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A golden age for ectoparasitoids of Embioidea: Cretaceous Sclerogibbidae (Hymenoptera, Chrysoidea) from Kachin (Myanmar), Charentes (France) and Choshi (Japan) ambers

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ABSTRACT

Sclerogibbid wasps are obligate parasitoids of webspinners (Embiodea). Both groups have a particularly scarce geological record and are known since the Cretaceous: there are only four species of webspinners known from Burmese amber, and only two sclerogibbids were described from Barremian Lebanese and Cenomanian Burmese ambers. Here we report transferred genus from Aptian Choshi (Japan) amber and new sclerogibbids from Cenomanian Burmese and Charentese (France) ambers. The taxa described from Burmese amber are: *Burmasclerogibba aptera* gen. et sp. nov., *Cretosclerogibba* gen. nov. (with *C. antennalis* sp. nov., *C. contractocollis* sp. nov., *C. neli* sp. nov. and *C. rasnitsyni* sp. nov.) and *Edrossia vetusta* gen. et sp. nov. The first European fossil sclerogibbid *Gallosclerogibba alnensis* gen. et sp. nov. is described from Charentese amber. The holotype of *Chosia yamadai* Fujiyama, from Choshi amber, is re-described; it appears to be the oldest Laurasian sclerogibbid. The significant abundance and variety of Burmese sclerogibbid wasps (60% of fossil species known worldwide), as proxy of their hosts, were probably caused by the protection granted to them by the silk webs and possibly by the limited predation from ornithuromorph birds or crown-group ants. While all three extant sclerogibbid genera have apterous females, genera with winged females (*Cretosclerogibba* and *Edrossia*) dominated in Burmese amber. Small silk galleries from hosts may have favored the preservation of wings in females of Cretaceous sclerogibbids. Most new species described in the present paper, in addition to *C. yamadai*, are characterized by a very slender neck and a very long frontal process concealing the antennal toruli. These characters disappeared in extant species. We suggest that this loss was caused by a change in the fauna of predators, penalizing species with long neck and rostrum.

1. Introduction

Sclerogibbidae are a small and still poorly documented family of chrysidoid wasps, hitherto with only 24 species recognized in three extant and two extinct genera (Table 1). All extant

sclerogibbids are obligate ectoparasitoids, and koinobionts, on webspinners (order Embiodea), the females laying one or more egg in the host's abdomen anchoring it or them deeply, with one-third of each egg embedded inside the host body. Larvae feed until the host is consumed (Ross, 2000; Olmi, 2005; Martynova et al., 2019a). The family is distributed almost exclusively in the tropics, similarly to their hosts, though a few species occur in warm temperate regions (Olmi, 2005). Webspinners (1500 estimated species, roughly 400 of which have been named: Edgerly, 2018 and references herein) live in silk galleries, therefore female sclerogibbids have to enter their nests to lay eggs.

The systematics of the family has been clarified only recently thanks to a comprehensive revision of the world fauna by Olmi (2005). Yet, despite the few studies published on sclerogibbids for over a century after the discovery of the first species by Riggio and De Stefani-Perez (1888), there has been a large consensus of cladistic analyses on the relationships of sclerogibbids with other chrysidoid families. Indeed, the family was retrieved as sister to the clade (Embolemidae + Dryinidae) in all morphological analyses (e.g., Carpenter, 1999; Brothers and Carpenter, 1993; Brothers, 1999, 2011; Ronquist et al., 1999) as well as in the single molecular analysis that incorporated a sclerogibbid (Branstetter et al., 2017).

While the distinction between genera and species can be challenging, sclerogibbids are rather easily recognized among chrysidoid wasps by the antennal toruli located under prominent frontal lobes or processes (so that antennae are inserted ventrally), the presence of numerous antennomeres (14–39 segments) and the wing venation reduced (5 closed cells on fore wing, rarely 4 or 6; hind wing with at most Radial vein present). Males and females are very dimorphic, the females of extant genera being always apterous, probably as an adaptation to 'troglobiotic-like' life in silken tunnels of webspinner galleries (but four extinct genera are known with macropterous females) and with the mesosoma distinctly modified (pronotum elongate and fore coxae and femora much broadened). Apterous females can be superficially confused with those of Embolemidae or Dryinidae, and even with Pompilidae (Martynova et al., 2019a).

Sclerogibbids have rarely been encountered in the geological record: only two extinct species have been described from Miocene Dominican amber (Olmi, 2005), one species from mid-Cretaceous Burmese amber (Martynova et al., 2019a), and one species from Lower Cretaceous Lebanese amber (Engel and Grimaldi, 2006). Additionally, the family has been reported as compression fossils from the Laiyang Formation (late phase of the Jehol Biota; 120–122.5 Ma) of Shandong Province in China (Zhang et al., 2010).

Extant webspinners are rarely seen because of their cryptic mode of life, the apterism of females and short life of winged males. They comprise only 0.1 % of all animals normally found in traps according to Solórzano Kraemer et al. (2015). Fossil webspinners are also extremely rare, although recent records from Burmese amber reveal the abundance of these insects in the Burmese mid-Cretaceous amber forest.

Here we report the discovery of 13 new fossil sclerogibbids from lowermost Upper Cretaceous (Cenomanian) amber from Kachin (Myanmar) and Charentes (France). The new material comprise five female and eight male specimens representing four new genera and seven new species, as well as additional material of *Sclerogibba cretacica* Martynova et al., 2019. We also re-examine *Chosia yamadai* Fujiyama, 1994 from Lower Cretaceous Choshi amber, and we transfer it from Stephanidae to Sclerogibbidae.

2. Material and methods

The piece of Japanese amber containing *Chosia yamadai* was collected near Choshi, Chiba Prefecture, Kanto Region, Honshu, Japan. Choshi amber is found in the Inubouzaki Formation (Choshi Group) which is considered to be Early Cretaceous (latest early Aptian) in age (about 121–122 Ma) (Rasnitsyn et al., 2016).

All pieces of Burmese amber examined here were collected from the Noiye Bum site (26° 29' N, 96° 35' E) in the Hukawng Valley of Kachin State, Myanmar. The age of Kachin amber was

previously considered to be late Albian to Cenomanian based on palynology and ammonite stratigraphy (Cruickshank and Ko, 2003). It is now radiometrically dated as 98.79 ± 0.62 Ma based on U-Pb zircon dating of the volcanoclastic matrix and shown to be earliest Cenomanian in age (Shi et al., 2012; Smith and Ross, 2018; Zhang et al., 2018; Yu et al, 2019).

The piece of Charentese amber containing one sclerogibbid was collected from a lignitic lens exposed during low tides on the “Plage de la Vierge” at Fouras, Charente-Maritime department, France. The lignitic lens was embedded within alternating layers of sand and glauconitic clay composing the lithological unit B2 described by Néraudeau et al. (2003), and dated biochronologically as early Cenomanian. A location map and details on the geology and paleontology of this deposit are available in Néraudeau et al. (2003), Perrichot et al. (2010), or Cockx et al. (2016), and an updated stratigraphic section of the locality with discussion on the associated palynomorphs was recently provided by Peyrot et al. (2019). This specimen was originally preserved in syninclusion with 53 other arthropods and 3 plant fragments, in a piece of yellowish amber (numbered IGR.FRS-7; see list of syninclusions in Cockx et al., 2016). Because the piece comprised multiple layers, polishing of its outer surface did not allow for a clear view deep into the amber matrix, so the piece was cut into several fragments using a scalpel blade as a micro-saw. Each fragment containing at least one organic inclusion was then embedded into mineralogical-grade epoxy Epotek 301-2 using a vacuum chamber, and the resulting blocks were polished for an optimal view of the fossils. A total of 34 fossiliferous fragments were prepared, and collection numbers IGR.FRS-7.1 to IGR.FRS-7.34 were assigned. The sclerogibbid wasp described herein is now preserved with two undetermined mites (Acari) in fragment IGR.FRS-7.27.

Photographs of the specimens were taken at multiple focal planes and stacked using the equipment available in the institutions visited for the present study: a Zeiss AXIO Zoom V16 stereomicroscope equipped with a Zeiss Axiocam 512 camera, with ZEN 2.3 and Helicon Focus softwares at the Nanjing Institute of Geology and Palaeontology (China); a Leica Z16 APO stereomicroscope equipped with a Leica DFC 450 camera, with LAS V 3.8 and Adobe Photoshop

software at the Schmalhausen Institute of Zoology (Kiev, Ukraine); an Olympus SZX10 stereomicroscope equipped with an Olympus E-5 camera, processed with Zerene Stacker (Zerene Systems, USA) at the Entomological Laboratory of the Kyushu University (Motooka, Japan).

The descriptions herein follow the terminology used by Martynova et al. (2019a) and Olmi (2005). The measurements reported are relative, except for the total length (from head to abdominal tip, excluding antennae) that is given in millimetres. The term “metapectal-propodeal complex” is here used in the sense of Kawada et al. (2015). It corresponds to the term “propodeum” *sensu* Olmi (2005). The nomenclature for cells and veins of the fore wing are here used in the sense of Olmi (2005) and Martynova et al. (2019a).

All fossil and extant species of Sclerogibbidae reported here were examined personally, except for the holotype of *Sclerogibbodes embioleia*. The type specimens are deposited in the following collections: AMNH (American Museum of Natural History, New York, USA); DAFS (Department of Agriculture and Forestry Sciences, University of Tuscia, Viterbo, Italy); IGR (Geological Department and Museum, University of Rennes 1, France); LYU (Institute of Geology and Paleontology, Linyi University, Linyi, Shandong, China); NHMIC (Natural History Museum and Institute of Chiba, Japan); NIGPAS (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, Jiangsu, China). Other collections examined during this study are PMC (Patrick Müller’s collection, Käßhofen, Germany) and PAC (George O. Poinar, Jr. amber collection, maintained at Oregon State University, Corvallis, Oregon, USA).

3. Results

3.1. Key to the genera of extant and fossil Sclerogibbidae

Females

1. Macropterous (extinct species) (Figs. 2, 8) 2

- Apterous (extant and extinct species) (Figs. 1B, 1C, 11A) 5
- 2. Frons with anterior process concealing antennal toruli in dorsal view and showing a pointed apophysis (Fig. 1A) *Pterosclerogibba* Olmi, 2005
 - Frons with anterior process concealing antennal toruli in dorsal view but without pointed apophysis (Fig. 4C) 3
- 3. Frons with very long anterior process concealing antennal toruli in dorsal view (head about 2.7× as long as anterior frontal process) (Fig. 4C); head separated from pronotum by very long narrow neck (Fig. 4C) (head about 3.5× as long as neck) *Cretosclerogibba* **gen. nov.**
 - Frons with short anterior process concealing antennal toruli in dorsal view (head about 6.6–10× as long as anterior frontal process) (Fig. 7A); neck not or hardly visible (Fig. 7A) 4
- 4. Head about 2.2× as long as thick *Sclerogibbodes* Engel and Grimaldi, 2006
 - Head less than twice as long as thick (1.6) *Edrossia* **gen. nov.**
- 5. Head with very long anterior process concealing base of antennae (Fig. 1B) (head about 4× as long as anterior process); mesoscutum slightly shorter than mesoscutellum, situated only minimally between two posterior lateral angles of pronotum; mesopleuron thick, projecting outwards on sides of mesoscutellum and forming a step *Burmasclerogibba* **gen. nov.**
 - Head with short anterior process concealing antennal toruli in dorsal view (head about 6.6–10× as long as anterior frontal process) (Figs. 11A, 11E); mesoscutum very small, much shorter than mesoscutellum, situated completely at the posterior extremity of the pronotum, between two posterior lateral angles of pronotum (Fig. 11A); mesopleuron not thick, not projected outwards on sides of mesoscutellum, not forming a step 6
- 6. Mesosoma crossed by a straight suture separating the metanotum and mesoscutellum from the metapectal-propodeal complex and distinctly crossing the body (Fig. 11C); metanotum composed of two very large pieces situated on the sides of the mesoscutellum (Fig. 11C); head usually with two, rarely three ocelli (Fig. 11C); eye usually small, approximately situated half-way in the head lateral margin (Fig. 11C); occasionally eye larger and situated in the posterior third of the head;

anterior flat surface of hypostomal bridge as long as first antennal segment, or slightly shorter (Fig. 14); tibial spurs 1/1/2 *Caenosclerogibba* Yasumatsu, 1958

– Mesosoma never crossed by a straight suture separating the metanotum and mesoscutellum from the metapectal-propodeal complex (Figs. 11A, 11F); metanotum usually composed of two narrow pieces situated on the sides of the mesoscutellum (Figs. 11A, 11F); occasionally the above pieces are large, but in this case the suture separating the metanotum and mesoscutellum from the metapectal-propodeal complex is always curved; head with three ocelli (Figs. 11A, 11F); eye always large, situated in the posterior two thirds of the head (Figs. 11A, 11F) 7

7. Tibial spurs formula 1/1/2; anterior flat surface of hypostomal bridge as long as scape, or slightly shorter (Fig. 14) *Probethylus* Ashmead, 1902

– Tibial spurs formula 1/2/2; scape at least twice as long as anterior flat surface of hypostomal bridge (Fig. 14) *Sclerogibba* Riggio and De Stefani-Perez, 1888

Remarks: Females of *Chosia* Fujiyama, 1994 and *Gallosclerogibba* **gen. nov.** are unknown.

Males

1. Frons with very long anterior process concealing antennal toruli in dorsal view (head about 2.4–5.0× as long as anterior process) (Figs. 2, 6); propleuron extended into a very long neck-like prolongation, exposed dorsally (Fig. 6A) (neck usually about a fourth-half of head length; rarely neck not visible) 2

– Frons with short anterior process concealing antennal toruli in dorsal view, about a tenth of head length (Fig. 8D); propleuron not extended into a neck-like prolongation (Figs. 8A, 9C), or rarely with very short neck not dorsally exposed 3

2. Fore wing cells 1M and 2Cu enclosed by pigmented veins (Fig. 2E) *Chosia* Fujiyama, 1994

– Fore wing cell 1M enclosed by pigmented veins; cell 2Cu absent (Fig. 6) *Cretosclerogibba* **gen. nov.**

3. Fore wing with submarginal vein (Rs + M) petiolate on marginal (Rs) (Fig. 8) and pterostigma present (Fig. 9A); notauli usually complete, very rarely incomplete (in such case, shape of cells 1R1 and 2R1 different from those of the two following genera (Figs. 11B, 11E) . . . 4

– Fore wing with submarginal vein (Rs + M) sessile on marginal (Rs) (Figs. 11B, 11D) and without pterostigma (Figs. 11B, 11D); rarely, fore wing with submarginal vein (Rs + M) petiolate on marginal (Rs) and with pterostigma (in such case, notauli incomplete and shape of cells 1R1 and 2R1 different) . . . 5

4. Fore wing with cells 1M and 2Cu enclosed by pigmented veins (Fig. 8C) . . . *Gallosclerogibba* **gen. nov.**

– Fore wing at most with cell 1M enclosed by pigmented veins (Fig. 9A) . . . *Sclerogibba* Riggio and De Stefani-Perez, 1888

5. Metapectal-propodeal complex almost completely smooth, shiny and unsculptured or very slightly granulate . . . *Caenosclerogibba* Yasumatsu, 1958

– Metapectal-propodeal complex dull and reticulate rugose . . . *Probethylus* Ashmead, 1902

Remarks: The males of *Burmasclerogibba* **gen. nov.**, *Edrossia* **gen. nov.**, *Pterosclerogibba* Olmi, 2005, and *Sclerogibbodes* Engel and Grimaldi, 2006 (all fossil genera) are unknown.

