Diversity and phylogeny of the Mesozoic wasp family Stigmaphronidae (Hymenoptera: Ceraphronoidea)

Michael S. ENGEL & David A. GRIMALDI

Abstract: The extinct, parasitoid wasp family Stigmaphronidae (Proctotrupomorpha: Ceraphronoidea) is reviewed and a cladistic analysis of relationships undertaken. Stigmaphronids are presently known principally in Cretaceous amber from Siberia, Alaska, Canada, New Jersey, Myanmar, and Lebanon, but also from a few compressions from the Early Cretaceous of Siberia and Mongolia. As a result of the study the following new taxa are proposed, more than doubling the size of the family: *Elasmophron kurthi* nov.gen. et sp. (New Jersey amber), *Libanophron astarte* nov.gen. et sp. (Lebanese amber), *Burmaphron tridentatum* nov.gen. et sp. (Burmese amber), *B. prolatum* nov.sp. (Burmese amber), *Tagsmiphron muesebecki* nov.gen. et sp. (New Jersey amber), *T. gigas* nov.sp. (New Jersey amber), *T. ascalaphus* nov.sp. (New Jersey amber), and *T. canadense* nov.sp. (Canadian amber). The genus *Elasmomorpha* KOZLOV is proposed as a junior synonym of *Allocotidus* MUESEBECK (nov.syn.) resulting in *Allocotidus melpomene* (KOZLOV) nov.comb. Relationships are well supported, so the lack of any stratigraphic-clade rank correlation strongly suggests poor stratigraphic sampling of what was probably a very diverse lineage.

Key words: Stigmaphronidae, taxonomy, Cretaceous, amber, biogeography, phylogeny.

Santrauka: Straipsnyje aptariama išnykusi parazitinų vapsvelių šeima Stigmaphronidae (Proctotrupomorpha: Ceraphronoidea). Atlikta kladistinė filogenetinių šeimos ryšių analizė. Dauguma šios šeimos rūšių yra aprašytos iš kreidos gintarų, tokių kaip Sibiro, Aliaskos, Kanados, Nju Džersio, Mijanmaro ir Libano, bet keletas pavyzdžių yra rasta ir nuosėdinėse ankstyvosios kreidos uolienose Sibire ir Mongolijoje. Tyrimų išdavoje skelbiami šie nauji taksonai: *Elasmophron kurthi* nov.gen. et sp. (Nju Džersio gintaras), *Libanophron astarte* nov.gen. et sp. (Libano gintaras), *Burmaphron* nov.gen., *Burmaphron tridentatum* nov.sp. (Mijanmaro gintaras), *B. prolatum* nov.sp. (Mijanmaro) gintaras, *Tagsmiphron* nov.gen., *Tagsmiphron muesebecki* nov.sp. (Nju Džersio gintaras), *T. gigas* nov.sp. (Nju Džersio gintaras), *T. ascalaphus* nov.sp. (Nju Džersio gintaras) ir *T. canadense* nov.sp. (Kanados gintaras). Šioje publikacijoje naujai aprašomų rūšių skaičius viršija iki tol aprašyt rūšių skaičių. Gentis *Elasmomorpha* KOZLOV suvedama į genties *Allocotidus* MUESEBECK jaunesniuosius sinonimus (nov.syn.), todėl sudaroma nauja kombinacija *Allocotidus melpomene* (KOZLOV) nov.comb. Atskirų taksonų tarpusavio ryšiai yra gerai pagrįsti, todėl stratigrafinių-kladistinių eilių tarpusavio koreliacijos nebuvimas aiškinamas silpnu stratigrafiniu praeityje buvusios labai įvairios šeimos ištirtumu.

Raktiniai žodžiai: Stigmaphronidae, taksonomija, kreidos gintaras, biogeografija, filogenija.

Introduction

Wasps of the family Stigmaphronidae are one of a few extinct, monophyletic lineages recognized in the order Hymenoptera. These diminutive (0.80-2.0 mm in length) wasps were widespread during the Cretaceous, apparently flourishing during the mid- to Late Cretaceous but became extinct sometime prior to the infamous K-T boundary, 65 Ma (GRIMALDI & ENGEL 2005). Stigmaphronids coexsited for a brief interlude of time with their modern relatives, the Ceraphronidae and Megaspilidae, the three families together comprising the Ceraphronoidea. While definitive ceraphronids remain undocumented in the fossil record, megaspilids are known from a variety of deposits, principally as amber inclusions but including two compressions in oil shale, ranging in age from the Late Cretaceous to the Miocene (ALEKSEEV & RASNITSYN 1981; PEÑALVER & ENGEL 2006).

Today the superfamily comprises approximately 660 species – about 300 in Megaspilidae, about 360 in Ceraphronidae – with both families of cosmopolitan distribution (JOHNSON & MUSETTI 2004). Biological data on these minute parasitoids is scant. Megaspilids retain the ancestral ectoparasitic mode of parasitoidism (with at least one derived species feeding initially as an endoparasitoid: DESSART 1995), while ceraphronids are ecto- and endoparasitoids (DESSART 1995). Both families parasitize species of Coniopterygidae and Chrysopidae (Neuroptera), and Cecidomyiidae (Diptera) (e.g., PRIESNER 1936; PARNELL 1963; DESSART 1972, 1973,

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1995). Ceraphronids have been additionally recorded attacking thrips (Thysanoptera), caddisfly pupae (Trichoptera), caterpillars (Lepidoptera), and the puparia of higher flies, as well as being hyperparasitoids on Microgastrinae (Hymenoptera: Braconidae) (e.g., DESSART 1978, 1979, 1995). There is also some evidence to suggest that some species may use apoid wasp larvae as hosts (MELO & CAMPOS 1993). Megaspilidae have a similarly broad range of hosts that further includes Coccidae (Hemiptera), Hemerobiidae (Neuroptera), Boreidae (Mecoptera), Syrphidae, Chloropidae, Chamaemyiidae, and Muscidae (all Diptera), and species may also act as hyperparasitoids (e.g., DESSART 1972, 1973, 1987, 1990, 1995; COOPER & DESSART 1975; BENNETT & SULLIVAN 1978; FERGUSSON 1980). While the biology of stigmaphronids is entirely unknown, it may be safely presumed that they were parasitoids and, given the ancestral retention of ectoparasitoidism in Megaspilidae, they may have been ectoparasitoids on Neuroptera and/or Diptera (the hosts most common to all ceraphronoid families and accordingly an aspect of their biology perhaps shared ancestrally with Stigmaphronidae).

Placement of Stigmaphronidae, and ceraphronoids in general, among other lineages of Hymenoptera has historically been confused. Stigmaphronids superficially resemble Elasminae (Chalcidoidea: Eulophidae), by the compact, laterally-flattened body; possession of a large mesoscutellum (in the Elasminae, though, the dorsal triangular structure is largely the lamella, projecting from beneath the mesoscutellum); a very large, flat, plate-like metacoxa; enlarged metatibial spurs; and metafemur thick and flattened. Naturally, elasmines exhibit typical chalcidoid apomorphies such as the presence of a stigmal vein and flagellomeres with longitudinal sensilla (COOTE 1997). The elasmine-stigmaphronid similarity is clearly convergence, since stigmaphronids have none of these, nor any other chalcidoid characters: i.e., no longitudinal sensilla on flagellomeres; no costal cell, and base of the forewing is in contact with the pronotum (as in proctotrupoids), not distant from it.

RASNITSYN (1975, 2002) has considered Ceraphronoidea, including Stigmaphronidae, as related to the Megalyroidea in the Evaniomorpha. This was largely based on the apparent loss of vein A in the hind wing beyond cu-a. However, in many minute wasps the hind wing venation is entirely lost and, indeed, in the proctotrupomorphan superfamilies Chalcidoidea, Proctotrupoidea, Cynipoidea, and Platygastroidea this vein is similarly lost. As such, this character cannot conclusively place Ceraphronoidea among the Evaniomorpha. The proctotrupomorphan families are purportedly united by characters not exhibited in Ceraphronoidea, such as the absence of a medial mesoscutal line. However, this sulcus can vary from dramatically reduced to effectively absent in Ceraphronoidea as well, while faint median lines also occur in some Proctotrupomorpha. Across the taxa in question this feature does not appear to be conclusively fixed one way or the other and may be easily lost, and accordingly is a tenuous trait upon which to unite or exclude large heterogeneous clades. Other features purportedly uniting Proctotrupomorpha are largely wing vein losses that apply equally to Ceraphronoidea (e.g., loss of 3rs-m, 2rs-m, loss of particular cells in the hind wing) or are enigmatically identical to the feature purportedly placing ceraphronoids in Evaniomorpha (i.e., the aforementioned loss of hind wing vein A) (RASNITSYN 2002). GIBSON (1985) identified the conditions of the mesothoracic spiracle (appearing on the pronotum – not discernable in stigmaphronid specimens) and the spiracular occlusor muscle (also not observable in the fossils) as being potential synapomorphies for Ceraphronoidea and Megalyroidea. These features are clearly a single, complex character (position on pronotum and the associated pronotal apodeme origination of the associated muscle) and are indeed suggestive, as are the coxal articulations of the superfamilies. However, critical analyses of these and other data for modern Hymenoptera have recovered a relationship between Ceraphronoidea and Platygastroidea or Platygastroidea + Chalcidoidea + Mymarommatoidea in the Proctotrupomorpha (e.g., RONQUIST et al. 1999; SHARKEY & ROY 2002). Accordingly we have herein considered ceraphronoids to belong to the Proctotrupomorpha, noting that the controversy regarding their phylogenetic placement remains real.

