

A primitive sapygid wasp in Burmese amber (Hymenoptera: Sapygidae)

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Abstract. A primitive wasp of the family Sapygidae is described and figured from a male preserved in mid-Cretaceous (latest Albian, ca. 100 Ma) amber from Myanmar. The fossil is described as a new genus and species, *Cretosapyga resinicola*, and a new subfamily, Cretosapyginae, is proposed. The phylogenetic placement of the fossil is discussed. *Cretosapyga* is the oldest and first formally described fossil for the lineage, the only other record being a putative species of *Sapyga* (Sapyginae) in Baltic amber (Eocene: Lutetian, ca. 45 Ma).

Key words: Hymenoptera, Apocrita, Vespomorpha, Aculeata, Euaculeata, Tiphiiiformes, phylogeny, new species, Cretaceous, Albian, Myanmar.

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I. INTRODUCTION

Sapygids are typically, moderately robust wasps the biology of which is poorly understood. Where known, species are either ectoparasitoids or cleptoparasites of larval eumenine wasps or solitary bees of the Megachilinae and Xylocopini (e.g., PATE 1947; TORCHIO 1972, 1979; BONELLI 1977; WESTRICH 1983). The family is divided into two subfamilies – the Fedtschenkiinae, with the sole genus *Fedtschenkia*, and the Sapyginae. The five species of *Fedtschenkia* are relict, occurring disjunctly in xeric areas of western North America, the Middle East, and Central Asia. Sapygines presently comprise 13 genera and approximately 67 species occurring throughout the world except the Australian region. KURZENKO (1996) has provided a key to the Holarctic genera, while PATE's (1947) key includes the South American genera *Huarpea* and *Araucania*; only *Parasapyga* is known from the Oriental region. No cladistic analysis has yet been attempted for the family.

Herein we provide the description of the first Mesozoic representative of the Sapygidae and, although a putative species of *Sapyga* has been recorded from Baltic amber (Eocene: Lutetian, ca. 45 Ma) (LARSSON 1978; SPAHR 1987), the first formally proposed fossil of the family. A single male of a primitive sapygid was discovered in Burmese amber. The age of Burmese amber had historically been considered to be of Tertiary age (e.g., NOETLING 1892; STUART 1923: but see COCKERELL 1917, who, ahead of his time, believed that the insect inclusions suggested a Cretaceous age!). Re-

newed study of amber from northern Myanmar in the last five years has conclusively demonstrated that the deposits are of mid-Cretaceous age (ZHERIKHIN & ROSS, 2000; GRIMALDI et al., 2002; CRUICKSHANK & KO 2003), perhaps as old as the latest Albian (ca. 100 Ma).

The fossil described herein possesses key synapomorphies for the mutillid + sapygid clade and it likely represents an extinct, stem group basal either to modern Sapyginae or Sapyginae + Fedtschenkiinae. Both hypotheses are consistent with a subfamily rank nomen and thus a new, extinct subfamily, *Cretosapyginae* is erected to receive this species.

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II. SYSTEMATIC PALEONTOLOGY

Family SAPYGIDAE LATREILLE

Subfamily *Cretosapyginae* subfam. nov.

T y p e g e n u s. *Cretosapyga* gen. nov.

