

Phylogenetic analyses elucidate the inter-relationships of Pamphilioidea (Hymenoptera, Symphyta)

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Abstract

The phylogeny of the superfamily Pamphilioidea is reconstructed using morphology and DNA sequence data of living and fossil taxa by employing two phylogenetic methods (maximum parsimony and Bayesian inference). Based on our results, the monophyly of Pamphilioidea and Pamphiliidae are corroborated, whereas two extinct families, Xyelydidae and Praesiricidae, are not monophyletic. Because members of Praesiricidae together with *Megalodontes* form a monophyletic group, we propose that the paraphyletic Praesiricidae is synonymized under Megalodontesidae (syn. nov.). The origin of Pamphilioidea is hypothesized to be as early as the Early Jurassic. To better understand morphological evolution in the early lineages of Pamphilioidea, ancestral states of the first flagellomere and the first and second abdominal terga are reconstructed on the morphology-based tree. In addition, three new genera (*Medilyda*, *Brevilyda*, *Strenolyda*) with five new species (*Medilyda procera*, *M. distorta*, *Brevilyda provecta*, *Strenolyda marginalis* and *S. retrorsa*) are described based on well-preserved xyelydid fossils from the Middle Jurassic Jiulongshan Formation of north-eastern China.

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Hymenoptera is one of the largest orders of insects with over 153 000 described species (Huber, 2009; Aguilar et al., 2013). Hymenopterans are the sister group to the remaining holometabolous insect orders (Rasnitsyn, 1969, 1988; Wiegmann et al., 2009; Beutel et al., 2011; Misof et al., 2014) and play an important role in the natural world. ‘Symphyta’, the basal grade in Hymenoptera, are distinguished by their broad ‘waists’ and their phytophagous feeding habits in addition to the small, ectoparasitic family Orussidae (Heraty et al., 2011). Recently, total-evidence dating estimated that divergence times of stem lineages of Hymenoptera occurred in the Late Carboniferous, 70 Myr earlier than the date of the earliest fossil record (Ronquist et al., 2012).

In general, fossil record completeness and fossil temporal position close to the ancestor of a phylogenetic clade improve divergence time estimates (Huelsenbeck, 1991; Solodovnikov et al., 2012). This is applicable to the superfamily Pamphilioidea, a small group of distinctive sawflies, characterized by a massive head, isolated mandibular foramina and a modified ovipositor (Rasnitsyn, 1969, 1980). The superfamily consists of two Holarctic-distributed extant families, Megalodontesidae and Pamphiliidae, and two extinct families, Xyelydidae and Praesiricidae (Rasnitsyn, 1969, 1983). The latter two families may be, in part, placeholders for poorly preserved fossil specimens. The relationships of these four families are poorly understood (Ronquist et al., 2012).

The family Pamphiliidae has ten extant genera containing about 330 reported species (Taeger et al., 2010), and four extinct genera containing eight species

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described from the Mesozoic, Palaeogene and Neogene of China, Russia, USA and Spain (Rasnitsyn, 1983; Penälvér and Arillo, 2002; Nel, 2004; Wang et al., 2014a). It is typified by having a medially split second tergum, lateral folding of the abdominal terga above the spiracle, and fore wing with vein A markedly sinuate (Viitasaari, 2002). Extant members of Pamphiliidae are restricted to temperate regions of North America and Eurasia (Eidt, 1969; Xiao et al., 1992), and their larvae typically feed on conifers, spinning silk to build tents or webs (Cephalciinae), or rolling angiosperm leaves to form tubes (Pamphiliinae), where they feed (Benson, 1945; Achterberg and Aartsen, 1986; Goulet, 1993; Viitasaari, 2002). In addition to the two extant subfamilies, a third subfamily, Juralydinae, was proposed by Rasnitsyn (1977), based on one genus, *Juralyda*, described from a single fore wing.

The family Megalodontesidae is a small family with only one extant genus, *Megalodontes* Latreille, 1803, containing about 88 described species, all of which are distributed in Eurasia (Taeger et al., 2010). In contrast to Pamphiliidae, Megalodontesidae is typified by having pectinate antennae and no lateral keels on the abdomen (Benson, 1968; Goulet, 1993). The family has only one extinct representative, *Jibaissodes giganteus* from the Early Cretaceous of China (Ren et al., 1995), which was transferred from Baissodidae to Megalodontesidae by Rasnitsyn (2000).

During study of 35 specimens of xyelydids from the Middle Jurassic of China in our collections, we found that it was difficult to place them in the present taxonomic hierarchy using the diagnostic characters in the literature. These new specimens show continuous variations in many of the key taxonomic characters. We propose a novel classification using specific ranges of character variations, and present a dichotomous key to xyelydid genera.

The early evolution of flagellar morphology has been difficult to unravel. However, a series of publications (Rasnitsyn, 1968, 1969, 1980, 1988, 1996; Wang et al., 2013) demonstrated that an enlarged first flagellomere is the ancestral state for Hymenoptera. The morphology of the first two abdominal terga is also useful in understanding the basal phylogeny of Hymenoptera. Matsuda (1976) and Vilhelmsen (2000) showed that a divided first abdominal tergum and an undivided second tergum represent the ancestral states in Hymenoptera. Herein, we conduct ancestral-state reconstructions of these three characters in the superfamily Pamphilioidea based on our new fossil specimens.

To shed new light on pamphilioid developmental trends, as well as on the evolution of hymenopterans and insects in general, we carried out simultaneous morphological and molecular phylogenetic analyses of the Pamphilioidea. This is accomplished by incorporating morphological characters of selected representatives of

extant species, as well as almost all the type specimens of fossils, and DNA sequence data from representative extant species. Our goals are (i) to explore the interrelationships of the four families of Pamphilioidea, (ii) to address the controversial question of whether the extinct families Xyelydidae and Praesiricidae are monophyletic, and (iii) to redefine familial limits based on synapomorphic characters.

Background

A review of published data on pamphilioid phylogeny

Rasnitsyn's (1988, 2002) works on hymenopteran fossils were the starting point for phylogenetic studies of Hymenoptera. Ronquist et al. (1999), Vilhelmsen (2001), Schulmeister et al. (2002), and Sharkey and Roy (2002) critically examined previously used characters and added more characters based on newly published data. Over the past decade, phylogenetic analyses of the order Hymenoptera were conducted and relationships within symphytans were well resolved (Sharkey et al., 2012; Klopstein et al., 2013). Malm and Nyman (2015) demonstrated Pamphilioidea to be the sister group to {Tenthredinoidea, [Cephidae, (Siricoidea, Xiphydriidae, Vespina)]} with strong branch support; and the two extant families Megalodontesidae and Pamphiliidae were firmly supported as monophyletic. Additionally, the two extant subfamilies in Pamphiliidae, Cephalciinae and Pamphiliinae, were also recovered as monophyletic groups. The latter was consistent with the results of Ronquist et al. (2012) except for the position of *Neurotoma*.

A review of published data on Mesozoic pamphilioid fossils

The described fossils of Pamphilioidea, summarized by Rasnitsyn et al. (2006), Gao et al. (2013a), Wang et al. (2014a,b,c, 2015a,b), and the EDNA fossil insect database (EDNA, 2014), comprise 28 genera and 59 species. For this study, we reviewed and summarized all published data on Mesozoic pamphilioid fossils (Table 1), with particular focus on species assigned into Xyelydidae and Praesiricidae, covering the period from the Early Jurassic (200 Ma, the putatively earliest record) to the end of the Cretaceous (65 Ma).

The earliest pamphilioid records were xyelydids, *Sagulyda* spp. and *Ferganolyda* spp., from the Early or Middle Jurassic of the Sogul Formation in Kyrgyzstan, dated to approximately 180–170 Ma (Rasnitsyn, 1983; Rasnitsyn et al., 2006). Recently, more complete fossils of *Ferganolyda* have been reported, displaying significant sexual dimorphism in body size, exaggerated head and antenna morphologies (Rasnitsyn et al., 2006;

Table 1
List of fossil Pamphilioidea of the world

Family	Taxa	Locality	Horizon	Guiding literature
Xyelydidae	<i>Ferganolyda cubitalis</i> Rasnitsyn, 1983	Kyrgyzstan	J2	Rasnitsyn (1983)
	<i>F. radialis</i> Rasnitsyn, 1983	Kyrgyzstan	J2	Rasnitsyn (1983)
	<i>F. sogdiana</i> Rasnitsyn, 1983	Kyrgyzstan	J2	Rasnitsyn (1983)
	<i>F. scylla</i> Rasnitsyn, Zhang & Wang, 2006	China	J2	Rasnitsyn et al. (2006)
	<i>F. charybdis</i> Rasnitsyn, Zhang & Wang, 2006	China	J2	Rasnitsyn et al. (2006)
	<i>F. chungkuei</i> Rasnitsyn, Zhang & Wang, 2006	China	J2	Rasnitsyn et al. (2006)
	<i>F. eucalla</i> Wang, Rasnitsyn, Shih & Ren, 2014	China	J2	Wang et al. (2014c)
	<i>F. insolita</i> Wang, Rasnitsyn, Shih & Ren, 2014	China	J2	Wang et al. (2014c)
	<i>Mesolyda jurassica</i> Rasnitsyn, 1963	Kazakhstan	J3	Rasnitsyn (1963)
	<i>M. sibirica</i> Rasnitsyn, 1983	Russia	J3	Rasnitsyn (1983)
	<i>Novalyda cretacea</i> Gao, Engel, Shih & Ren, 2013	China	K1	Gao et al. (2013b)
	<i>N. decora</i> Wang, Rasnitsyn, Shih & Ren, 2015	China	K1	Wang et al. (2015b)
	<i>Prolyda karatavica</i> Rasnitsyn, 1968	Kazakhstan	J3	Rasnitsyn (1968)
	<i>P. depressa</i> Rasnitsyn, 1969	Kazakhstan	J3	Rasnitsyn (1969)
	<i>P. xylocera</i> Rasnitsyn, 1968	Kazakhstan	J3	Rasnitsyn (1968)
	<i>Rectilyda sticta</i> Wang, Rasnitsyn, Shih & Ren, 2014	China	K1	Wang et al. (2014b)
	<i>Strophandria grossa</i> Rasnitsyn, 1968	Kazakhstan	J3	Rasnitsyn (1968)
	<i>S. moderata</i> Rasnitsyn, 1983	Kazakhstan	J3	Rasnitsyn (1983)
	<i>Sagulyda arcuata</i> Rasnitsyn, 1983	Kyrgyzstan	J2	Rasnitsyn (1983)
	<i>S. ferganica</i> Rasnitsyn, 1983	Kyrgyzstan	J2	Rasnitsyn (1983)
	<i>S. magna</i> Rasnitsyn, 1983	Kyrgyzstan	J2	Rasnitsyn (1983)
	<i>Xyelyda excellens</i> Rasnitsyn, 1968	Kazakhstan	J3	Rasnitsyn (1968)
	<i>Fissilyda compta</i> Wang, Rasnitsyn, Shih & Ren, 2015	China	K1	Wang et al. (2015b)
	<i>F. alba</i> Wang, Rasnitsyn, Shih & Ren, 2015	China	K1	Wang et al. (2015b)
	<i>F. parilis</i> Wang, Rasnitsyn, Shih & Ren, 2015	China	K1	Wang et al. (2015b)
	<i>Medilyda procera</i> sp. nov.	China	J2	This paper
	<i>M. distorta</i> sp. nov.	China	J2	This paper
	<i>Brevilyda provecta</i> sp. nov.	China	J2	This paper
	<i>Strenolyda marginalis</i> sp. nov.	China	J2	This paper
	<i>S. retrorsa</i> sp. nov.	China	J2	This paper
'Praesiricidae'	<i>Praesirex hirtus</i> Rasnitsyn, 1968	Russia	K1	Rasnitsyn (1968)
	<i>Xyelodontes sculpturatus</i> Rasnitsyn, 1983	Mongolia	K1	Rasnitsyn (1983)
	<i>Aulidontes mandibulatus</i> Rasnitsyn, 1983	Kazakhstan	J3	Rasnitsyn (1983)
	<i>Turgidontes magnus</i> Rasnitsyn, 1990	Russia	K1	Rasnitsyn (1990)
	<i>Rudisiricicus belli</i> Gao, Rasnitsyn, Shih & Ren, 2010	China	K1	Gao et al. (2010)
	<i>R. crassinodus</i> Gao, Rasnitsyn, Shih & Ren, 2010	China	K1	Gao et al. (2010)
	<i>R. scelsus</i> Gao, Rasnitsyn, Shih & Ren, 2010	China	K1	Gao et al. (2010)
	<i>R. validus</i> Wang, Rasnitsyn, Shih & Ren, 2015	China	K1	Wang et al. (2015a)
	<i>R. ferox</i> Wang, Rasnitsyn, Shih & Ren, 2015	China	K1	Wang et al. (2015a)
	<i>R. ater</i> Wang, Rasnitsyn, Shih & Ren, 2015	China	K1	Wang et al. (2015a)
	<i>R. tenellus</i> Wang, Rasnitsyn, Shih & Ren, 2015	China	K1	Wang et al. (2015a)
	<i>R. membranaceus</i> Wang, Rasnitsyn, Shih & Ren, 2015	China	K1	Wang et al. (2015a)
	<i>R. parvus</i> Wang, Rasnitsyn, Shih & Ren, 2014	China	K1	Wang et al. (2015a)
	<i>Archoxyelyda mirabilis</i> Wang, Rasnitsyn & Ren, 2013	China	K1	Wang et al. (2013)
	<i>Hoplitolyda duolunica</i> Gao, Shih, Rasnitsyn & Ren, 2013	China	K1	Gao et al. (2013a)
	<i>Decorisiricicus patulus</i> Wang, Rasnitsyn, Shih & Ren, 2015	China	K1	Wang et al. (2015c)
	<i>D. latus</i> Wang, Rasnitsyn, Shih & Ren, 2015	China	K1	Wang et al. (2015c)
	<i>Limbsiricicus aequalis</i> Wang, Rasnitsyn, Shih & Ren, 2015	China	J2	Wang et al. (2015c)
	<i>L. complanatus</i> Wang, Rasnitsyn, Shih & Ren, 2015	China	J2	Wang et al. (2015c)
	<i>Pallorisiricicus distortus</i> Wang, Rasnitsyn, Shih & Ren, 2015	China	J2	Wang et al. (2015c)
Pamphiliidae	<i>Juralyda udensis</i> Rasnitsyn, 1977	Russia	J3	Rasnitsyn (1977)
	<i>Scabolyda orientalis</i> Wang, Rasnitsyn, Shih & Ren, 2014	China	J2	Wang et al. (2014a)
	<i>S. incompleta</i> Wang, Rasnitsyn, Shih & Ren, 2014	China	K1	Wang et al. (2014a)
	<i>Atocus defessus</i> Scudder, 1892	USA	E	Rasnitsyn (1983)
	<i>A. cockerelli</i> Rohwer, 1908	USA	E	Rasnitsyn (1983)
	<i>Tapholyda caplani</i> Rasnitsyn, 1983	USA, Russia	E	Rasnitsyn (1983)
	<i>Acantholyda</i> (?) <i>ribesalbensis</i> Penälvér and Arillo, 2002	Spain	M	Penälvér and Arillo (2002)
	<i>A. grangeoni</i> Riou, 1999	France	M	Nel (2004)
	<i>Jibaissodes giganteus</i> Ren, Lu, Guo & Ji, 1995	China	K1	Ren et al. (1995)