Stigmaphronidae presently comprise five genera. The genus *Aphrostigmon* RASNITSYN (*Aphrostigmon bontsaganicum* RASNITSYN, *A. priapulus* RASNITSYN, and *A. vitimense* RASNITSYN) is known strictly as compressions from the Early Cretaceous of Central Asia (RASNITSYN 1991) and is only putatively included in the family since most defining features cannot be observed. A further four genera have been described, all in Late Cretaceous amber: *Stigmaphron* KOZLOV (*S. orphne* KOZLOV), *Elasmomorpha* KOZLOV (*E. melpomene* KOZLOV), *Hippocoon* KOZLOV (*H. evadne* KOZLOV), all in Siberian amber; and *Allocotidus* MUESEBECK (*A. bruesi* MUESEBECK), in Alaskan amber. KOZLOV (1975) was the first to recognize that *Allocotidus* (originally described as a ceraphronid) was related to the Siberian amber genera although he, like all subsequent authors, did not examine MUESEBECK's type material. Herein we provide a revision of those definitive members of the family Stigmaphronidae (i.e., all of those preserved in amber) and the first cladistic analysis of relationships among the genera.

Material and Methods

Type material of all previously described species was studied and coded for cladistic analysis and the classification of the family revised. In addition, we document a further eight new species in Late Cretaceous amber from New Jersey and Canada, mid-Cretaceous amber from Myanmar, and Early Cretaceous amber from Lebanon (Table 1). The age and origin of New Jersey amber has been overviewed by GRIMALDI et al. (2000); that of Canadian amber by PIKE (1994, 1995); that of Burmese amber by ZHERIKHIN & ROSS (2000), GRIMALDI et al. (2002), and CRUICKSHANK & KO (2003); and that of Lebanese amber by AZAR (2000). The following institutional acronyms are employed herein and their designation refers to the depository of types and other material: AMNH, American Museum of Natural History (New York); AZAR, Dany AZAR Lebanese Amber Collection, Museum National d'Histoire Naturelle (Paris); PIN, Paleontological Institute, Russian Academy of Sciences (Moscow); RTMP, Royal Tyrell Museum of Paleontology (Drumheller); UCMP, University of California Museum of Paleontology (Berkeley).

Material in the AMNH collection was prepared according to the protocols of NASCIMBENE & SILVERSTEIN (2000) and photomicrography was undertaken using a Nikon D1x digital camera attached to an Infinity® K-2 long-distance microscopic lens. Line drawings were prepared by the junior author using a camera lucida attached to a Leica stereomicroscope. Methods for phylogenetic analysis are detailed under "Cladistics" (vide infra).

Table 1: Classification of Stigmaphronidae (Hymenoptera: Ceraphronoidea) as recognized herein. All species are preserved as inclusions in amber except those of *Aphrostigmon*, which are compressions in stone. For each species is provided the geographic location and geological age of the deposit.

—Family STIGMAPHRONIDAE KOZLOV—		
Genus *Elasmophron* nov.gen.		
E. kurthi nov.sp.	New Jersey	Turonian
Genus *Libanophron* nov.gen.		
L. astarte nov.sp.	Lebanon	Neocomian
Genus *Hippocoon* KOZLOV, 1975		
H. evadne KOZLOV, 1975	Siberia	Santonian
H. sp.?	Spain	Albian
Genus *Allocotidus* MUESEBECK, 1963		
A. bruesi MUESEBECK, 1963	Alaska	Cenomanian
A. melpomene (KOZLOV, 1975)	Siberia	Santonian
Genus *Burmaphron* nov.gen.		
B. tridentatum nov.sp	Myanmar	Albian-Cenomanian
B. prolatum nov.sp.	Myanmar	Albian-Cenomanian
Genus *Stigmaphron* KOZLOV, 1975		
S. orphne KOZLOV, 1975	Siberia	Santonian
Genus *Tagsmiphron* nov.gen.		
T. muesebecki nov.sp.	New Jersey	Turonian
T. gigas nov.sp.	New Jersey	Turonian
T. ascalaphus nov.sp.	New Jersey	Turonian
T. canadense nov.sp.	Canada	Campanian
—Incertae Sedis—		
Genus *Aphrostigmon* RASNITSYN, 1991		
A. vitimense RASNITSYN, 1991	Siberia	Berriasian
A. bontsaganicum RASNITSYN, 1991	Mongolia	Aptian
A. priapulus RASNITSYN, 1991	Mongolia	Aptian

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Family Stigmaphronidae KOZLOV

Stigmaphronidae KOZLOV, 1975: 75.

Type genus: *Stigmaphron* KOZLOV, 1975.

Diagnosis: Non-aculeate apocritans with generally compact body; head hemispherical, with sharply angled preoccipital ridge, occiput evenly concave, smooth, accommodating convex anterior of mesosoma; scape primitively long, inserted near clypeal base in apical-ventral part of face; flagellum with 7-10 flagellomeres; compound eyes well developed, large, encompassing lateral surface of head (except reduced in *Stigmaphron*); ocelli present. Mesoscutellum enlarged. Forewing C and Sc+R fused, although sometimes with faint impression indicating former presence of two veins; pterostigma distinct, large; Rs long, upcurved (absent only in *Stigmaphron*); hind wing slender, typically without venation although sometimes with apparent costa on apical margin, with 1-4 distal hamuli; wing membranes hyaline, with scattered microtrichia, veins light brown. Metacoxa large, flattened, covering lateral view of propodeum; metafemur typically crassate (except in basal genera); tibial spur formula 2-2-2, although 1-2-2 in some derived genera (KOZLOV's assertion of a 1-2-3 formula is erroneous), mesotibial spurs elongate; metatibial spurs stout, frequently greatly elongate (except in basal genera); pretarsal ungues (i.e., claws) simple, arolium present but typically very small. First metasomal segment forming a short, narrow petiole, largely obscured by second metasomal segment; second metasomal segment not distinctly larger than succeeding metasomal segments.

Comments: The family is known only from the Cretaceous, principally from Cretaceous ambers [Siberian (Santonian), Canadian (Campanian), New Jersey (Turonian), Alaskan (Cenomanian), French (Early Cenomanian: PERRICHOT et al. 2007, non visum), Burmese (Albian-Cenomanian), Spanish (Albian: DELCLÒS et al. 2007), and Lebanese (Neocomian: Barremian?): Table 1].

In addition to the specimens described herein, three additional stigmaphronids were discovered although all were too poorly preserved to permit identification beyond the level of family. We report these specimens here for future researchers to potentially examine with new techniques: AZAR L-142 from Hammana/Mdeirij, Le-

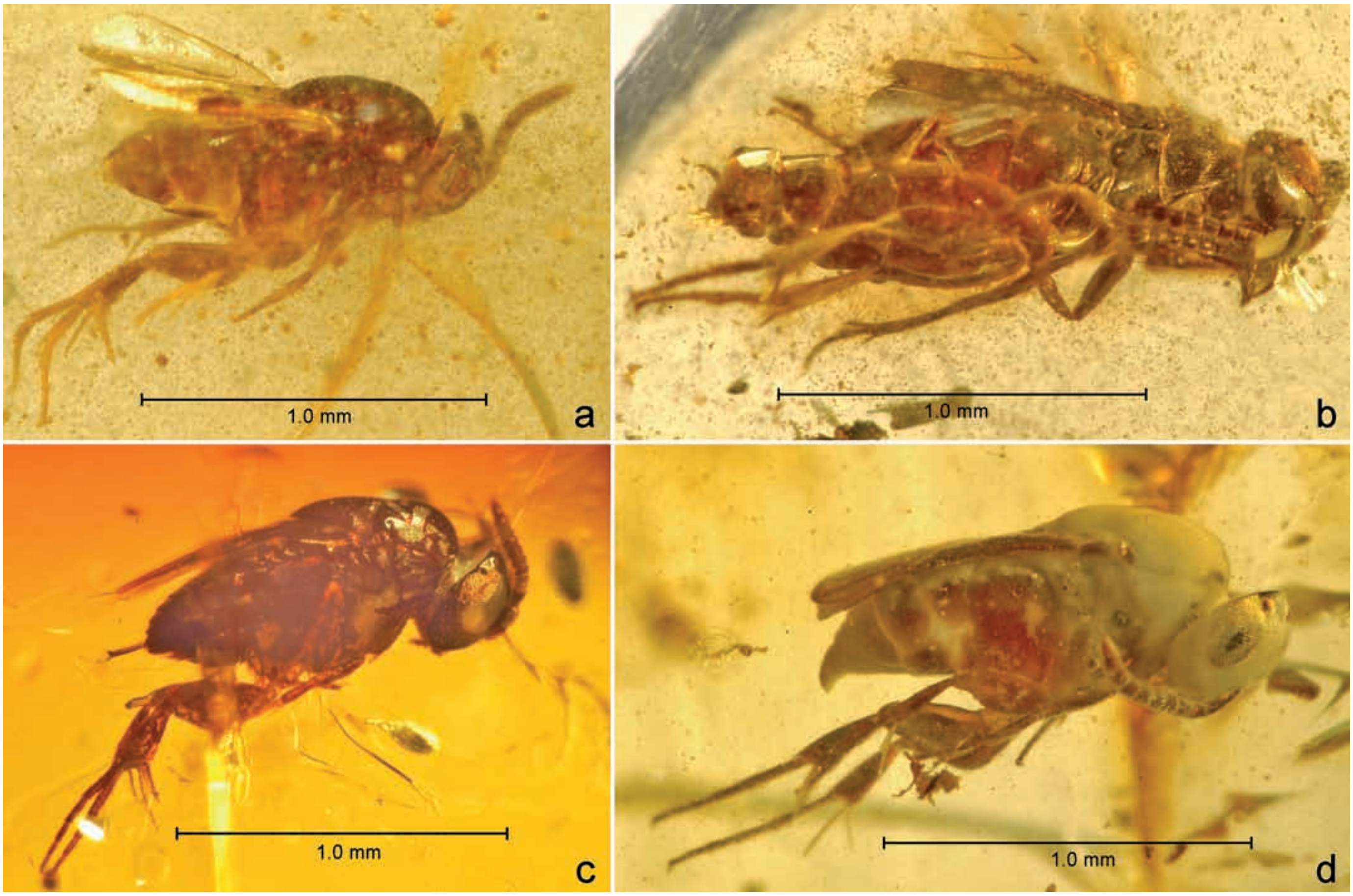

Fig. 1: Photomicrographs of stigmaphronid wasps in Turonian-aged New Jersey amber: (**a**) paratype of *Tagsmiphron muesebecki* nov.gen. et sp. (AMNH NJ-701); (**b**) holotype of *Elasmophron kurthi* nov.gen. et sp. (AMNH NJ-1127); (**c**) holotype of *T. muesebecki* nov.gen. et sp. (AMNH NJ-697); (**d**) holotype of *T. ascalaphus* nov.gen. et sp. (AMNH NJ-1128).

banon (Early Cretaceous: Neocomian), and AMNH NJ-1003 and NJ-1022 both from Sayreville, Middlesex County, New Jersey (Late Cretaceous: Turonian).

