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Long-Tailed Wasps (Hymenoptera: Megalyridae) from Cretaceous and Paleogene European amber

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Abstract.—Fifty-two fossils of megalyrid wasps from various collections of European amber were examined. A male neotype for *Prodinapsis succinalis* Brues and a female neotype for *P. minor* Brues are designated. The two species are redescribed and illustrated from Eocene and Oligocene amber, and males are tentatively distinguished by the length of their forewing. Three new species are described: *P. pumilio* Perrichot & Perkovsky n. sp., from a single female preserved in upper Eocene Rovno amber (Ukraine); *P. janzeni* Perrichot n. sp., from three males in Eocene Baltic and Rovno amber; and *P. oesiensis* Perrichot n. sp., from a single male preserved in lower Eocene French amber. A key for the identification of the five species of *Prodinapsis* is provided. *Megazar elegans* Perrichot n. gen. and n. sp., and *Megalava truncata* Perrichot n. gen. and n. sp., are described from Albian French and Spanish amber, respectively, and are placed in a new tribe Megazarini Perrichot n. tribe, which is characterized by the mesothoracic spiracle not being surrounded by pronotal cuticle posteriorly, the inner margin of the metathoracic trochanter, femur, tibia, and first two tarsomeres having comblike spines or stiff setae, the forewing with M+Cu being tubular, the basal segment of Rs being very long, and a narrow medial cell [1M]. The following new fossil genera and species are also described and illustrated: *Ukrainosa prolata* Perrichot & Perkovsky n. gen. and n. sp., from Eocene Rovno amber; *Rubes bruesi* Perrichot n. gen. and n. sp. from Eocene Baltic amber; *Megallica parva* Perrichot n. gen. and n. sp., from upper Albian amber of France; and *Valaa delclosi* Perrichot n. gen. and n. sp., from lower Albian amber of Spain. A second specimen of *Megalyra baltica* Poinar & Shaw is illustrated from Baltic amber and discussed. A key for the identification of all known fossil and extant genera is provided. The new fossils extend significantly our knowledge of the evolutionary history of Megalyridae *sensu stricto* (i.e., excluding Cleistogastridae) that hitherto comprised eight modern and two extinct genera. They also emphasize the relictual distribution of the family that is now mainly restricted in tropical and austral regions, while it obviously occurred widely in ancient forests of the northern hemisphere during the Mesozoic and Cenozoic era.

Keywords: Insecta, Hymenoptera, Apocrita, megalyrid wasp, Mesozoic, Cenozoic, Tertiary

INTRODUCTION

The Megalyridae is a small family of infrequently collected wasps comprising eight living genera of mostly pantropical and austral distribution and associated with relict primary tropical forests (Shaw, 2007). Megalyrids are characterized by a unique combination of characters that occur individually in other hymenopteran families. This includes, among the most diagnostic features, a flat mesoscutum divided by the median mesoscutal sulcus, large triangular axillae, antennae with 14 segments inserted below the ventral margin of the compound eyes, and a long to very long ovipositor. Their biology is still largely unknown, except for a few species of *Megalyra* Westwood, which are ectoparasitoids on larvae of bostrichid, buprestid, and cerambycid beetles, and a single host record within sphecid wasps (Froggatt, 1906; Rodd, 1951; Naumann, 1987; Shaw, 1990a).

Most recent works on the phylogeny of Hymenoptera suggest a placement of Megalyridae in its own, monotypic superfamily Megalyroidea (Dowton & others, 1997; Dowton & Austin, 2001; Castro & Dowton, 2006; Sharkey, 2007; Vilhelmsen, Mikó, & Krogmann, 2009), while Ronquist and others (1999) included it among a large clade of Evaniomorpha, and Rasnitsyn (1988,

