Gonypetyllis Wood-Mason, 1891	-	Gonypetyllina
Haania Saussure, 1871	Haaniae Giglio-Tos, 1915	Haanioidea, -idae, -inae, -ini
Hagiomantis Saussure & Zehntner, 1894	-	Hagiomantini
Hapalomantis Stål, 1871	Hapalomantini Beier, 1964	Hapalomantinae, -ini
Hestiasula Saussure, 1871	Hestiasulae Giglio-Tos, 1871	Hestiasulini
Heterochaeta Westwood, 1843	Heterochaetae Brunner de Wattenwyl, 1893	Heterochaetinae
Heterochaetula Wood-Mason, 1889	-	Heterochaetulini
Heterovates Saussure, 1872	Heterovatini Svenson et al. 2015	Heterovatina
Hierodula Burmeister, 1838	Hierodulae Brunner de Wattenwyl, 1893	Hierodulinae, -ini
Hoplocorypha Stål, 1871	Hoplocoryphae Giglio-Tos, 1916	Hoplocoryphoidea, -idae
Humbertiella Saussure, 1869	Humbertiellae Brunner de Wattenwyl, 1893	Humbertiellina
Hymenopus Audinet-Serville, 1831	Hymenopodinae Giglio-Tos, 1915	Hymenopoidea, -idae, -inae, -ini, -ina
Idolomantis Uvarov, 1940	Idolomantini Ehrmann & Roy, 2002	Idolomantini
Idolomorpha Burmeister, 1838	Idolomorphini Ehrmann & Roy, 2002	Idolomorphina
Iridopteryx Saussure, 1869	Iridopteryginae Giglio-Tos, 1915	Iridopteryginae, -ini, -ina
Ischnomantis Stål, 1877	Ischnomantes Giglio-Tos, 1916	Ischnomantini
Iris Saussure, 1869	Irides Westwood, 1889	Iridinae, -ini, -ina
Leptocola Gerstaecker, 1883	Leptocolae Giglio-Tos, 1916	Leptocolini, -ina
Leptomantella Uvarov, 1940	-	Leptomantellidae
Leptomiopteryx Chopard, 1912	-	Leptomiopterygini
Ligaria Stål, 1877	Ligariae Giglio-Tos, 1915	Ligariini
Litaneutria Saussure, 1869	Litaneutriidae Jantsch, 1999	Litaneutriina
Liturgousa Saussure, 1869	Liturgusae Giglio-Tos, 1915	Liturgusidae, -ini
Macromantis Saussure, 1871	Macromantides Brunner de Wattenwyl, 1893	Macromantinae
Majanga Wood-Mason, 1891	Majangae Giglio-Tos, 1915	Majangidae, -inae, -ini
Mantis Linné, 1758	Mantides Latreille, 1802	Mantoidea, -idae, -inae
Mantoida Newman, 1838	Mantoidae Giglio-Tos, 1919	Mantoidoidea, -idae
Melliera Saussure, 1892	Mellierae Giglio-Tos, 1915	Mellierinae, -ini
Metallyticus Westwood, 1835	Metallytici Giglio-Tos, 1917	Metallyticoidea, -idae
Microphotina Beier, 1935	-	Microphotinaini
Miobantia Giglio-Tos, 1917	Miobantiinae Roy, 2013	Miobantiinae
Miomantis Saussure, 1870	Miomantides Westwood, 1889	Miomantoidea, -idae, -inae
Musoniella Giglio-Tos, 1916	-	Musoniellinae, -ini
Nanomantis Saussure, 1871	Nanomantes Brunner de Wattenwyl, 1893	Nanomantoidea, -idae, -inae
Neomantis Giglio-Tos, 1915	-	Neomantini
Nilomantis Werner, 1907	Nilomantinae Ehrmann & Roy, 2002	Nilomantini
Oligonyx Saussure, 1869	Oligonyx Saussure, 1892	Oligonychini, -ina
Omomantis Saussure, 1899	Omomantes Giglio-Tos, 1916	Omomantinae
Orthodera Burmeister, 1838	Orthoderites Saussure, 1869	Orthoderinae
Orthoderella Giglio-Tos, 1897	Orthoderellae Giglio-Tos, 1919	Orthoderellina
Otomantis Bolivar, 1890	Otomantes Giglio-Tos, 1915	Otomantini
Oxyelaea Giglio-Tos, 1917	-	Oxyelaeini

(*continued*)

(*Continued*).