'Praesiricidae' means it is a synonymization in the present paper; J1, Early Jurassic; J2, Middle Jurassic; J3, Late Jurassic; K1, Early Cretaceous; E, Eocene; M, Miocene.

Wang et al., 2014c). The oldest fossil of Pamphiliidae (*Scabolyda orientalis*) was also reported from the Middle Jurassic of the Jiulongshan Formation in China (Wang et al., 2014a), but fossils of Megalodontesidae were still lacking from the same epoch.

In the Cretaceous, the number of xyelydids appeared to have declined rapidly with only three genera (*Novolyda*, *Fissilyda* and *Rectilyda*) discovered, and no more xyelydids have been described after that. In contrast to Xyelydidae, the species of Praesiricidae in the Early Cretaceous were relatively abundant. Initially being misunderstood (Rasnitsyn, 1968, 1969), this family together with Megalodontesidae has been later revealed as a monophylum (Rasnitsyn, 1983) and of complicated structure. Four subfamilies were identified, two of which being known in the Early Cretaceous only (Praesiricinae with *Praesirex*, *Xyelodontes* and *Turgidontes*, and Archoxyelidinae with *Archoxyelyda* and *Xyelodontes*), and two other (Rudisiriciinae with *Rudisiricius* and *Aulidontes*, and Decorisiriciinae with *Decorisiricius*, *Limbisiricius* and *Pallorisiricius*) spanning from the Jurassic to the Cretaceous (Gao et al., 2010; Wang et al., 2013, 2015a, c).

Hoplitolyda duolunica, with a body length estimated to be more than 55.0 mm, and a wing span of >92.0 mm, is the largest fossil hymenopteran discovered to date. It possessed characters that bear resemblance to Praesiricidae and therefore Gao et al. (2013a) tentatively assigned the species to this family and did not assign it to a particular subfamily.

To date, the research on pamphilioid phylogeny omits fossil material because of the paucity of data from the fossil record and the inconsistency in scoring characters between extant and fossil taxa, which often results in significantly lower nodal support values across phylogenies. Nevertheless, Ronquist et al. (2012) used fossils to calibrate divergence times in a total-evidence analysis. Their majority-rule consensus tree showed that most of the fossils were poorly placed; for example, extinct genera belonging to Xyelydidae and Praesiricidae were not united (*Rudisiricius*, *Ferganolyda*, etc.), and most formed a polytomy with the exception that *Turgidontes* was the sister to the extant genus *Megalodontes*.

Materials and methods

Depositions of fossils

All new fossil specimens studied in this paper were from the Jiulongshan Formation of Inner Mongolia, China, and deposited in the Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University (CNU), in Beijing, China (Ren Dong, Curator). The specimens

were examined and then photographed, either dry or wetted with 95% ethanol, with a Leica DFC500 digital camera (Wetzlar, Germany) attached to a Leica MZ165C dissecting microscope. The colours of fossils described below are not reliably known because of the absence of a counterpart fossil, which is just the direct presentation from the surface of fossils. The wing venation nomenclature used in this paper was modified after Rasnitsyn (1969, 1980).

The Jiulongshan Formation is well known for yielding feathered dinosaurs, mammals, conifers, bennettitaleans and 20 orders of insects that have contributed significantly to our understanding of the evolution of these groups (Zhang and Zheng, 1987; Xu and Zhang, 2005; Huang and Nel, 2009; Ren et al., 2010, 2012; Gao et al., 2012; Wang et al., 2012a,b). Because of new calibrations for the Jurassic, this deposit is now considered as latest Middle Jurassic (late Callovian) in age (Walker et al., 2013), approximately 165–164 Ma.

Exemplar taxa

We sampled 44 terminals, comprising nine extant taxa, 30 fossil taxa and five outgroups. The extant pamphiliid genera that we sampled represented two of three subfamilies of Pamphiliidae and the sole genus of Megalodontesidae. The sampled genera were *Cephalcia* Panzer, 1803, *Caenolyda* Konow, 1897 and *Acantholyda* Costa, 1894 in Cephalciinae, *Neurotoma* Konow, 1897, *Pamphilius* Latreille, 1803, *Onycholyda* Takeuchi, 1938, *Kelidoptera* Konow, 1897 and *Pseudocephaleia* Zirngiebl, 1937 in Pamphiliinae, and *Megalodontes* Latreille, 1803 of Megalodontesidae. The specimens of extant Pamphiliidae and Megalodontesidae examined for the analyses were deposited in the Entomological Museum, University of Kentucky, Lexington, USA (UK); the National Zoological Museum of China, Institute of Zoology, Chinese Academy of Sciences, Beijing, China (NZMC, IOZ, CAS); the Beijing Forestry University, Beijing, China (BJFU); and the American Museum of Natural History, New York, USA (AMNH). Most of the type species of Xyelydidae and Praesiricidae were included in the analyses. In addition, we selected specimens with relative completeness and maximum morphological information to achieve the most complete morphological matrix.

We excluded *Sagulyda* Rasnitsyn, 1983 (Xyelydidae), *Xyelodontes* Rasnitsyn, 1983 (Praesiricidae), *Juralyda* Rasnitsyn, 1977 (Pamphiliidae) and *Jibaissodes* Ren, Lu, Guo & Ji, 1995 (Megalodontesidae) from the matrix due to their poor preservation (solely fragmentary wings or distorted bodies). *Hoplitolyda duolunica* Gao, Shih, Rasnitsyn & Ren, 2013 was originally described based on a male specimen and tentatively assigned to Praesiricidae. Examination of a newly discovered female of this species shows that it has a

weak fore wing SC, and a unique cell 1mcu of the fore wing. Because of these characters and the fact that the ovipositor and antennae are similar to those of Siricoidea (our personal observation), it is our opinion that the taxonomic position of this species needs re-evaluation. It was therefore excluded from the analyses.

The outgroup taxa were selected based on their phylogenetic proximity to Pamphilioidea (Malm and Nyman, 2015) and their putatively plesiomorphic wing venation, antennae and ovipositors. We chose *Macroxylela* Kirby, 1882, *Abrotoxylela* Gao, Ren & Shih, 2009 and *Platxyylela* Wang, Ren & Shih, 2012 of Xyeloidea, and *Xyelotoma* Rasnitsyn, 1968 and *Tenthredo* Linnaeus, 1758 of Tenthredinoidea.

Morphological data

The morphological data were mainly taken from earlier studies (Ronquist et al., 1999, 2012; Vilhelmsen, 2001; Schulmeister, 2003; Sharkey et al., 2012), but some characters were excluded because they cannot be satisfactorily examined in fossil species. We also introduced new characters that were well suited to examination in fossils. Forty-five adult characters (Appendix 1; Figs 1 and 2) were coded for the 39 ingroup and five outgroup taxa. All characters were treated as unordered and with equal weight, and we favoured a missing data entry over a potentially incorrect homology assessment. Inapplicable and unknown characters were coded with ‘-’ and ‘?’, respectively.

Molecular data

Molecular data for the seven extant taxa (five species of Pamphiliidae and Megalodontesidae, and two

outgroup species from Xyeloidea and Tenthredinoidea; Appendix S1) were downloaded from GenBank. Seven gene fragments, widely applied in hymenopteran phylogenetic studies, were used: 12S, 16S, 18S and 28S rRNA, cytochrome c oxidase subunit I (COI), and two copies of elongation factor 1 α (EF1 α F1 and EF1 α F2) (Ronquist et al., 2012). Protein-coding genes (COI and two copies of EF1 α) were aligned individually based on codon-based multiple alignments using the Muscle algorithm implemented in MEGA 6.06 (Tamura et al., 2013). Sequences of rRNA genes were aligned using the ClustalW algorithm in MEGA. Alignments were then checked manually for quality and to ensure that protein-coding genes were in the correct reading frame. Genes were concatenated and the final data set includes a total of 5255 aligned base pairs.

The optimal partition strategy and models of molecular data were selected by PartitionFinder v. 1.1.1 (Lanfear et al., 2012, 2014). We created an input configuration file that contained 13 pre-defined partitions: four partitions for four rRNA genes and nine partitions for codon positions of COI, EF1 α F1 and EF1 α F2. We use the ‘greedy’ algorithm with branch lengths estimated as “unlinked” and used the Bayesian information criterion (BIC) to search for the best-fit scheme. The data were partitioned into four parts as follows: (i) 12S and 16S rRNAs and first codon positions of COI with the GTR+G model; (ii) 18S and 28S rRNAs, second codon positions of COI, and first and second codon positions of EF1 α F1 and EF1 α F2 with the SYM+I+G model; (iii) third codon positions of COI with the HKY+G model; and (iv) third codon positions of EF1 α F1 and EF1 α F2 with the GTR+G model.