Key to Genera of Stigmaphronidae

1 Metatibial spurs short, length shorter than or scarcely longer than apical metatibial width (Figs 1b, 2) 2

– Metatibial spurs stout, thick, elongate, much longer than apical metatibial width (Figs 1a, 1c-d, 5-7) 3

2 Posterior border of mesoscutellum rounded (Fig. 2); metafemur slender; metatibial apex with short comb of fine, thin setae . . *Elasmophron* nov.gen.

– Posterior border of mesoscutellum pointed (Figs 3a, 4a); metafemur swollen dorsally (but transversely not widened); metatibial apex without comb of fine setae . . . . *Libanophron* nov.gen.

3 Forewing with Rs present, either tubular or nebulous (Figs 2-4, 6, 7) 4

– Forewing with Rs absent. . . *Stigmaphron* KOZLOV

4 Preoccipital area not ridged immediately anterior to sharply angled posterior border of head (Fig. 7); distal margin of metatibia without spicules. 5

– Preoccipital area ridged immediately anterior to sharply angled posterior border of head (Fig. 6); distal margin of metatibia with comb of 5–7 long, thin spicules (Fig. 6) . . . . . *Burmaphron* nov.gen.

5 Funicular articles of antenna variable but never entirely compact, with width much greater than length, typically basal articles slightly wider than long, tapering apically to articles that are as wide as long or longer than wide. 6

– Funicular articles of antenna extremely compact, short, transverse, width much greater than length. . . . . *Hippocoon* KOZLOV

6 Forewing Rs faint, nebulous (Fig. 4c); protibia slender, with two spurs . . *Allocotidus* MUESEBECK

– Forewing Rs well developed, tubular (Fig. 7); protibia with a single spur (most species) or, if with two spurs, then protibia greatly expanded and spurs stout and elongate (*T. canadense*) . . . . *Tagsmiphron* nov.gen.

Genus *Elasmophron* nov.gen.

Type species: *Elasmophron kurthi* ENGEL & GRIMALDI nov.sp.

Diagnosis: Scape slender, elongate, about 5.5 times longer than apical width; funicular articles not compact, gradually increasing in length; compound eye occupying large portion of lateral surface of head; preoccipital ridge sharply angled, carinate, without defined elevation anterior to angle. Mesoscutum with exceedingly faint medial line, more evident anteriorly and medially, with exceedingly faint notauli more evident anteriorly; mesoscutellum rounded posteriorly, not obscuring propodeum. Forewing with faint impression apically in C+Sc+R; Rs present, tubular, and well developed. Protibia slender, with two protibial spurs of approximately equal design, inner spur slightly shorter than outer spur; metafemur slender, posterior margin of metafemur without a row of spicules, without stiff, fine spicules on distal margin; metatibia slender, metatibial spurs short, outer spur scarcely longer than metatibial apical width, inner spur shorter than metatibial apical width, metatibia with comb of 7–8 fine, thin setae on apicolateral edge; metabasitarsus shorter than metafemur, with sparse, short setae on inner surface, without spicules or spines on inner surface.

Etymology: The new genus-group name combines the prefix and suffix of two other stigmaphronid genera: Elasmomorpha and Stigmaphron. The name is neuter.

Elasmophron kurthi nov.sp. (Figs 1b, 2)

Holotype: AMNH NJ-1127; Late Cretaceous (Turonian, Raritan Formation) amber; Sayreville, Middlesex County, New Jersey.

Additional material: AMNH NJ-77; Late Cretaceous (Turonian, Raritan Formation) amber; Sayreville, Middlesex County, New Jersey.

Diagnosis: As for the genus (vide supra).

Description: Total body length 1.76 mm; forewing length 0.92 mm. Integument dark brown, where evident except tarsi slightly lighter; integument of head and mesosoma with dense, minute, fine punctures; integument of metasoma imbricate. Head slightly wider than long; lateral ocellus separated from compound eye by ocellar diameter; median ocellus separated from preoccipital carinate angle by 3.5 ocellar diameters; nine flagellar articles, basal articles slightly wider than long, tapering to articles about as wide as long apically; apicalmost article longest, tapering to bluntly rounded apex. Mesoscutellum with transverse, V-shaped sulcus present although exceedingly faint; metanotum with distinct, coarse punctures contrasting with fine, minute punctures elsewhere on mesosoma. Metatibia slender, with apex slightly dilated, with comb of fine, thin setae on inner margin, with two metatibial spurs not greatly expanded, scarcely longer than apical width of metatibia. Metasoma distended with gas in holotype, so exact proportions difficult to discern; apparently longer and more slender than in other stigmaphronids except *Libanophron* (vide infra); segments roughly quadrate.

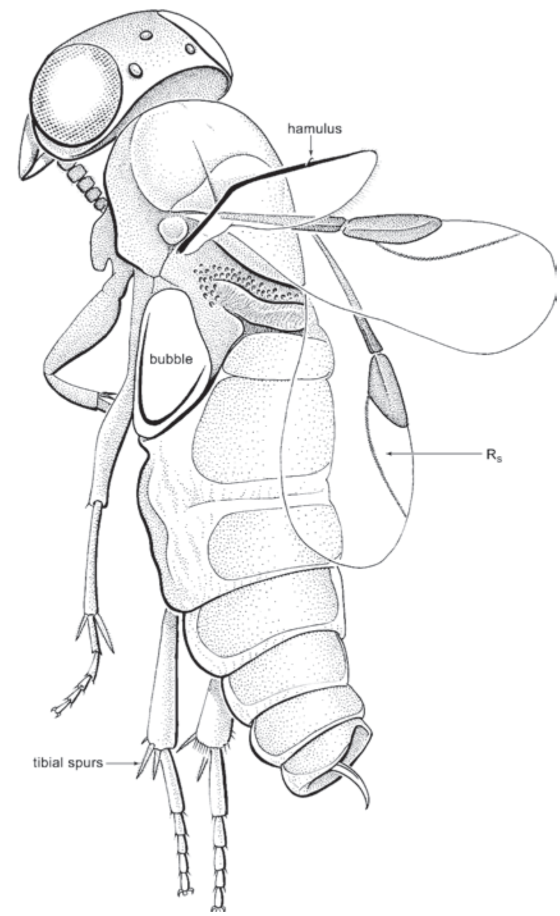

Fig. 2: Dorsal habitus of holotype of *Elasmophron kurthi* nov.gen. et sp. (AMNH NJ-1127) (note that faint notauli and medial line on mesoscutum are not portrayed).

Etymology: The specific epithet is a patronymic honoring Steven KURTH, collector and donator of the holotype and several other wonderful New Jersey amber fossils to the AMNH.

Genus *Libanophron* nov.gen.

Type species: *Libanophron astarte* ENGEL & GRIMALDI nov.sp.

Diagnosis: Scape slender, elongate, about 5 times longer than apical width; funicular articles not compact, gradually increasing in length; compound eye occupying

Fig. 3: Photomicrographs of holotype of *Libanophron astarte* nov.gen. et sp. (AZAR L-139): (**a**) dorsal habitus of holotype; (**b**) detail of forewing venation showing tubular Rs.

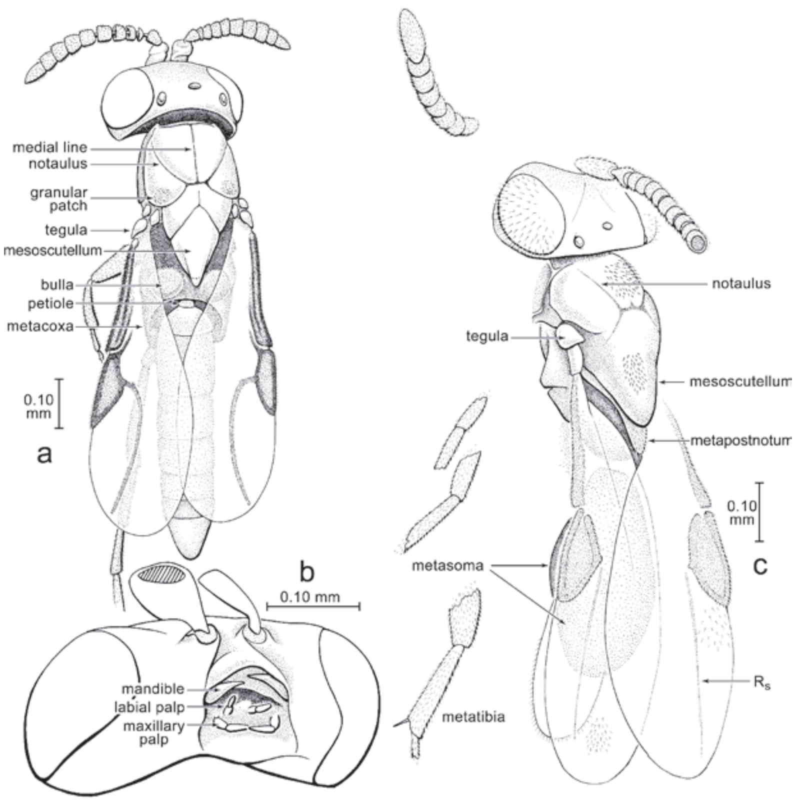

Fig. 4: Illustrations of two stigmaphronid wasps: (**a**) dorsal habitus of holotype of *Libanophron astarte* nov.gen. et sp. (AZAR L-139); (**b**) ventral aspect of head of *L. astarte* showing exposed mouthparts; (**c**) dorsal habitus of fragmentary holotype of *Allocotidus bruesi* Muesebeck (UCMP 12875) (note that the legs are broken at the amber surface and the inner margin of the metatibia is missing and may, therefore, have been expanded with an elongate spur). Only portions of microtrichial vestiture are portrayed.

large portion of lateral surface of head; preoccipital ridge sharply angled, carinate, without defined elevation anterior to angle; mandibles reduced, short, not meeting medially, apices simple (Fig. 4b). Mesoscutum with medial line deeply impressed; mesoscutellum pointed posteriorly, not obscuring propodeum. Forewing with faint impression apically in C+Sc+R; Rs present, tubular, and well developed. Protibia slender, with two protibial spurs of approximately equal design, inner spur slightly shorter than outer spur; metafemur greatly swollen, posterior margin of metafemur without a row of spicules, without stiff, fine spicules on distal margin; metatibia slender, metatibial spurs short, outer spur scarcely longer than metatibial apical width, inner spur shorter than metatibial apical width; metabasitarsus shorter than metafemur, with sparse, short setae on inner surface, without spicules or spines on inner surface.