2002) in the Stephanoidea *sensu lato.* In fact, its exact phylogenetic relationships remain controversial among apocritans: Ronquist and others (1999), Rasnitsyn (1988), and Dowton's papers (listed above) discussed unclear sister-group relationships with the Stephanidae and Trigonalidae; alternatively, Sharkey (2007) hypothesized a sister-group relationship with the Ceraphronoidea in an intuitive tree based on morphological evidence combined with most recent results on molecular phylogeny. This sister-group relationship was retrieved in most analyses of the mesosomal anatomy by Vilhelmsen, Mikó, and Krogmann (2009). The internal phylogeny of the family is not resolved either. The sole cladistic analysis was conducted by Shaw (1990b) and resulted in a classification into six tribes, four of which were new [Note 1: he proposed the tribe Prodinapsini to include *Prodinapsis* Brues and *Cretodinapsis* Rasnitsyn, but he overlooked Rasnitsyn's work that previously created the Cretodinapsini (Rasnitsyn, 1977); Prodinapsini is thus invalid since it includes the type genus of an older family-group name, and according to the Principle of Priority (ICZN, 1999: Art. 23), the correct tribal name is Cretodinapsini Rasnitsyn, 1977. Note 2: he based the tribe Megalyrideini upon the incorrect spelling *Megalyridea* of the genus *Megalyridia* Hedqvist; the correct stem is Megalyridi-, according to the formation and treatment of family-group names (ICZN, 1999: Art. 35.4); the correct name for the tribe is Megalyridiini Shaw, 1990b, *nomen correctum*.] This tribal classification does not consider the fossil group Cleistogastrinae Rasnitsyn, which was originally considered as a subfamily within Megalyridae (Rasnitsyn, 1975), but Kovalev (1994), following Shaw (1988), segregated the Cleistogastridae from the Megalyridae and erected the new superfamily Cleistogastroidea. Rasnitsyn (2002, 2008) did not follow Kovalev's statement and retained the Cleistogastrinae within the Megalyridae. He considered the latter to be paraphyletic, however, representing the ancestral group of seven families that he included in the Ceraphronoidea (Rasnitsyn, 2002). Compared to the standard features displayed by all modern megalyrids, the Cleistogastrinae/-idae have a variable number of antennomeres (10–21, with only 10 of the 42 species having 14 antennomeres, as in all megalyrids), a much more complete wing venation, and notauli present on the mesoscutum, which arguably exclude them from Megalyridae. Therefore, taxa currently attributed to this group, the seven genera *Cleistogaster* Rasnitsyn, *Brachycleistogaster* Rasnitsyn, *Microcleistogaster* Rasnitsyn, *Leptocleistogaster* Rasnitsyn, *Neocleistogaster* Rasnitsyn, *Mesaulacinus* Martynov, and *Yanocleistogaster* Ren (Martynov, 1925; Rasnitsyn, 1975, 1986; Ren, 1995), have yet to be better justified in their exact assignment, and they are considered herein as a separate family.

The Megalyridae have a sparse representation in the fossil record. Only one extinct species from Eocene Baltic amber has been assigned to the modern genus *Megalyra* (Poinar & Shaw, 2007), and three species have been described in two exclusively extinct genera: *Prodinapsis* from Baltic amber (Brues, 1923, 1933) and *Cretodinapsis* from Cenomanian amber of Azerbaijan (Rasnitsyn, 1977). Additional fossils have been mentioned or figured from Turonian New Jersey amber (Grimaldi, Shedrinsky, & Wampler, 2000, fig. 46h), Albian Burmese amber (Grimaldi, Engel, & Nascimbene, 2002), and one specimen was also found in Campanian Canadian amber (M. Engel, personal communication, June 2009), but they have yet to be described. The mid-Cretaceous family Maimetshidae, originally composed of the monotypic genus *Maimetsha* Rasnitsyn, from Santonian Taimyr amber (Rasnitsyn, 1975), was synonymized with the Megalyridae by Shaw (1988, 1990b, 2007), who suggested that it could represent a basal lineage within megalyrids. *Maimetsha*'s similarities with Megalyridae include the antennae being inserted below the level of the ventral margin of the eyes, the presence of a median mesoscutal sulcus, and the ovipositor being externalized, though short. All these characters are plesiomorphic, however, and the exact position of *Maimetsha* has been debated (see Rasnitsyn, 2002; Perrichot, Nel, & Néraudeau, 2004; Grimaldi & Engel, 2005). Rasnitsyn and Brothers (2009) recently described some additional genera related to *Maimetsha* from the Turonian of Botswana, which allowed a redefinition of the Maimetshidae as a distinct family. Differences with Megalyridae include the absence of a subantennal groove, 16 to 20 antennomeres, mandibles with 4 teeth (rarely asymmetrical, with 4 and 3 teeth), notauli present and well developed, a more complete wing venation resembling that of the Cleistogastridae, and the attachment of the first metasomal segment to the propodeum reduced to a small ring.