3.2. Systematic paleontology

Order Hymenoptera Linnaeus, 1758

Suborder Apocrita Gerstaecker, 1867

Superfamily Chrysidoidea Latreille, 1802

Family Sclerogibbidae Ashmead, 1902

Genus *Burmasclerogibba* Perkovsky, Olmi, Zhang & Martynova **gen. nov.**

(Figs. 1B, 1C)

Type species. *Burmasclerogibba aptera* Perkovsky, Olmi, Zhang & Martynova **sp. nov.**, by monotypy and present designation.

Diagnosis. Female: apterous (Figs. 1B, 1C); head with very long anterior frontal process, concealing base of antennae (Fig. 1B) (head about four times as long as anterior process); ocelli absent; hypostomal bridge much longer than scape (Fig. 1C); proximal part of scape narrow and situated under anterior frontal process, distal part broader and not concealed under frontal process (Fig. 1B); no neck present between head and pronotum; mesoscutum slightly shorter than mesoscutellum, situated only minimally between two posterior lateral angles of pronotum; mesopleuron thick, projecting outwards on sides of mesoscutellum and forming a step; tibial spurs 1/2/2. **Male:** unknown.

Species. One.

Distribution. Cretaceous genus, known only from Burmese (Kachin) amber.

Etymology. The new genus-group name is a combination of Burma (or Myanmar, where the material was found) and *Sclerogibba*, the type genus of the family Sclerogibbidae. Name feminine.

Burmasclerogibba aptera Perkovsky, Olmi, Zhang & Martynova **sp. nov.**

(Figs. 1B, 1C)

Diagnosis. As for the genus, by monotypy.

Description. Female (Figs. 1B, 1C): apterous; length 3.8 mm. Apparently brown; palps testaceous. Antenna filiform, composed of 20 antennomeres; scape much longer than pedicel (12:4), with proximal part of scape narrow and situated under anterior frontal process, distal part broader and not concealed under frontal process (Fig. 1B); flagellar segments in following proportions: 4:4:4:4:4:4:4:4:4:4:4:4:3:3:3:4. Antenna slightly shorter than mesosoma (75:84). Teeth of mandible not distinct. Head dull, unsetose, flat, with sculpture not distinct, much shorter than mesosoma (41:84). Frons with anterior process concealing base of antennae. Head about four times

as long as anterior process (41:10 = 4.1). Head more than twice as long as thick (41:13). Frontal line absent. Hypostomal bridge much longer than scape (21:12). Occipital carina not distinct. Eye much shorter than head (11:41). Ocelli absent. Palpal formula 6/3. No neck visible between head and pronotum. Mesosoma longer than metasoma (84:63). Pronotum dull, unsetose, with sculpture not distinct, much shorter than head (28:41). Mesoscutum slightly shorter than mesoscutellum (9:13), situated only minimally between two posterior lateral angles of pronotum. Notauli not distinct. Metanotum much shorter than mesoscutellum (4:13). Metapectal-propodeal complex slightly swollen, about as long as pronotum, with no distinction between disc and propodeal declivity, with sculpture not distinct. Petiole much shorter than metasoma (6:63). Mesopleuron thick, projecting outwards on sides of mesoscutellum and forming a step. Fore leg ratio: 18 (coxa): 4 (trochanter): 27 (femur): 19 (tibia): 8:2:3:2:3 (protarsomeres I-V). Midleg ratio: 17 (coxa): 4 (trochanter): 27 (femur): 26 (tibia): 14:6:6:3:4 (mesotarsomeres I-V). Hind leg ratio: 14 (coxa): 5 (trochanter): 26 (femur): 25 (tibia): 16:8:6:3:5 (metatarsomeres I-V). Metafemur much larger than mesofemur but smaller than profemur. Tibial spurs 1/2/2.

Male. Unknown.

Material examined. Type: Holotype ♀, NIGP171716 (NIGPAS): MYANMAR: specimen in Upper Cretaceous Burmese amber (about 99 Ma) from Noiye Bum, Kachin State.

Etymology. The specific epithet is formed from the Greek prefix a- (alpha privative, expressing negation or absence) and the Greek noun *pteron* (= wing), in reference to the absence of wings.

Genus *Chosia* Fujiyama

(Fig. 2)

Chosia Fujiyama, 1994: 1.

Type species. *Chosia yamadai* Fujiyama, 1994, by monotypy and original designation.

Revised diagnosis. Male: macropterous, with frons produced into very long anterior process, concealing antennal toruli in dorsal view (head about 4.0 times as long as frontal process length) (Figs. 2C, 2D); ocelli present; antenna composed of 20 antennomeres, as long as mesosoma + metasoma combined; scape regularly cylindrical, longer than pedicel; prothorax tapered anteriorly, forming a neck-like prolongation behind head (Figs. 2C, 2D) (neck about a third of head length); submarginal vein (Rs + M) petiolate (Rs+M connects to r-m crossvein distally, and 'sessil' when Rs+M connects to RS distally) on marginal (Rs); pterostigma present; discoidal cell (1M; = first medial cell) present, rectangular, three times as long as broad (3:1) (Figs. 2B, 2E); subdiscoidal cell (= second cubital cell, 2Cu) present, closed by weakly pigmented veins (Figs. 2B, 2E); vein M straight; marginal cell (2R1; = second radial 1 cell) very large; metapectal-propodeal complex reticulate rugose. **Female:** unknown.

Species. one.

Distribution. Cretaceous genus, known only from Choshi (Japan) amber.

***Chosia yamadai* Fujiyama**

(Fig 2)

Chosia yamadai Fujiyama, 1994: 2.

Diagnosis. As for the genus, by monotypy.

Re-description. Male (Figs. 2B–2E): macropterous; length 3.6 mm. Apparently dark brown, except antenna and tarsi paler. Antenna filiform, rising under frontal projection, composed of 20 antennomeres, about as long as mesosoma + metasoma combined; scape 3.5 times as long as pedicel (3.5:1.0). Flagellomeres in following proportions:

2:2:2:2:2:2:2:2:2:1.8:1.5:1.5:1.5:1.5:1.5:1.2:2.2. Mandible tridentate; palpus not distinct. Head subsphaerical, covered with short setae, swollen, with very long frontal anterior process produced

over antennal toruli (Figs. 2C, 2D). Head 4.0 times as long as frontal process; posterior part of head broken. Clypeus not distinct. Frontal line not distinct. Occipital carina not distinct. Head much shorter than mesosoma (3:8). Ocelli present. POL = 1.2; OL = 1.0; OOL = 2.2; greatest width of posterior ocelli about half as long as OL. Eye much shorter than head (9:20). Head separated from pronotum by very long narrow neck-like prolongation (Figs. 2C, 2D) (neck about a third of head length). Mesosoma slightly shorter than metasoma (53:66). Anterior region of propleura very narrow, surrounding neck. Propleuron dorsally exposed (Fig. 2C), about 0.2 times as long as head length. Pronotum triangular. Pronotal tubercles reaching tegulae. Mesoscutum flat, slightly longer than pronotum (7:8). Mesoscutum sculpture not distinct; however, left parapsidal line and tracks of notauli are visible. Notauli subparallel, posteriorly well separated each other. Mesoscutellum and metanotum not distinct. Metapectal-propodeal complex longer than mesoscutum (5:7), areolate. Disc of metapectal-propodeal complex and propodeal declivity situated on the same plane. Disc of metapectal-propodeal complex areolate. Mesopleuron and metapleuron smooth. Fore wing (Fig. 2E) hyaline, not darkened; pterostigma present; discoidal cell (1M; = first median cell) closed, rectangular, three times as long as broad (3:1) (Fig. 2E); second cubital cell (2Cu) closed, rectangular, twice as long as broad (2:1) (Fig. 2E); cu-a antefurcal, cu-a and anal veins weakly pigmented; distal apex of anal vein indistinct, but not reaching fore wing border; marginal (2R1; = second radial cell) and submarginal cells (1R1; = first radial cell) surrounded by sclerotized veins; submarginal vein (Rs + M) petiolate on marginal (Rs); petiole (P) of submarginal vein (Rs + M) shorter than pterostigma (1:3); vein M straight, reaching fore wing border; marginal cell 2R1 very large. Fore leg ratio: 6.0 (coxa): 2.0 (trochanter): 13.0 (femur): 11.0 (tibia): 5.0:1.5:1.0:1.0:3.5 (protarsomeres I-V). Profemur very large and swollen. Midleg ratio: 6.0 (coxa): 2.0 (trochanter): 8.0 (femur): 12.0 (tibia): 8.0:3.0:2.0:1.5:2.5 (mesotarsomeres I-V). Hind leg ratio: 6.0 (coxa): 3.0 (trochanter): 11.0 (femur): 18.5 (tibia): 8.5:4.0:2.0:1.0:3.0 (metatarsomeres I-V). Metafemur not toothed ventrally. Tibial spurs ?/?/2.

Female. Unknown.

Material examined. Type: Holotype ♂, CBM-PI 000001 (NHMIC): JAPAN: specimen in Lower Cretaceous Choshi amber (Fig. 2A), Inubouzaki Formation (Choshi Group), upper lower Aptian (about 121–122 Ma). Obtained from Honshu, Kanto Region, Chiba Prefecture, Choshi, Katsuhiko Yamada leg.

Remarks. *Chosia* was tentatively assigned to Stephanidae by Fujiyama (1994), mainly based on the neck between the head and mesosoma, but later the genus was excluded from Stephanidae (Engel and Grimaldi, 2004 and references therein). The typical characters of Stephanidae are absent: the head has no tooth-like spines around the median ocellus (spines present in Stephanidae); the neck is formed mostly by the propleura (neck formed by anterior region of pronotum in Stephanidae); the fore wing has a costal vein between tegula and pterostigma (no costal vein in Stephanidae); the metafemur is ventrally simple (toothed in Stephanidae); and the gaster is attached low on the metapectal-propodeal complex (high in Stephanidae), although in basal taxa the proximal extremity of the metasoma is wide (high) making false appearance of high attachment) (Mason, in Goulet & Huber, 1993; Townes, 1949). On the other hand, the anterior frontal process concealing the antennal toruli and the fore wing venation are typical of Sclerogibbidae, so we attribute this species to this family. The neck between head and mesosoma and the extraordinary length of the anterior frontal process are not found in extant sclerogibbids, but they are known in basal extinct genera from Burmese amber (see *Cretosclerogibba* **gen. nov.** and *Burmasclerogibba* **gen. nov.** herein). *Chosia* looks also similar to some Scolebythidae (Engel and Grimaldi, 2004), but differs mainly by the antennae (13 antennomeres in Scolebythidae, 20 in *Chosia*; and antennal toruli concealed under the frontal process in *Chosia* and all Sclerogibbidae, while in the few scolebythid species with a frontal process, antennal toruli are located on the sides of the process) (Evans, 1963; Nagy, 1975; Finnamore and Brothers, in Goulet and Huber, 1993; Azevedo, 1999; Cai et al., 2012; Engel, 2015; Zhang et al., 2020). The venation is strongly reduced in extant sclerogibbid genera (all with wingless females) compared to winged females of *Cretosclerogibba* **gen. nov.**, but *Chosia* retains

the vein 2Cu as well as very long wings (wing/body ratio equals 3:4), so apterism of *Chosia* females is highly unlikely.

Genus *Cretosclerogibba* Perkovsky, Olmi, Zhang & Martynova **gen. nov.**

(Figs. 3–6)

Type species. *Cretosclerogibba rasnitsyni* Perkovsky, Olmi, Zhang & Martynova **sp. nov.**, by present designation.

Diagnosis. Female: macropterous (Fig. 4); scape regularly cylindrical, shorter than pedicel; frons with very long anterior process concealing antennal toruli in dorsal view (head about 2.7 times as long as anterior frontal process) (Fig. 4A); propleuron extended into a very long neck, dorsally exposed (Fig. 4A) (neck length about one third of head length); fore wing with submarginal vein (Rs + M) petiolate on marginal (Rs) (Fig. 4B) and pterostigma present (Fig. 4B); tibial spurs 1/2/2.

Male: macropterous (Fig. 6); frons with very long anterior process, concealing antennal toruli in dorsal view (head about 3.5–5.0 times as long as frontal process length) (Fig. 6); propleuron extended into a very long neck, dorsally exposed (neck between one fourth and one half of head length) (Fig. 6); rarely neck not visible; fore wing with submarginal vein (Rs + M) petiolate on marginal (Rs) (Fig. 6) and pterostigma present (Fig. 6); discoidal cell (1M; = first medial cell) enclosed by pigmented veins (Fig. 6); notauli complete, posteriorly separated; metapectal-propodeal complex dull, slightly transversely striate; tibial spurs 1/2/2.

Hosts. Unknown.

Species. Four.

Distribution. Cretaceous genus, known only from Burmese (Kachin) amber.

Etymology. The new genus-group name is a combination of Cretaceous and *Sclerogibba*, the type genus of the family Sclerogibbidae. Name feminine.

Key to species of *Cretosclerogibba***Females**

Only the female of *C. neli* is known.

Males

1 Neck not visible in dorsal and lateral view (Fig. 5) *C. contractocollis* **sp. nov.**

– Propleuron extended into a very long neck-like prolongation, dorsally exposed (neck slightly less than one third of head length) (Figs. 3, 6) 2

2 Antenna slightly longer than combined length of mesosoma + metasoma (Fig. 3) *C. antennalis* **sp. nov.**

– Antenna shorter than combined length of mesosoma + metasoma (Fig. 6) *C. rasnitsyni* **sp. nov.**

Cretosclerogibba antennalis Perkovsky, Olmi, Zhang & Martynova **sp. nov.**

(Fig. 3)

Diagnosis. Male: macropterous; frons produced into a long anterior process concealing antennal toruli in dorsal view (head about 3.5 times as long as frontal process length); ocelli present; antenna (Fig. 3) composed of 22 antennomeres, slightly longer than mesosoma + metasoma combined; propleuron extended into a very long neck-like prolongation, dorsally exposed (neck about half of head length) (Fig. 3); submarginal vein (Rs + M) petiolate on marginal (Rs); pterostigma present; discoidal cell (1M; = first medial cell) present, rectangular, more than twice as long as broad (11:5); vein M straight; marginal cell (2R1; = second radial cell) very large (Fig. 3). **Female:** unknown.