D i a g n o s i s. **Male.** Stout-bodied wasp. Compound eyes with inner margins entire, not emarginate (emarginate in Sapyginae). Toruli widely spaced, separated by twice width of an individual torulus; dorsal rim of torulus forming oblique lamella (lamellae of toruli divergent) and extending slightly over radicle; radicle apparently partly concealed in base of scape but seemingly without cup or depression at base of scape. Occipital carina present. Humeral (anterolateral) angle of pronotum rounded but medial dorsal area with sharp declivity; posterodorsal margin of pronotum more or less straight between tegulae (at most weakly concave), with suture between pronotum and mesoscutum strong; posterolateral angle of pronotum rounded toward tegula. Mesoscutum strongly rounded, appearing “humped” (at least in part due to distortion of light by amber); mesoscutum with notauli and parapsidal furrows present; strongly impressed margin between mesoscutum and mesoscutellum. Mesopleuron and metapleuron strongly swollen yet strongly impressed between them at meso-metapleural suture. Propodeum broadly concave posteriorly; posterior margin with oblique triangular flange. Forewing with all veins tubular; marginal cell closed; three submarginal cells present, third submarginal cell wider along its anterior margin than posteriorly; first discal cell much shorter than sub-basal cell; wing membrane hyaline, not textured, membrane with scattered, short pubescence. Hind wing with distinct jugal lobe (partially folded under wing but evident). Legs generally slender, not fossorial (metafemora somewhat expanded); mesosternum not expanded posteromedially over bases of mesocoxae; meso- and metacoxae contiguous (or nearly so); metacoxae not concealed by lamellae; metacoxa with dorsal longitudinal carina; tibiae and apices of tarsi spinose; tibial spur formula 1-2-2; protibial spur straight, unmodified; tarsi pentamerous; pretarsal claws simple except for a minute medial tooth. Metasoma somewhat elongate, slender apically, sessile; metasomal T1–2 without felt line but with lateral, longitudinal carina extending along length of terga (paralleling margin of terga); posterior margin of metasomal T1 as wide as anterior margin of metasomal T2, laterally forming continuous curve; metasomal S1 separated from S2 by distinct constriction, S1 apparently not overlapping S2 and with distinct posterior, vertical surface; constriction between S4 and S5. **Female.** Unknown.

R e m a r k s. *Cretosapyga* superficially and plesiomorphically resembles primitive mutillids of the subfamily Myrmosinae (as might be expected for any early fossil of the Mutillidae + Sapygi-

dae clade). However, as discussed later (*vide* Discussion, *infra*), the fossil lacks synapomorphies of the Mutillidae and cannot be included in this family. It can similarly be excluded from more basal tiphiiiform families (i.e., Pompilidae and Tiphiiidae) owing to the absence of apomorphies for each of these families while simultaneously possessing synapomorphies of the Mutillidae + Sapygidae clade (*vide* Discussion, *infra*). As we discuss below, the most conservative placement of *Cretosapyga* is as a subfamily basal within Sapygidae but discovery of more completely preserved specimens and additional character data may require its elevation to familial status.

Cretosapyga is unique in its form of constriction between metasomal S1 and S2. Some form of constriction between metasomal S1 and S2 is found in many, if not most, vespid taxa, usually formed by non-overlapping slanted or rounded margins of S1 and or S2. However, the form of constriction found in *Cretosapyga*, particularly the precipitous apex to S1, is clearly not as common. Yet some form similar to this is found in at least some Sapygidae (weak in *Eusapyga*, *Sapyga* and *Fedtschenkia* may have vestigial forms of this same constriction), anthoboscine tiphiiids, and some Rhopalosomatidae. In the latter, the posterior surface of S1 is angled anteriorly and has posterior projections laterally. Thus it is arguably not homologous with the constriction found in the former taxa. Given the possession of some form of this trait in *Cretosapyga*, basal tiphiiids, as well as in some other sapygids, it may be a synapomorphy for the Tiphiiiformes outside of pompilid wasps. If this is the case, it has subsequently been lost in the common ancestor of mutillid wasps, and separately in higher tiphiiids and some sapygids (a decidedly less than parsimonious interpretation). The form of S1-S2 constriction should be critically re-evaluated across Vespoidea and a series of revised, character states identified to be more thoroughly evaluated for their phylogenetic utility in combination with other characters. Among all of the taxa, the conditions in *Cretosapyga* and *Eusapyga* are clearly the most similar.

Genus *Cretosapyga* gen. n.

T y p e s p e c i e s. *Cretosapyga resinicola* sp. n.

D i a g n o s i s. As for the subfamily (*vide supra*).