Until now, *Prodinapsis* comprised two species described from inclusions preserved in Eocene Baltic amber, *P. succinalis* and *P. minor* (Brues, 1923, 1933). Brues's type material was in the collection of the Albertus Universität in Königsberg (now Kaliningrad, Russia), which was partly destroyed during World War II. Some material was saved, however, and now constitutes important amber collections in the Museum of Comparative Zoology at Harvard University and in the Geological Museum at the University of Göttingen. A personal examination of the Göttingen material in December 2008 recovered no type specimen of *Prodinapsis;* however, two unidentified males were found. They probably belong to the 16 male specimens examined by Brues, but lack any label, and Brues mentioned that he was unable to assign males to either of the two species (Brues, 1933). Indeed, he distinguished both species on the basis of female specimens only. Apart from the two males recovered from the Göttingen collection, two other Baltic amber specimens assignable to *Prodinapsis* were figured from the former collection of Jens-Wilhelm Janzen: a male (Weitschat & Wichard, 2002, pl. 67a) that is now in the private collection of Jürgen Velten; and an exquisitely preserved female (Janzen, 2002, fig. 297) that is now housed in the American Museum of Natural History, New York. Shaw (1990b) mentioned a specimen of unknown sex in the Harvard University Museum of Comparative Zoology.

During the present study, I examined 39 specimens from different amber collections that match the original description and illustrations provided by Brues for the genus, and I hereby consider them as congeneric. A male neotype for *P. succinalis* and a female neotype for *P. minor* are designated herein (the sex was chosen in order to match the original holotype as closely as possible), and both species are redescribed and newly illustrated, with a tentative distinction of males based on forewing length relative to the head length, which is preferred to comparison of the body length or position of wing apex relative to that of the metasoma, because the latter is easily distorted by preservation in amber (see metasoma in Fig. 4.3, 7.2, and 14.3) while the head is mostly intact. Three new species from Eocene Baltic, Rovno (Ukraine), and Oise (France)

amber, two new genera and species preserved in Eocene Baltic and Rovno amber, and four new genera and species preserved in Cretaceous French and Spanish amber are also described.

MATERIAL AND METHODS

The specimens treated herein were studied and imaged under incident and transmitted light with a Leica M205 C stereomicroscope and a Leica DM2500 M microscope, and measurements were made with an ocular micrometer. Drawings were made with a camera lucida attached to the stereomicroscope. Photomicrographs were made with a Leica DFC420 C camera attached to the stereomicroscope, and stacks of multiple images were merged using Helicon Focus software (HeliconSoft Ltd.). The terminology of Huber and Sharkey (1993) is employed throughout for the description of morphological features of the body and wings (see Fig. 1 for labels of wing veins and cells), except for the nomenclature of surface sculpturing, which follows Harris (1979).

This study is based on specimens obtained from the following amber collections, listed with their abbreviations, and the names of curators or persons who facilitated loans of specimens are given in parentheses: GZG, Museum des Geowissenschaftlichen Zentrums der Universität Göttingen, Germany (Mike Reich); JVC, Jürgen Velten personal collection, Idstein, Germany (Jürgen Velten, Jens-Wilhelm Janzen); KU-NHM-ENT, University of Kansas Natural History Museum, Division of Entomology, Lawrence, Kansas, USA (Michael Engel); MCNA, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain (Rafael López del Valle, Xavier Delclòs); MfN, Museum für Naturkunde Berlin, Germany (Christian Neumann); MNHN, Muséum National d'Histoire Naturelle, Paris, France (André Nel); RMRS, Rovno Museum of Regional Studies, Rovno, Ukraine (Anatoliy Vlaskin); SIZK, Schmalhausen Institute of Zoology, Kiev, Ukraine (Evgeny Perkovsky).

Bitterfeld (Saxonian) amber.—One female and three males belonging to *P. succinalis* were found complete and well preserved in four distinct pieces from the amber collection of the MfN. Two additional males of the same species are also preserved in a single piece from the former collection of Manfred Kutscher, which was recently acquired by the GZG. The age of this amber, found in the Goitsche mine near Bitterfeld (Sachsen-Anhalt, Germany), is still in dispute. The amber-bearing sediments were first assigned to the lower Miocene (Barthel & Hetzer, 1982). Several authors suggested a redeposition of Eocene Baltic amber (Röschmann, 1997; Weitschat, 1997; Weitschat & Wichard, 2002), while the independent origin of the Bitterfeld amber has been emphasized based on sedimentological and paleogeographical studies (Kosmowska-Ceranowicz & Krumbiegel, 1989; Knuth & others, 2002; Fuhrmann, 2005). Most recent works on the biostratigraphy and paleogeography of the deposits suggest no connection with Baltic amber and support an age of 23–24 Ma for the amber-bearing layers, from upper Oligocene (Wimmer, Pester, & Eissmann, 2008) to lower Miocene (Standke, 2008). A part of this amber may be redeposited, however, and the study of its fossil content shows both similarities and differences with that of the Baltic amber. The pieces were polished in order to obtain flat surfaces for clear views of the fossils.