Description. Male (Fig. 3): macropterous; length 2.9 mm. Apparently brown. Antenna filiform, composed of 21 antennomeres, slightly longer than mesosoma + metasoma combined (136:131);

scape more than twice as long as pedicel (7:3). Flagellomeres in following proportions: 7:7:8:7:8:8:8:7:6:6:6:6:6:6:5:5:5:7. Mandible and palpal formula not distinct. Head unisetose, shiny, with sculpture not distinct, with very long frontal anterior process produced over antennal toruli. Head about 3.5 times as long as frontal anterior process (17:5). Clypeus not distinct. Frontal line absent. Occipital carina complete, not present dorsally behind posterior ocelli, surrounding foramen magnum. Head much shorter than mesosoma (17:64). Ocelli present. POL = 5; OL = 4; OOL = 7; greatest breadth of posterior ocelli much shorter than OL (2:4). Eye slightly shorter than head (15:17). Mesosoma slightly shorter than metasoma (64:67). Propleuron extended into a very long neck-like prolongation, dorsally exposed (neck about half of the head length (9:17) (Fig. 3). Dorsal surface of mesosoma not distinct. Mesopleuron and metapleuron not distinct. Fore wing hyaline, not darkened; pterostigma present; discoidal cell (1M) closed, rectangular, more than twice as long as broad (11:5); marginal (2R1) and submarginal (1R1) cells surrounded by sclerotized veins; submarginal vein (Rs + M) petiolate on marginal (Rs); petiole (P) of submarginal (Rs + M) vein much shorter than pterostigma (6:12); vein M straight, apparently not reaching fore wing border; marginal cell (2R1) very large (Fig. 3). Legs and tibial spurs not distinct.

Female: unknown.

Material examined. Type: Holotype ♂, NIGP171717 (NIGPAS): MYANMAR: specimen in Upper Cretaceous Burmese amber (about 99 Ma) from Noiye Bum, Kachin State.

Etymology. The specific epithet refers to the length of the antenna (slightly longer than mesosoma + metasoma).

Cretosclerogibba neli Perkovsky, Olmi, Zhang, Zheng & Martynova **sp. nov.**

(Fig. 4)

Diagnosis. Female: macropterous; frons produced into a long anterior process concealing antennal toruli in dorsal view (head about 2.7 times as long as anterior frontal process) (Fig. 4); antenna

composed of 18 antennomeres (Fig. 4), shorter than mesosoma; scape regularly cylindrical, shorter than pedicel; propleuron extended into a very long neck-like prolongation, dorsally exposed (head about 3.5 times as long as neck) (Fig. 4); submarginal vein (Rs + M) petiolate on marginal (Rs) (Fig. 4A); pterostigma present (Fig. 4B); marginal cell (2R1) very large (Fig. 4B). **Male:** unknown.

Description. Female (Fig. 4): macropterous; length 3.8 mm. Apparently brown. Antenna composed of 18 antennomeres, shorter than mesosoma (70:80); scape regularly cylindrical, longer than pedicel (9:5). Flagellomeres in following proportions: 5:5:5:5:4:4:4:5:4:5:4:5:4:4:5. Mandible and palpal formula not distinct. Head flat, covered with long setae, shiny, with sculpture not distinct, with very long frontal anterior process produced over antennal toruli (Fig. 4A). Head about seven times as long as thick and about 2.7 times as long as frontal anterior process (35:13). Clypeus not distinct. Frontal line apparently absent. Occipital carina not distinct. Head much shorter than mesosoma (35:80). Ocelli and eye not distinct. Mesosoma slightly shorter than metasoma (80:88). Propleuron extended into a very long neck-like prolongation, dorsally exposed (head about 3.5 times as long as neck) (35:10) (Fig. 4A). Dorsal surface of mesosoma not distinct. Mesopleuron and metapleuron not distinct. Fore wing (Fig. 4A) hyaline, not darkened; pterostigma present, longer than broad (9:5); discoidal cell (1M) not visible; marginal cell (2R1) very large, surrounded by sclerotized veins; submarginal cell (1R1) not visible; submarginal vein (Rs + M) petiolate on marginal (Rs); petiole (P) of submarginal vein (Rs + M) much shorter than pterostigma (4:9); vein M not visible. Legs not completely distinct. Hind leg ratio: 29 (tibia): 19:7:5:3:7 (metatarsomeres I-V). Tibial spurs 1/2/2. Paratype ♀: similar to holotype, length 3.2 mm; antenna composed of 18 antennomeres; head more than twice as long as eye (2.6); POL = 2; OL = 2; OOL = 3; OPL = 3; TL = 3; greatest breadth of lateral ocelli about as long as OOL; pronotum, mesoscutum and mesoscutellum dull, alutaceous; notauli complete, posteriorly broadly separated; minimum distance between notauli about twice as long as OOL (6:3); mesoscutellum subtriangular (Fig. 4B). Paratype ♀: similar to holotype, length 3.2 mm.

Male: unknown.

Material examined. Type: Holotype ♀, NIGP171718 (NIGPAS): MYANMAR: specimen in Upper Cretaceous Burmese amber (about 99 Ma) from Noiye Bum, Kachin State. Paratype: 1 ♀, LY-HY-007-1 (LYU), same locality as holotype.

Etymology. The specific epithet is a patronym honoring Prof. André Nel (Muséum national d'Histoire naturelle, Paris, France).

Remarks. There is the possibility that *S. neli* is the female of one of the three male-based new species of *Cretosclerogibba*. Females of Sclerogibbidae are very different from males. Association of opposite sexes can be obtained only by DNA analysis or rearing.

***Cretosclerogibba contractocollis* Perkovsky, Olmi, Zhang & Martynova sp. nov.**

(Fig. 5)

Diagnosis. Male: macropterous; frons produced into a long anterior process concealing antennal toruli in dorsal view (head about 5.0 times as long as frontal process length) (Fig. 5A); antenna (Fig. 5) composed of 16 antennomeres, shorter than mesosoma + metasoma combined; propleuron not extended into a neck-like prolongation (Fig. 5); submarginal vein (Rs + M) petiolate on marginal (Rs) (Fig. 5B); pterostigma present; discoidal cell (1M) present, rectangular, more than twice as long as broad (11:5); marginal cell (2R1) very large (Fig. 5B). **Female:** unknown.

Description. Male (Fig. 5): macropterous; length 2.6 mm. Apparently brown. Antenna filiform, composed of 16 antennomeres, shorter than mesosoma + metasoma (90:114); scape slightly shorter than pedicel (3:4). Flagellomeres in following proportions: 4:5:5:6:5:5:5:5:5:5:5:5:5:5:5:5.

Mandible and palpal formula not distinct. Head unisetose, shiny, with sculpture not distinct, with very long frontal anterior process produced over antennal toruli (Fig. 5A). Head about 5.0 times as long as frontal anterior process (25:5). Clypeus not distinct. Frontal line and occipital carina not distinct. Head much shorter than mesosoma (25:50). Ocelli not distinct. Eye much shorter than head (13:25). Mesosoma shorter than metasoma (50:64). Propleuron not extended into a neck-like

prolongation (Fig. 5). Dorsal surface of mesosoma not distinct. Mesopleuron and metapleuron not distinct. Fore wing (Fig. 5B) hyaline, not darkened; pterostigma present, much longer than broad (11:3); discoidal cell (1M) closed, rectangular, more than twice as long as broad (8:3); marginal cell (2R1) very large (Fig. 5B); submarginal cell (1R1) not distinct; submarginal vein (Rs + M) petiolate on marginal (Rs) (Fig. 5B); petiole (P) of submarginal vein (Rs + M) much shorter than pterostigma (6:11); vein M vein. Fore leg ratio: 10 (coxa): ? (trochanter): 20 (femur): 14 (tibia): protarsomeres not distinct. Midleg ratio: 7 (coxa): 2 (trochanter): 14 (femur): 10 (tibia): mesotarsomeres not distinct. Hind leg ratio: 9 (coxa): 3 (trochanter): 20 (femur): 20 (tibia): metatarsomeres not distinct. Tibial spurs not distinct.

Female: unknown.

Material examined. Type: Holotype ♂, NIGP171719 (NIGPAS): MYANMAR: specimen in Upper Cretaceous Burmese amber (about 99 Ma) from Noiye Bum, Kachin State.

Etymology. The specific epithet derives from *contractus* (Latin, adjective meaning short) and *collis* (Latin noun meaning “neck”) = *contractocollis*, indicating the very short neck.

Cretosclerogibba rasnitsyni Perkovsky, Olmi, Zhang, Zheng & Martynova **sp. nov.**

(Fig. 6; fig. 8 in Zhang et al., 2018)

Diagnosis. Male: macropterous; face produced into a long anterior process concealing antennal toruli in dorsal view (head about 3.5 times as long as frontal process length) (Fig. 6A); ocelli present; antenna (Fig. 6A) composed of 14–15 antennomeres, much shorter than mesosoma + metasoma; propleuron extended into a very long neck-like prolongation, dorsally exposed (neck about a fourth of head length) (Fig. 6A); submarginal vein (Rs + M) petiolate on marginal (Rs) (Fig. 6B); pterostigma present; discoidal cell (1M) present, rectangular, more than twice as long as broad (8:3) (Fig. 6B); M vein straight; marginal cell (2R1) very large (Fig. 6B); metapectal-propodeal complex dull, slightly transversely striate. **Female:** unknown.

Description. Male (Fig. 6): macropterous; length 1.9 mm. Apparently brown, except head black. Antenna filiform, composed of 15 antennomeres, much shorter than mesosoma + metasoma combined (73:99); scape slightly longer than pedicel (5:4). Flagellomeres in following proportions: 6:5:5:5:5:5:5:5:5:5:4.5:4.5:5. Mandible with four small teeth. Palpal formula 6/3. Head unisetose, swollen, shiny, smooth, with very long frontal anterior process produced over antennal toruli (Fig. 6A). Head about 3.5 times as long as frontal anterior process (21:6). Clypeus swollen. Frontal line absent. Occipital carina complete, not present dorsally behind posterior ocelli, surrounding foramen magnum. Head much shorter than mesosoma (21:46). Ocelli present. POL = 4; OL = 3; OOL = 6; greatest breadth of posterior ocelli about as long as OL. Eye much shorter than head (10:21). Mesosoma slightly shorter than metasoma (46:53). Propleuron extended into a very long neck-like prolongation, dorsally exposed (neck about one fourth of head length (5:21)) (Fig. 6A). Pronotum swollen, smooth, twice as long as neck (10:5). Pronotal tubercles reaching tegulae. Mesoscutum flat, smooth, slightly longer than pronotum (11:10). Notauli complete, posteriorly separated; minimum distance between notauli slightly shorter than neck (4:6). Mesoscutellum smooth, shorter than mesoscutum (8:11). Metanotum much shorter than mesoscutellum (4:8). Metapectal-propodeal complex about as long as mesoscutum, sculptured by slight transverse keels. Disc of metapectal-propodeal complex and propodeal declivity situated on the same plane. Disc of metapectal-propodeal complex slightly rugose, much shorter than propodeal declivity (1:10). Mesopleuron and metapleuron dull, with sculpture not distinct. Fore wing (Fig. 6) hyaline, not darkened; pterostigma present; discoidal cell (1M) closed, rectangular, more than twice as long as broad (8:3); marginal (2R1) and submarginal (1R1) cells surrounded by sclerotized veins; submarginal vein (Rs + M) petiolate on marginal (Rs); petiole (P) of submarginal vein (Rs + M) much shorter than pterostigma (4:12); M vein straight, reaching fore wing border; marginal cell (2R1) very large. Fore leg ratio: 9 (coxa): 3 (trochanter): 17 (femur): 14 (tibia): 6:1:1:1:3 (protarsomeres I-V). Midleg ratio: 9 (coxa): 3 (trochanter): 11 (femur): 14 (tibia): 4:3:2.5:2:4 (protarsomeres I-V). Hind leg ratio: 10 (coxa): 4 (trochanter): 18 (femur): 23 (tibia): 10:4:3:2:3 (protarsomeres I-V). Tibial spurs 1/2/2. Paratype

(Fig. 6C): similar to holotype; length 1.6 mm; antenna composed of 14 antennomeres; POL = 1; OL = 1; OOL = 2; OPL = 1; TL = 1.5; greatest breadth of lateral ocelli as long as POL; neck about a third of head length (3:9).

Female: unknown.

Material examined. Type: Holotype ♂, NIGP171720 (NIGPAS): MYANMAR: specimen in Upper Cretaceous Burmese amber (about 99 Ma) from Noiye Bum, Kachin State. Paratype: 1 ♂, LY-HY-007 (2) (LYU): same locality as holotype.

Etymology. The specific epithet is a patronym honoring Prof. Alexandr Rasnitsyn (A.A. Borissiak Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia), who first recognized this new sclerogibbid wasp among the rich material deposited at NIGPAS (Zhang et al., 2018).

Genus *Edrossia* Perkovsky, Olmi, Zhang & Martynova **gen. nov.**

(Fig. 7)

Type-species. *Edrossia vetusta* Perkovsky, Olmi, Zhang & Martynova **sp. nov.**

Diagnosis. Female (Fig. 7): macropterous; head with posterior margin much longer than anterior one; eyes very large and situated in posterior half of head; head swollen, about 1.7 times as long as eye (33:19), about 1.6 times as long as thick (33:21); frons with short anterior process concealing antennal toruli in dorsal view (head about 5 times as long as anterior frontal process) (Fig. 7A); head more than four times as long as neck (Fig. 7D); antenna (Figs. 7A, 7D) composed of 17 antennomeres, shorter than mesosoma; scape longer than pedicel; propleuron extended into a very short neck (Fig. 7A); fore wing with distinct pterostigma, with submarginal vein (Rs + M) petiolate on marginal (Rs) (Figs. 7A, 7B); marginal cell (2R1) very large (Fig. 7B); profemur strongly enlarged (Figs. 7D, 7E); fore leg with arolium much larger than those of mid and hind legs. **Male:** unknown.

Species. One.

Distribution. Cretaceous genus, known only from Burmese (Kachin) amber.

Etymology. The new genus-group name is a patronym honoring the late specialist of webspinners, Edward S. Ross. Name feminine.

Edrossia vetusta Perkovsky, Olmi, Zhang & Martynova **sp. nov.**

(Fig. 7)

Diagnosis. As for the genus, by monotypy.

Description. Female (Fig. 7): macropterous; length 3.6 mm. Brown, except head black. Antenna filiform, composed of 17 antennomeres, much shorter than mesosoma + metasoma combined (52:148); scape longer than pedicel (7:3). Flagellomeres in following proportions: 3:3:3:3:3:3:3:3:3:3:3:2:3. Teeth of mandible not distinct. Palpal formula not distinct. Head unisetose, flat, dull, granulate, less than twice as long as thick (33:21), with short frontal anterior process produced over antennal toruli (Fig. 7A). Head about 5 times as long as frontal anterior process. Clypeus not distinct. Frontal line absent. Occipital carina not distinct. Head much shorter than mesosoma (33:67). Ocelli present. POL = 6; OL = 4; OOL = 6; OPL = 3; greatest breadth of posterior ocelli shorter OL (3:4). Temple about as long as OOL. Head less than twice as long as eye (33:19). Mesosoma shorter than metasoma (67:81). Head longer than pronotum (33:20). Propleuron extended into a very short neck-like prolongation (Fig. 7A) (head more than four times as long as neck). Pronotum dull, granulate, with disc flat, much longer than anterior collar (14:6). Pronotal tubercles reaching tegulae. Mesoscutum, mesoscutellum and metanotum not distinct. Notauli not distinct. Metapectal-propodeal complex about as long as pronotum, apparently reticulate rugose, with strong median longitudinal keel. Metapectal-propodeal complex regularly inclined towards petiole; disc of metapectal-propodeal complex and propodeal declivity not clearly separated. Mesopleuron and metapleuron not distinct. Fore wing (Fig. 7B) darkened; pterostigma present, much longer than broad (9:3); discoidal cell (1M) closed, rectangular, more than twice as long as

broad (9:4) (Fig. 7B); marginal (2R1) and submarginal (1R1) cells surrounded by sclerotized veins; submarginal vein (Rs + M) petiolate on marginal (Rs) (Fig. 7B); petiole (P) of submarginal vein (Rs + M) shorter than pterostigma (7:9); vein M short (Fig. 7B); marginal cell (2R1) very large (Fig. 7B). Legs only partly distinct. Tibial spurs not distinct. Paratype: similar to holotype; length 2.7 mm; antenna composed of 18 antennomeres; POL = 3; OL = 2; OOL = 3; OPL = 2; head swollen, about 4.6 times as long as neck.