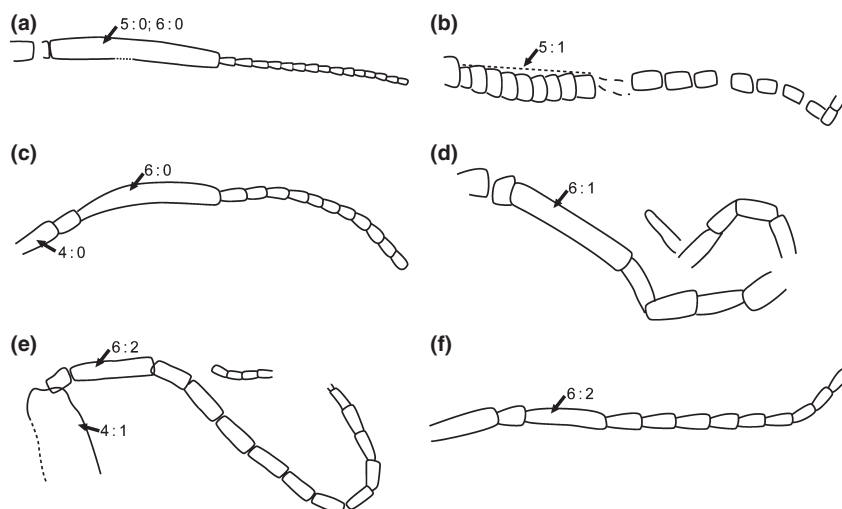


Fig. 1. Antenna of Pamphilioidea. (a) *Platxyylela unica* (Xyelidae); (b) *Archoxyylela mirabilis* (Praesiricidae); (c) *Novalyda cretacea* (Xyelidae); (d) *Scabolyda orientalis* (Pamphiliidae); (e) *Rudisiricius validus* (Praesiricidae); (f) *Pamphilius hortorum* (Pamphiliidae). Numbers refer to characters and states, see Appendix 1.

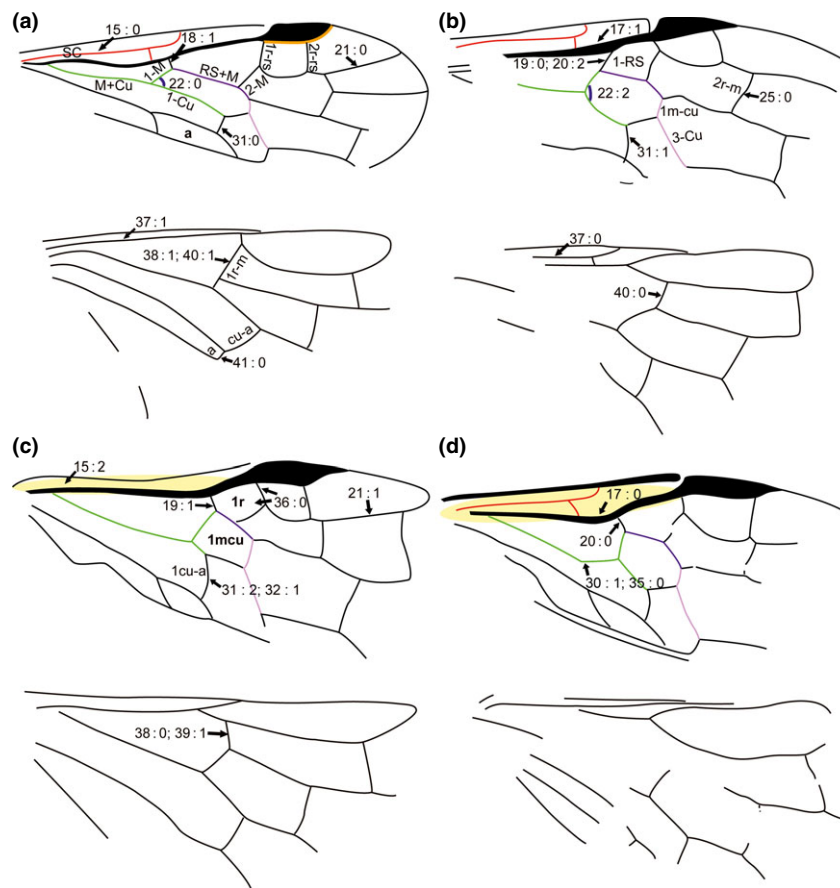


Fig. 2. Wings of Pamphilioidea. (a) *Platyxyela unica* (Xyelidae); (b) *Rectilyda sticta* (Xyelidae); (c) *Decorisiricius patulus* (Praesiricidae); (d) *Scabolyda orientalis* (Pamphiliidae). Major wing veins of fore wing are highlighted in colour. Red indicates SC; green indicates M+Cu, 1-M and 1-Cu; purple indicates RS+M and 2-M; pink indicates 1m-cu and 3-Cu; orange indicates distance between 1r-rs and 2r-rs and between 2r-rs and apex of pterostigma; yellow shadow indicates costal area. Numbers refer to characters and states, see Appendix 1.

Phylogenetic methods

Because the DNA sequence data were only available from species of the extant families Pamphiliidae and Megalodontesidae (~12.8% of all ingroup terminals), it was difficult to resolve the phylogeny of Pamphilioidea based on molecular data or total-evidence data. We analysed two data sets, as follows: (i) to evaluate the phylogenetic signal of the data and to construct a robust hypothesis of the relationships among the genera of Pamphilioidea, we employed a morphological data set containing 44 species (39 pamphilioids and five outgroups) and 45 morphological characters (Appendix S2); (ii) to clarify the inner relationships of Pamphiliidae, a total-evidence data set including 17 species (12 pamphilioids and five outgroups), 45 morphological characters and seven genes was used (Appendix S3). All trees were rooted on *Macroxyela ferruginea*.

Maximum parsimony (MP) analysis. MP analysis of the morphological data set (Appendix S2) was

conducted with TNT v. 1.1 (Goloboff et al., 2003) using the traditional search option under the following parameters: memory set to hold 500 000 trees; zero random seed, tree bisection reconnection (TBR) branch swapping algorithm with 50 000 replications saving 10 trees per replicate. Branch support was calculated using bootstrap support values (Felsenstein, 1985). The characters were mapped in WinClada (Nixon, 2002).

To further evaluate phylogenetic relationships, rather than just selecting a 'preferred MP tree' from a set of source trees, we used weighted compromise trees (Sharkey et al., 2013) and successive weighting (SW) using the maximum rescaled consistency index in PAUP*4.0b10 (Swofford, 2002).

Bayesian inference (BI). Bayesian analysis was performed in MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). Five data partitions were used: four partitions for molecular data with the best model selected by the software PartitionFinder, and the fifth partition for morphological data with the Mk model (Lewis, 2001)

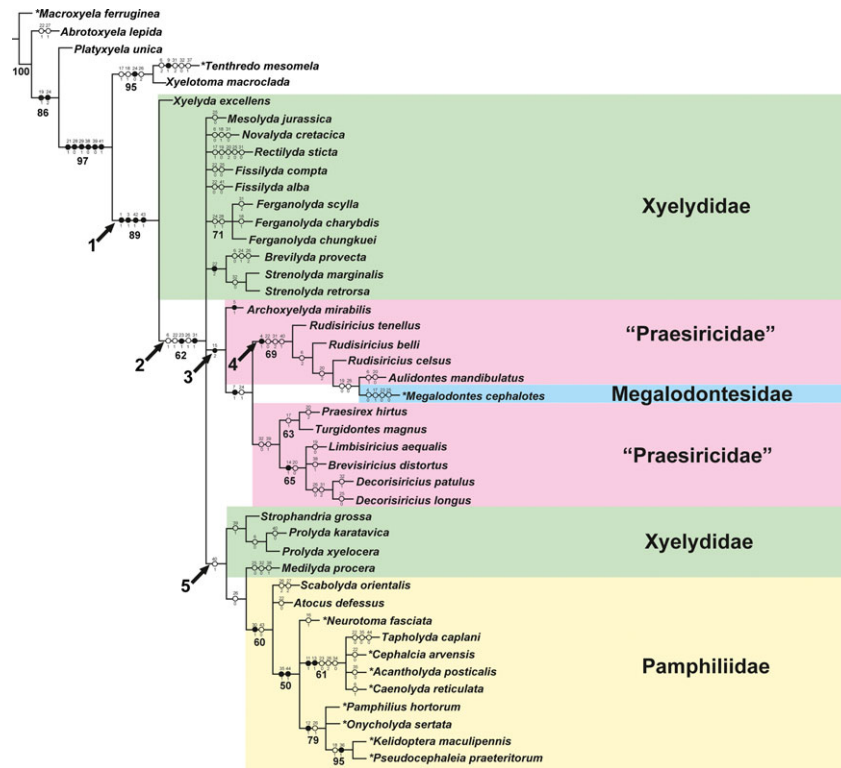


Fig. 3. Phylogeny of extant and extinct Pamphilioidea. Strict consensus tree recovered from parsimony analyses of morphological characters. Character state changes are plotted on each node with bootstrap support values > 50%. An asterisk indicates extant species.

and gamma distribution (Appendix S3). Two separate runs, each having unlinked partitions and four Bayesian Markov chain Monte Carlo (MCMC) chains (three heated and one cold) ran simultaneously for a total of 10 million generations, with sampling every 1000 generations and the first 25% discarded as burn-in. Stationarity was considered to be reached when the average standard deviation of split frequencies was below 0.01. A majority-rule consensus tree was computed with posterior probabilities (PP) for each node.

Reconstruction of ancestral character states

Ancestral states for the first flagellomere (Char. 6), and the first (Char. 43) and second (Char. 44) terga were reconstructed in Mesquite v. 2.75 (Maddison and Maddison, 2014) with MP optimization. We based ancestral state reconstructions on the strict consensus tree from MP analysis of 44 terminals with 45 morphological characters.

Results

Phylogeny

Phylogenetic results from MP analysis based on morphological characters. Parsimony analysis of the

morphological data set (Appendix S2) yielded 48 most parsimonious trees, with the following characteristics: tree length = 137, consistency index (CI) = 0.41 and retention index (RI) = 0.74. To alleviate the potential effect of homoplasy, a reweighted tree and a weighted w-consensus tree were generated. Both results were isomorphic with the strict consensus tree. Thus we explored the group's overall classification, taxonomic refinements and evolution of morphological features mainly based on the present parsimony framework (Fig. 3).

The superfamily Pamphilioidea was recovered as monophyletic with moderate support and with multiple unambiguous morphological characters (Fig. 3, clade 1). Within Xyelydidae, *Xyelyda* was sister to the remaining pamphilioids (Fig. 3, clade 2), three genera (*Strophandria*, *Prolyda* and *Medilyda*) constituted a grade basal to Pamphiliidae (Fig. 3, clade 5), and the remaining were scattered and formed a polytomy at the base of Pamphilioidea. Thus, the monophyly of Xyelydidae was not recovered. The monophyly of Pamphiliidae, two extant subfamilies Pamphiliinae (except *Neurotoma*) and Cephalciinae, were supported, respectively. However, most inter-generic relationships among Pamphiliidae were poorly resolved.