Baltic amber.—Three specimens of the amber collection of the GZG, originally from the former Königsberg collection, were examined. One is a male *P. succinalis*, one a female *P. minor*, and the third one is a nicely preserved female of a distinct new genus. The exact provenance is unknown, but Baltic amber from the Königsberg collection has been collected largely from the so-called Blue Earth layers of the Samland Peninsula (Grimaldi, 1996; Weitschat & Wichard, 2002) that are upper Eocene in age (Priabonian, 34–37 Ma) (Kasinski & Kramarska, 2008). The University of Kansas Division of Entomology recently purchased a part of Janzen's Baltic amber collection, which contains 21 males and females of *Prodinapsis*, as well as six females of a new genus, and one female specimen of *Megalyra baltica* Poinar and Shaw. Four other specimens examined from the private collection of Jürgen Velten are also attributable to *Prodinapsis.* The amber pieces containing the specimens were polished to allow detailed observations.

Rovno amber.—Five megalyrids from the SIZK collection and one from the RMRS collection are studied herein. One female and four males are assignable to *Prodinapsis,* and two are new species. One female is assignable to a new genus. Ukrainian amber from Klesov in the Rovno region has sometimes been interpreted as being of Oligocene age but should be referred to the upper Eocene (Perkovsky & Fedotova, 2004; Perkovsky & others, 2007).

French Eocene amber.—A complete male specimen, assigned to a new species of *Prodinapsis*, was found in amber from Oise in the MNHN collection. The age is lower Eocene (Ypresian), ca. 53 Ma (Nel & others, 1999).

French Cretaceous amber.—Two complete specimens representing two genera are fossilized in Cretaceous amber from southwestern France: one female from the locality of Cadeuil and one male from Archingeay-Les Nouillers, with both amber-bearing strata being upper Albian in age (Néraudeau & others, 2002, 2008). They were each found preserved with other fossil arthropods in their respective pieces of amber, were separated using a scalpel as a microsaw, and then embedded in Canada balsam or epoxy resin. They are deposited in the MNHN collection.

Spanish amber.—The MCNA collection contains two fossil megalyrids of two different species, preserved in thin pieces of amber that have been embedded in epoxy resin blocks for consolidation and preservation and then polished. One subcomplete male is well preserved, but some structures are weakly visible, blurred by fissures or detrital material. The other specimen lacks the entire metasoma, but preserved parts show diagnostic features of the Megalyridae. The amber was collected from the fossil site Peñacerrada 1, near Moraza, in the Basque-Cantabrian province of Álava, from the lower Albian middle member of the Escucha Formation (Martínez-Torres, Pujalte, & Robles, 2003; Delclòs & others, 2007).

Abbreviations used in figures and tables.—AG, inner axillar groove; AL, antennal length; AmP, anteromedial pronotum; Av, aedegus valves; BL, body length (excluding antennae and ovipositor); CC, coxal carinae; Ce, cerci; CN, clypeal anteromedian notch; CSG, dorsal carina of subantennal groove; CT, convex temple; FCS, femoral comblike setae; FES, femoral erect setae; FMM, fore metapleural margin; FOC, foveate occipital carina; FT, flat temple; FWCu1, forewing basal segment Cu1; FWL, forewing length; FWRs, forewing apical segment Rs; HL, head length; HW, head width; Hy, hypopygium; IG, interaxillar groove; Ma, mandible; ML, metasomal length; mL/mW, ratio mesoscutal length/

mesoscutal width; MMS, median mesoscutal sulcus; MSV, median sulcus of vertex; OC, occipital carina; OL, ovipositor length; Pa, paramere; PC, postorbital carina; PFR, anterior propodeal foveate row; PG, postorbital groove; PGW, postorbital groove width; Pp, parapside; PV, punctate vertex; SG, subantennal groove; Sp, spiracle exposed posteriorly; TB, tibial brush of stiff setae; TS, tibial spur; VMP, vertex and mesoscutal pilosity.