Male: unknown.

Material examined. Type: Holotype ♀, NIGP171721 (NIGPAS); MYANMAR: specimen in Upper Cretaceous Burmese amber (about 99 Ma) from Noiye Bum, Kachin State. Paratype: 1 ♀, NIGP171722, same locality as holotype.

Etymology. The specific epithet derives from *vetusta* (Latin adjective meaning “very old”), in reference to the antiquity of Burmese amber.

Genus *Gallosclerogibba* Perrichot, Gantier & Olmi **gen. nov.**

(Fig. 8)

Type species. *Gallosclerogibba alnensis* Perrichot, Gantier & Olmi **sp. nov.**

Diagnosis. Male (Fig. 8): macropterous; frons with short anterior process concealing antennal toruli and base of scape in dorsal view (head about 10 times as long as anterior frontal process) (Fig. 8A, 8D); antenna composed of 25 antennomeres; ocelli present; mandible tridentate; propleuron extended into a very short neck not exposed in dorsal view (Figs. 8A, 8D); notauli complete (Fig. 8A); fore wing with pterostigma (Fig. 8C), submarginal vein (Rs + M) petiolate on marginal (Rs) (Fig. 8C), and cells 1M and 2Cu enclosed by pigmented veins (Fig. 8C). Tibial spurs 1/2/2. **Female:** unknown.

Species. One.

Distribution. Cretaceous genus, known only from Charentese amber (France).

Etymology. The new genus-group name is a combination of Gallia, the former Latin name for France, and *Sclerogibba*, the type genus of the family Sclerogibbidae. Name feminine.

Gallosclerogibba alnensis Perrichot, Gantier & Olmi **sp. nov.**

(Fig. 8)

Diagnosis. As for the genus, by monotypy.

Description. Male: macropterous (Figs. 8A– 8C); length 3.7 mm. Head apparently black; antennae brown, except antennomeres 4-6 whitish; mesosoma apparently black, except prothorax testaceous; metasoma testaceous, except posterior half brown; legs brown-testaceous. Head dull, apparently granulated, with short anterior frontal process concealing antennal toruli (head about 10 times as long as anterior frontal process) (Fig. 8D); frons with median longitudinal furrow; ocelli large, POL = 4.5; OL = 3; OOL = 3; OPL = 4; temple absent; head less than twice as long as eye (29:18). Antenna as long as combined length of mesosoma and metasoma, progressively tapering toward apex; scape longer than pedicel (12:7); proportions of flagellomeres: 13:14:10:10:13:13:12:12:12:11:11:10:10:10:10: 10:10:10:9:9:8:7:10. Clypeus projecting as a median lobe. Mandibles rectangular, with 3 teeth. Maxillary palps with 4 visible segments, labial palps with 3 visible segments. Pronotum shiny, unsetose, alutaceous, apparently with complete median longitudinal furrow. Mesoscutum with sculpture not visible, with notauli complete, posteriorly separated. Minimum distance between notauli slightly shorter than scape (6:5). Mesoscutum longer than mesoscutellum (15:10). Mesoscutellum with sculpture apparently granulated. Mesoscutellum longer than metanotum (10:3). Metanotum with sculpture not visible. Metapectal propodeal complex longer than mesoscutellum (14:10), reticulate rugose. Fore wing hyaline, not darkened; pterostigma present, not completely visible; submarginal vein (Rs + M) petiolate on marginal (Rs); discoidal cell (1M; = first medial cell) present, rectangular, less than three times as long as broad (20:8) (Fig. 8C); subdiscoidal cell (= second cubital cell, 2Cu) present,

closed by pigmented veins (Fig. 8C); vein M slightly curved; marginal cell not visible. Legs robust, procoxa not exaggeratedly larger than meso- and metacoxae; fore femur and tibia not exaggeratedly broadened; tibial spurs 1/2/2; pretarsal claws with a preapical tooth.

Female: unknown.

Material examined. Type: Holotype ♂, IGR.FRS-7.27 (IGR): FRANCE: specimen in Upper Cretaceous (lower Cenomanian, about 98 Ma) amber from Fouras, Charente-Maritime, SW France.

Etymology. The specific epithet derives from ‘Aunis’ (Latin *pagus Alnensis*), a historical French province from the Middle Age, and now “Pays d’Aunis” to which belongs the *locus typicus* Fouras of the new species.

Genus *Sclerogibba* Riggio & De Stefani-Perez

(Figs. 9, 11A)

Sclerogibba Riggio & De Stefani-Perez, 1888: 19.

Type-species. *Sclerogibba crassifemorata* Riggio & De Stefani-Perez, 1888, by monotypy.

Diagnosis. Female: apterous (Fig. 11A); head with short anterior process concealing antennal toruli in dorsal view (head about 6.6–10 times as long as anterior frontal process) (Fig. 11A); head with three ocelli (Fig. 11A); eye always large, situated in posterior two thirds of head (Fig. 11A); scape at least twice as long as anterior flat surface of hypostomal bridge; mesosoma never crossed by a straight suture separating the metanotum and scutellum from the metapectal-propodeal complex (Fig. 11A); mesoscutum very small, much shorter than mesoscutellum, situated completely at the posterior extremity of the pronotum, between two posterior lateral angles of pronotum (Fig. 11A); mesopleuron not thick, not projected outwards on sides of mesoscutellum, not forming a step; metanotum usually composed of two narrow pieces situated on the sides of the mesoscutellum (Fig. 11A); occasionally the above pieces are large, then the suture separating the metanotum and mesoscutellum from the metapectal-propodeal complex is always curved; tibial spurs 1/2/2. **Male**

(Fig. 9): macropterous; frons with short anterior process, concealing antennal toruli in dorsal view, about a tenth of the head length (Fig. 9C); propleuron not extended into a neck-like prolongation (Fig. 9); notauli usually complete, very rarely incomplete; fore wing with submarginal vein (Rs + M) petiolate on marginal (Rs) (Fig. 9B); pterostigma of fore wing present (Fig. 9).

Species. Sixteen (fifteen extant and one extinct species).

Distribution. Extant species are spread worldwide. The unique fossil species is known from mid-Cretaceous Burmese (Kachin) amber.

Remarks. Fossil females of *Sclerogibba* are unknown.

***Sclerogibba cretacica* Martynova, Olmi, Müller & Perkovsky**

(Fig. 9)

Sclerogibba cretacica Martynova, Olmi, Müller & Perkovsky, 2019: 1573.

Diagnosis (taken from Martynova et al., 2019a). **Male** (Fig. 9): macropterous; fore wing with submarginal vein (Rs + M) petiolate on marginal (Rs) (Figs. 9A, 9B); pterostigma present (Figs. 9A, 9B); discoidal cell (1M) present, rectangular, more than twice as long as broad (Figs. 9A, 9B); vein M straight (Figs. 9A, 9B); marginal cell (2R1) very large (Figs. 9A, 9B); metapectal-propodeal complex dull and reticulate rugose.

Complemental description. **Male** (Fig. 9): macropterous; body length 2.7 mm (holotype), 2.8 mm (NIGP171723), 3.0 mm (NIGP171724), 1.8 mm (PMC BUB3206). Black, except antennae and legs brown. Antenna filiform, composed of 19 antennomeres in holotype, 14 antennomeres in specimen NIGP171724; 16 antennomeres in specimen BUB3206 (PMC); antennal segment 1 about twice as long as segment 2 (10:5). Mandible with teeth not distinct. Head hairy, shiny, granulate. Frontal line not distinct. Occipital carina complete. Head visible only in lateral view, much shorter than mesosoma (30:60). Ocelli not distinct. Eye much shorter than head (18:30). Mesosoma slightly

longer than metasoma (60:59), visible only in lateral view. Pronotum, mesoscutum, mesoscutellum and metanotum visible only in lateral view, their sculpture being not distinct. Notauli not distinct. Pronotal tubercles not distinct. Metapectal-propodeal complex visible only in lateral view, reticulate rugose, with areolae very wide. Mesopleuron and metapleuron with sculpture not distinct. Fore wing (Fig. 9) hyaline, not darkened; pterostigma present; discoidal cell (1M) closed, rectangular, more than twice as long as broad (12:5); marginal (2R1) and submarginal (1R1) cells surrounded by sclerotized veins; submarginal vein (Rs + M) petiolate on marginal (Rs); petiole (P) of submarginal vein (Rs + M) very long, much shorter than pterostigma (7:21); M vein straight; marginal cell (2R1) very large. Palpal formula not distinct. Tibial spurs 1/2/2.

Female: unknown.

Material examined. Type: holotype ♂, DAF2760 (DAFS): MYANMAR: specimen in mid-Cretaceous Burmese amber (about 99 Ma) from Noiye Bum, Kachin State. **Other material:** 2♂♂, NIGP171723; NIGP171724 (NIGPAS): same locality label; 1♂, BUB3206 (PMC): same locality label.

Distribution. Known only from Cretaceous Burmese (Kachin) amber.

Remarks. *S. cretacica* shows a discoidal cell (1M) in the fore wing, similarly to the following five extant species of *Sclerogibba*: *S. africana* (Kieffer, 1904); *impressa* Olmi, 2005; *rossi* Olmi, 2005; *rugosa* Olmi, 2005; and *turneri* Richards, 1939. But the new species different from the above five extant species because of the rectangular shape of the discoidal cell (1M) (Figs. 9A, 9B), which is more than twice as long as broad (less than twice in the above five species (Fig. 129)).

***Sclerogibbodes* Engel & Grimaldi**

Sclerogibbodes Engel & Grimaldi, 2006: 3.

Type species: *Sclerogibbodes embioleia* Engel & Grimaldi, 2006, by monotypy and original designation.

Diagnosis (re-formulated; see also Engel & Grimaldi, 2006): **Female:** macropterous (Fig. 10); head about 2.2 times as long as eye (Fig. 10); frons with short anterior process concealing antennal toruli in dorsal view (head about 7 times as long as anterior frontal process) (Fig. 10); antenna composed of 14 antennomeres; neck not or hardly visible (Fig. 10); pterostigma present; fore wing with submarginal vein (Rs + M) petiolate on marginal (Rs) (Fig. 10); tibial spurs 1/2/2.

Male. Unknown.

Species. One.

Distribution. Cretaceous genus, known only from Lebanese amber.

***Sclerogibbodes embioleia* Engel & Grimaldi**

Sclerogibbodes embioleia Engel & Grimaldi, 2006: 3.

Diagnosis. As for the genus, by monotypy.

Description. Female (Fig. 10): macropterous (Fig. 10); length 2.3 mm. Apparently black, except antennae and tarsi dark brown. Antenna clavate, composed of 14 antennomeres, with flagellomeres of approximately same shape, except distal two flagellomeres distinctly wider than long; apex of distalmost flagellomere tapering. Head length 0.47 mm, width 0.36 mm. Head (Fig. 10) about 2.2 times as long as eye, tapering strongly beyond lower tangent of compound eyes; frons with anterior prominence strongly pronounced. Compound eye with short, scattered setae; inner margins of compound eyes widely separated, separated by distance slightly less than compound eye length. Mesosoma elongate and narrow, approximately three times as long as wide. Notauli not visible. Metasoma narrow (sting extruded in holotype: fig. 2 in Engel & Grimaldi 2006). Wings hyaline, not darkened. Fore wing approximate length 1.2 mm, venation only partly visible. Pterostigma present. Fore wing with submarginal vein (Rs + M) petiolate on marginal (Rs) (Fig. 10); discoidal cell not

visible. Profemur greatly swollen, width slightly more than three times protibial width. Body with scattered short setae, those of mesosoma and metasoma arising from setigerous punctures.

Male: unknown.

Material. Type: Holotype ♀, LB-AE-3-20 (AMNH), LEBANON: specimen in Lower Cretaceous (lower Barremian) Lebanese amber from Bcharreh (Azar et al., 2010).

4. Discussion

In extant Sclerogibbidae, females are always apterous and males macropterous (Olmí, 2005). In fossil species, the only known male was also macropterous (*Sclerogibba cretatica*, from Kachin amber; Martynova et al., 2019a), but females were shown to be either apterous (*Probethylus poinari*, Dominican amber) or macropterous (*Pterosclerogibba antiqua* (Fig. 1), Dominican amber; *Sclerogibbodes embioleia* (Fig. 10), Lebanese amber). In this paper, the newly described fossils confirm male macroptery (*Chosia yamadai*, Choshi amber; *Cretosclerogibba antennalis*, *C. contractocollis* and *C. rasnitsyni*, Kachin amber; and *Gallosclerogibba alnensis*, Charentese amber) and female aptery (*Burmasclerogibba aptera*, Kachin amber) or macroptery (*Cretosclerogibba neli* and *Edrossia vetusta*, Kachin amber). For the first time, apterous and macropterous females are found together in the same fossil Lagerstätte (Kachin amber), demonstrating that apterous females existed not only in the Miocene, but also already in the mid-Cretaceous of West Burma.

One of the main distinctive morphological characters of Sclerogibbidae is the anterior frontal process concealing the antennal toruli in dorsal view (Figs. 1B, 1C, 6A) in both sexes. In extant species, this process is always short (head about 6.6–10 times as long as anterior frontal process) (Fig. 11E). On the contrary, in fossil species, it can be short (in *Edrossia*, *Gallosclerogibba*, *Probethylus*, *Pterosclerogibba*, *Sclerogibba*, *Sclerogibbodes*) or long (head about 2.4–5 times as long as anterior frontal process in *Burmasclerogibba*, *Chosia*, *Cretosclerogibba*). Thus, this long anterior process is known only in pre-Cenozoic genera from the

Kachin and Choshi ambers (99 and 121 Ma, respectively), but it was already short in some species including the oldest known sclerogibbid (*Sclerogibbodes embioleia*, from Lebanese amber; about 130 Ma).

In some fossil genera, the head of both sexes is separated from the pronotum by a very long narrow neck (Figs. 4, 6) formed by the propleura (head about 2–4 times as long as neck). This character is present in *Chosia* and in almost all species of *Cretosclerogibba*, except the male of *Cretosclerogibba contractocollis*, where the neck is absent. A neck formed by elongate propleura is characteristic also of some other hymenopteran groups, e.g., Xiphydriidae, Gasteruptiidae (Gasteruptiinae and Aulacinae), some Anaxyelidae and some Cephidae.