The extinct Praesiricidae together with *Megalodontes* (Megalodontesidae) (Fig. 3, clade 3) formed a monophyletic group supported by one synapomorphic

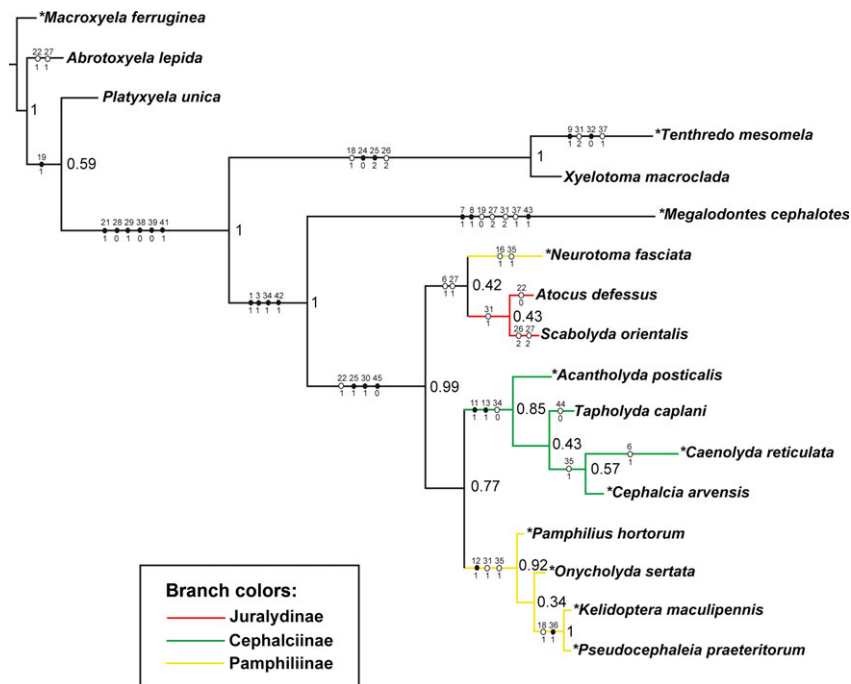


Fig. 4. Phylogeny of extant and extinct Pamphiliidae. Consensus tree recovered from Bayesian analysis of combined morphological characters and DNA sequence data. Bayesian posterior probability values are included at nodes. Synapomorphic characters mapped on each node are recovered from parsimony optimization of morphological characters alone. An asterisk indicates extant species.

character state: subcosta (SC) of fore wing absent (15:2). *Megalodontes* combined with Rudisiricinae (*Rudisiricius* + *Aulidontes*) as a monophyletic lineage (Fig. 3, clade 4) shared an unambiguous synapomorphic character state: the antenna with a long scape, which is uniformly thick or thickened apically, and is at least twice as long as wide (4:1); this inferred a reversal to 4:0 in *Megalodontes*. Additionally, the subfamily Decorisiricinae, including *Limbsiricius*, *Brevisiricius* and *Decorisiricius*, was also recovered as monophyletic, supported by a very narrow basal costal area of the fore wing (14:1).

In summary, based on our results, the monophyly of the superfamily Pamphilioidea and the extant family Pamphiliidae were both well supported. The extinct family Praesiricidae was not monophyletic, with *Megalodontes* as a derived branch within this family. Xyelididae was paraphyletic, with the relationships among the genera inadequately resolved.

Phylogenetic results from BI analysis based on total evidence (morphology + molecular data). As mentioned above, the inter-relationships among Pamphiliidae genera were poorly supported. Previous studies found that the addition of molecular data increased the resolution of fossil taxa (Shaffer et al., 1997; Rothwell and Nixon, 2006; Wiens et al., 2010). Herein, when analyzing a total-evidence data set of Pamphiliidae (Fig. 4), this family was recovered as monophyletic with strong statistical support (PP: 0.99)

and consisted of two major groups, i.e. three heterogeneous genera (*Scabolyda*, *Atocus* and *Neurotoma*) as the sister-group to the other genera. *Neurotoma* was sister to *Scabolyda* + *Atocus* with very weak posterior probability (0.42) and supported with two homoplastic character states: the first flagellomere is distinctly shorter than the head and is several times longer than the second one (6:1), and the length of M+Cu of the fore wing is less than twice as long as cell 1mCu (27:1). Cephalciinae and Pamphiliinae were sisters with moderate posterior support (PP: 0.77). Cephalciinae comprised the extant genera *Caenolyda*, *Cephalcia* and *Acantholyda*, together with the fossil genus *Tapholyda*, and was recovered with moderate statistical support (PP: 0.85) with *Acantholyda* sister to the clade [*Tapholyda*, (*Caenolyda*, *Cephalcia*)]. Pamphiliinae was recovered with strong statistical support (PP: 0.92) with *Pamphilius* sister to the clade [*Onycholyda*, (*Kelidoptera*, *Pseudocephaleia*)].

Ancestral-state reconstructions

The first flagellomere (Fig. 5a) ancestral state for all Pamphilioidea was ambiguous. There were at least three independent transitions to a very short first flagellomere (i.e. much shorter than head and at most twice as long as second one) from a relatively long first flagellomere ancestor (i.e. distinctly shorter than head and at least three times longer than the second one) within pamphiliids and praesiricids.

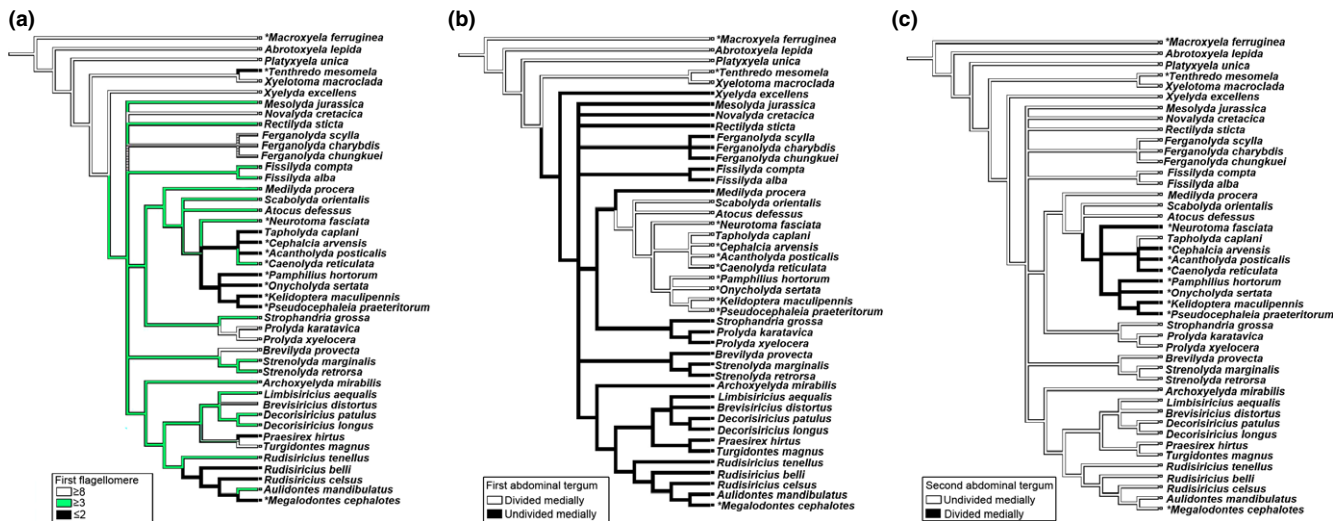


Fig. 5. Ancestral character state reconstruction for three morphological characters of Pamphilioidea. Input tree is the strict consensus tree from MP analysis of 44 terminals with 45 morphological characters. (a) MP optimization of the first flagellomere (Char. 6); (b) MP optimization of the first abdominal tergum (Char. 43); (c) MP optimization of the second abdominal tergum (Char. 44). Numbers in (a) indicate the length ratio of the first flagellomere to second flagellomere.

The common ancestor to all pamphilioids possessed an undivided first abdominal tergum (Fig. 5b). There was a single transition from the undivided first tergum to a divided one in Pamphiliidae. In addition, the divided second tergum arose once in extant pamphiliids (Fig. 5c).

Discussion

Taxonomy and relationships among Pamphilioidea

Pamphiliidae. Our results corroborate the results of Ronquist et al. (2012), who also recovered both subfamilies of Pamphiliidae, Cephalciinae (conifer needle feeders) and Pamphiliinae (angiosperm leaf feeders), as monophyletic. In our study, *Neurotoma* is located in a basal position, similar to studies that exclude fossils (Vilhelmsen, 2001; Schulmeister, 2003); however, *Neurotoma* is sister-group to *Atocus* + *Scabolyda* with weak Bayesian posterior probability (PP: 0.42). These three heterogeneous genera (*Scabolyda*, *Atocus*, *Neurotoma*) have existed across a time span from 165 to 50 Ma to the present, respectively. Wang et al. (2014a) emended the subfamily Juralydinae and proposed to transfer *Atocus* from Pamphiliinae to Juralydinae, mainly based on its symplesiomorphies shared with Juralydinae (i.e. the first flagellomere about twice to three times as long as the second one, long 1-RS of fore wing, etc.). *Neurotoma* possesses a similarly long first flagellomere (i.e. at most three times as long as the second one), except *N. tropica* with the first flagellomere almost 3.7 times as long as the second one (Shinohara, 1986). In

spite of *Scabolyda* and *Atocus* plus *Neurotoma* forming a clade with weak support, we tentatively recommend to expand the concept of Juralydinae to include the small extant genus *Neurotoma* mainly based on its relatively long first flagellomere (6:1) under the present total-evidence analysis shown (Fig. 4).

Praesiricidae. Due to limited praesiricid fossils and available data, few systematic studies have focused on this family. Wang et al. (2015c) conducted the first phylogenetic analysis of inter-generic relationships of Praesiricidae, using 18 morphological characters covering three outgroups and 15 ingroups. They concluded that Praesiricidae was paraphyletic, in agreement with Rasnitsyn (1988, fig. 1) who placed it as ancestral (= paraphyletic) with respect to Megalodontesidae. In the present study, we revised the morphological data set of Wang et al. (2015c), using 28% of their characters, and expanded it to include 31 genera of Pamphilioidea. It is not surprising that our present results are nearly identical to theirs (see details in Wang et al., 2015c), i.e. Praesiricidae is confirmed as a paraphyletic group. Praesiricidae in conjunction with *Megalodontes* form a monophylum with the SC of the fore wing absent; Decorisiricinae is also recovered as a monophyletic group with relatively strong support. Our results corroborate their decision to synonymize Praesiricidae under Megalodontesidae.

In summary, we reach a similar conclusion to Wang et al. (2015c) that Praesiricidae is paraphyletic with regard to Megalodontesidae; therefore, Megalodontesidae should be redefined to encompass all the praesiricid lineages. *Megalodontes* is placed in Rudisiricinae and therefore the subfamily must be renamed Megal-

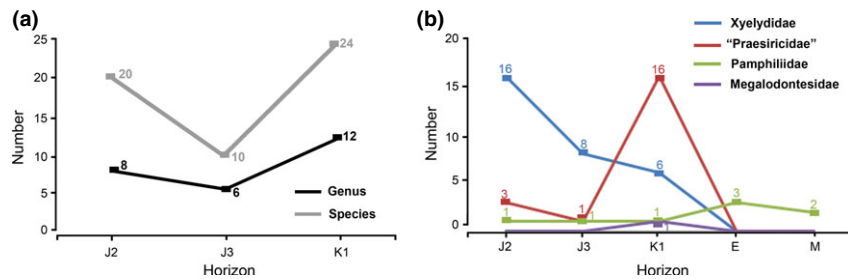


Fig. 6. Histograms of genera and species richness of Pamphilioidea during the mid Mesozoic. (a) Total number of genera and species of Pamphilioidea in the Mesozoic; (b) number of species among four families of Pamphilioidea in Mesozoic. J2, Middle Jurassic; J3, Late Jurassic; K1, Early Cretaceous; E, Eocene; M, Miocene.

odontesinae. Thus, the family Megalodontesidae is redefined and divided into four primary clades, allocated to four subfamilies: Decorisiricinae, Megalodontesinae, Praesiricinae and Archoxyelydinae.

Xyelydidae. All praesiricid species are highly distinctive and easy to identify, whereas xyelydids are very similar morphologically, and even the genera are defined by rather ambiguous and variable characters (Rasnitsyn, 1983; Wang et al., 2014b). The addition of recently discovered fossils to our analyses further demonstrates the ambiguity of these characters.