Etymology: The new genus-group name combines the name of Lebanon and the suffix of *Stigmaphron*, type genus of the family. The name is neuter.

Libanophron astarte nov.sp. (Figs 3, 4a-b)

Holotype: Azar L-139; Early Cretaceous (Neocomian: Barremian?) amber; Hammana/Mdeirij, Lebanon.

Diagnosis: As for the genus (vide supra).

Description: Total body length 1.20 mm; forewing length 0.75 mm; intertegular distance 0.19 mm. Integument dark brown except legs and mouthparts brown; integument of head and mesosoma with dense, minute, fine punctures; integument of metasoma imbricate. Head wider than long; lateral ocellus separated from compound eye by less than ocellar diameter; median ocellus separated from preoccipital carinate angle by two ocellar diameters; nine flagellar articles, basal flagellar article annellus-like, much wider than long, basal funicular articles wider than long, tapering to about as wide as long apically; apicalmost flagellar article longest, tapering to pointed apex. Mesoscutellum with transverse, V-shaped sulcus present and strongly impressed; propodeum dorsolaterally with bullae comprising rounded areas of minute velvet setae. Metatibia slender, with apex slightly dilated, with two metatibial spurs not greatly expanded, scarcely longer than apical width of metatibia. Metasoma longer and more slender than in other stigmaphronids except *Elasmophron* (vide supra); segments roughly quadrate except second slightly longer than wide.

Etymology: The specific epithet is the name of the Phoenician goddess of heaven. Astarte, a form of the great "mother goddess", is more famously known by her Akkadian counterpart Ishtar, the Egyptian goddess Isis, and/or the Greco-Roman Artemis or Diana.

Genus *Hippocoon* KOZLOV

Hippocoon KOZLOV, 1975: 80.

Type species: *Hippocoon evadne* KOZLOV, 1975, by original designation.

Diagnosis: Scape exceedingly short, about as long as wide; funicular articles extremely compact, short and transverse, much wider than long; compound eye occupying large portion of lateral surface of head; preoccipital ridge sharply angled, carinate, without defined elevation anterior to angle. Mesoscutellum pointed posteriorly, projecting over dorsal surface of propodeum, obscuring dorsal view of propodeum. Forewing Rs present and well developed. Protibia slender, with two protibial spurs of approximately equal design; metafemur greatly swollen, posterior margin of metafemur without a row of spicules, without stiff, fine spicules on distal margin; metatibia distinctly and greatly broadened apically, metatibial spurs stout and elongate, much greater than apical width of metatibia; metabasitarsus shorter than metafemur, with sparse, short setae on inner surface, without spicules or spines on inner surface.

Comments: A new species of what appears to be *Hippocoon* occurs in Late Albian amber from Spain (DELCLÒS et al. 2007), although in this specimen some affinity with *Burmaphron* was also evident so assignment to *Hippocoon* must be considered tentative. We were kindly permitted to examine a specimen of this not uncommon Álava amber species by Dr. Xavier DELCLÒS (Universitat de Barcelona). An account of the species is being prepared by a team of Spanish paleoentomologists who will clarify its identity and phylogenetic position in a forthcoming contribution.

Genus *Burmaphron* nov.gen.

Type species: *Burmaphron tridentatum* ENGEL & GRIMALDI nov.sp.

Diagnosis: Scape slender, elongate, about 5 times longer than apical width; funicular articles not compact, gradually increasing in length; compound eye occupying large portion of lateral surface of head; preoccipital ridge sharply angled, carinate, with defined elevation anterior to angle. Mesoscutum with medial line absent, notauli present but weakly impressed; mesoscutellum pointed posteriorly, projecting over dorsal surface of propodeum, obscuring dorsal view of propodeum. Forewing Rs present, nebulous. Protibia slender, with two protibial spurs, inner spur vestigial, drastically shorter than outer spur; metafemur greatly swollen, posterior margin of metafemur without a row of spicules, with 5-7 long, fine spicules (or setae) on ventral distal margin; metatibia distinctly and greatly broadened apically; metatibial spurs stout and elongate, much greater than apical width of metatibia; inner surface of metabasitarsus with scattered, short setae, without spicules or spines on inner surface.

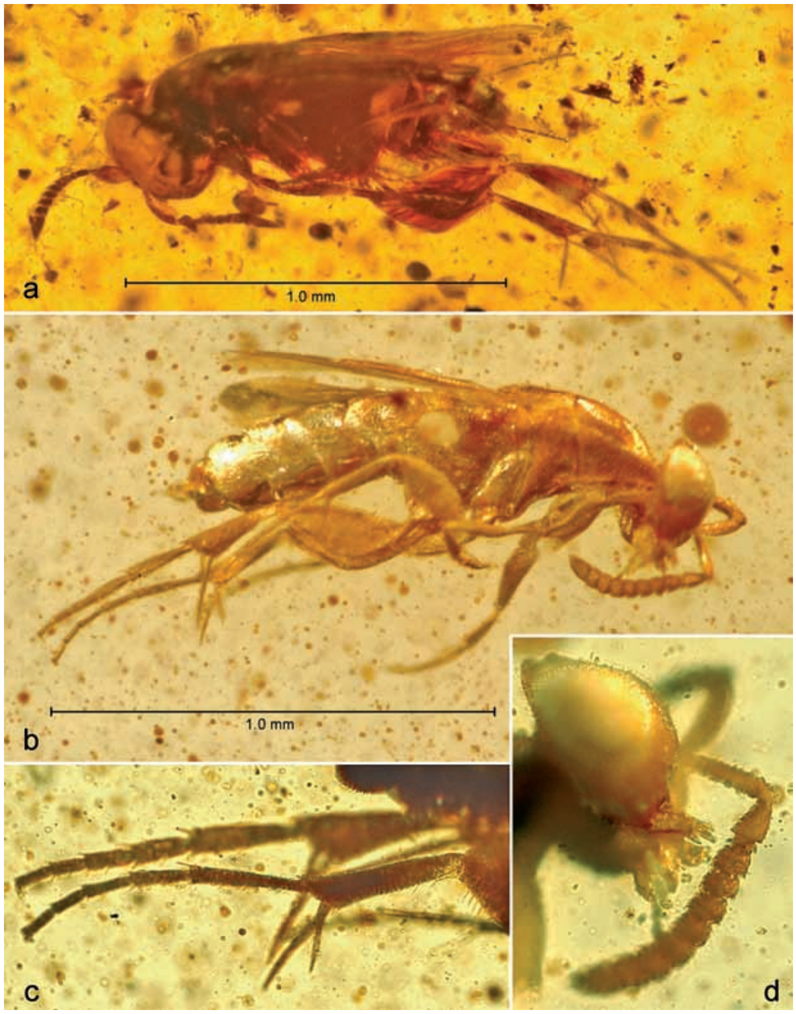

Fig. 5: Photomicrographs of Burmese amber stigmaphronid wasps: (**a**) lateral habitus of holotype of *Burmaphron prolatum* nov.gen. et sp. (AMNH Bu-671); (**b**) lateral habitus of holotype of *B. tridentatum* nov.gen. et sp. (AMNH Bu-677); (**c**) hind legs of *B. tridentatum* depicting enlarged metatibial spurs (note that metatibia in foreground is angled into the amber, making it appear foreshortened and not as wide as the metatibia in the background. Both metatibiae are actually expanded.); (**d**) detail of holotype of *B. tridentatum* depicting antenna and mouthparts, with tridentate mandible, clearly visible.

Etymology: The new genus-group name combines the name Burma, a former name for the Union of Myanmar, and the suffix of *Stigmaphron*, type genus of the family. The name is neuter.