E t y m o l o g y. The new genus-group name is a combination of Cretaceous and *Sapyga* (type genus of the family). The name is feminine.

Cretosapyga resinicola sp. n.

Fig. 1

D i a g n o s i s. As for the genus (*vide supra*).

D e s c r i p t i o n. As described for the subfamily, with the following additions: **Male.** Total body length 6.62 mm; forewing length 3.92 mm. Integument appearing imbricate; color apparently dark brown to black without maculations. Head width 1.30 mm, length 1.00 mm. Antenna with 11 flagellomeres; flagellomeres longer than wide, each individual length ranging from ca. 3-4 times width, shortest near pedicel and progressively and slightly longer toward distal flagellomere. Intertegular distance 0.83 mm. Profemur and protibia subequal in length; probasitarsus about two-thirds length of protibia; mesotrochantellus narrow, ring-like; mesofemur swollen medially and flattened, about one-third as wide as long; mesotibia subequal in length to mesofemur and flattened, about one-seventh as wide medially as long; mesotibial spurs elongate, each about one-half length of mesobasitarsus; mesobasitarsus about one-half length of mesotibia and about equal in length to combined lengths of remaining mesotarsomeres. Metafemur swollen medially, flattened, apparently twisted, and slightly shorter than metatibia; metatibial spurs elongate, inner spur longest, about one-half length of metabasitarsus. Metasoma slender apically and somewhat elongate; apices of parameres exposed, acutely rounded but not pointed, bearing dense, short, simple setae. **Female.** Unknown.

H o l o t y p e. ♂, Myanmar (Burma): Middle Cretaceous (Albian-Cenomanian), Kachin: Tanai Village (on Ledo road, 105 km NW Myitkyna), KU-NHM-ENT-Bu022. Deposited in the