It is interesting to discuss the phylogenetic significance of the long frontal process and the long neck, both characters being absent in extant species. It is noteworthy that all sclerogibbids with long neck also have a long frontal process (the reverse is not always correct). The long anterior frontal process can be found only in *Chosia yamadai* from the Aptian Choshi amber, and the following species from the Cenomanian Kachin amber: *Burmasclerogibba aptera*, female, apterous; and all species of *Cretosclerogibba*, macropterous females and males. The neck is absent or very short only in *Cretosclerogibba contractocollis*, *Sclerogibba cretacica* and *Gallosclerogibba alnensis* (males) and *Sclerogibbodes embioleia*, *Edrossia vetusta* and *Burmasclerogibba aptera* (females). Apparently, a long anterior frontal process and long neck lengthen the body of both females and males. These characters can facilitate the capture of webspinners. Extant sclerogibbids run inside or less frequently over the silk tubes to catch webspinners. It is possible that Cretaceous sclerogibbids with a long neck explored the silk tubes only from the outside, and opened a hole in the silk wall to enter the tube with the anterior part of the body when a webspinner was detected. A long and narrow body likely helped in fast prey capture. But staying outside the silk tubes instead of inside gives a greater exposure to natural predators such as ants and birds, which may explain why long-neck sclerogibbids are now extinct. Cretaceous sclerogibbids with short or no neck were probably running inside the silk tubes similarly to recent species. Assessing the function of the long

anterior frontal process is tricky. This could help projecting the antennae forward, but the toruli facing downwards under the long process likely favoured the antennal movement backwards only laterally or ventrally, not dorsally. In fact, from outside the silk tubes it is more complicated to explore a large area of wall, but sclerogibbids are able to spin their antennae under the frontal process, left and right, to explore the outer surface of the silk tubes.

Unstable number of flagellomeres is typical of sclerogibbids, while being unknown in other Aculeata (Rasnitsyn, 1980). The number of antennomeres in sclerogibbids varies from 16 to 39 in extant males and 16 to 34 in extant females, but it is limited to 14–25 in extinct males and 14–20 in extinct females (Table 2). The fossil genera with winged females retain the minimal number of antennomeres among all Sclerogibbidae (14 in males and females). Along with ‘enlargement’ of the female body length the number of antennomeres increases too, but actually insignificantly if compared to extant genera with wingless females. For example, extant females ranging from 2.7 to 4.0 mm have 19–34 antennomeres, but similarly sized *Edrossia vetusta* and *Cretosclerogibba neli* (2.7–3.8 mm long) have only 17 or 18 antennal segments; and even more important is the fact that extant females with a length more than 3.2 mm have 24–34 antennomeres (9 species studied, unpublished data). Cenomanian wingless *Burmasclerogibba* (3.8 mm) has 20 antennomeres, far from 26–34 antennomeres of most extant females of similar body length (but a female of *Sclerogibba vagabunda* (Bridwell, 1919) from Sakha, Egypt, with length 3.75 mm, has 24 antennomeres). The largest fossil male known to date, *Gallosclerogibba alnensis* (3.7 mm), has 25 antennomeres, while extant males of similar or greater body length have 30–39 antennomeres (unpublished data, from 10 species in MO collection). The Aptian *Chosia yamadai* (3.5 mm) has only 20 antennomeres, while extant species with body length 3.1–3.7 mm have 27–33 antennomeres. The male of the Cenomanian *Cretosclerogibba antennalis* (2.9 mm, 21 antennomeres) is close to species of the extant genera *Caenosclerogibba* and *Probethylus* in the number of antennomeres (Table 2). All in all, it seems that the level of antennal polymorphism had

risen from the Barremian to Cenomanian, but in the Cenomanian the number of antennomeres was much less than in extant species of the same body length.

Chosia yamadai and *Gallosclerogibba alnensis* are the sole fossil sclerogibbid wasps known from the Choshi and Charentese ambers respectively. Their fore wing with cells 2Cu and 1M completely enclosed by pigmented veins (Fig. 2) readily differentiates them from all other extant and fossil Sclerogibbidae. In the other genera, the fore wing pattern is always the same: three basal cells (C, R, 1Cu), and cells 1M, 1R1, 2R1 enclosed by pigmented veins (Fig. 9). In addition, the submarginal vein (Rs + M) is always petiolate on the margin (Rs) and the petiole (P) is always complete, except in *Sclerogibba cretacica* and *Gallosclerogibba alnensis*, where it is plesiomorphically interrupted. The interruption is a bulla that gives way to a fold running below from the pterostigmal base towards M and then turns distally in front of M (Figs. 8, 9) to cross Rs + M (Rasnitsyn, 1969). In extant Sclerogibbidae, the fore wing pattern is the same in most *Sclerogibba* species (Figs. 12, 13), but cell 1M is enclosed by pigmented veins only in five of the 15 species known in this genus (Fig. 12). In other extant genera, *Caenosclerogibba*, and *Probethylus*, the fore wing pattern is quite different because 1M is not enclosed by pigmented veins and the submarginal vein (Rs + M) is sessile on the marginal vein (Rs) (Figs. 11B, 11E).

The most complete fore wing pattern is therefore found in the macropterous *Chosia yamadai* and *Gallosclerogibba alnensis*, the only two known Laurasian sclerogibbids (the Lebanese and Kachin ambers have Gondwanan affinities). Macropterous species in Kachin amber, although coeval with *G. alnensis*, have the fore wing with cell 1M present but cell 2Cu absent in both sexes (Figs. 4, 9). In mid-Cretaceous Kachin amber almost all species are macropterous but the earliest apterous female is recorded (*Burmasclerogibba aptera*) (Figs. 1B, 1C). Males have remained macropterous throughout the ages. The main result of the above evolution is a fore wing simplification, with the gradual loss of cells 2Cu and 1M. Unfortunately *Sclerogibbodes embioleia*, the oldest known fossil sclerogibbid, cannot be considered in this scheme. According to Grimaldi and Engel (2006), the fore wing of the holotype is in fact “mostly obscured in ventral view by the

body and in dorsal view by fractures and debris in amber, so that only extreme anterior margin (i.e., C, Sc + R, pterostigma, basal portion of r-rs, and R anteriorly bordering the marginal cell is evident) is visible from behind the body in ventral view, the marginal cell being apparently long, extending slightly more than half the distance between the pterostigma and fore wing apex” (Fig. 10).

Extant webspinners live in silk galleries produced by glands situated in the first protarsomere of both sexes. According to Martynova et al. (2019a), life in silk galleries cannot be considered as the primary mode of living in Embiodea. In fact, the probable ancestral families of the Embiodea (Alexarasniidae Gorochoy, 2011 and Sinembiidae Huang & Nel, 2009) did not live in silk galleries, as demonstrated by the absence of modified protarsomeres, but probably lived in protected microhabitats under bark or in wood or forest litter. Alexarasniidae are known from Permian deposits (Shcherbakov, 2015). This family is most similar to Mesorthopteridae Tillyard, 1922, a Permian-Jurassic family of eoblattids. Mesorthopterids differ from alexarasniids mainly in the wide costal field or the multiple branching RS. Actually, mesorthopterids exhibit all the characters of alexarasniids except for the radial sinus and homonomous wings (Aristov, 2017a). This makes Mesorthopteridae the possible ancestors of Alexarasniidae, which adapted their behaviour to living in protected microhabitats and lost the paranota of the pronotum, the enlarged anal lobe of the hind wing, and the ovipositor (Aristov, 2017b). Both eoblattids and embiodeans have asymmetrical male genitalia (Aristov, 2017b). The main reasons for the assignment of Alexarasniidae to webspinners are the homonomous wings, the thick R of the fore wing, the presence of hyaline folds, the shift of the beginning of RS and first branches of M and CuA to the wing base, oligomerization of RS, MA and MP veins, and the merging of bases of the main veins along the posterior wing margin (Shcherbakov, 2015). According to Martynova et al. (2019a) and despite the generally accepted opinion, palaeontological data enable us to hypothesize that the slender body, short legs, enlarged hind femora, cerci with a small number of segments and the flexible wings with sinuses along the veins evolved in the ancestors of webspinners that had already adapted to living in secluded microhabitats long before their descendants evolved the ability to spin

silk galleries (Shcherbakov, 2015). Ross (in Engel et al., 2011) even questioned the assignment of Jurassic Sinembiidae to webspinners because of the absence of probasitarsal modifications, fully winged females, etc. But the appearance of flexible wings with sinuses along the veins turned out to be a pre-adaptation to living inside the silk galleries.

According to Ross (2000), the first true webspinners (Ross missed Alexarasniidae and Sinembiidae, discovered in the following years) probably possessed fairly inflexible wings similar to those of most other winged insects. However, because of the necessity of quick reverse movements inside silk galleries, the apices of the wings would probably have frequently snagged against opposing gallery walls which would have slowed or prevented escape. According to Martynova et al. (2019a), the true embioidan ancestors had long evolved an extraordinary wing flexibility. As a result, when in a resting position over the back, the wings of all modern webspinners readily fold transversely and slide forward towards the head, thereby reducing the likelihood of snagging. Obviously, the ultimate adaptation for rapid reverse movement in galleries is the complete wing elimination, now universal in females and found in many males.

To date, seven Cenozoic species and four Cretaceous species (all in Burmese amber) of webspinners are recognized. But adult webspinners are much larger than their parasitoids and the last meal of the adult males occurs during the penultimate instar (Edgerly, 2018 and references therein) so they are very rare in amber fauna biased towards small inclusions, with an exception in Burmese amber. Their obligate parasitoids, sclerogibbid wasps, reveal an even more striking situation: Burmese amber has yielded almost 60% of the specific diversity (7/12 species) and nearly 50% of the generic diversity (4/9 genera) of fossil Sclerogibbidae, with taxa represented by numerous specimens. The prevalence of alate female sclerogibbids in the Burmese fauna is also characteristic, although this fauna is known to contain clothodid webspinners, which means that large colonies did exist by that time (clothodids have large colonies and we suppose that apterism is an adaptation in large colonies (Martynova et al., 2019a)). However, wingless females were present, as attested by *Burmasclerogibba aptera* described in this paper.

Similar to webspinners, the extant sclerogibbids have apterous females and fully winged males. However, as highlighted by Martynova et al. (2019a) and the present paper, both sexes of webspinners and sclerogibbids have been alates during the major events of the evolutionary and distributional history of the orders and female apterism must have convergently occurred later in sclerogibbids with and without a long frontal process: the description of *Burmasclerogibba* supports this suggestion. According to Olmi et al. (2016), apterism was accompanied by a modification of the metasoma being maintained in a vertical and oblique position (Figs. 1B, 1C, 6A) to push against the upper wall of the silk galleries and make movement easier and faster. This behaviour is also present in all males to facilitate movements inside the galleries while looking for the opposite sex. This position of the metasoma is typical of all extant sclerogibbids of both sexes and is present also in many fossil females and males, suggesting that this behaviour existed as early as in the Cretaceous. Apparently, it is absent in few macropterous females and males, but this may be only a result of preservation in the resin.

Sclerogibbidae are a small family which comprises only 20 extant species in three genera. The Burmese amber fauna is already known to contain four genera and seven species – as much as all of the Indochinan Peninsula, which has the highest extant diversity of sclerogibbid wasps, and almost as much as Southeast Asia or India (nine species each). Indo-China has 167 times the area of the Hukawng valley that yielded Burmese amber, South-East Asia is 350 times larger, and India is 227 times larger. Of course, the amber was deposited from a huge territory during thousands (or rather tens of thousands) of years; still, its relative diversity is notably greater than that of any other extant or fossil fauna. Martynova et al. (2019b) showed that Sclerogibbidae were previously known to comprise only 20 extant species out of 7438 extant chrysidoids (0.27%), and only four species from 198 fossil chrysidoids (2%). Furthermore, the Cretaceous fauna had a comparatively higher percentage of sclerogibbids (2 of 87 species, 2.3%) (Martynova et al., 2019b; Colombo et al., 2020; Zhang et al., 2020) which significantly increases with transfer of *Chosia* and descriptions of new taxa herein (10 of 95 species, 10.6%).

The fauna of Burmese amber forest was even richer, with 12.7% of Sclerogibbidae (7 from 55 species). Burmese amber bethylids are very understudied, but we can usefully compare the diversity of Burmese sclerogibbids and dryinids, which are nearly equally studied: the number of described Burmese dryinids is only 2.9 times higher than the number of sclerogibbids (Martynova et al., 2019b). The latter is incomparable to the ratio of the extant fauna. For example, in the recently reviewed Afrotropical fauna of Dryinidae (Olmi et al., 2019), Dryinidae comprise 430 described extant species, in contrast to 16 species (including introduced taxa) of Sclerogibbidae (26.9 times higher). In the Oriental fauna 368 dryinids (Martynova et al., 2020) were recorded versus 12 sclerogibbids (31 times more); in the Neotropics 503 dryinid species are known (Martynova et al., 2020), but just three sclerogibbids (168 times more). Burmese amber reveals a similar species proportion of Sclerogibbidae to Dryinidae specimens (Zhang et al., 2018): 46 in contrast to 11 (Dryinidae specimens are 4.2 times more numerous than Sclerogibbidae). Thus, sclerogibbid wasps and their hosts were unexpectedly abundant and diverse in the Burmese amber forest. What could be the reason for such diversity? Extant sclerogibbids have apterous females. They are transported widely by their hosts, either directly (females carrying sclerogibbid larvae) or indirectly (as cocoons spun in the silk tubes). Webspinners form silk galleries on many types of materials, including wood and grain. Humans extensively transport these materials along with webspinners. In this way, apterous females are intercontinentally dispersed. For example, a species of *Sclerogibba* was found in Manaus (Brazil), where there is an important harbour, although species of this genus are typical of the Old World. Humans are surely responsible for the spread of apterous females as well as the winged males born in these galleries. This dispersal can happen at the species and genus level. For example, the New World genus *Probethylus* is found in many African countries, where it coexists with *Sclerogibba* and *Caenosclerogibba*. In the Cretaceous, the predominance of fully winged forms suggests that the spread of species and genera depended mostly on the autonomous dispersal of macropterous sclerogibbid females. Apterous fossil sclerogibbids would have had a very limited dispersal potential. A tree trunk transported by a river

after a storm could host webspinners galleries, carrying sclerogibbids long distances. We believe, however, that their high diversity in the Burmese fauna is surely associated with complete wings in their females.

We suggest that the preservation of winged females in Burmese genera was mainly a result of the richness of webspinners in the Burmese fauna, and secondarily of modest pressure from natural predators, mainly birds and ants. Enantiornithine birds (named “opposite birds”) (Zelenkov, 2017; Perkovsky et al., 2019) probably did not play an important role in the biological control of Cretaceous webspinners because of their manner of eating (named “cranioinertial”, i.e., once the food is taken with the beak, the head and neck are rapidly thrust backwards and the beak is simultaneously opened, releasing the prey). Cranioinertial feeding would have been an obstacle for consuming small (less than 10 mm) arboreal insects (most opposite birds were arboreal), and three of the four described Burmese species of webspinners are very small (Engel and Grimaldi, 2006; Engel et al., 2016). They would likely have been feeding on the large webspinners, which would have been, however, protected by their moderately-sized silk webs. It seems significant that both known extant passerine birds that are recorded as tearing open webspinner silk with their beaks and grabbing tropical webspinners are small (Edgerly, 1994). Their weight is 20–37 grams, while most enantiornithines were much bigger, at least as large as a starling (75 grams) (Zelenkov, pers. com.); their precocial hatchlings (enantiornithines were arboreal, but precocial, i.e., able to feed themselves upon hatching) were smaller (Xing et al., 2017)). Also, the eggs of some solitary female webspinners would have escaped detection and not been consumed by egg parasitoids (Edgerly, 1994).