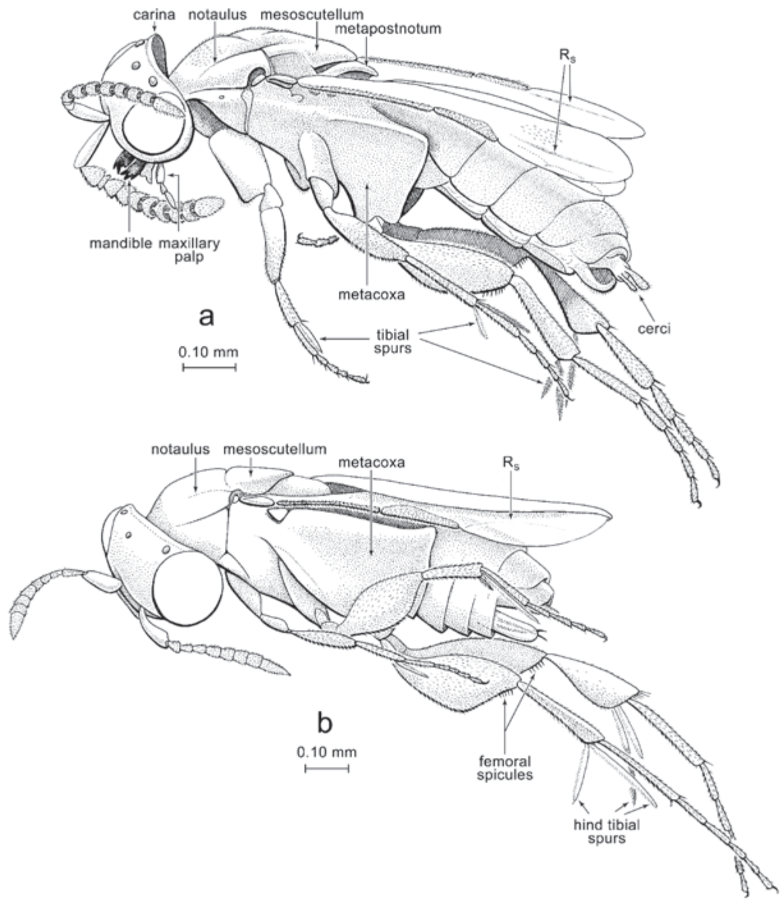

Fig. 6: Illustrations of the lateral habitus of Burmese amber stigmaphronid wasps: (**a**) holotype of *Burmaphron tridentatum* nov.gen. et sp. (AMNH Bu-677); (**b**) holotype of *B. prolatum* nov.gen. et sp. (AMNH Bu-671).

Key to Species of *Burmaphron*

1 Metabasitarsus slightly shorter than metatibia (Figs 5c, 6a); preoccipital ridge strongly produced anterior to sharply angled edge at posterior of head (Fig. 6a); flagellum with nine articles . . . . *B. tridentatum* nov.sp.

– Metabasitarsus longer than metatibia (Fig. 6b); preoccipital ridge weakly produced anterior to sharply angled edge at posterior of head (Fig. 6b); flagellum with seven articles . . . . *B. prolatum* nov.sp.

Burmaphron tridentatum nov.sp. (Figs 5b-d, 6a)

Stigmaphronidae sp. Grimaldi et al. 2002: 50, fig. 33a.

Holotype: AMNH Bu-677; mid-Cretaceous (Albian-Cenomanian) amber; Tanai Village (on Ledo Road, 105 km NW Myitkyina), Kachin, Myanmar.

Diagnosis: *Burmaphron tridentatum* can be most readily separated from its congener (vide infra) by the shorter metabasitarsus, the more strongly developed ridge anterior to the preoccipital carinate angle, the larger number of flagellar articles, and the smaller metacoxa (as measured transversely at midlength). Additional interesting features of *B. tridentatum* include the distinctly tridentate mandible, with the medial tooth longest. Unfortunately, the mouthparts of *B. prolatum* cannot be seen and so this is presently not considered a defining feature of the genus or a true autapomorphy of *B. tridentatum*. Hopefully further material shall be recovered in the future permitting a more thorough account of these two species.

Description: Total body length 1.0 mm; forewing length 0.69 mm; intertegular distance 0.15 mm. Integument light brown and imbricate except head and mesosoma with dense, minute, fine punctures. Mandible well developed, short, tridentate, medial tooth longest (Fig. 5d); lateral ocellus separated from compound eye by about an ocellar diameter; median ocellus separated from preoccipital carinate angle by approximately two ocellar diameters; swollen ridge anterior to preoccipital carinate angle strong (Fig. 6a); nine flagellar articles, basalmost article annellus-like, exceedingly wider than long, funicular articles slightly wider than long, apicalmost article longest, tapering to bluntly rounded apex. Legs with scattered, short, fine, subappressed setae; protibia not enlarged, with one long spur and one exceedingly minute (vestigial) spur (sometimes difficult to see and can be confused with a stout, apical seta); metafemur crassate, widest near midlength; metatibia expanded apically, metabasitarsus slightly shorter than metatibia. Metasoma relatively short, apex barely exceeding wing apex; not compressed laterally or dorsoventrally, integument imbricate, with sparse, short, subappressed setae.

Etymology: The specific epithet is a combination of the Latin terms tri (meaning, "three") and dentatum (meaning, "toothed").

Burmaphron prolatum nov.sp. (Figs 5a, 6b)

Holotype: AMNH Bu-671; mid-Cretaceous (Albian-Cenomanian) amber; Tanai Village (on Ledo Road, 105 km NW Myitkyina), Kachin, Myanmar.

Diagnosis: This species differs most notably from *B. tridentatum* in the longer metabasitarsus, the weaker development of the swollen ridge anterior to the preoccipital carinate angle, the smaller number of flagellar articles, and the more medially swollen metacoxa. The holotype also has a significantly darker integument relative to *B. tridentatum* but this may be a result of preservation and is therefore not considered a key character.

Description: Total body length 0.99 mm; forewing length 0.80 mm; intertegular distance 0.19 mm. Integument dark brown except tarsi brown. Mouthparts not visible; lateral ocellus separated from compound eye by less than ocellar diameter; median ocellus separated from preoccipital carinate angle by approximately 3.5 ocellar diameters; swollen ridge anterior to preoccipital carinate angle weak (Fig. 6b); seven flagellar articles, basalmost article not annellus-like, longer than wide, funicular articles tapering from longer than wide to about as wide as long, apicalmost article longest, tapering to acutely rounded apex. Metabasitarsus longer than metatibia. Metasoma short, apex not exceeding wing apex; not compressed laterally or dorsoventrally, integument imbricate, with sparse, short, subappressed setae.

Etymology: The specific epithet is based on the Latin "prolatus" (meaning, "elongate").

Genus *Allocotidus* MUESEBECK

Allocotidus MUESEBECK, 1963: 129. Type species: *Allocotidus bruesi* MUESEBECK, 1963, by original designation.
Elasmomorpha KOZLOV, 1975: 78. Type species: *Elasmomorpha melpomene* KOZLOV, 1975, by original designation. **Syn.nov.**

Diagnosis: Scape short, 1.5-2.5 times longer than apical width; funicular articles extremely compact, funicular articles not compact, slightly increasing in length toward antennal apex; compound eye occupying large portion of lateral surface of head; preoccipital ridge sharply angled, carinate, without defined elevation anterior to angle. Mesoscutum without median line; mesoscutellum pointed posteriorly, projecting over dorsal surface of propodeum, obscuring dorsal view of propodeum. Forewing Rs present, faint, nebulous.

Key to Species of *Allocotidus*

1 Larger species, length c. 1.3 mm; medial line exceedingly faint, disappearing anteriorly; mesoscutum with distinct scattered, minute setae; lateral ocellus separated from compound eye by approximately a single ocellar diameter . . . . *A. bruesi* MUESEBECK

– Smaller species, length c. 1.1 mm; medial line strongly impressed; mesoscutum without apparent setae; lateral ocellus separated from compound eye by less than ocellar diameter . . . . *A. melpomene* (KOZLOV)

Allocotidus bruesi MUESEBECK (Fig. 4c)

Allocotidus bruesi MUESEBECK, 1963: 129, fig 1, pl. 17-4; KOZLOV 1975: 77.

Holotype: UCMP 12875; Late Cretaceous (Cenomanian) amber; Pugnik #2, Kuk Inlet (immediately south of Wainwright), Alaska.

Diagnosis: *Allocotidus bruesi* can be distinguished from *A. melpomene* by its slightly larger size (c. 1.3 mm in total length, although as more material is discovered this gap may prove to be artificial), the exceedingly faint medial line that largely disappears anteriorly, the distinct setae of the mesoscutum, and the separation of the lateral ocellus from the compound eye by approximately a single ocellar diameter.

Comments: Contrary to MUESEBECK's (1963) published description and illustrations of *A. bruesi* the forewing Rs is distinctly present, although faint and nebulous (under some lighting the vein is challenging to see and perhaps this led to MUESEBECK's interpretation that the vein was absent). It is likely that had KOZLOV (1975) had the opportunity to study MUESEBECK's holotype in addition to recognizing the species as a stigmaphronid he would have also noted that his *Elasmomorpha melpomene* was congeneric. As it was, KOZLOV never had the chance to examine MUESEBECK's material and only had the original, incomplete, and incorrect description upon which to base his conclusions regarding *Allocotidus*.

Allocotidus melpomene (KOZLOV) comb.nov.

Elasmomorpha melpomene KOZLOV, 1975: 80, fig 89.

Holotype: PIN 3311/66; Late Cretaceous (Santonian, Kheta Formation) amber; Taymyr (Yantardakh), Siberia, Russia.

Diagnosis: *Allocotidus melpomene* can be recognized by the following combination of traits: smaller body size (1.1 mm in total length), strongly impressed medial line, mesoscutum apparently bare, and lateral ocellus separated from the compound eye by less than a single ocellar diameter. In addition, *A. melpomene* possesses a slender protibia with two spurs that are not greatly elongate, with the inner spur slightly shorter than the outer; a greatly expanded metafemur, with the posterior margin of the metafemur lacking a row of spicules and lacking stiff, fine spicules on the ventral distal margin; a distinctly and greatly broadened metatibia, with stout and elongate metatibial spurs, much greater than the apical width of the metatibia; a metabasitarsus shorter than the metafemur, with scattered sparse and short setae on the inner surface, not intermingled with spicules or spines. These latter features will likely prove to be generic once more complete material of *A. bruesi* is discovered.