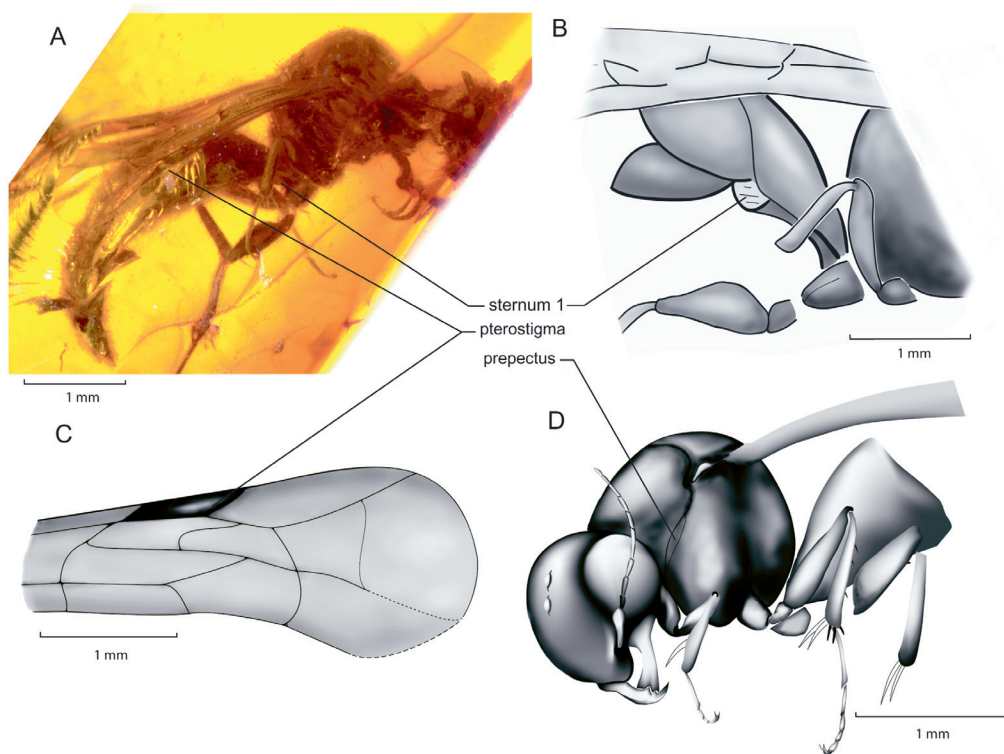


Fig. 1. Holotype male of *Cretosapyga resinicola* (KU-ENT-Bu-022); all line figures are drawn *as preserved* (i.e., with bends and distortions). A. Photomicrograph of entire specimen. B. Posterior-oblique view of anterior metasoma and posterior mesosoma. C. Apical half of forewing. D. Anterior-oblique view of head, mesosoma, and anteriormost metasoma.

Fossil Insect Collection, Division of Entomology, University of Kansas Natural History Museum. The specimen is preserved close to the amber surface which is slightly curved, thereby preventing an optimal view of many structures. Similarly, the fossil is bordered on its other side by a large elaterid beetle, preventing further preparation of the amber piece to expose a view from the other side of the specimen. Indeed, any cuts into the piece would result in either damage to the wasp or to the beetle and so further preparation is not possible.

E t y m o l o g y. The specific epithet is a combination of the Latin words *resina* (meaning, “resin”) and *-cola* (meaning, “inhabiting”).

III. DISCUSSION

The stinging wasps (Aculeata: Table 1) are first, definitively known from the earliest Cretaceous. The latest Jurassic family Bethylonomidae has been regarded as the sister group to Aculeata (e.g., RASNITSYN 1975, 1988). Certainly bethylonomids are strongly suggestive of plesiomorphic aculeates owing to their bethylid-like habitus and apparently short ovipositor, but the definitive apomorphy (i.e., the modification of the ovipositor into a sting) is not conclusively known for the family. The first diversity of definitive aculeates is in the Early Cretaceous, with a diversity of taxa of all three superfamilies known from numerous deposits around the world.

Table I

Hierarchical classification of Aculeata and its putative sister group †Bethylony-moidea (*vide etiam* GRIMALDI & ENGEL 2005)

PARVORDER †PARACULEATA ENGEL	
Superfamily †Bethylonymoidea RASNITSYN Family †Bethylonymidae RASNITSYN	
PARVORDER ACULEATA SCOPOLI	
Superfamily Chrysoidea LATREILLE Family Plumariidae BISCHOFF Family Scolebythidae EVANS Section Chrysidiformes nov. Family Bethylidae HALIDAY Family Chrysididae LATREILLE Section Dryiniiformes nov. Family Sclerogibbidae ASHMEAD Family Embolemidae FÖRSTER Family Dryinidae HALIDAY	
NANORDER EUACULEATA GRIMALDI & ENGEL	
Superfamily Vespoidea LATREILLE Family Sierolomorphidae KROMBEIN Section Vespiformes nov. Family Rhopalosomatidae ASHMEAD Family Bradynobaenidae SAUSSURE Family †Falsiformicidae RASNITSYN Family †Armaniidae DLUSSKY Family Formicidae LATREILLE Family Vespidae LATREILLE Family Scoliidae LATREILLE Section Tiphiiiformes nov. Family Tiphiiidae LEACH Family Pompilidae LATREILLE Family Mutillidae LATREILLE Family Sapygidae LATREILLE	Superfamily Apoidea LATREILLE Family †Angarosphecidae RASNITSYN Family Heterogynaidae NAGY Family Ampulicidae SHUCKARD Family Sphecidae LATREILLE Family Crabronidae LATREILLE Section Anthophila LATREILLE Family Colletidae LEPELETIER Family Halictidae THOMSON Family Andrenidae LATREILLE Family †Paleomelittidae ENGEL Family Melittidae SCHENCK Family Megachilidae LATREILLE Family Apidae LATREILLE