Rather small and distant host colonies would have been more accessible for winged sclerogibbid females. The wings of parasitoids could have been preserved unbroken in host colonies with small silk galleries. After appearance of such effective predators as ornithuromorph (modern type) arboreal birds, first seen in the Cenozoic (Zelenkov, 2017; Perkovsky et al., 2018), and crown-group ants with large colonies (LaPolla et al., 2013; Perkovsky and Wegierek, 2018 and

references therein), large silk webs protected webspinners but they lost former abundance and diversity: the earliest Eocene Cambay amber (Gujarat, India) has yielded only two males of a single webspinner species, not related to Cretaceous genera (Engel et al., 2011). That was the reason of extinction of sclerogibbids with fully winged females. Following analysis of Cretaceous faunas, two zoogeographic realms of the Northern Hemisphere (“*Baeomorpha*” and “Isoptera”) were recognized (Gumovsky et al., 2018): the *Baeomorpha* Realm, with a temperate or warm temperate climate, characterized by the presence of very numerous and diverse parasitic wasps of the genus *Baeomorpha* (Rotoitidae), very abundant aphids (eight families of four superfamilies endemic to this realm), few termites, and no webspinners; and the Isoptera Realm (Fig. 15), which had a warmer climate, contained almost no Rotoitidae (Huber et al., 2019), no or few aphids (often with strongly reduced hind wings), but with abundant and diverse termites and webspinners (Perkovsky and Vasilenko, 2019). Here, we demonstrate the abundance and diversity of webspinners in the Isoptera realm (inferred by sclerogibbids as a proxy for the presence of webspinners in the Cretaceous Old World that belonged to this Realm). We add it to the main characteristics of the Isoptera Realm (Perkovsky and Vasilenko, 2019).

Conclusions

To date, seven Cenozoic fossil species (in four families) and four Cretaceous species (in four families) of webspinners are recognized, and two species of Cenozoic extinct sclerogibbids vs. ten Cretaceous species (seven in Burmese amber, three from Lebanese, Choshi and Charentese amber) are revealed. Thus, unexpected abundance and diversity of Burmese amber sclerogibbids (two genera with winged and two genera with apterous females, including one extant genus) are explained by the uncommon abundance, diversity and specific features of their hosts, represented in the Burmese amber forest.

Even moderately-sized silk galleries provided effective protection to webspinners against opposite birds and ants, that results in the abundance and diversity of sclerogibbid hosts in Burmese amber. It is possible that sclerogibbids with long neck explored the silk tubes only from outside; the long neck is present in 3 from 7 Burmese species. The change of character of predator pressure led to extinction of sclerogibbids with long neck and rostrum (6 from 10 Cretaceous species had the long rostrum), most common in the Cretaceous Laurasia.

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FIGURES

Fig. 1. Female holotype of *Pterosclerogibba antiqua* Olmi, 2005, specimen H-10 59C (A) and holotype male of *Burmasclerogibba aptera* gen. et sp. nov., specimen NIGP171716 (B, C): A. Ventral view. B. Lateral view. C. Ventrolateral view. Scale bars 0.5 mm.

Fig. 2. Holotype male of *Chosia yamadai* Fujiyama, 1994, specimen CBM-PI 000001: A. Choshi amber piece containing holotype. B. Scheme of fore wing venation. C. Dorsal view. D. Head, mesosoma and part of metasoma in lateral view. E. Right fore wing. Scale bar 1 mm for C, 0.5 mm for D, E.

Fig. 3. Holotype male of *Cretosclerogibba antennalis* gen. et sp. nov., specimen NIGP171717, in dorsolateral view. Scale bar 0.5 mm.

Fig. 4. *Cretosclerogibba neli* gen. et sp. nov.: A. Holotype female, specimen NIGP171718, in lateral view. B, C. Paratype female, specimen LY-HY-007-1, in dorsal (B) and lateral (C) view. Scale bar 0.5 mm.

Fig. 5. Holotype male of *Cretosclerogibba contractocollis* gen. et sp. nov., specimen NIGP171719: A. Lateral view. B. Dorsolateral view. Scale bars 0.5 mm.

Fig. 6. *Cretosclerogibba rasnitsyni* gen. et sp. nov.: A, B. Holotype male, specimen NIGP171720 in lateral (A) and dorsolateral (B) view. C. Paratype male, specimen LY-HY-007-2, in lateral view. Scale bars: 0.5 mm for A, 0.2 mm for B, C.

Fig. 7. *Edrossia vetusta* gen. et sp. nov.: A. Holotype female, specimen NIGP171721, in dorsal view. B. Fore wing and metapectal-propodeal complex of holotype female. C, D, E. Paratype

female, specimen NIGP171722, fore wing (C) and body in dorsal (D) and ventral (E) view. Scale bars 0.5 mm.

Fig. 8. Holotype male of *Gallosclerogibba alnensis* gen. et sp. nov., specimen IGR.FRS-7.27: A. Dorsal view. B. Ventral view. C. Fore wing. D. Head in dorsal view. Scale bars 1 mm for A, B, 0.5 mm for C, D.

Fig. 9. *Sclerogibba cretacica* Martynova, Olmi, Müller & Perkovsky, 2019: A. Holotype male, specimen DAF2760, in left lateral view. B. the same, scheme of fore wing venation. C. Male specimen NIGP171724 in lateral view. Scale bars 0.5 mm. A and B reproduced from Martynova et al. (2019a) with permission, “©The Trustees of the Natural History Museum, London, 2019”.

Fig. 10. *Sclerogibbodes embioleia* Engel and Grimaldi, 2006. Female holotype AMNH LB-AE-3-20 in ventral view. Fore wing venation indicated by black. Scale bar 0.5 mm.

Fig. 11. Extant sclerogibbid wasps: A. *Sclerogibba magrettii* (Kieffer, 1913), female from Yemen, Beit Baus (from Olmi, 2005). B. *Caenosclerogibba longiceps* (Richards, 1958), male from India, 24 mi. SW Rajmahal Hills (from Olmi, 2005). C. *Caenosclerogibba longiceps* (Richards, 1958), female from China, Nanjing. D. *Probethylus callani* Richards, 1939, female from Trinidad, St. Augustine (from Olmi, 2005). E. *Probethylus callani*, male from Yemen, Sana’a (from Olmi, 2005). F. *Probethylus callani*, female paratype from Trinidad in lateral view (from Olmi, 2005). Scale bars 1 mm for A, D, E, F, 0.5 mm for B, C.

Figure 12. Fore wings of extant males of *Sclerogibba* species with discoidal cell (from Olmi, 2005).

Figure 13. Fore wings of extant males of *Sclerogibba* species without discoidal cell (from Olmi, 2005).

Figure 14. Head in ventral view of females of extant Sclerogibbidae (from Olmi, 2005) (a = antenna, h = hypostomal bridge).

Figure 15. Scheme showing known localities of Cretaceous sclerogibbids and their hosts: 1– Lebanese amber, Lebanon; 2 – Choshi amber, Japan; 3 – Kachin amber (Hukawng Valley), Myanmar; 4 – Charentese amber (Fouras), France.

Credit author statement

Evgeny E. Perkovsky: Supervision, Writing- Original draft preparation. Ekaterina V. Martynova: Investigation, Writing- Original draft preparation. Toshiharu Mita: Resources, Methodology. Massimo Olmi: Conceptualization, Writing- Reviewing and Editing. Yan Zheng: Resources, Writing- Editing. Patrick Müller: Resource, Writing- Editing. Qi Zhang: Resources, Writing- Reviewing and Editing. Flavie Gantier: Visualization, Data curation. Vincent Perrichot: Resources, formal analysis.

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Table 1. Diversity and distribution of world Sclerogibbidae. Abbreviations of zoogeographical regions: Afr. = Afrotropical; Au. = Australasian; Or. = Oriental; Nea. = Nearctic; Neo. = Neotropical; Pal. = Palaeartic.

Genera	Species	Distribution
† <i>Burmasclerogibba</i> gen. nov.	† <i>B. aptera</i> sp. nov.	Burmese amber, Cenomanian (99 Ma)
<i>Caenosclerogibba</i> Yasumatsu, 1958	3 extant	Afr., Neo., Or., Pal.
† <i>Chosia</i> Fujiyama, 1994	† <i>C. yamadai</i>	Japanese amber, Aptian (121-122 Ma)
† <i>Cretosclerogibba</i> gen. nov.	† <i>C. antennalis</i> sp. nov.	Burmese amber, Cenomanian (99 Ma)
	† <i>C. contractocollis</i> sp. nov.	Burmese amber, Cenomanian (99 Ma)
	† <i>C. neli</i> sp. nov.	Burmese amber, Cenomanian (99 Ma)
	† <i>C. rasnitsyni</i> sp. nov.	Burmese amber, Cenomanian (99 Ma)
† <i>Edrossia</i> gen. nov.	† <i>E. vetusta</i> sp. nov.	Burmese amber, Cenomanian (99 Ma)
† <i>Gallosclerogibba</i> gen. nov.	† <i>G. alnensis</i> sp. nov.	French amber, Cenomanian (98 Ma)
<i>Probethylus</i> Ashmead, 1902	† <i>P. poinari</i>	Dominican amber, Miocene (15-20 Ma)
	2 extant	Afr., Nea., Neo.
† <i>Pterosclerogibba</i> Olmi, 2004	† <i>P. antiqua</i>	Dominican amber, Miocene (15-20 Ma)
<i>Sclerogibba</i> Reggio & De Stefani-Perez, 1888	† <i>S. cretatica</i>	Burmese amber, Cenomanian (99 Ma)
	15 extant	Afr., Au., Or., Pal.
† <i>Sclerogibbodes</i> Engel & Grimaldi, 2006	† <i>S. embioleia</i>	Lebanese amber, Barremian (125-129 Ma)

Table 2. Antennal polymorphism in sclerogibbid taxa

No	Sclerogibbid taxa	Male: number of antennomeres / size, mm	Female: number of antennomeres / size, mm	Reference
1	<i>Caenosclerogibba longiceps</i> (Richards, 1958)	20 / 1.8–2.4	16–17 / 1.3–2.2	Olmi, 2005
2	<i>Caenosclerogibba rossi</i> Olmi, 2005	20–22 / 2.2–2.9	17–19 / 2.2–3.3	Olmi, 2005
3	<i>Caenosclerogibba probethyloides</i> Olmi, 2005	16–18 / 2.0–2.8	16–18 / 1.6–3.4	Olmi, 2005
4	<i>Probethylus callani</i> Richards, 1939	19–32 / 1.4–4.4	15–25 / 1.3–5.0	Olmi, 2005
5	<i>Probethylus schwarzi</i> Ashmead, 1902	17–23 / 1.2–3.0	18–23 / 1.6–4.5	Olmi, 2005
6	<i>Probethylus poinari</i> Olmi, 2005	—	18 / 2.3	Olmi, 2005
7	<i>Sclerogibba africana</i> (Kieffer, 1904)	25–30 / 2.8–3.6	24–34 / 3.0–3.5	Olmi, 2005
8	<i>Sclerogibba algerica</i> Benoit, 1963	27–29 / 3.0–4.5	30 / 4.8–5.2	Olmi, 2005
9	<i>Sclerogibba berlandi</i> Benoit, 1963	21–38 / 1.8–5.0	20–27 / 2.7–4.0	Olmi, 2005
10	<i>Sclerogibba crassifemorata</i> Riggio & De Stefani-Perez, 1888	25–36 / 1.3–5.6	24–31 / 2.9–6.6	Olmi, 2005
11	<i>Sclerogibba cretacica</i> Martynova et al., 2019	14–19 / 1.8–3.0	—	this paper
12	<i>Sclerogibba embiopterae</i> Dodd, 1939	22–35 / 2.0–5.3	19–30 / 1.6–6.1	Olmi, 2005
13	<i>Sclerogibba impressa</i> Olmi, 2005	25–31 / 2.2–4.1	23–26 / 1.2–4.5	Olmi, 2005
14	<i>Sclerogibba madegassa</i> Benoit, 1952	24–31 / 1.4–3.8	20–27 / 2.4–4.4	Olmi, 2005
15	<i>Sclerogibba magrettii</i> (Kieffer, 1913)	27–38 / 2.5–4.6	26–30 / 2.7–5.4	Olmi, 2005
16	<i>Sclerogibba rapax</i> Olmi, 2005	31–36 / 2.3–5.6	24–31 / 2.9–6.6	Olmi, 2005
17	<i>Sclerogibba rossi</i> Olmi, 2005	28 / 3.8	19–25 / 2.7–4.0	Olmi, 2005
18	<i>Sclerogibba rufithorax</i> (Cameron, 1904)	19–34 / 1.4–4.0	26–32 / 3.4–7.0	Olmi, 2005
19	<i>Sclerogibba rugosa</i> Olmi, 2005	31–36 / 3.9–5.0	—	Olmi, 2005
20	<i>Sclerogibba talpiformis</i> Benoit, 1950	28–37 / 3.4–5.3	25–34 / 3.5–6.0	Olmi, 2005
21	<i>Sclerogibba turneri</i> Richards, 1939	30–39 / 2.8–5.4	28–32 / 4.3–5.6	Olmi, 2005
22	<i>Sclerogibba vagabunda</i> (Bridwell, 1919)	23–32 / 1.8–4.0	20–28 / 2.8–4.4	Olmi, 2005
23	<i>Pterosclerogibba antiqua</i> Olmi, 2005	—	14 / 2	Olmi, 2005
24	<i>Edrossia vetusta</i> sp. nov.	—	17 / 2.7–3.6	this paper
25	<i>Sclerogibbodes embioleia</i> Engel & Grimaldi, 2006	—	14 / 2.3	Engel & Grimaldi, 2006
26	<i>Burmasclerogibba aptera</i> sp. nov.	—	20 / 3.8	this paper
27	<i>Chosia yamadai</i> Fujiyama, 1994	20 / 3.5	—	this paper
28	<i>Cretosclerogibba rasnitsyni</i> sp. nov.	14–15 / 1.6–1.9	—	this paper
29	<i>Cretosclerogibba antennalis</i> sp. nov.	21 / 2.9	—	this paper
30	<i>Cretosclerogibba neli</i> sp. nov.	—	18 / 3.2–3.8	this paper
31	<i>Cretosclerogibba contractocollis</i> sp. nov.	15 / 2.6	—	this paper
32	<i>Gallosclerogibba alnensis</i> sp. nov.	25 / 3.7	—	this paper

Graphical abstract

Highlights

New Cretaceous sclerogibbids from Burmese amber and Laurasia (France and Japan)