Our phylogenetic analysis (Fig. 3) corroborates the paraphyly of *Xyelydidae*. *Xyelyda* is placed as sister to the remaining pamphilioids, possessing a long and enlarged first flagellomere and proclival 1-RS, which are ancestral characters for Pamphilioidea. Moreover, three genera (*Strophandria*, *Prolyda*, *Medilyda*), together with Pamphiliidae, form a monophyletic group with weak character support. Therefore, we prefer not to transfer these three genera to Pamphiliidae until they can be better characterized through the study of more material. The monophyly of *Xyelydidae* is not confirmed and highly doubtful, but we propose it is better to leave subsets of *Xyelydidae* here rather than recommend reassignment based on incomplete data.

In summary, although the inter-relationships within the superfamily Pamphilioidea are not fully and satisfactorily resolved, there are a few clades that are well supported by our phylogenetic analyses, such as a much more robust placement of the primitive and ancient fossil taxa (xyelydids and praesiricids) in the parsimony tree. This is to be expected as our analyses constitute an initial probe into the internal phylogeny of Pamphilioidea, including morphological and molecular data with the most comprehensive sampling of fossils and extant genera. Notwithstanding, the bias in character sampling is always a serious issue owing to limited available characters preserved on fossils (Prevosti and Chemisquy, 2009; Pattinson et al., 2015). As a result, the phylogenetic inference and affinity are mostly dependent on the wing venation characters (Li et al., 2013; Yang et al., 2014). Our present study also has a similar issue men-

tioned above, i.e. the predominance of wing venation characters in morphological character sampling (~62%). Future fossil discoveries and additional structural evidence will provide a more secure placement of the less character-rich taxa, and contribute to refining the phylogeny of the Pamphilioidea.

Origin, early evolution and diversity of Pamphilioidea

From the histograms of specific and generic richness for the Pamphilioidea (Fig. 6a), the diversity of genera and species seems to have been fairly even from the late Middle Jurassic at 165 Ma to the mid Early Cretaceous at 125 Ma, with generic diversity reaching a peak in the Early Cretaceous and very rare after that as indicated by their relict status in the Cenozoic. A comparison of the diversity of species between families (Fig. 6b) shows that the number of species of *Xyelydidae* peaked in the Middle Jurassic and decreased in the Late Jurassic and Early Cretaceous. Contrastingly, the number of species in *Megalodontesidae* (*sensu nov.*) shows a significant increase during the Early Cretaceous. The earliest known fossils of the extant family Pamphiliidae originate from the Middle Jurassic, and the number of species is low from the Middle Jurassic to the Early Cretaceous and even to the Cenozoic. As the earliest known *Megalodontesidae* (*sensu nov.*) of the Middle Jurassic are attributed to Decorisiricinae, the lineage of Megalodontesinae (*Megalodontes*, *Jibaissodes* and former Rudisiricinae) should have also originated during the Middle Jurassic or possibly earlier. But to date, they are only known from the Late Jurassic (*Aulidontes*) and the Cretaceous (*Rudisiricius*, *Jibaissodes*).

Ronquist et al. (2012) estimated that the earliest divergence time of Pamphiliidae based on total-evidence dating was in the Early Cretaceous *c.* 130 Ma, 10 million years earlier than that predicted by molecular clock approaches using the independent gamma rates (IGR) model (*c.* 120 Ma). However, the hitherto earliest record of Pamphiliidae is *Scabolyda orientalis* from the late Middle Jurassic (*c.* 165 Ma). This fossil

timing indicated that the diversification within the above-mentioned clades could have occurred no later than the Middle Jurassic, pushing the time of their origin and initial divergence significantly deeper in time, possibly to the Early Jurassic period.

After decades of studies, it is known that the morphology of the first flagellomere is very diverse in lower hymenopterans, and that a long, broad first flagellomere is a plesiomorphic character state of Hymenoptera (Rasnitsyn, 1980, 1996). However, when considering the morphological evolution of Pamphilioidea, it is notable that the first flagellomere exhibits significant variations. The first flagellomere is several times as long as the head and also several times (at least eight times) as long as the second flagellomere in some now-extinct genera of pamphilioids (Fig. 1a, c), i.e. *Novalyda*, *Turgidontes*, *Prolyda* and *Xyelyda*. Besides, the first flagellomere is distinctly shorter than the head but still at least three times as long as the second flagellomere (Fig. 1d), as in most xyelydids, some *Neurotoma*, *Scabolyda*, *Atocus* and *Archoxyelyda*, Decorisiricinae, and some *Rudisiricius*. Furthermore, in *Megalodontes*, most pamphiliids and most *Rudisiricius*, the first flagellomere is shorter than the head and at most twice as long as the second flagellomere (Fig. 1e, f). The character state of first flagellomere is polymorphic in Pamphilioidea, namely the ancestral state is considered unchanged (xyelid-like), with other states appearing multiply (fig. 12 in Rasnitsyn, 1996; nodes 13, 14, 20, 22, 24). However, our ancestral-state reconstruction (Fig. 5a) indicates that the configuration of the first flagellomere of the ancestor of Pamphilioidea is ambiguous, but at least several times (no fewer than three times) as long as the second. In Pamphilioidea, there are at least three independent transitions to the relatively shorter first flagellomeres from the longer first flagellomere ancestor, within pamphiliids, *Praesirix*, *Rudisiricius* + *Megalodontes* (Fig. 5a), and originated in the early Cretaceous.

The character of whether the first two terga are split varies among lower Hymenoptera. The hymenopteran ancestral state is a medially split first tergum and undivided second (most ‘Symphyta’). The Pamphilioidea ancestral condition includes having both terga undivided. Our ancestral-state reconstruction of abdominal terga suggests that the ancestor of Pamphiliidae had a medially split first tergum, implying that it reversed to the plesiomorphic state (Fig. 5b). There was also a single transition from an undivided second tergum to a divided one within extant pamphiliids (Fig. 5c).

Conclusions

Our investigation represents the first phylogenetic study of Pamphilioidea that includes most extinct and

extant genera, and combines molecular and morphological data. Our phylogenetic analyses of the superfamily Pamphilioidea corroborate the monophyly of Pamphilioidea and Pamphiliidae, and also demonstrate that the extinct families Praesiricidae and Xyelydidae are not monophyletic. All members of Praesiricidae were therefore transferred to Megalodontesidae. Rudisiricinae, including *Megalodontes*, was renamed as Megalodontesinae. Based on fossil evidence, the origin and initial divergence of Pamphiliidae is pushed back deeper in time, possibly as early as the Early Jurassic. The relatively old lineages, xyelydids and praesiricids, span from the Middle Jurassic to the Early Cretaceous, undergoing origination, diversification, declination and finally becoming extinct. The modern groups of pamphilioids are now a combination of relict and younger lineages. Discovery and examination of more fossils from a variety of geological locations and periods, improving taxonomic coverage, and increasing molecular data will enable more complete analyses and probably lead to a more robust phylogenetic hypothesis.

Taxonomy

Hymenoptera Linnaeus, 1758

Pamphilioidea Cameron, 1890

Megalodontesidae Konow, 1897 (as Megalodontidae, not Megalodontidae Morris & Lycet 1853).

= Praesiricidae Rasnitsyn, 1968, **syn. nov.**

See above for the reasons of synonymy.

Megalodontesinae Konow, 1897

= Rudisiriciinae Gao, Shih, Rasnitsyn & Ren, 2010, **syn. nov.**

See above for the reasons of synonymy.

Xyelydidae Rasnitsyn, 1968

***Medilyda* Wang & Rasnitsyn gen. nov.**

Type species. Medilyda procera sp. nov.

Diagnosis. Head circular and massive, at least as wide as mesonotum. Fore wing with pterostigma sclerotized completely, the latter narrow and long; SC very close to R; posterior branch of SC extremely short and almost diminished; 2r-rs meeting pterostigma almost at its mid-length; cell 1r at least as long as cell 2r. In hind wing, 1-RS short, at most half of 1r-m.

Etymology. The generic name is a combination of the Latin ‘Medi-’ meaning middle (referring to 2r-rs of fore wing intersecting the middle of pterostigma) and *Lyda*, a junior synonym of *Pamphilius* Latreille, 1802, often used as a suffix for generic names in Pamphilioidea. Gender feminine.

Included species. *M. procera* sp. nov., *M. distorta* sp. nov.

Remarks. For comparison with other genera, see key below.

***Medilyda procera* Wang & Rasnitsyn sp. nov.**

Fig. 7, Fig. S1

Diagnosis. In addition to the generic diagnosis, 1-M as long as 1-Cu and 2-Cu; 1cu-a located almost at middle of cell 1mcu; RS+M just slightly shorter than 2-M; 2r-m far from 2r-rs by longer than half of its own length; cell 2r rather small, almost one-third of cell 3r in length.

Etymology. The specific name is derived from the Latin word ‘procerus’ meaning tall and high, referring to the larger body size of this species.

Material examined. Holotype, No. CNU-HYM-NN-2012143; Paratype, No. CNU-HYM-NN-2012144

Locality and horizon. Jiulongshan Formation; Dahugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China (41°18.979’N, 119°14.318’E); latest Middle Jurassic of late Callovian age.

Description. As preserved, body (Fig. 7a) moderately infuscated, first three abdominal segments slightly darker than remaining parts. Head (Fig. 7b)

with eyes placed at the mandibular base, 0.3 times head length; mandible strong and long, sickle-like, arching in basal half, with sub-apical tooth short and acute, positioned three-fifths to the apical, and apical tooth with inner margin poorly preserved (with no serration visible). Pronotum short with wide and shallowly incurved hind margin; mesoprescutum short, 0.3 times as long as mesonotum; metascutellum nearly round. Abdomen with the third and fourth segments slightly wider than remaining abdominal segments; first tergum not split medially.

Fore wing (Fig. 7d) with basal part of vein R curved anteriorly and then distinctly angular at RS base; 1-RS short and proclival, inclined toward wing apex, about 0.37 times as long as 1-M; 1r-rs parallel to 2r-rs, the latter about 1.38 times as long as the former, with RS between them arching towards wing base; M+Cu bent gently; 2r-m separated from 2r-rs by 0.54 times its own length, located distal to middle of cell 2mcu; 3r-m separated from apex of cell 3r by just slightly shorter than half of its length, and 1.35 times as long as 2r-m; 1m-cu 0.54 times and 0.26 times as long as 2-Cu and 3-Cu, respectively; 1cu-a bent distinctly towards wing apex, 1.16 times as long as 2-Cu; 2m-cu straight, at middle of cell 3rm; cell 1mcu 1.28 times as long as wide, and 0.63 times as long as cell 2rm; cell 2rm almost as long as 3rm, and 0.75 times as long as and 0.55 times as wide as cell 2mcu; cell 2r rather small, and cell 3r three times as long as cell 2r. Hind wing with SC present, anterior branch arched and meeting with C almost at origin of 1-RS; 1-RS rather

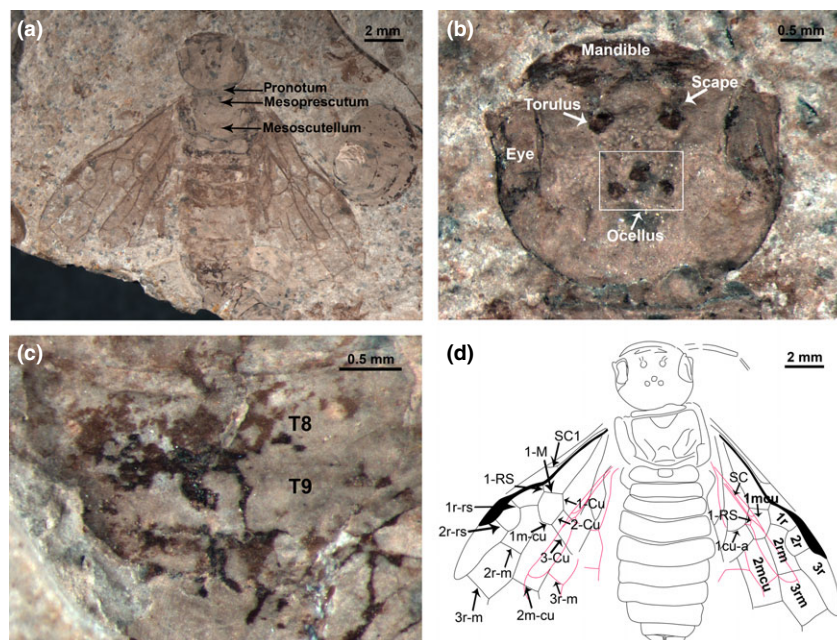


Fig. 7. *Medilyda procera* gen. et sp. nov. Holotype, CNU-HYM-NN-2012143. (a) Photo of habitus; (b) head; (c) genitalia; (d) line drawing.