Aculeate wasps are relatively well represented in Burmese amber (e.g., ANTROPOV 2000; GRIMALDI et al. 2002; ENGEL 2003, in press; ENGEL & GRIMALDI unpubl. data). Fossils of the Tiphiiiformes (Table I) are rare and most are known from Tertiary resins. Previously, the sole Mesozoic record of the section was an anthoboscine tiphiiid from the Early Cretaceous of Brazil (DARLING & SHARKEY 1990). *Cretosapyga*, along with a recently discovered pompilid in Burmese amber (GRIMALDI et al. 2002; ENGEL & GRIMALDI in prep.), are the second oldest records of the Tiphiiiformes. These Burmese amber fossils are the oldest records of their respective families.

The characters in the preferred tree of BROTHERS & CARPENTER (1993) for aculeate phylogeny are arguably the most important for determining the phylogenetic position of *Cretosapyga*. Considering only these characters, the fossil can be placed convincingly within the Tiphiiiformes and outside of the Pompilidae and the Tiphiiidae by the form of the prepectus, lack of a transverse mesopleural sulcus, antennal sockets forming a tubercle, a radical axis inserted at an angle with re-

spect to the scape, and the metacoxa with a dorsal, longitudinal carina (e.g., Fig. 2A). An exact position within this group, however, is less clear. By reference to traditional characters historically used in delineation of these groups (e.g., BROTHERS 1975) and combined with those synapomorphies highlighted by BROTHERS & CARPENTER (1993) for relevant clades, a few likely hypotheses emerge. The fossil clearly falls outside of the Mutillidae and each of the sapygid subfamilies as defined by modern taxa. This is evident by the lack of key synapomorphies for mutillids (i.e., a radicle inserted on a depression or invagination on scape, prepectus with line of fusion to mesepisternum obliterated except at two ventral pits), Sapyginae (emarginate eyes, meso- and metatibial spines apparent only as spiniform setae, large clypeus), and Fedtschenkiinae (loss of occipital carina in males, lack of strongly concave posterodorsal margin of pronotum; robust, fossorial body form; greatly enlarged labiomaxillary complex).

The possibility that the fossil may represent an extinct family basal to Mutillidae + Sapygidae cannot be entirely excluded. Evidence for this is in the lack of an anterior pronotum that is strongly declivitous widely to lateral margins (though it is declivitous medially) and the fossil is possibly without a straight lateroventral margin of the pronotom (summarized in Figure 2A). However, the latter character is dubious owing to lack of a clear view and without further corroborating characters