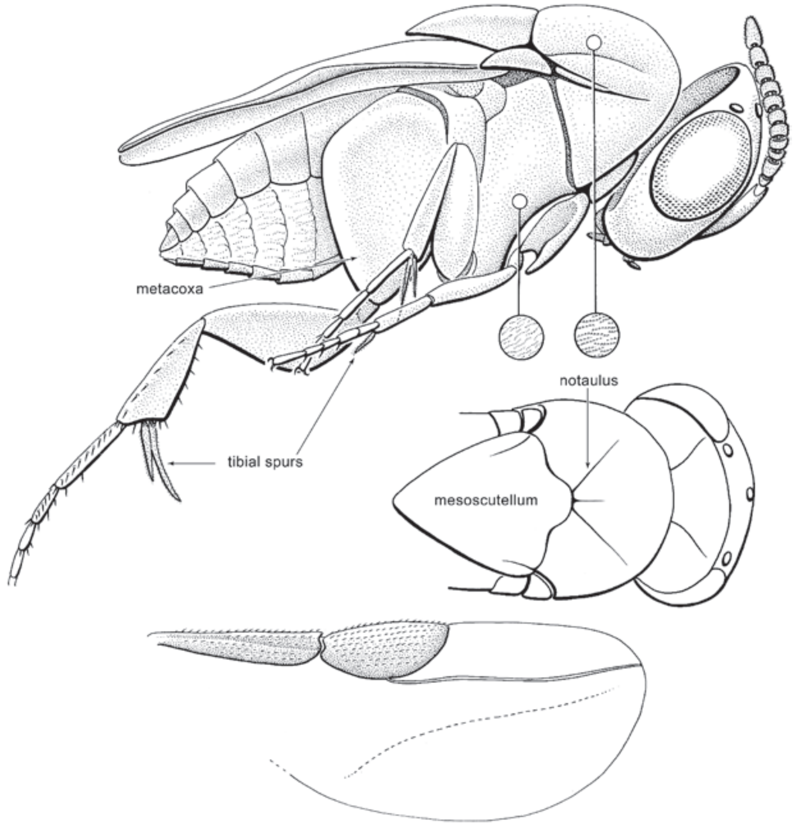

Fig. 7: Illustrations of holotype of *Tagsmiphron muesebecki* nov.gen. et sp. (AMNH NJ-697) in Late Cretaceous amber from New Jersey; lateral habitus above, detail of mesoscutum and forewing venation beneath.

Genus *Stigmaphron* KOZLOV

Stigmaphron KOZLOV, 1975: 77.

Type species: *Stigmaphron orphne* KOZLOV, 1975, by original designation.

Diagnosis: Scape slender, elongate, about 5 times longer than apical width; funicular articles not compact, gradually increasing in length; compound eye reduced, set posteriorly on head and occupying small portion of lateral surface of head; preoccipital ridge sharply angled, carinate, without defined elevation anterior to angle. Mesoscutellum pointed posteriorly, projecting over dorsal surface of propodeum, obscuring dorsal view of propodeum. Forewing Rs absent. Protibia slender, with a single protibial spur; metafemur greatly swollen, posterior margin of metafemur without a row of spicules, without stiff, fine spicules on distal margin; metatibia distinctly and greatly broadened apically; metatibial spurs stout and elongate, much greater than apical width of metatibia; metabasitarsus shorter than metafemur, inner surface of metabasitarsus with scattered, short setae, without spicules or spines on inner surface.

Genus *Tagsmiphron* nov.gen.

Type species: *Tagsmiphron muesebecki* ENGEL & GRIMALDI nov.sp.

Diagnosis: Scape slender, long to very long about 3-5.5 times longer than apical width; funicular articles not compact, gradually increasing in length; compound eye occupying large portion of lateral surface of head; preoccipital ridge sharply angled, carinate, without defined elevation anterior to angle. Mesoscutellum pointed posteriorly, projecting over dorsal surface of propodeum, obscuring dorsal view of propodeum. Forewing Rs present, well developed. Protibia slender or expanded, with one or two protibial spurs (two spurs only present in *T. canadense*); metafemur greatly swollen, posterior margin of metafemur with a longitudinal row of spicules, without stiff, fine spicules on ventral distal margin but with four very short, stub-like teeth on inner distal margin; metatibia distinctly and greatly broadened apically; metatibial spurs stout and elongate, lengths much greater than apical width of metatibia; metabasitarsus shorter than metafemur, inner surface of metabasitarsus with scattered, short setae, with a longitudinal row of short spicules (most species) or stout spines (only in *T. canadense*) on inner surface.

Etymology: The genus-group name is an anagram of *Stigmaphron*, type genus of the family. The name is neuter.

Key to Species of *Tagsmiphron*

1 Protibia with a single, short, slender spur; protibia slender, not expanded like mesotibia; inner surface of metabasitarsus with row of short spicules 2

– Protibia with two, stout, elongate spurs (similar to those of metatibia); protibia slightly expanded like mesotibia; inner surface of metabasitarsus with stout spines . . . . *T. canadense* nov.sp.

2 Scape elongate, length c. 5 times apical width. 3

– Scape shorter, length 3-3.5 times apical width. . . . . *T. ascalaphus* nov.sp.

3 Small species, forewing length 0.75-0.76 mm (total length 1.10-1.19 mm); metatibial spur elongate but relatively slender, basal width less than basal width of metabasitarsus, length slightly shorter than metabasitarsal length; mesotibial outer apex without three short spicules . . . . *T. muesebecki* nov.sp.

– Larger species, forewing length c. 1.60 mm (total length c. 2 mm); metatibial spur elongate and thick, basal width greater than basal width of metabasitarsus, length longer than metabasitarsus; mesotibial outer apex with transverse row of three short spicules . . . . *T. gigas* nov.sp.

Tagsmiphron muesebecki nov.sp. (Figs 1a, 1c, 7)

Stigmaphronidae sp. GRIMALDI & ENGEL 2005: 427, fig 11.27.

Holotype: AMNH NJ-697; Late Cretaceous (Turonian, Raritan Formation) amber; Sayreville, Middlesex County, New Jersey.

Paratype: AMNH NJ-701; Late Cretaceous (Turonian, Raritan Formation) amber; Sayreville, Middlesex County, New Jersey.

Additional material: AMNH NJ-708; Late Cretaceous (Turonian, Raritan Formation) amber; Sayreville, Middlesex County, New Jersey.

Diagnosis: *Tagsmiphron muesebecki* can be distinguished from its congeners by the following combination of features: scape elongate, five or more times longer than apical width; protibia slender, with single spur; row of spinulose setae on outer posterior margin of metatibia extending along metatibial length; inner metabasitarsal surface with longitudinal row of short, stublike spicules.

Description: Total body length 1.19 mm (1.10 mm); forewing length 0.76 mm (0.75 mm); intertegular distance 0.31 mm (0.28 mm). Integument dark brown except legs tending to be slightly lighter. Head with dense, minute, fine punctures; lateral ocellus separated from compound eye by less than ocellar diameter; median ocellus separated from preoccipital ridge by 2.5-3 ocellar diameters; scape slender, long, 5-5.6 times longer than apical width; 10 flagellar articles, basal funicular articles wider than long, tapering to slightly longer than wide by penultimate article, apicalmost article longest, tapering to bluntly rounded apex. Mesosoma with fine, minute, dense punctures, integument between punctures with fine connecting grooves (like fingerprints) (Fig. 7); notauli present but disappearing anteriorly. Forewing with Rs relatively straight. Legs with scattered, short, fine, subappressed setae; protibia not enlarged, with a single spur; metafemur crassate, widest near midlength; metatibia expanded apically, outer margin with posterior, longitudinal row of spinulose setae (Fig. 7); longest metatibial spur as long as or slightly shorter than metabasitarsus, base of spur narrower than metabasitarsal base; inner surface of metabasitarsus with scattered, short setae, with a longitudinal row of short spicules on inner surface. Metasoma short, tapered to narrow apex; apex barely reaching to level of wing apex; not compressed laterally or dorsoventrally, integument imbricate, with sparse, short, subappressed setae.

Etymology: The specific epithet is a patronym honoring Dr. Carl Frederick William MUESEBECK (1894-1987) who described the first fossil stigmaphronid, although he placed his species in the related family Ceraphronidae.

Tagsmiphron gigas nov.sp.

Holotype: AMNH NJ-1126; Late Cretaceous (Turonian, Raritan Formation) amber; Sayreville, Middlesex County, New Jersey.

Diagnosis: This species can be most readily recognized by its "prodigious" proportions relative to all other Stigmaphronidae (2.0 mm in length versus 0.9-1.7 mm). In addition, the exceedingly stout and thickened metatibial spur that is wider basally than the metabasitarsus and which is similarly longer than the metabasitarsus are unique features of the species.

Description: As described for *T. muesebecki* except as follows: total body length 2.0 mm; forewing length 1.59 mm; intertegular distance 0.43 mm. Holotype largely covered in a microscopic froth of bubbles and obscuring many features. Integument (where evident) dark brown except tarsi apparently light brown. Nine flagellar articles, basal funicular articles wider than long, tapering to slightly longer than wide by penultimate article, apicalmost article longest, tapering to bluntly rounded apex. Metatibia expanded apically, outer margin with posterior, longitudinal row of spinulose setae confined to apical half, apically three such setae clustered together; longest metatibial spur longer than metabasitarsus, base of spur wider than metabasitarsal base; inner surface of metabasitarsus with scattered, short setae, with a longitudinal row of short spicules on inner surface. Metasoma short, apparently tapered to narrow apex; apex reaching to level of wing apex; not compressed laterally or dorsoventrally.

Etymology: The specific epithet is the Latin word "gigas", meaning "giant".

Tagsmiphron ascalaphus nov.sp. (Fig. 1d)

Holotype: AMNH NJ-1128; Late Cretaceous (Turonian, Raritan Formation) amber; Sayreville, Middlesex County, New Jersey.

Paratypes: AMNH NJ-654 and NJ-363b; both in Late Cretaceous (Turonian, Raritan Formation) amber; Sayreville, Middlesex County, New Jersey.

Additional material: AMNH NJ-1125 and NJ-1129; both in Late Cretaceous (Turonian, Raritan Formation) amber; Sayreville, Middlesex County, New Jersey.