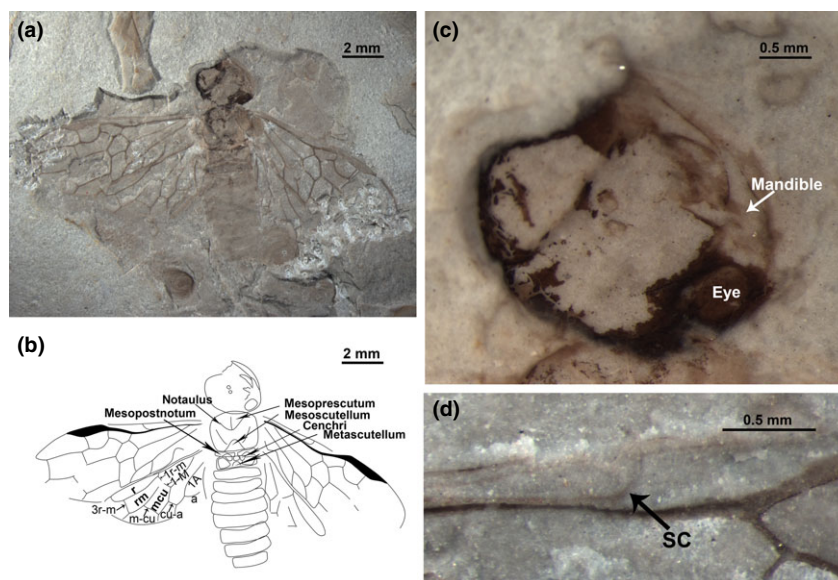


Fig. 8. *Medilyda distorta* sp. nov. Holotype, CNU-HYM-NN-2012171. (a) Photo of habitus; (b) line drawing; (c) head; (d) subcosta (SC) of fore wing.

short; 3r-m separated from apex of cell r by almost its own length; cell r becoming rounded apically.

Measurements (in mm). Body length (excluding antenna) 15.0, head length including mandible 3.3, width 3.8, fore wing length up to end of cell 3r 11.1, hind wing length up to end of cell r 7.0.

***Medilyda distorta* Wang & Rasnitsyn sp. nov.**

Fig. 8

Diagnosis. In addition to the generic diagnosis, 1-Cu short; 1-M slightly longer than 1-Cu; 2-Cu longer than 1-Cu; 1cu-a located proximal to middle of cell 1mcu; RS+M half of 2-M; 2r-m separated from 2r-rs by almost half of its own length; cell 2r almost half of cell 3r in length.

Etymology. The specific name is derived from the Latin word ‘distortus’ meaning separated, referring to the head departed from the body.

Material examined. Holotype, No. CNU-HYM-NN-2012171

Locality and horizon. Jiulongshan Formation; Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China (41°18.979'N, 119°14.318'E); latest Middle Jurassic of late Callovian age.

Description. As preserved, body (Fig. 8a) moderately pale with part of head slightly darker and abdomen paler than thorax; pterostigma sclerotized

completely. Head (Fig. 8c) with eye 0.23 times head length; mandibles sickle-like, strong but rather short, and inner side of apical tooth with serration.

Mesonotum (Fig. 8b) with all main sulci present; mesoprescutum with notauli short and meeting at angle of 106°; mesoscutellum large, and almost the same size as mesoprescutum; mesopostnotum rectangular, about 0.47 times as long as metanotum; cenchri relatively large and long, reaching nearly the mid-length of metanotum; metascutellum rounded triangular.

Fore wing (Fig. 8b, d) with pterostigma about 5.2 times as long as wide; 1-RS half of 1-M; M+Cu rather straight; 2-M as long as 2-Cu, and 1-M 0.7 times as long as the former; 2r-m separated from 2r-rs by slightly longer than half of its own length, located distal to middle of cell 2mcu; 3r-m separated from apex of cell 3r by 0.6 times of its length, and 1.4 times as long as 2r-m; 1m-cu 0.5 times and 0.43 times as long as 2-Cu and 3-Cu, respectively; 1cu-a bent distinctly towards wing apex, 0.8 times as long as 2-Cu, almost placed slightly proximal to middle of cell 1mcu; cell 1mcu 1.33 times as long as wide, and 0.69 times as long as cell 2rm; cell 2rm almost as long as 3rm, and 0.77 times as long as and 0.6 times as wide as cell 2mcu; cell 2r rather small, and cell 3r 2.45 times as long as cell 2r. In hind wing (Fig. 8b), cell r rounded apically; 1-RS rather short; cross-vein 1r-m just located at bases of both RS and M; 3r-m separated from apex of cell r by almost its own length; cross-vein m-cu wavy, longer than 3r-m, joining 2-M distal to mid-length of cell rm, separated from 3r-m by a distance equivalent to nearly its length; cross-vein cu-a nearly at the middle of cell mcu; vein M+Cu almost

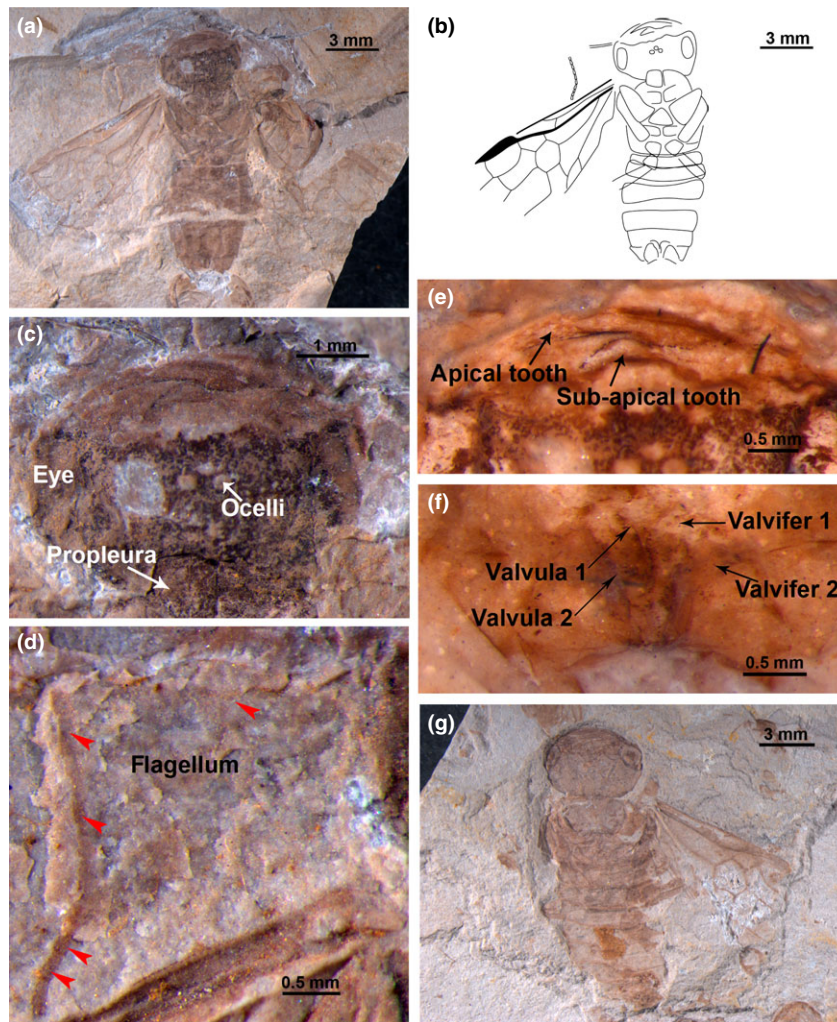


Fig. 9. *Brevilyda provecta* gen. et sp. nov. Holotype (a–f), CNU-HYM-NN-2012151. Paratype (g), CNU-HYM-NN-2012149. (a) Photo of habitus; (b) line drawing; (c) head; (d) part of antenna; (e) mandible; (f) genitalia; (g) photo of habitus.

straight, 1A arched towards upward, and cross-vein a proximal to cu-a by at least 0.8 times as long as its own length.

Measurements (in mm). Body length (excluding antenna) 9.63, head length including mandible 2.29, width 2.8, fore wing length up to end of cell 3r 8.2, hind wing length up to the end of cell r 5.19.

***Brevilyda* Wang & Rasnitsyn gen. nov.**

Type species. *Brevilyda provecta* sp. nov.

Etymology. The generic name is a combination of the Latin ‘Brevi-’ meaning short (referring to the short RS+M of fore wing) and *Lyda*, a junior synonym of *Pamphilus* Latreille, 1802, often used as a suffix for generic names in Pamphilioidea. Gender feminine.

Included species. *B. provecta* sp. nov.

Diagnosis. Head big and widened, head width at least 0.43 times fore wing length (up to apex of cell 3r); mesopseudosternum triangular, reaching the fore margin of mesoventropleuron; fore wing with pterostigma sclerotized completely, narrow and long, almost 4.5 times as long as wide; SC1 almost equal to SC2 in length; 1-RS subvertical, more or less 0.4 times as long as 1-M; 2r-m antefurcal; cell 2r large, at least 1.5 times as long as cell 1r; cell 1mcu forming a hexagon, and at least 1.1 times as long as wide.

Remarks. For comparison with other genera, see key below.

***Brevilyda provecta* Wang & Rasnitsyn sp. nov.**

Fig. 9, Fig. S2

Diagnosis. As for genus.

Etymology. The specific name is derived from the Latin word ‘provectus’, meaning anterior and before, referring to 2r-m of fore wing antefurcal.

Material examined. Holotype, No. CNU-HYM-NN-2012151; Paratypes, No. CNU-HYM-NN-2012149; No. CNU-HYM-NN-2012150(p/c).

Locality and horizon. Jiulongshan Formation; Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China (41°18.979’N, 119°14.318’E); latest Middle Jurassic of late Callovian age.

Description. As preserved, body (Fig. 9a) moderately dark, including head (excluding mandible) slightly darker than thorax and abdomen. Head (Fig. 9c) about 1.5 times as wide as mesothorax, 1.68 times as wide as long, its fore (clypeal) margin wavy with small teeth; mandible (Fig. 9e) sickle-shaped, reaching opposite side of head when closed, with apical tooth long and curved, sub-apical one short, placed at about 0.5 mandible length; three ocelli small and well preserved, forming an acute triangle; antenna

(Fig. 9d) thin and narrow, with at least ten antennal segments preserved.

Prothorax with propleurae narrow, about 0.36 times as wide as mesopleuron; mesopseudosternum triangular, relatively large, 1.8 times as wide as high. Legs ordinary, with hind trochanter large, almost the same size as hind coxa; femur narrow, 0.7 times as wide as the first abdominal segment. Ovipositor (Fig. 9f) poorly preserved; if correctly interpreted, very short, with basal stylets stretched into its sixth segment, wide apart and meeting only at their apices.