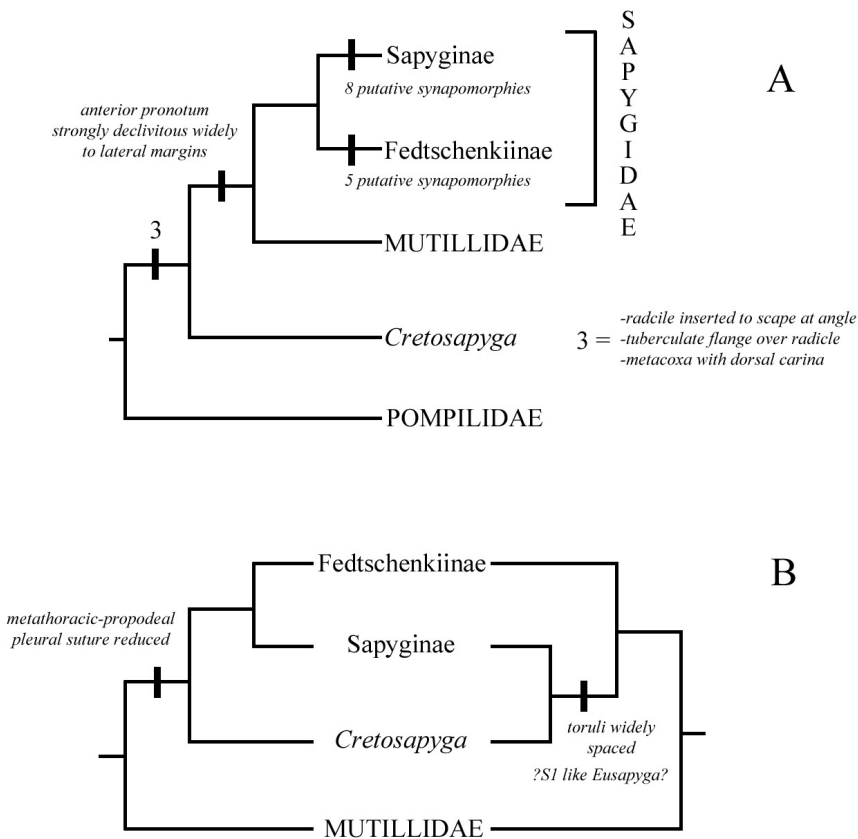


Fig. 2. Phylogenetic hypotheses for the placement of *Cretosapyga*. Only pertinent traits relating to the placement of *Cretosapyga* are discussed or mapped. Refer to BROTHERS & CARPENTER (1993) for their complete list of characters and for evidence of the various nodes. A. The least well-supported hypothesis with the fossil outside of the Mutillidae + Sapygidae clade. B. The most well-supported hypotheses with *Cretosapyga* within Sapygidae.