Diagnosis: This species is generally similar to most *Tagsmiphron* in the presence of a single protibial spur. However, it shares with *T. canadense* the shorter scape but can be separated from that species by the slender protibia, the unmodified protibial spurs, and the presence of stublike spicules rather than stout spines on the inner metabasitarsal surface, in addition to the single

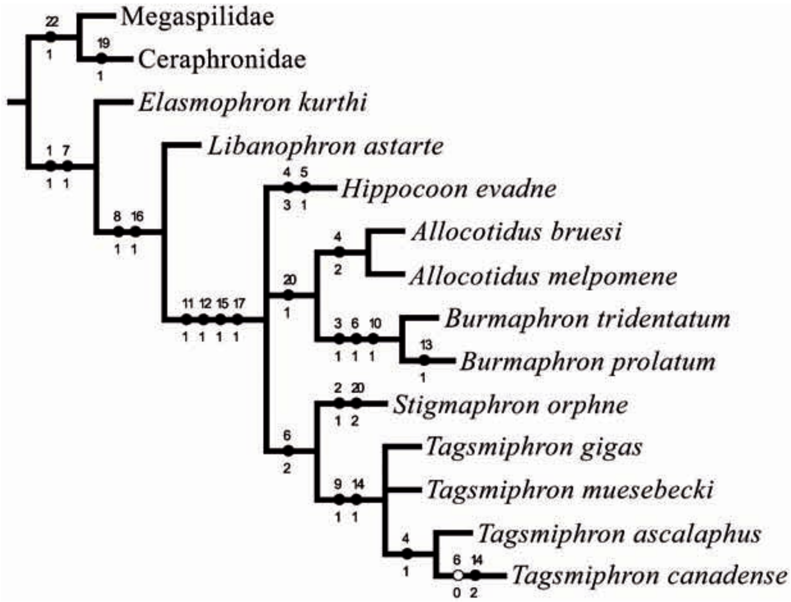

Fig. 8: Cladogram of Stigmaphronidae (length 28, CI 95, RI 97), with unambiguous apomorphies denoted by black circles, reversals in white. Character numbers appear above the branch and state numbers beneath the branch.

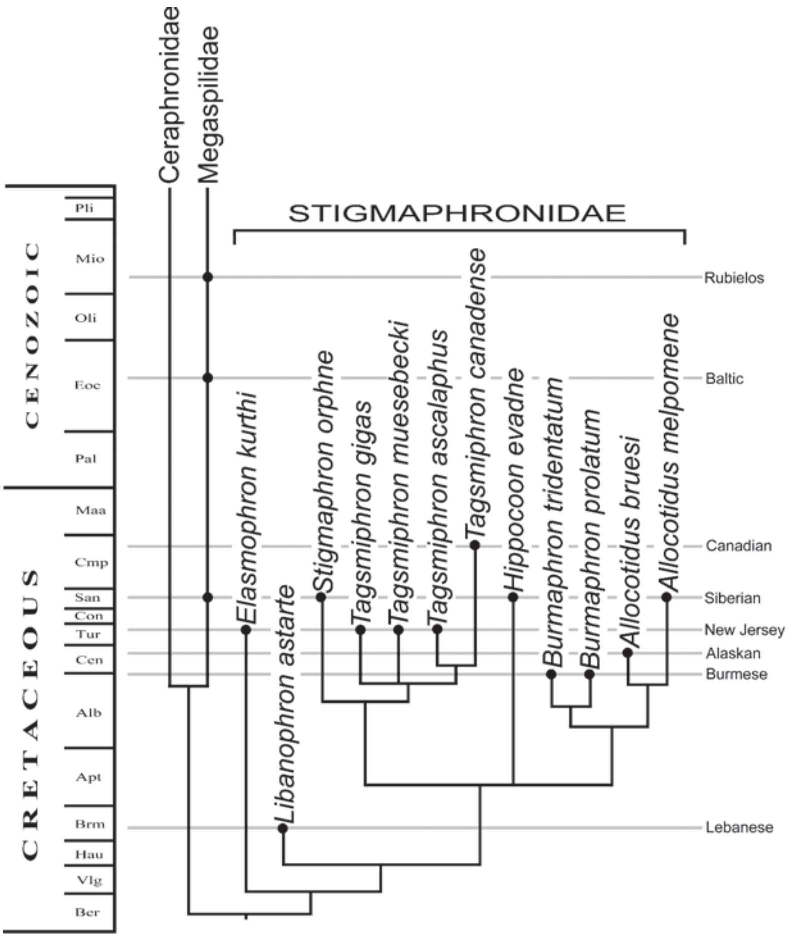

Fig. 9: Phylogeny of Stigmaphronidae (based on cladogram from Fig. 8). Dark circles indicate fossil records of Megaspilidae, no fossils of Ceraphronidae are yet documented.

protibial spur and other features of the highly autapomorphic *T. canadense* (vide infra).

Description: As described for *T. muesebecki* except as follows: total body length 1.08 mm (1.06-1.20 mm); forewing length 0.74 mm (0.74-0.80 mm); intertegular distance 0.25 mm (0.25-0.30 mm). Scape slender, c. 3.5 times longer than apical width. Mesosoma with fine, minute, dense punctures, integument between punctures (where evident) smooth; notauli not evident; medial line either exceedingly faint or absent (difficult to discern in available specimens).

Etymology: The specific epithet is a Latin transliteration of the Greek name Askalaphos (Ασκαλαφος). Askalaphos, son of Akheron and Orphne (for whom the type species of *Stigmaphron* was named; a.k.a. Gorgyra), was the underworld spirit who managed the orchards of Hades and to whom he tattled on Persephone after she ate of the pomegranate seeds. Persephone was forced to spend a part of each year with Hades away from her mother Demeter, thereby bringing on winter as a result of Demeter's sorrow. Demeter punished Askalaphos by burying him under a stone, much like this fossil was long buried (when he was subsequently freed by Herakles he was turned into an owl by Persephone herself as she threw water from the river Phlegethon into his face).

Tagsmiphron canadense nov.sp.

Holotype: RTMP 964.705; Late Cretaceous (Campanian, Foremost Formation) amber; Grassy Lake, Alberta, Canada.

Diagnosis: *Tagsmiphron canadense* can be immediately recognized by the expanded protibia, with two stout spurs (all other *Tagsmiphron* species have a single, short protibial spur), and the stout spines on the metabasitarsus.

Description: Total body length 1.24 mm. Integument dark brown to black except tarsi and spurs brown; integument where evident imbricate. Head apparently about as long as wide (difficult to discern owing to distortion of specimen), with exceedingly sparse, short setae, with dense, minute, fine punctures; scape about three times longer than apical width; flagellar articles about as wide as long, tapering to slightly longer than wide by penultimate flagellar article, apicalmost flagellar article short, much more narrow and tapering to acute point. Mesosoma with exceedingly sparse, short setae. Legs generally with numerous, fine, short, subappressed setae; protibia distinctly expanded apically, with two stout, elongate spurs, outer spur nearly as long as probasitarsus (nearly three-quarters length of protibia), inner spur almost one-half probasitarsal length, with short spicules on outer surface of protibia and probasitarsus; metatibial spur exceedingly long, nearly length of metatibia; metabasitarsus with longitudinal row of distinct, stout, erect spines, such spines present on inner surface of metatarsomeres II-IV; outer surface of metabasitarsus with dense comb of very short, stub-like spicules along length. Wings not preserved. Metasoma largely crushed, surface apparently imbricate with scattered, short, subappressed setae.

Etymology: The specific epithet is based on the country in which the amber originates, Canada.

Comments: The holotype of *T. canadense* is unfortunately quite poorly preserved, with the wings lost at the surface of the amber and the entire specimen badly laterally compressed. Nonetheless, sufficient character information could be coded for the specimen to permit its inclusion in the cladistic analysis (vide infra). Initially the peculiar protibial structure, enlarged protibial spurs, and stout spines on the metabasitarsus suggested placement in a new genus but the cladistic analysis indicates an affinity among the New Jersey amber species and we have, therefore, considered them as congeneric despite the considerable autapomorphies of the Canadian species. Hopefully more complete material will eventually be recovered to permit a more thorough characterization of the species and a critical test as to whether it is correctly placed within *Tagsmiphron*.

Cladistics

A cladistic analysis of stigmaphronid species was undertaken using the characters and states outlined in Appendix 1. Twenty-two characters were identified and coded for analysis. The analysis included all described stigmaphronid species as well as the new taxa considered herein. To these were added codings of representatives for the remaining ceraphronoid families, *Lagynodes* (for Megaspilidae) and *Ceraphron* (for Ceraphronidae), as well as a third composite outgroup consisting of a generalized higher proctotrupomorphan. While much confusion remains concerning the higher-level affinities of major hymenopteran clades (e.g., GRIMALDI & ENGEL 2005), such a matter is well outside the scope of the present study. We have therefore not attempted to readdress the position of Ceraphronoidea among Proctotrupomorpha (or Evaniomorpha) nor the monophyly of the infraorder including this superfamily. We have largely relied upon Megaspilidae (represented by *Lagynodes*) and Ceraphronidae (represented by *Ceraphron*) for outgroup polarization, although we should note that the generalized coding for Proctotrupomorpha would apply equally for a generalized coding of Evaniomorpha for the characters under examination. The complete data matrix is presented in Table 2. A parsimony analysis of the data matrix using the wh* and max* commands in NONA (GOLOBOFF 1997) via the WinClada interface (NIXON 2002) resulted in a single topology of length 28, CI 0.95, and RI 0.97 (Fig. 8). The analysis recovered a monophyletic Stigmaphronidae as well as a clade comprising the modern families of Ceraphronoidea. An extensive search for characters regarding relationships among or within modern Ceraphronoidea was not made and so little can be discerned regarding these two families. Nonetheless, while related to Ceraphronidae the Megaspilidae share many features primitively with Stigmaphronidae and no autapomorphy was immediately evident for megaspilids. The possibility that Ceraphronidae is actually derived from within Megaspilidae should be critically investigated, and the former may represent a post-Eocene radiation of a "megaspiline" clade. A great deal of phylogenetic work remains to be done on modern ceraphronoids as well as Apocritan relationships as a whole.