SYSTEMATIC PALEONTOLOGY
Class INSECTA Linnaeus, 1758
Order HYMENOPTERA Linnaeus, 1758
Family MEGALYRIDAE Schletterer, 1889

Type genus.—*Megalyra* Westwood, 1832, p. 419, pl. 66,*4;* pl. 106,*4a–f.*

Diagnosis.—Antennae filiform, inserted below level of ventral margin of eyes, with 14 segments, with scape short and globular; subantennal groove present, with or without dorsal carina; eyes large, with posterior orbit smooth or margined by a groove and/or carina; mandibles symmetrical, with 3 teeth, rarely with 4 or 5. Pronotum reduced medially, barely visible dorsally; median mesoscutal sulcus present; notauli absent; mesoscutum with parapsides exceptionally present; large triangular axillae separated anteriorly by a foveate groove; mesothoracic spiracle generally completely surrounded by pronotal cuticle, rarely exposed posteriorly. Wing venation reduced; forewing veins 2r-m, 3r-m, and 2m-cu absent; M+Cu absent or spectral, rarely tubular; hind wing without enclosed cell, with Rs usually not extending beyond middle of wing. Legs with metacoxa large and metafemur swollen; first metasomal segment inserted low on propodeum, very close to metacoxal foramina; ovipositor external, at least half as long as metasoma.

Key to Genera of Megalyridae

1. Forewing with vein Rs between Rs+M and r-rs spectral or tubular for at least a short distance (Fig. 1.8, 15.2, 18.2, 19.1) 2

   Forewing with vein Rs between Rs+M and r-rs absent (Fig. 1.1–1.7), apical segment of Rs absent or spectral (Fig. 1.1–1.8) 9

2. Forewing with apical segment of Rs tubular, arched toward stigma (Fig. 15, 18, 19) 3

   Forewing with apical segment of Rs spectral, directed toward wing tip (Fig. 1.8) ..... ***Cretodinapsis*** Rasnitsyn

3. Anterior thoracic spiracle posteriorly not surrounded by pronotal cuticle (Fig. 16.3); parapsides present (Fig. 16.2, 17.1); metafemur with comblike spines along inner margin (Fig. 15.3, 16.4, 17.2); forewing with veins M+Cu and distal segments of Cu present, tubular (Fig. 15.2, 17.1) 4

   Anterior thoracic spiracle entirely surrounded by pronotal cuticle; parapsides absent; metafemur without comblike spines; forewing with veins M+Cu and distal segments of Cu absent or at most spectral 5

4. Vertex without longitudinal median sulcus; mandibles with 4 teeth; occipital carina, median mesoscutal sulcus, and inner axillar grooves smooth (Fig. 16.2); forewing with marginal cell narrow, large submarginal cell entirely closed by tubular veins, and prebasal segment Cu1 forming a small pentagonal medial cell (Fig. 15.2)..... ***Megazar*** n. gen.

   Vertex with a distinct longitudinal median sulcus; occipital carina foveate, median mesoscutal sulcus smooth, and inner axillar grooves crenulate; forewing with small rectangular medial cell, veins Cu and M tubular (Fig. 17.1)..... ***Megalava*** n. gen.

5. Vertex without longitudinal median sulcus 6

   Vertex with a distinct longitudinal median sulcus (Fig. 19.1, 20.2)..... ***Megallica*** n. gen.

6. Posterior ocular orbits with groove and/or carina present (Fig. 3.5, 4.4)..... 7

   Posterior ocular orbits without groove or carina (Fig. 16.5, 16.6, 18) ..... ***Valaa*** n. gen.

7. Posterior orbital groove foveate (Fig. 20.5; Shaw & van Noort, 2009, fig. 2D); forewing veins 1m-cu and Cu1 absent..... 8

   Posterior orbital groove not foveate; forewing veins 1m-cu and Cu1 present (Baltazar, 1962, fig. 1) ..... ***Ettchellsia*** Cameron

8. Forewing vein A posterior of 1cu-a present at least as a darkened line; metacoxa with a longitudinal carina; metasoma compact (Waterston, 1922, pl. 11)..... ***Dinapsis*** Waterston

   Forewing vein A posterior of 1cu-a absent; metacoxa without longitudinal carina; metasoma elongate (Shaw, 1987, fig. 3, 6)..... ***Neodinapsis*** Shaw

9. Vertex with longitudinal median sulcus distinct or faintly impressed (Fig. 5, 7, 8) 10

   Vertex without longitudinal median sulcus 12

10. Eyes not fully covering head length; frons in dorsal view wider than eye, temples convex (Fig. 5, 6.4, 7.1, 8, 9.1, 10) 11

    Eyes very large, fully covering head length; frons in dorsal view narrower than eye, temples nearly flat (Fig. 13, 14)..... ***Rubes*** n. gen.