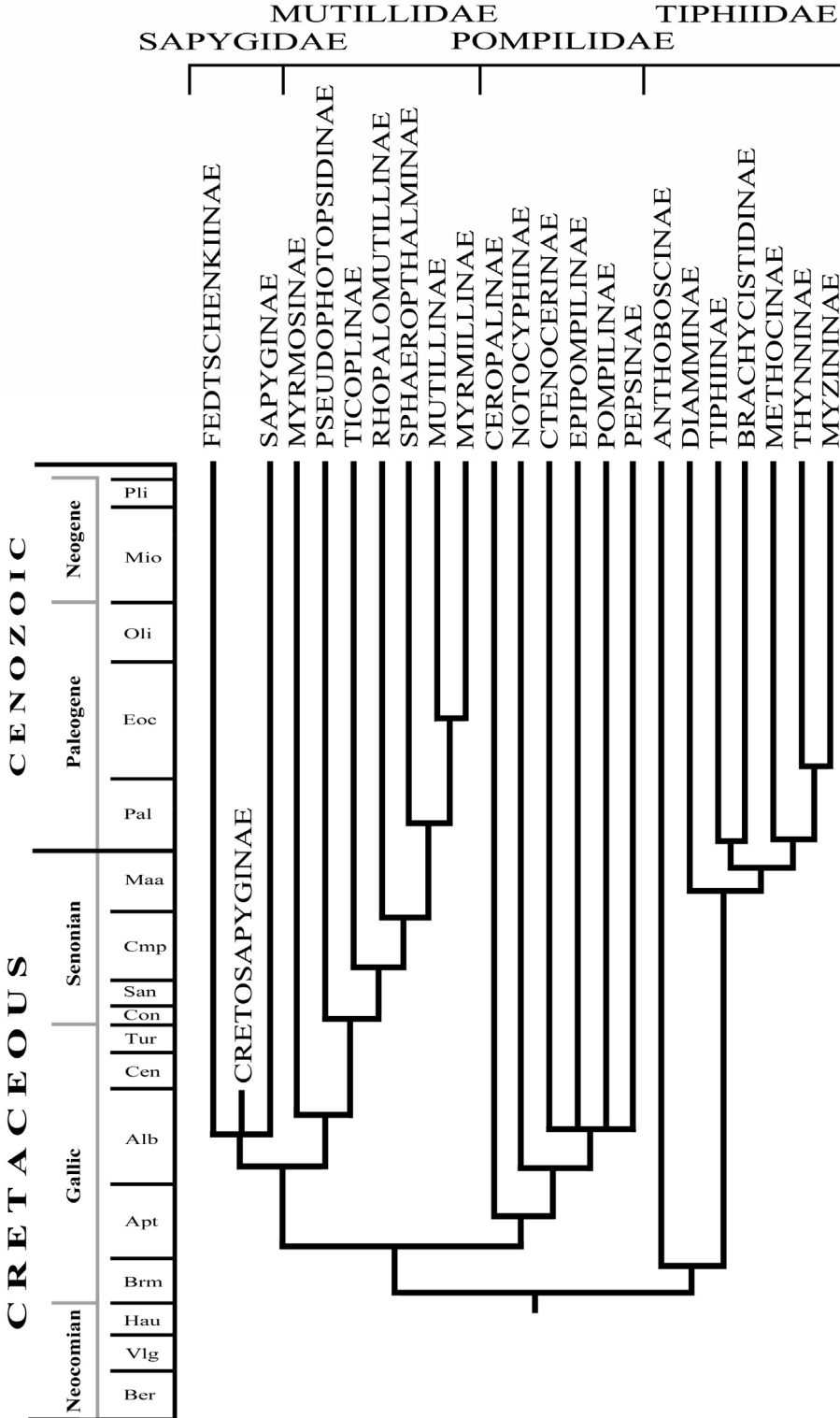


Fig. 3. Phylogeny of the Tiphiiiformes indicating the most conservative placement of Cretosapyginae as well as putative ages of various clades.

to support the former, this hypothesis is only weakly supported. It is more likely, and given the structure of the three characters shortly to be discussed, that *Cretosapyga* belongs inside of the Sapygidae + Mutillidae clade and, in fact, is basal to one or both extant sapygid subfamilies (as shown in Figure 2B). Evidence for this is in the form of the reduced metathoracic-propodeal pleural suture (as in Sapygidae) and the wide spacing of the toruli (as in Sapyginae) and the similar construction of S1 to *Eusapyga*. Whether *Cretosapyga* should be considered as a stem group to modern Sapygidae (i.e., left-hand arrangement of taxa in Fig. 2B) or as related to Sapyginae (i.e., right-hand arrangement of taxa in Fig. 2B) is not as clear as it might appear. The sole, unambiguous trait uniting the fossil with Sapyginae is the widely spaced toruli (the fossil apparently lacking the seven other apomorphies for the subfamily). While the structure of the posterior margin of S1 is very similar to *Eusapyga* (with a distinctly declivitous posterior surface), the polarity of this trait is difficult to ascertain without understanding the placement of *Eusapyga*. Regardless, if *Eusapyga* is not basal within Sapyginae (which on the surface appears likely), then the conditions in the former and the fossil is likely convergent, while if *Eusapyga* were basal, then the similarity would perhaps be plesiomorphic. Given the diversity of S1 constrictions and posterior margins across Tiphiiiformes it is challenging to a priori ascertain the correct polarity of this trait but given the structure seen in Fedtschenkiinae and Mutillidae it seems unlikely that the *Eusapyga-Cretosapyga* condition is plesiomorphic and is more likely convergent between the two (in which case the S1 construction is apomorphic for the fossil). The position of *Cretosapyga* is likely to be one of those shown in figure 2B. While placement of the fossil in Sapygidae *s. lato* (as in Figs 2B, 3) seems most strongly supported, given the uncertainties just discussed we feel it most conservative to consider the fossil as belonging to an extinct subfamily and in a trichotomy with Fedtschenkiinae and Sapyginae (e.g., Fig. 3).

If the fossil possessed more synapomorphies of one of the sapygid subfamilies, then assignment to a particular modern subfamily would be favored. However, since this is not the case and since both trees shown in figure 2B are cladistically consistent with separate subfamilial status, a new, extinct subfamily is proposed. It is greatly hoped that additional material of *Cretosapyga* (particularly a female!) will eventually be discovered along with further Cretaceous tiphiiiform wasps. It is from such taxa that we will gain the greatest insights into vespoid phylogeny and evolution.

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