Sclerogibbids archaic in Laurasian and much more diverse in the Burmese amber

low predator pressure cause abundance of webspinners in Burmese amber forest

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Figure 1

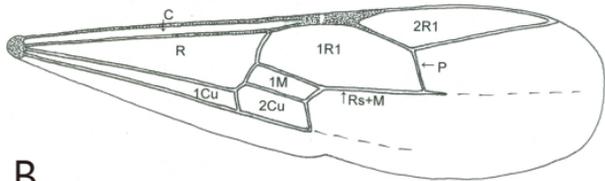


Figure 2

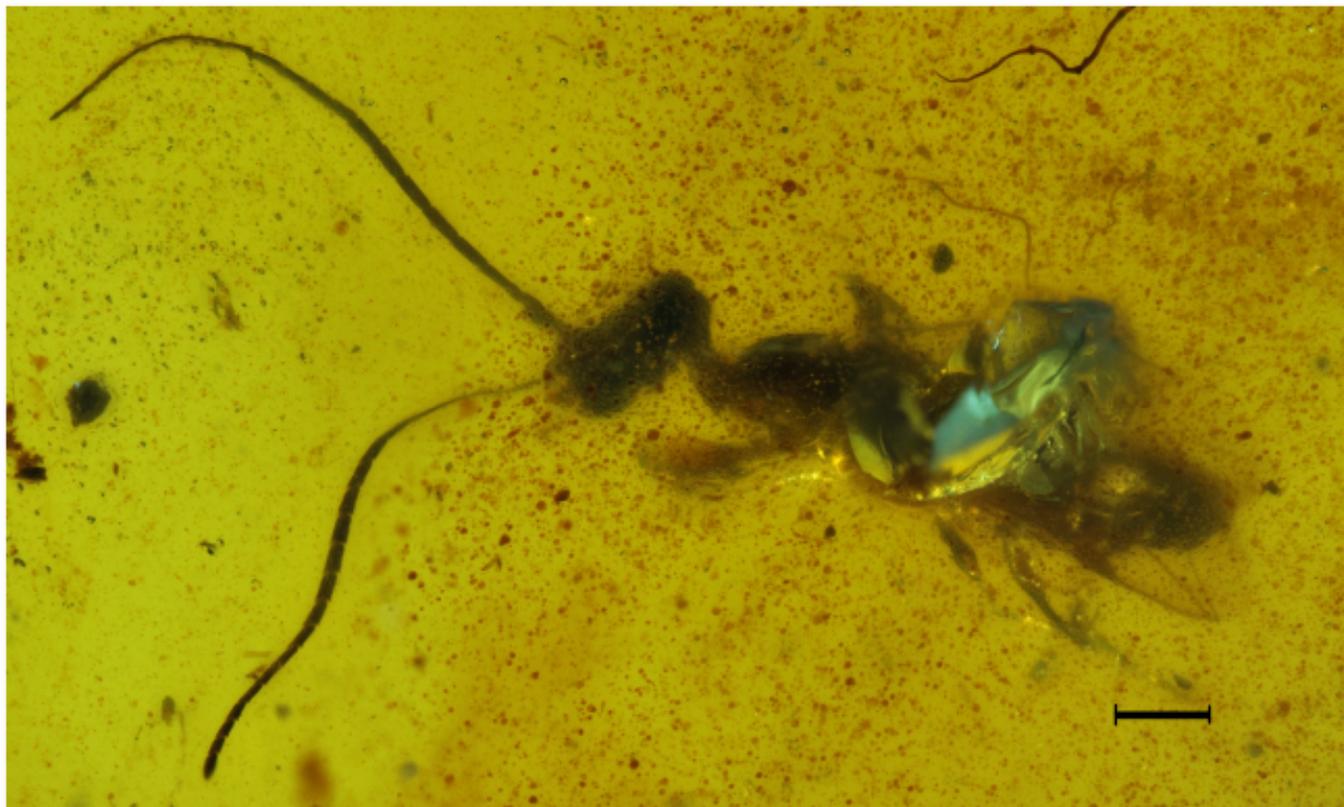


Figure 3



Figure 4



Figure 5



Figure 6

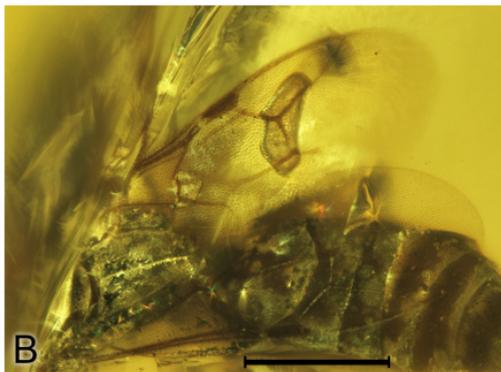
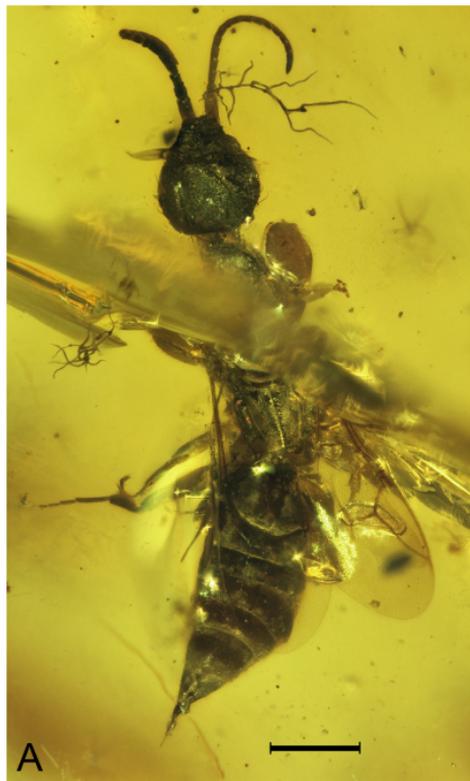


Figure 7

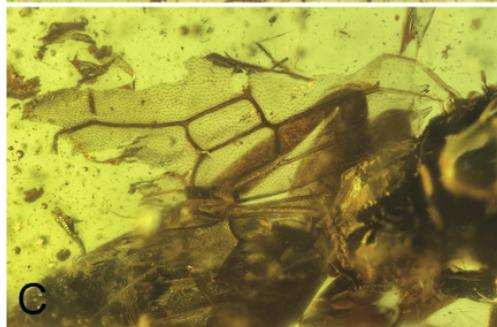
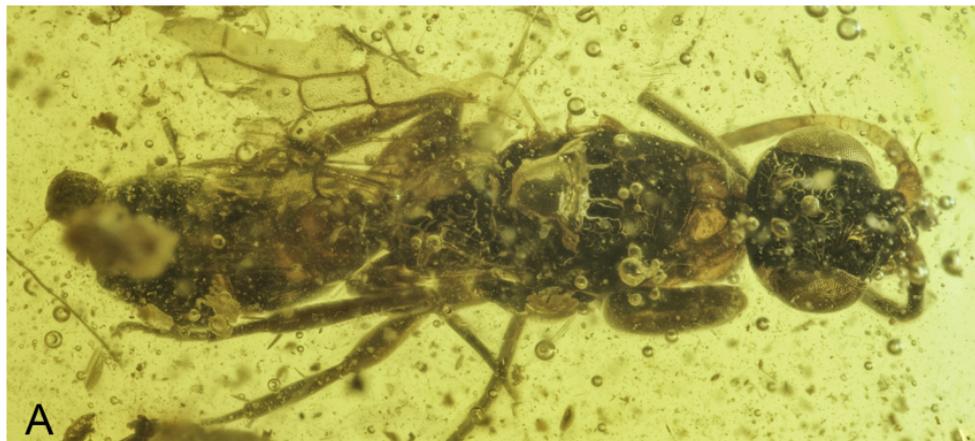


Figure 8

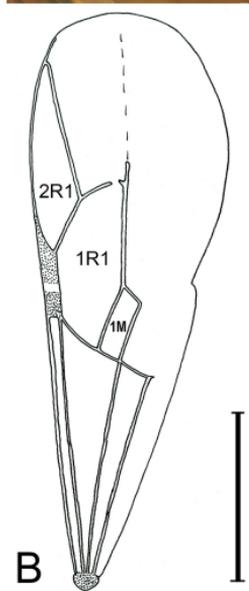


Figure 9

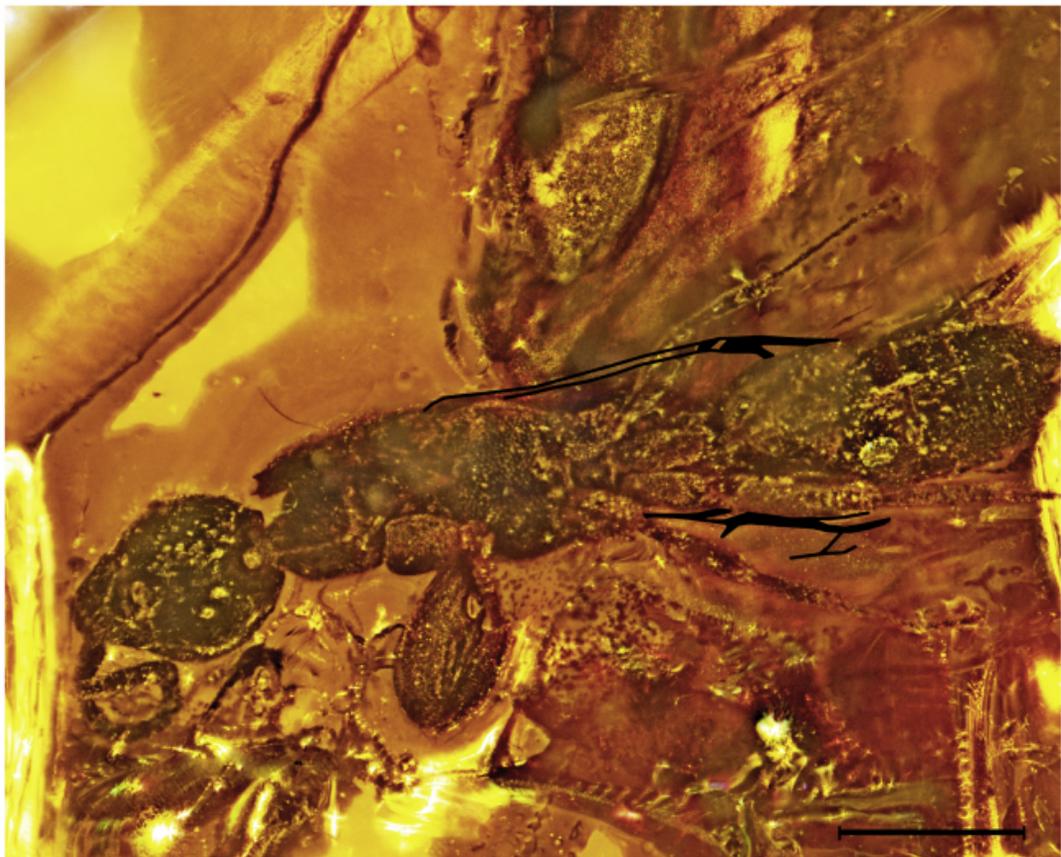


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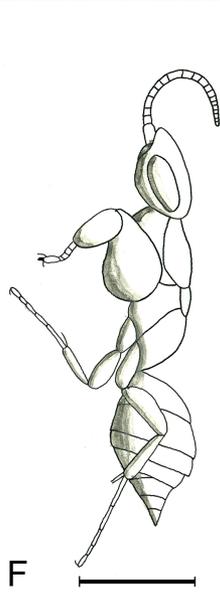
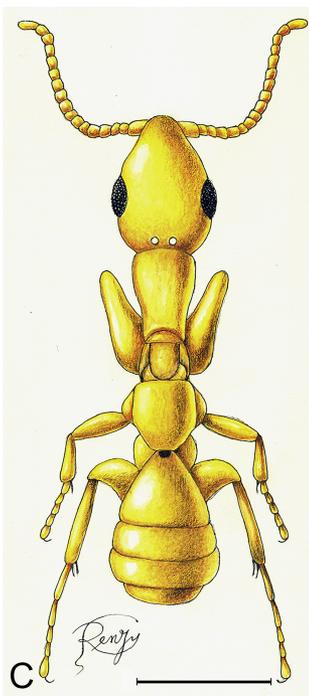
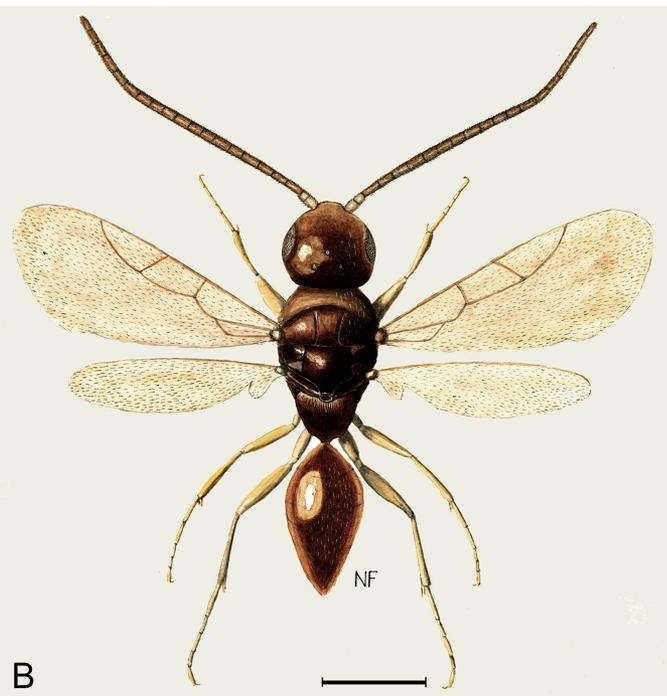
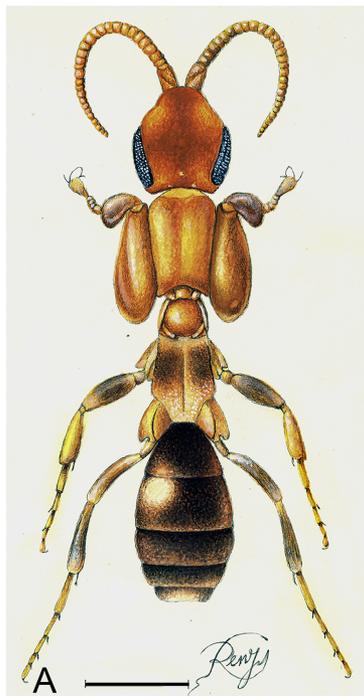