11. Head progressively narrowed behind eyes (Fig. 5, 7, 8, 10); posterior ocular orbits with groove reduced or absent and carina present, sharp, or reduced (Fig. 3.5, 6.1, 6.6); forewing vein Cu nebulous or absent (Fig. 1.1–1.5) ..... ***Prodinapsis*** Brues

    Head sharply narrowed behind eyes; posterior ocular orbits without groove or carina; forewing vein Cu tubular (Fig. 1.6)..... ***Ukrainosa*** n. gen.

12. Dorsal carina of subantennal groove present 13

    Dorsal carina of subantennal groove absent (Shaw, 1987, fig. 1, 4)... ***Rigel*** Shaw

13. Flagellomeres compact; forewing R1 absent; hind wing Rs absent (Shaw, 1988, fig. 1)..... 14

    Flagellomeres elongate; forewing R1 present; hind wing Rs present 15

14. Pterostigma absent; metacoxa shagreened; metatibia with two apical spurs (Shaw, 1988, fig. 1)..... ***Carminator*** Shaw

    Pterostigma present, only swelling at junction with Rs; metacoxa rugose; metatibia with only one apical spur (Shaw, 1987, fig. 2, 5)... ***Cryptalyra*** Shaw

15. Head and mesosoma shagreened; face with a distinct short longitudinal median groove; pronotal spiracle without internal fringe of setae; metacoxa shagreened; metatibia with two apical spurs (Hedqvist, 1959, fig. 1) ..... ***Megalyridia*** Hedqvist

    Head and mesosoma coarsely foveate-reticulate; face without median groove; pronotal spiracle with an internal fringe of setae; metacoxa rugose; metatibia with only one apical spur (Fig. 20.3–20.6)..... ***Megalyra*** Westwood

Tribe CRETODINAPSINI Rasnitsyn, 1977
Genus PRODINAPSIS Brues, 1923

Type species.—*Prodinapsis succinalis* Brues, 1923, p. 32.

Diagnosis.—Head hypognathous, slightly broader than thorax, obliquely narrowed behind eyes; compound eyes large, widely sepa-

rated; posterior orbital groove narrow or absent, without foveae; lateral ocelli closer to eye margin than to each other; vertex with a distinct longitudinal median sulcus originating behind central ocellus, crenulate or not; occipital margin raised by a small foveate carina; face with a distinct longitudinal median sulcus anterior to central ocellus; antennae inserted below ventral margin of eyes, closer to each other than to eye margin; subantennal grooves deeply excavated, usually with a dorsal carina. Pronotum short, not visible dorsally; mesoscutum with anterolateral carina along vertical portion, with median mesoscutal sulcus usually crenulate; large triangular axillae not meeting at inner angles, connected by a foveate groove, separated from scutellum by grooves that are usually crenulate; propodeum with a transverse row of small, shallow to deep foveae anteriorly, irregularly areolate-rugose in other parts; anterior thoracic spiracle small, entirely surrounded by pronotal cuticle; posterior margin of mesopleuron foveolate; fore metapleural margin nearly straight. Forewing with pterostigma short, only swelling at junction with r-rs; vein r-rs curved toward wing tip, not branching; distal segment of Rs, veins M+Cu, 1m-cu, Cu1, and distal part of A spectral or absent. Hind wing venation reduced to Sc+R, R1, and Rs, with Rs reaching middle of wing. Anterior and median legs slender; hind legs stout, with coxae large, femora swollen, and tibiae enlarged apically; protibia with one long curved spur, meso- and metatibiae with one and two short straight spurs, respectively. Abdomen longer than thorax in females, of variable length in males, with 7 nearly equal segments, spiracles not visible; small cerci spatulate, trilobed and with very fine setae at apex; male genitalia symmetrical, projecting downward or forward, with two simple, spinelike aedeagus valves between parameres; female ovipositor barely longer than half body length.