Table 2: Data matrix for cladistic analysis of Stigmaphronidae; character descriptions provided in Appendix 1; all characters considered non-additive.

Taxon/Character	**1111111111222** **1234567890123456789012**
Allocotidus bruesi MUESEBECK	10020?1???????11110110
Allocotidus melpomene (KOZLOV)	1002001100110011110110
Burmaphron prolatum nov.sp.	1010011101111011110110
Burmaphron tridentatum nov.sp.	1010011101110011110110
Elasmophron kurthi nov.sp.	1000001000000000010010
Hippocoon evadne KOZLOV	100310110011 00?1110010
Libanophron astarte nov.sp.	1000001100000001010010
Stigmaphron orphne KOZLOV	110002110011 00?1110210
Tagsmiphron ascalaphus nov.sp.	100102111011 01?1110010
Tagsmiphron canadense nov.sp.	1001001110110 2??????10
Tagsmiphron gigas nov.sp.	100002111011 01?1110010
Tagsmiphron muesebecki nov.sp.	1000021110110111110010
Lagynodes sp. (Megaspilidae)	0000000000000000010011
Ceraphron sp. (Ceraphronidae)	0000000000000000011011
General Proctotrupomorpha	0000000000000000000000

Discussion

The Stigmaphronidae are an interesting example of a monophyletic radiation of late Mesozoic wasps, which presumably became extinct sometime prior to the end of the Cretaceous. Unlike many Cretaceous hymenopterans that represent primitive grades to particular families, subfamilies, or other lineages (e.g., ENGEL 2006; ENGEL & GRIMALDI 2005, 2006a, 2006b; GRIMALDI & ENGEL 2005; LIU et al. 2007; unpubl. data), the stigmaphronids are not paraphyletic to the surviving species of Ceraphronoidea, but instead possess unique synapomorphies and are definitively monophyletic. This is evidenced by the form of the peculiarly expanded and flattened metacoxa and the hemispherical head, with its occiput smoothly concave and an occipital surface tightly adjoining the anterior portion of the mesosoma. If *E. kurthi* in 90 Ma old New Jersey amber is indeed the sister group to the rest of the Stigmaphronidae, then basal divergence of the Stigmaphronidae from Ceraphronidae + Megaspilidae must have preceded the age of *Libanophron*, which is in older (c. 120 Ma) amber. Origin and basal-most divergences of Ceraphronoidea plausibly occurred in the earliest Cretaceous or even Late Jurassic. Given that Apocrita and even Proctotrupomorpha as a whole are documented from the Early Jurassic (GRIMALDI & ENGEL 2005), a latest Jurassic origin of Ceraphronoidea is certainly within reason, with subsequent diversification in the Cretaceous (definitive Evaniomorpha are not known until the Late Jurassic).

The phylogeny of the Stigmaphronidae (Fig. 9) reveals no stratigraphic-clade rank correlation. Lack of such a correlation is due either to: 1, an obscure or poorly supported phylogenetic hypothesis; 2, very incomplete stratigraphic sampling; or, both of these. Given that the present hypothesis (Fig. 8) has very little character conflict, we interpret the lack of a stratigraphic-clade rank correlation to reflect poor stratigraphic sampling. Clearly, we are only glimpsing at what must be a much more extensive diversity of these wasps (Fig. 9). Given this, the continued exploration of Cretaceous deposits will likely reveal many additional and important taxa, and undoubtedly these will revise our understanding of relationships within the family.

Stigmaphronidae were widespread during the Cretaceous, albeit with some provinciality in the distributions of genera and generic groups (e.g., a largely western Laurasia clade versus largely eastern Laurasia clade: Fig. 8). Species of the family are known in all major amber deposits of the period but by the end of the Cretaceous the family apparently became extinct. It is not understood why the family disappeared. Changes in climate are unlikely to have resulted in their disappearance, as most insect families were not dramatically affected by such shifts until the significant and permanent cooling of the Eocene-Oligocene transition (GRIMALDI & ENGEL 2005). It is possible that stigmaphronids specialized on a particular form of host which itself became extinct near the close of the Cretaceous. Unfortunately, nothing about their morphology can be correlated with a particular form of host and the diversity of modern ceraphronoid hosts (many of which were also present during the Cretaceous) precludes any immediate clue into the biology of stigmaphronids.

Finally, this study is typical of the type of inference that is possible with extinct taxa that are all preserved with life-like fidelity. An abundance of fossilized characters allows informed phylogenetic hypotheses, which in turn allows informed hypotheses on the origins, radiations, and extinction of taxa.

Zusammenfassung

Die Autoren revidieren eine ausgestorbene Familie parasitärer Wespen, die Stigmaphronidae (Proctotrupomorpha: Ceraphronoidea), und führen eine kladistische Analyse hinsichtlich ihrer Verwandschaftsverhältnisse durch. Stigmaphroniden sind hauptsächlich aus kreidezeitlichen Bernsteinen aus Sibirien, Alaska, Kanada, New Jersey, Burma und dem Libanon bekannt, kommen jedoch auch als kompaktierte Fossilien in normalen Sedimentgesteinen der Unterkreide Sibiriens und der Mongolei vor. Die Revision resultiert in der Beschreibung der folgenden neuen Taxa, welche die Diversität der Familie verdoppeln: *Elasmophron kurthi* nov.gen. et sp. (New Jersey Bernstein), *Libanophron astarte* nov.gen. et sp. (libanesischer Bernstein), *Burmaphron tridentatum* nov.gen. et sp. (burmesischer Bernstein), *B. prolatum* nov.sp. (burmesischer Bernstein), *Tagsmiphron muesebecki* nov.gen. et sp. (New Jersey Bernstein), *T. gigas* nov.sp. (New Jersey Bernstein), *T. ascalaphus* nov.sp. (New Jersey Bernstein), and *T. canadense* nov.sp. (kanadischer Bernstein). Des Weiteren wird die Gattung *Elasmomorpha* KOZLOV als jüngeres Synonym von *Allocotidus* MUESEBECK (nov.syn.) angesehen, was die neue Kombination *Allocotidus melpomene* (KOZLOV) nov.comb. zur Folge hat. Die Verwandtschaftsverhältnisse der kladistischen Analyse sind gut unterstützt, so dass das Fehlen jeglicher Korrelation zwischen stratigraphischem Auftreten und den "clade ranks" darauf hindeutet, dass die stratigraphische Beprobung dieser vermutlich sehr diversen Gruppe äußerst unzureichend ist.

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Address of authors:

Michael S. ENGEL
Division of Entomology (Paleoentomology)
Natural History Museum
1501 Crestline Drive – Suite 140
University of Kansas
Lawrence, Kansas 66049-2811, USA
E-Mail: msengel@ku.edu

David A. GRIMALDI
Division of Invertebrate Zoology (Entomology)
American Museum of Natural History
Central Park West at 79th Street
New York, New York 10024-5192, USA
E-Mail: grimaldi@amnh.org

Appendix 1

Characters used in cladistic analysis

Below are the characters and character states used in the cladistic analysis of stigmaphronid relationships. All of the characters were considered non-additive and of equal weight.

1. Body design: 0 = body more gracile, head not tightly fitted to pronotum; 1 = body relatively compact, with hemispherical head fitted to pronotum.
2. Compound eye: 0 = normal, occupying large portion of lateral surface of head (occupying 75% or more of lateral head surface); 1 = reduced, slender, set posteriorly on head, not occupying large portion of head's lateral surface (occupying less than 50% of head width).
3. Preoccipital ridge: 0 = sharply angled and carinate; 1 = with ridge prior to posterior angle.
4. Scape: 0 = slender, elongate, five or more times longer than apical width; 1 = slender, 3–3.5 times as long as wide; 2 = short, about 1.5–2.5 times as long as wide; 3 = exceedingly short, about as long as wide.
5. Funicular articles: 0 = gradually increasing in length, from transverse to longer than wide; 1 = all extremely short, compact, and transverse.
6. Protibial spurs: 0 = two well-developed spurs of approximately equal design; 1 = two spurs, with second drastically reduced and nearly vestigial; 2 = a single protibial spur present.
7. Metacoxa: 0 = slender and short, not covering lateral view of propodeum; 1 = greatly enlarged, flattened, and covering lateral view of propodeum.
8. Metafemur: 0 = slender; 1 = greatly swollen.
9. Row of short, stout spicules on posterior margin of metafemur: 0 = absent; 1 = present.
10. Five to seven long, fine, spicules on distal margin of metafemur: 0 = absent; 1 = present.
11. Metatibia: 0 = slender; 1 = greatly broadened apically.
12. Metatibial spurs: 0 = short, as long as or scarcely longer than metatibial apical width; 1 = greatly elongate, much greater than apical width of metatibia.
13. Metabasitarsus: 0 = as long as or shorter than metafemur; 1 = longer than metafemur.
14. Inner surface of metabasitarsus: 0 = with scattered setae; 1 = with row of short, stout spicules; 2 = with row of distinct spines.
15. Medial line of mesoscutum: 0 = present; 1 = absent.
16. Posterior border of mesoscutellum: 0 = rounded; 1 = pointed.
17. Mesoscutellum: 0 = not obscuring propodeum; 1 = obscuring propodeum.
18. Forewing veins C and Sc+R: 0 = distinct; 1 = fused.
19. Pterostigma: 0 = large, distinct; 1 = reduced, effectively absent.
20. Forewing Rs: 0 = present, well developed; 1 = present, nebulous; 2 = absent.
21. First metasomal segment: 0 = distinct; 1 = forming a short petiole largely obscured by second metasomal segment.
22. Second metasomal segment: 0 = not greatly larger than succeeding metasomal segments and comprising bulk of metasoma; 1 = greatly enlarged relative to succeeding metasomal segments and comprising bulk of metasoma.