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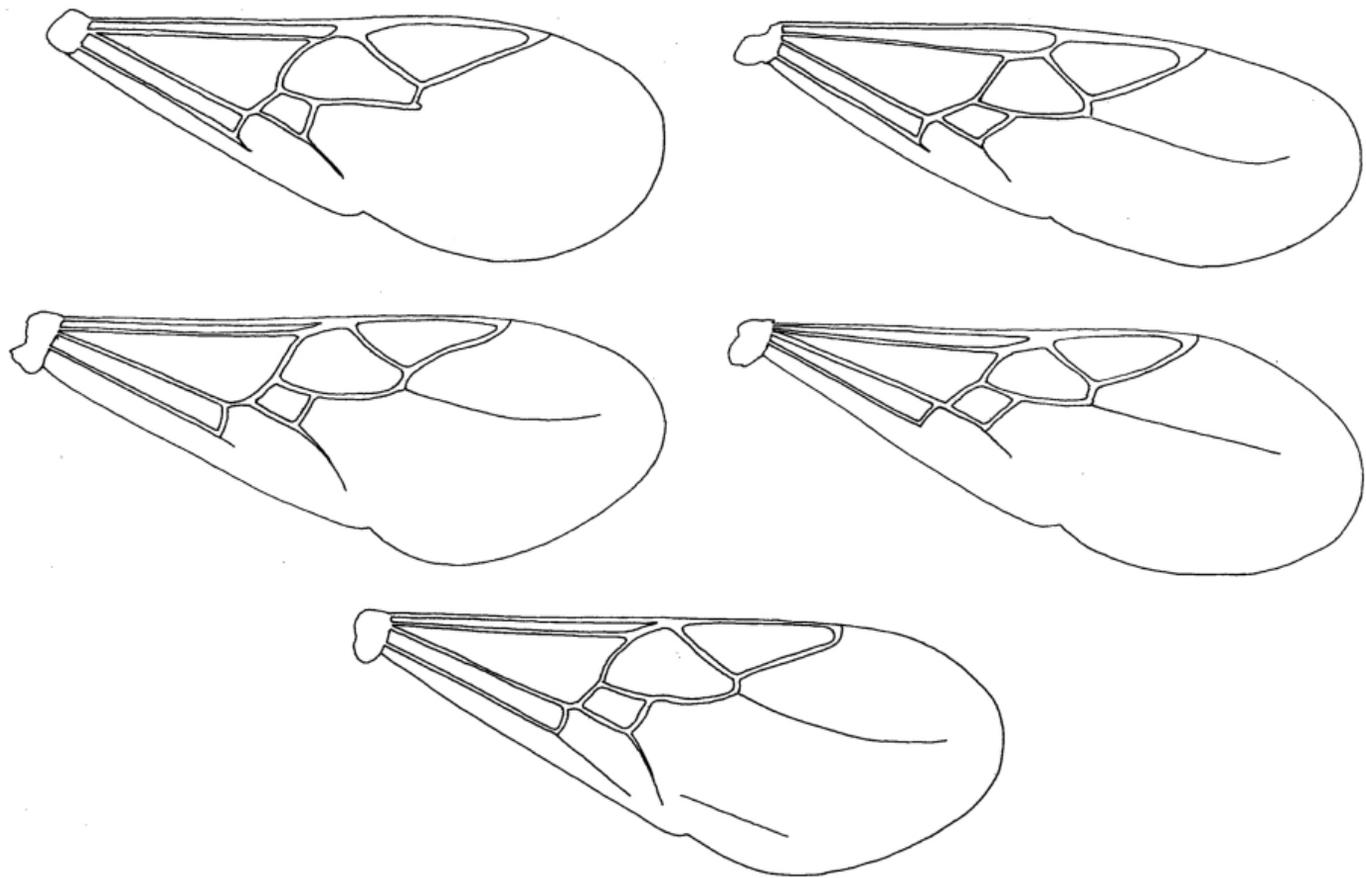


Figure 12

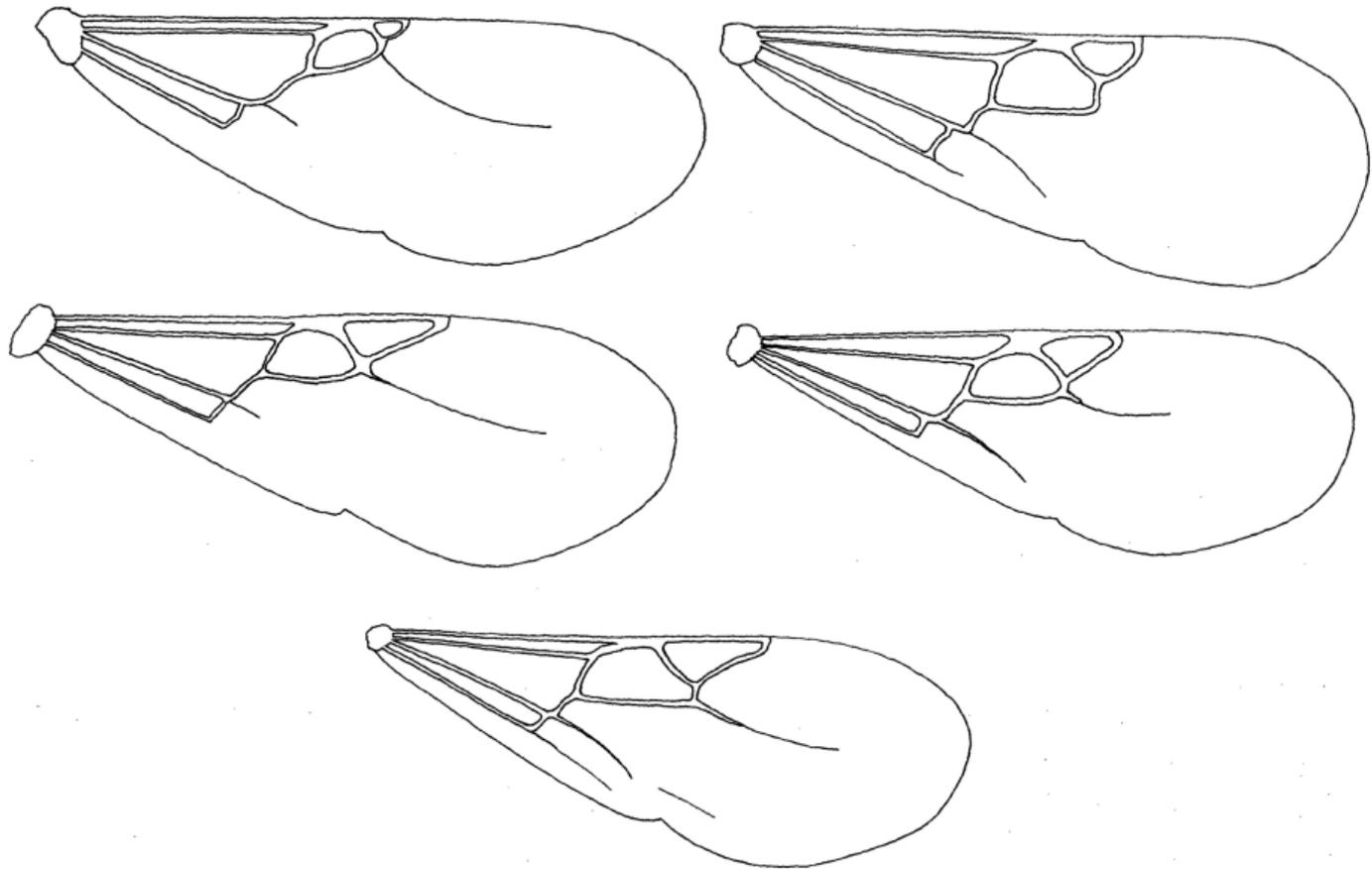


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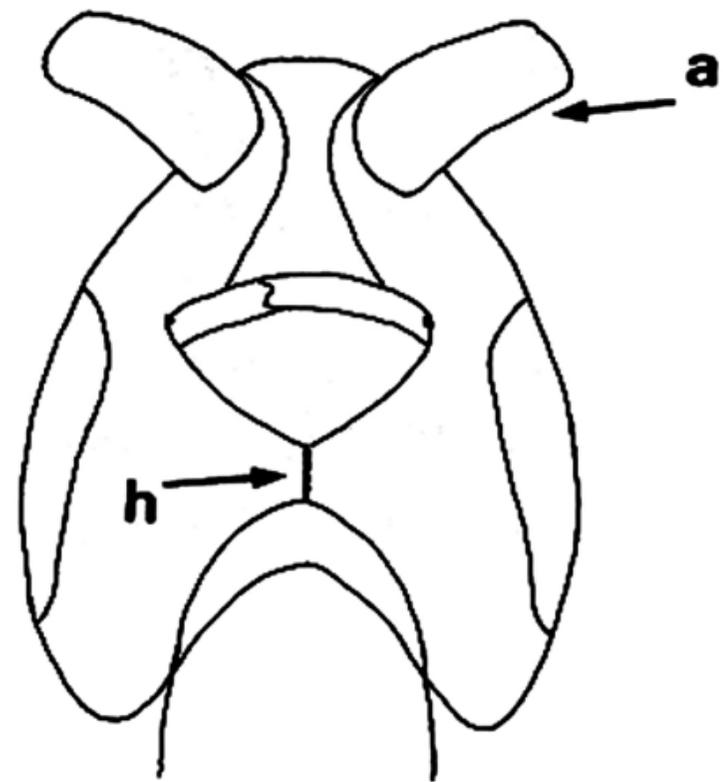
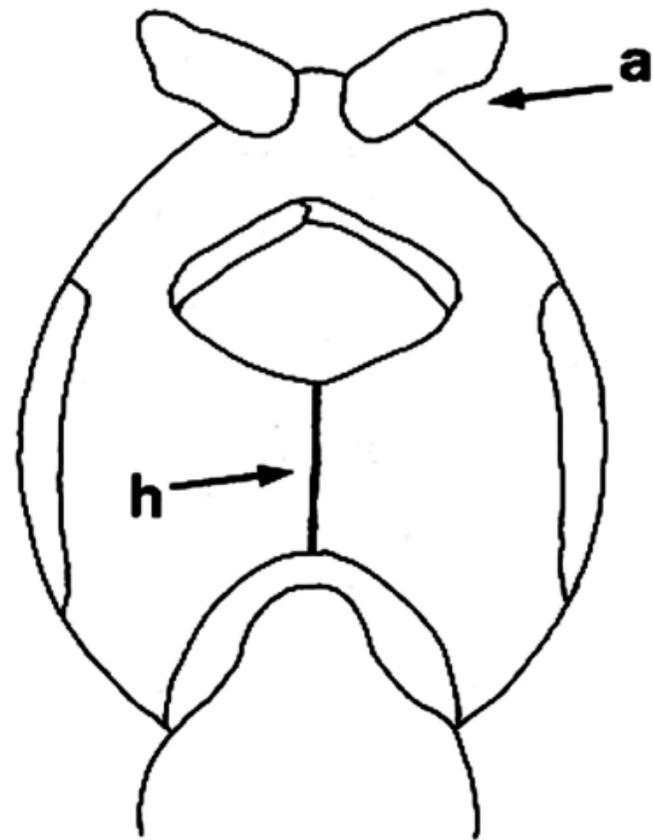
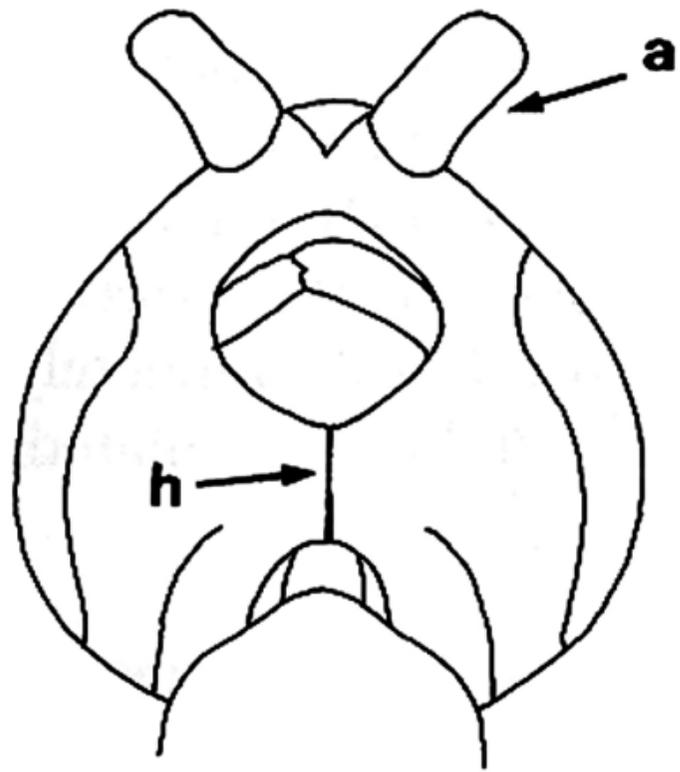


Figure 14

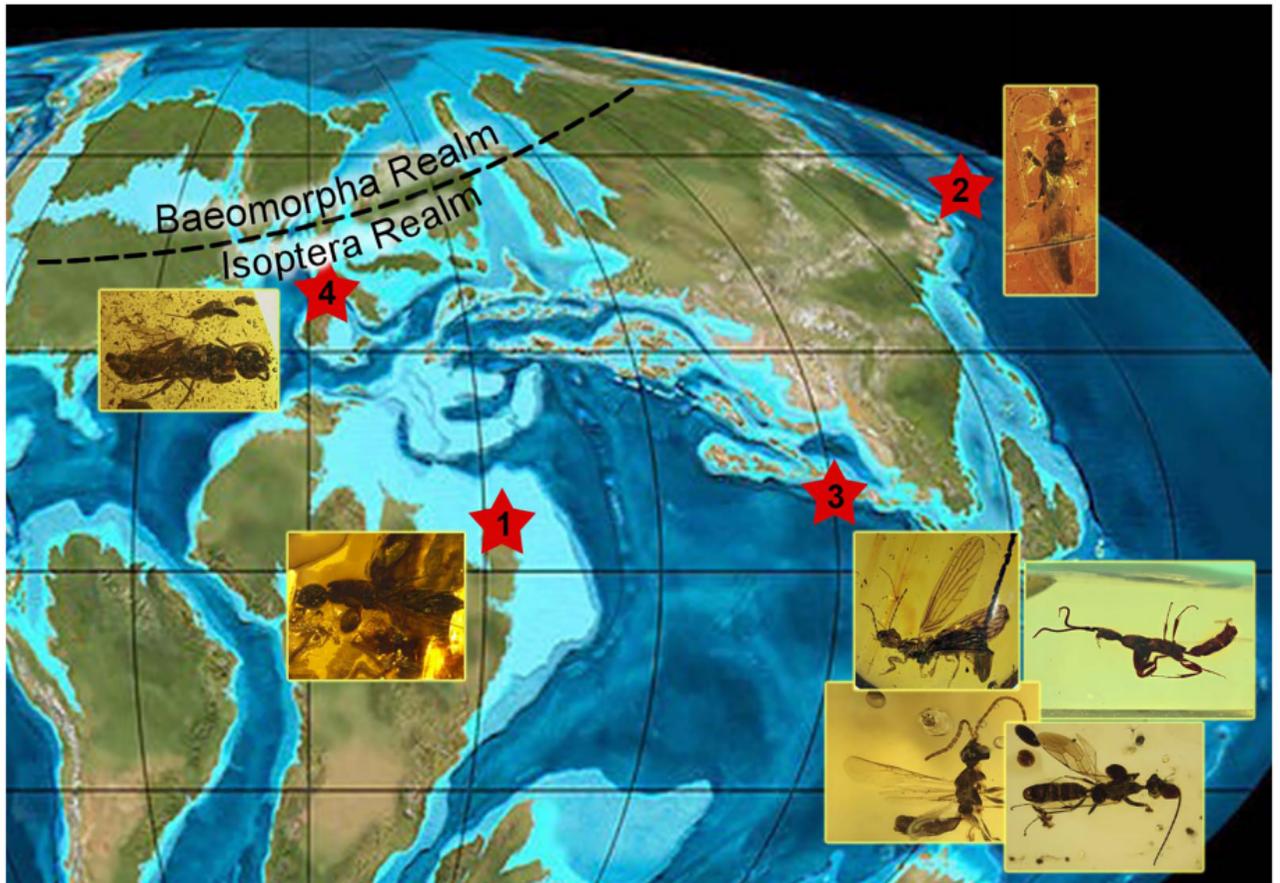


Figure 15