Fore wing (Fig. 9b) with SC bifurcate, at middle of cell c; R almost straight before RS base; 1-RS subvertical, 0.57 times as long as 1-M; 1-M nearly as long as RS+M; 1r-rs short and vertical, 0.46 times as long as 2r-rs and parallel to it, with RS between them arching towards wing base; 2r-rs intersecting pterostigma near its apex, and the latter narrow and long, about 4.45 times as long as wide; M+Cu curved sharply; 1-Cu 1.5 times as long as 1-M; 2r-m just slightly antefurcal, located distal to middle of cell 2mcu; 1m-cu relatively long, 0.67 times and 0.57 times as long as 2-Cu and 3-Cu, respectively; 1cu-a straight, slightly distal to middle of cell 1mcu; cell 1mcu forming a hexagon, 1.17

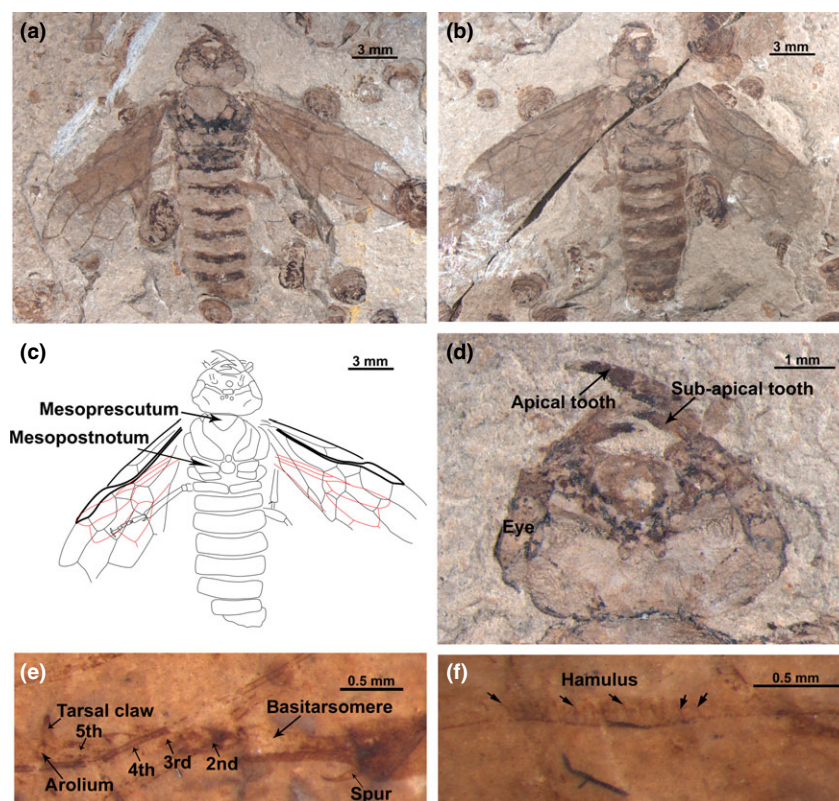


Fig. 10. *Strenolyda marginalis* gen. et sp. nov. Holotype, CNU-HYM-NN-2012166(p/c). (a) Photo of part; (b) photo of counterpart; (c) line drawing; (d) head; (e) tarsi; (f) hamulus on the hind wing.

times as long as wide, and 0.78 times as long as cell 2r-m.

Measurements (in mm). Body length (excluding antenna) 14.1, head length including mandible 3.0, width 4.9, fore wing length as preserved 10.0.

***Strenolyda* Wang & Rasnitsyn gen. nov.**

Type species. *Strenolyda marginalis* sp. nov.

Etymology. The generic name is a combination of the Greek ‘Stren-’ meaning strong and robust, and *Lyda*, a junior synonym of *Pamphilius* Latreille, 1802, often used as a suffix for generic names in Pamphilioidea. Gender feminine.

Included species. *S. marginalis* sp. nov., *S. retrorsa* sp. nov.

Diagnosis. Head massive and almost round; fore wing with pterostigma sclerotized completely or just around margins; SC1 longer or almost as long as SC2; 1-RS short, shorter than half of 1-M; angle between 1-M and 1-Cu 100–140°; 2r-m antefurcal, sometimes just slightly postfurcal; cell 1m-cu at least as long as wide, no more than 1.5 times as long as wide; cell 1r short, 0.6–0.7 times as long as cell 2r.

Remarks. For comparison with other genera, see key below.

***Strenolyda marginalis* Wang & Rasnitsyn sp. nov.**

Fig. 10, Fig. S3

Diagnosis. In addition to the generic diagnosis, fore wing with pterostigma sclerotized around margins; SC1 equal to SC2 in length; 2r-m antefurcal; 1-RS about one-third as long as 1-M; cell 1m-cu as long as wide; angle between 1-M and 1-Cu almost 130°; 1-Cu roughly equal to 2-Cu in length; cell 2r at least 1.5 times as long as cell 1r.

Etymology. The specific name is derived from the Latin word ‘marginalis’, meaning margin and border, referring to pterostigma sclerotized just around margins.

Material examined. Holotype: No. CNU-HYM-NN-2012166(p/c); Paratypes: No. CNU-HYM-NN-2012165; No. CNU-HYM-NN-2012170.

Locality and horizon. Jiulongshan Formation; Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China (41°18.979'N,

119°14.318'E); latest Middle Jurassic of late Callovian age.

Description. As preserved, body (Fig. 10a, b) moderately brown, including anterior margin of abdominal segments slightly darker than other structures. Head (Fig. 10d) 1.26 times as wide as mesonotum, nearly trapezoidal, 1.77 times as wide as long (excluding mandibles), with three ocelli at middle of head; clypeal margin slightly wavy; mandibles sickle-like, strong and long, reaching opposite side of head when closed, with apical tooth long, slanting sub-apical one placed basal of mandible.

Mesoprescutum almost 0.4 times as long as mesonotum length; mesopostnotum wide, about 2.4 times as long as wide. Hind femur narrow and long, 9.1 times as long as wide, and 0.67 times as long as first abdominal segment, with apical spurs preserved; basitarsomere almost equal to the remaining three tarsomeres combined, with big claws bearing prominent basal lobe, otherwise simple; tarsomere 1 : 2 : 3 : 4 : 5 = 3.1 : 1.4 : 1.1 : 1 : 1.4 (Fig. 10e).

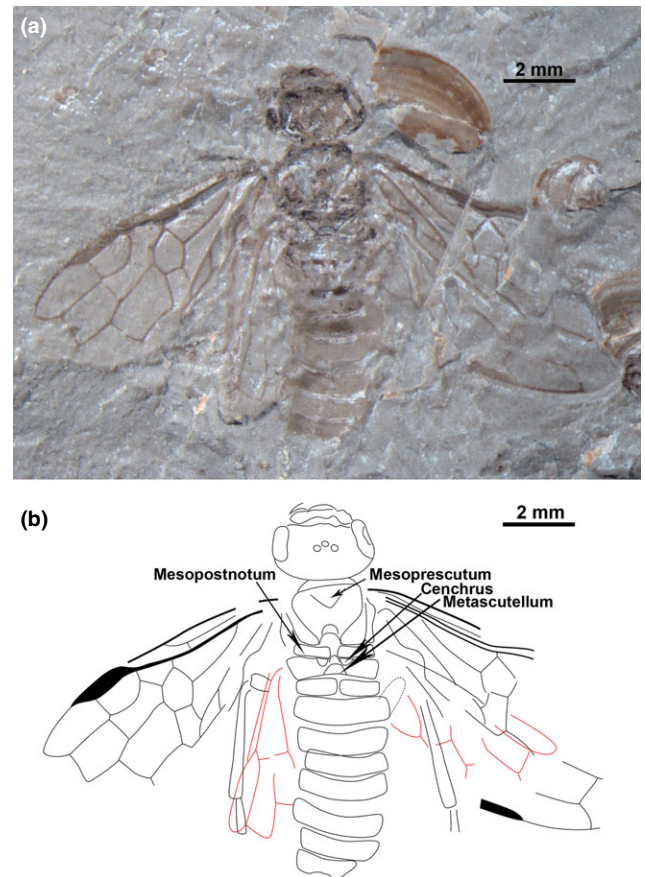


Fig. 11. *Strenolyda retrorsa* sp. nov. Holotype, CNU-HYM-NN-2012164. (a) Photo of habitus; (b) line drawing.

Fore wing (Fig. 10c) with 1-RS rather short, about 0.28 times as long as 1-M, RS+M almost equal to 1-M in length, and perpendicular to it; 2r-rs parallel to 1r-rs, and about 2.6 times as long as 1r-rs; 3r-m bent towards wing base, separated from apex of cell 3r by 0.73 times its own length; M+Cu bent gently; 1m-cu relatively long, 0.6 times and 0.5 times as long as 2-Cu and 3-Cu, respectively; 2m-cu placed in the middle of cell 3rm; cell 1mcu 0.69 times as long as cell 2rm; cell 2rm as long as cell 3rm, 0.7 times as long as and 0.5 times as wide as cell 2mcu. Hind wing with 19 hamuli present (Fig. 10f), and SC well developed with two branches; 1-RS 0.8 times as long as 1-M; cross-vein 1r-m distant from bases of both RS and M, about 0.68 times as long as 1-RS; 3r-m separated from cell r by almost its own length; cross-vein m-cu long, equal to 3r-m in length, joining 2-M slightly distal of mid-length of cell rm.

Measurements (in mm). Body length (excluding antenna) 16.9, head length including mandible 2.6, width (the widest part) 4.7, fore wing length up to end of cell 3r 13.0, hind wing length up to the end of cell r 8.0.

***Strenolyda retrorsa* Wang & Rasnitsyn sp. nov.**

Fig. 11, Fig. S4

Diagnosis. In addition to the generic diagnosis, fore wing with pterostigma sclerotized completely; SC1 long, at least three times as long as SC2; 2r-m postfurcal; 2m-cu located proximal to cell 3rm; 1cu-a distal to middle of cell 1mcu; cell 2r nearly 1.3 times as long as cell 1r.

Etymology. The specific name is derived from the Latin word ‘retrorsus’, meaning behind and posterior, referring to 2r-m slightly postfurcal.

Material examined. Holotype, No. CNU-HYM-NN-2012164; Paratypes, No. CNU-HYM-NN-2012167; CNU-HYM-NN-2012158; CNU-HYM-NN-2012163.

Locality and horizon. Jiulongshan Formation; Daohugou Village, Shantou Township, Ningcheng

County, Inner Mongolia, China (41°18.979'N, 119°14.318'E); latest Middle Jurassic of late Callovian age.

Description. As preserved, body (Fig. 11a) moderately brown including abdomen slightly paler than head and thorax. Head massive, widest behind middle length of head, 1.1 times as wide as mesothorax, with eyes relatively large, reniform, and 3.24 times as long as wide; mandible sickle-like, preserved poorly and clypeus slightly wavy.

Pronotum trapezoidal and short, about 7.1 times as wide as long; mesonotum with mesoprescutum almost 0.4 times as long as mesonotum length, with notauli at an angle of 98.7°; mesopostnotum rectangular, 3.4 times as wide as long, with a small round foramen in the middle; metanotum with cenchri and metascutellum preserved, and almost in the same length.

Tibiae almost as long as the first abdominal segment length, 6.76 times as long as wide and covered with dense setae. Abdomen with first terga split medially.

Fore wing (Fig. 11b) with posterior branch of SC short and subvertical, 1.55 times as long as 1-RS; 1-RS rather short, about 0.22 times as long as 1-M; RS+M almost equal to 1-M in length; 1r-rs twice as long as 1-RS, and 2r-rs about twice as long as 1r-rs; 3r-m bent towards wing base; M+Cu bent gently; 1-Cu as long as 1-M, the angle between them about 130°; 3r-m separated from apex of cell 3r by 0.82 times its own length, and nearly 1.25 times as long as 2r-m; 1cu-a nearly as long as 2-Cu, and placed apparently distal to middle of cell 1mcu; cell 1mcu as long as wide, and 0.63 times as long as cell 2rm; cell 2rm as long as 3rm, 0.79 times as long as and 0.5 times as wide as, cell 2mcu. In hind wing, cross-vein 1r-m linearly aligned with 1-M; 3r-m as long as m-cu, 0.88 times as long as 1r-m & 1-M; m-cu located slightly distal to mid-length of cell rm, separated from 3r-m by 1.35 times of its own length, with cross-vein cu-a at middle of cell mcu.