Type genus	Original name	Present names
Oxyopsis Caudell, 1904	Oxyopsides Giglio-Tos, 1914	Oxyopsidini
Oxyothespis Saussure, 1870	Oxyothespinae Giglio-Tos, 1916	Oxyothespinae, -ini
Oxypilus Audinet-Serville, 1831	Oxypilites Saussure, 1871	Oxypilinae, -ini
Parablepharis Saussure, 1870	Parablephares Giglio-Tos, 1915	Parablepharini
Paramantis Roy, 1973	Paramantini Roy, 1973	Paramantini, -ina
Paraoxypilus Saussure, 1870	Paraoxypilites Saussure, 1872	Paraoxypilina
Parathespis Saussure, 1869	Parathespinae Giglio-Tos, 1916	Parathespinae
Paroxyophthalmus Wood-Mason, 1889	-	Paroxyophthalmina
Perlamantis Guérin-Méneville, 1843	Perlamantinae Giglio-Tos, 1913	Perlamantinae
Photina Burmeister, 1838	Photininae Giglio-Tos, 1915	Photinaidae, -inae, -ini, -ina
Photiomantis Piza, 1968	-	Photiomantinae
Phyllocrania Burmeister, 1838	Phyllocraniae Brunner de Wattenwyl, 1893	Phyllocraniinae
Phyllothelys Wood-Mason, 1877	Phyllotheles Brunner de Wattenwyl, 1893	Phyllothelyinae, -ini
Pogonogaster Rehn, 1918	Pogonogasterees Beier, 1935	Pogonogasterina
Polyspilota Burmeister, 1838	Polyspilotae Giglio-Tos, 1917	Polyspilotina
Popa Stål, 1856	Popae Brunner de Wattenwyl, 1893	Popinae
Pseudempusa Brunner de Wattenwyl, 1893	Pseudempusae Rehn, 1911	Pseudempusina
Pseudocreobotra Saussure, 1870	Pseudocreobotrae Brunner de Wattenwyl, 1893	Pseudocreobotrina
Pseudomantis Saussure, 1869	Pseudomantides Brunner de Wattenwyl, 1893	Pseudomantina
Pseudopogonogaster Beier, 1942	-	Pseudopogonogastrinae
Pseudomiopteryx Saussure, 1870	Pseudomiopteriginae Giglio-Tos, 1915	Pseudomiopteryginae
Pseudoxyops Saussure & Zehntner, 1894	-	Pseudoxyopsidini
Rhodomantis Giglio-Tos, 1917	-	Rhodomantini
Rivetina Berland & Chopard, 1922	Rivetinini Ehrmann & Roy, 2002	Rivetinoidae, -inae, -ini
Schizocephala Audinet-Serville, 1831	Schizocephalites Saussure, 1869	Schizocephalini
Sibylla Stål, 1856	Sibyllae Giglio-Tos, 1915	Sibyllinae
Solygia Stål, 1877	Solygiinae Giglio-Tos, 1919	Solygiinae
Stagmatoptera Burmeister, 1838	Stagmatopterae Brunner de Wattenwyl, 1893	Stagmatopterini
Stagmomantis Saussure, 1869	Stagmomantes Brunner de Wattenwyl, 1893	Stagmomantinae, -ini
Stenomantis Saussure, 1871	Stenomantes Giglio-Tos, 1915	Stenomantini
Stenophylla Westwood, 1843	Stenophyllites Saussure, 1869	Stenophyllinae, -ini
Tarachina Werner, 1907	Tarachinae Giglio-Tos, 1915	Tarachininae, -ini
Tarachodes Burmeister, 1838	Tarachodes Giglio-Tos, 1917	Tarachodinae, -ini, -ina
Tenodera Burmeister, 1838	Tenoderae Brunner de Wattenwyl, 1893	Tenoderinae, -ini, -ina
Thespis Audinet-Serville, 1831	Thespites Saussure, 1869	Thespoidea, -idae, -inae, -ini
Toxodera Audinet-Serville, 1837	Toxoderites Saussure, 1869	Toxoderidae, -inae, -ini
Toxoderopsis Wood-Mason, 1889	Toxoderopsini Ehrmann & Roy, 2002	Toxoderopsini, -ina
Toxomantis Giglio-Tos, 1914	-	Toxomantina
Trachymantis Giglio-Tos, 1917	Trachymantes Giglio-Tos, 1917	Trachymantina
Tricondylomimus Chopard, 1930	-	Tricondylomimina
Tropidomantis Stål, 1877	Tropidomantes Giglio-Tos, 1915	Tropidomantinae
Vates Burmeister, 1838	Vatidae Stål, 1877	Vatinae, -ini, -ina