Measurements (in mm). Holotype: No. CNU-HYM-NN-2012164: Body length (excluding antenna) 10.7, head length including mandible 2.13, width 2.78, fore wing length up to end of cell 3r 7.83, hind wing length up to the end of cell r 5.2.

Key to genera of Xyelydidae

1.	1-RS reclival and not very short (Fig. 2b) - 1-RS not reclival unless very short	<i>Rectilyda</i> 2
2.	1m-cu at least half as long as 3-Cu - 1m-cu much shorter	<i>Sagulyda</i> 3
3.	RS+M & 2-M straight line. Head very large. 1r usually short - RS+M meeting 2-M at distinct angle. Head usually not large	<i>Ferganolyda</i> 4
4.	1r:2r = 0.6–0.77 - 1r:2r = 0.8 or more	5 6
5.	Head large (head width at least 0.43 times fore wing length up to apex of 3r cell) (Fig. 9c) - Head smaller (head width at most 0.4 times fore wing length) (Fig. 10d)	<i>Brevilyda</i> gen. nov. <i>Strenolyda</i> gen. nov.
6.	(4). Fore wing with pale spot at base of 1r-rs hiding adjacent sections of C, R and pterostigma - No such pale spot	<i>Fissilyda</i> 7
7.	1-RS almost absent. - 1-RS well developed even if short	<i>Novalyda</i> 8
8.	2r-m distal of 2r-rs for more than half 2r-rs length - 2r-m more proximal	<i>Mesolyda</i> 9
9.	M+Cu (measured straight from base to apex) 1.0–1.2 times as long as 1m-cu (measured from end of M+Cu till base of 3-M). 1-R 1.4–1.5 times as long as 2-R - M+Cu at least 1.6 times as long as 1m-cu. 1-R at least 1.7 times as long as 2-R	<i>Xyelyda</i> 10
10.	2r-rs 1.0–1.4 times as distant from 1r-rs as from apex of pterostigma (Fig. 7d) - 2r-rs at least 1.6 times as distant from 1r-rs as from apex of pterostigma	<i>Medilyda</i> gen. nov. 11
11.	M+Cu (measured straight from base to apex) 1.3–1.8 times as long as cell 1m-cu (measured from end of M+Cu till base of 3-M) - M+Cu 1.9–2.5 times as long as cell 1m-cu	<i>Prolyda</i> <i>Strophandria</i>

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of recent taxa, specimens and GenBank accession numbers.

Appendix S2. Morphological data matrix including 44 taxa (asterisk indicates extant species).

Appendix S3. Total evidence of pamphiliids and megalodontesids.

Appendix S4. Paratypes of new species descriptions.

Fig. S1. *Medilyda procera* sp. nov. Paratype, CNU-HYM-NN-2012144. (a) Photo of habitus; (b) line drawing; (c) head; (d) subcosta (SC) of fore wing; (e) setae on the wing; (f) ovipositor.

Fig. S2. *Brevilyda provecta* sp. nov. Paratype, CNU-HYM-NN-2012150(p/c). (a) Photo of part; (b) photo of counterpart; (c) line drawing of counterpart; (d) mesonotum; (e) part of legs; (f) tibia under alcohol; (g) SC of fore wing; (h) genitalia; (i) line drawing of hind wing.

Fig. S3. *Strenolyda marginalis* sp. nov. Paratypes, CNU-HYM-NN-2012165 (a–d); CNU-HYM-NN-2012170 (e, f). (a) Photo of habitus; (b) mandible

under alcohol; (c) tarsi under alcohol; (d) line drawing; (e) photo of habitus; (f) head under alcohol.

Fig. S4. *Strenolyda retrorsa* sp. nov. Paratypes, CNU-HYM-NN-2012167 (a, b); CNU-HYM-NN-2012158 (c, d); CNU-HYM-NN-2012163 (e–h). (a) Photo of habitus; (b) line drawing; (c) photo of habitus; (d) line drawing; (e) photo of habitus; (f) head under alcohol; (g) preapical spurs of hind tibia; (h) line drawing.

Appendix 1

Morphological characters coded in the phylogenetic analysis

Head (1–6)

1 **Head shape:** head not enlarged, narrower than mesothorax = 0; head massive, as wide as thorax or wider = 1.

2 **Mandibles** (Vilhelmsen, 1997a: 16; Ronquist et al., 1999: 24; Vilhelmsen, 2001: 26): neither highly asymmetric nor extremely long and curved = 0; highly asymmetric, with distinct molar process on the right mandible corresponding to a concavity on the left = 1; elongate and curved = 2.

3 **Oral and mandibular foramina** (Vilhelmsen, 1997a: 17; Ronquist et al., 1999: 4; Vilhelmsen, 2001: 14): confluent = 0; separated = 1.

4 **Scape** (Ronquist et al., 1999: 13): short, less than twice as long as wide, moderately narrow = 0 (Fig. 1c); long, uniformly thick or thickened apically, about as long as head, at least twice as long as wide = 1 (Fig. 1e).

5 **Structure of first flagellomere** (Ronquist et al., 1999: 14): entire, simple = 0 (Fig. 1a); with discernible subdivisions = 1 (Fig. 1b).

6 **First flagellomere:** about as long as or longer than head, and at least eight times as long and several times as wide as second flagellomere = 0 (Fig. 1c); distinctly shorter than head even though at least three times longer than second flagellomere = 1 (Fig. 1d); much shorter than head and at most twice as long as second flagellomere = 2 (Fig. 1e, f).

Thorax (7–13)

7 **Mesopseudosternum** (Ronquist et al., 1999: 49): short, distant from fore margin of ventropleuron = 0; widely sharing border with fore margin of ventropleuron = 1.

8 **Ratio of length to width of cenchri** (Vilhelmsen, 2000: 5; Vilhelmsen, 2001: 117): less than twice as wide as long = 0; at least twice as wide as long = 1.

9 **Length of pronotum medially in dorsal view** (Ronquist et al., 1999: 28): long = 0; moderately short = 1.

10 **Prepectus** (Ronquist et al., 1999: 40): large = 0; reduced in size = 1; absent = 2.

11 **Tips of apical protibial spurs:** (Basibuyuk and Quicke, 1995: C; Vilhelmsen, 2001: 73): pointed and sclerotized = 0; blunt and membranous = 1.

12 **Long bristles on the tarsal claws:** one = 0; two = 1.

13 **Inner tooth on tarsal claws:** developed and strong = 0; weak and small = 1.

Wings (14–41)

14 **1/3 to 1/2 of basal costal area of fore wing (compared with the widest costal area):** wide, ≥ 0.5 width of widest costal area = 0 (Fig. 2d); narrow, < 0.5 width of widest costal area = 1 (Fig. 2c).

15 **Subcosta (SC) of fore wing:** SC present as longitudinal stem (forked or not) = 0 (Fig. 2a); present as cross-vein only = 1; absent = 2 (Fig. 2c).

16 **Number of SC branches of fore wing:** SC forked apically = 0; not forked, reaching R only = 1.

17 **Form of R of fore wing:** with an angle at RS base and/or distinctly bent before it = 0 (Fig. 2d); straight, or bent very gently = 1 (Fig. 2b).

18 **1-RS of fore wing:** well developed = 0 (Fig. 2a); extremely short = 1.

19 **Length of 1-RS of fore wing:** no shorter than 1-M = 0 (Fig. 2b); shorter than 1-M = 1 (Fig. 2c).

20 **Shape of 1-RS of fore wing:** proclinal = 0 (Fig. 2d); perpendicular to R = 1; reclinal = 2 (Fig. 2b).

21 **Rs of fore wings apically** (Ronquist et al., 1999: 81; Vilhelmsen, 2001: 164): furcate = 0 (Fig. 2a); not furcate = 1 (Fig. 2c).

22 **Angle between 1-M and 1-Cu of fore wing:** $< 90^\circ$ = 0 (Fig. 2a); $\geq 90^\circ$, $< 110^\circ$ = 1; $\geq 110^\circ$ = 2 (Fig. 2b).

23 **Cell 1m-cu of fore wing length to width ratio:** ≥ 2 = 0; < 2 = 1.

24 **Ratio of length of 1m-cu to the length of 3-Cu of fore wing:** ≥ 1 = 0; ≥ 0.5 , < 1 = 1; ≤ 0.5 = 2.

25 **Cross-vein 2r-m of fore wing:** distinctly postfurcal, distal to 2r-rs for more than half of 2r-rs length = 0 (Fig. 2b); interstitial, or just slightly postfurcal = 1; distinctly antefurcal = 2.

26 **Distance between 2r-rs to 1r-rs and 2r-rs to apex of pterostigma:** < 1.5 = 0; ≥ 1.5 , ≤ 3 = 1; > 3 = 2.

27 **Length of M+Cu of fore wing (measured straight from base to apex) to cell 1m-cu length (measured from the end of M+Cu to base of 3-M):** < 1.5 = 0; ≥ 1.5 , ≤ 2 = 1; > 2 = 2.

28 **RS+M of fore wing:** with an angle at 2-M = 0 (Fig. 2d); in line with 2-M = 1 (Fig. 2c).

29 **Length of 1-M of fore wing:** shorter than half length of 1-Cu = 0 (Fig. 2a); half as long as 1-Cu or longer = 1 (Fig. 2c).

30 **M+Cu of fore wing:** straight, or slightly bent = 0; distinctly bent, and in some cases, with an additional crossvein, cu-a or its rudiment = 1 (Fig. 2d).

31 **Cross-vein 1cu-a of fore wing:** distinctly distal to mid-length of cell 1m-cu = 0 (Fig. 2a); at or very close to mid-length of cell 1m-cu = 1 (Fig. 2b); near base of cell 1m-cu = 2.

32 **Cross-vein 1cu-a of fore wing:** at or basal to mid-length of cell a = 0; apical to mid-length of cell a = 1 (Fig. 2c).

33 **Basal hamuli** (Basibuyuk and Quick, 1997; Vilhelmsen, 2001: 172): present = 0; absent = 1.

34 **Fore wing membrane:** coriaceous, without distinct folds = 0; corrugate, more or less folded apically = 1.

35 **Angled M+Cu of fore wing:** without extra M+Cu stub = 0 (Fig. 2d); with extra M+Cu stub, short or long = 1.

36 **Cross-vein 1r-rs of fore wing:** present, and shape of cell 1r almost pentagonal or somewhat quadrangular = 0 (Fig. 2c); absent, and shape of cell 1r nearly triangular = 1.

37 **SC of hind wing** (Ronquist et al., 1999: 101; Vilhelmsen, 2001: 178): present = 0 (Fig. 2b); absent = 1 (Fig. 2a).

38 **Cross-vein 1r-m of hind wing:** distant from bases of RS = 0 (Fig. 2a); located at base of RS = 1 (Fig. 2c).

39 **Length of 1r-m of hind wing:** shorter than 1-M = 0; as long as or longer than 1-M = 1 (Fig. 2c).

40 **Cross-vein 1r-m of hind wing:** forming a distinct angle with 1-M = 0 (Fig. 2b); in line with 1-M = 1 (Fig. 2a).

41 **Cross-vein a of hind wing:** meeting cu-a at apex of cu-a and therefore in line with cu-a = 0 (Fig. 2a); meeting cu-a basal to apex of cu-a and therefore not in-line with it = 1.

Abdomen and ovipositor (42–45)

42 **Structure of ovipositor (Vilhelmsen, 2001: 192; Sharkey et al., 2012: 384):** long and thin, saw-like = 0; short and wide, claw-like = 1.

43 **First abdominal tergum (Ronquist et al., 1999: 60; Vilhelmsen, 2001: 129):** longitudinally divided = 0; undivided = 1.

44 **Second abdominal tergum (Königsmann, 1977; Vilhelmsen, 2001: 187):** undivided = 0; longitudinally divided = 1.

45 **Pleural region of abdominal segments (Vilhelmsen, 2001: 188):** pleural regions surrounding the spiracles sclerotized, but at least partly separated from tergum of the corresponding segment by membranous lines = 0; pleural regions sclerotized and entirely fused with the tergites, membranous lines absent = 1.