Comment.—The original diagnosis of Brues is modified according to observations of the new material and also to accommodate the three new species described herein. With specimens occurring from the upper Eocene to the upper Oligocene, *P. succinalis* is now known to have existed for at least 12 m.y. As a whole, the genus *Prodinapsis* persisted for at least 30 m.y. and was obviously widely distributed from western to Central Europe.

Key to Species of *Prodinapsis*

1. Female.....2
   Male.....4
2. Antennae thickened at apex, flagellomeres compact (Fig. 5, 6.2, 6.5, 7); posterior orbits without groove, with carina small to weak; forewing with apical segment of Rs absent (Fig. 1.2–1.5); body at most 2.00 mm in length (excluding ovipositor).....3
   Antennae filiform, flagellomeres elongate (Fig. 1.1, 1.4, 3.5, 4.4, 8); posterior orbits with a distinct groove and a sharp carina (Fig. 3.5, 4.4); forewing with apical segment of Rs spectral (Fig. 1.1); body 2.30 to 4.00 mm in length (excluding ovipositor) ....***P. succinalis*** Brues
3. Posterior orbital carina small (Fig. 6.2); forewing with basal segment of Cu1 present, spectral (Fig. 1.2); body 1.60 to 2.00 mm in length .....***P. minor*** Brues
   Posterior orbital carina very weak (Fig. 6.6); forewing with basal segment of Cu1 absent (Fig. 1.3); body 1.40 mm in length..... ..... ***P. pumilio*** n. sp.
4. Antennae not extending beyond apex of metasoma; forewing with apical segment of Cu1 present, spectral (Fig. 1.1, 1.2, 1.5).....5
   Antennae extending beyond apex of metasoma; forewing with apical segment of Cu1 absent (Fig. 1.4).....***P. janzeni*** n. sp.
5. Median mesoscutal sulcus and axillar grooves crenulate.....6
   Median mesoscutal sulcus and axillar grooves smooth (Fig. 10, 11.4) .....***P. oesiensis*** n. sp.
6. Forewing length low relative to head length (3.5<FWL/HL<5) ....***P. succinalis*** Brues
   Forewing length high relative to head length (FWL/HL>5)..... .....***P. minor*** Brues

PRODINAPSIS SUCCINALIS Brues, 1923

Figures 1.1, 2–4

Prodinapsis succinalis Brues, 1923, p. 32, fig. 1 (holotype male, in former Königsberg collection, presumed destroyed).

Prodinapsis succinalis Brues, 1933, p. 21, pl. 2,*6* (type female, in former Königsberg collection, presumed destroyed).

Type material.—Neotype male (designated herein; the sex was chosen in order to match as closely as possible to the original holotype, in this case a male), specimen KU-NHM-ENT B-113, in Baltic amber from Samland Peninsula, upper Eocene.

Other material examined.—Bitterfeld amber: specimen MfN-MB.I-5446, one female; MfN-MB.I-5440, one male; MfN-MB.I-5650, one male; MfN-MB.I 5651, one male; GZG-BST-26981a,b, two males. Baltic amber: specimen GZG-BST-6498, one male; JVC-248, one male (Weitschat & Wichard, 2002, pl. 67a); JVC-307, one female; KU-NHM-ENT B-123, B-136, B-138, B-139, B-140, five females; KU-NHM-ENT B-114, B-115, B-116a, B-116b, B-117, B-119, B-121, B-122, B-124, B-127, B-134, eleven males. Rovno amber: SIZK-K-7092a, one male. Possible additional material: specimen RMRS-Ip253/13614, one male missing dorsal part of head and mesosoma; and SIZK-UA-881, one male. Both preserved in Rovno amber.

Diagnosis.—Longitudinal median sulcus on vertex extending from median ocellus to occipital carina; vertex minutely punctured posteriorly to lateral ocelli in females (Fig. 4.5); posterior orbits with a narrow but distinct groove and a sharp carina (Fig. 2.1, 2.4, 3.5, 4.4); antennae long, filiform; flagellomeres very elongate in females, moderately elongate in males; face with deep median depression separated from subantennal grooves by a sharp longitudinal carina extending from clypeus to torulus (Fig. 2.2); subantennal grooves with a sharp dorsal carina (Fig. 3.5, 4.4); clypeus with anterior margin bilobed. Median mesoscutal sulcus and axillar grooves crenulate; axillae widely separated at inner angles by foveate groove (Fig. 3.6); propodeum in females with a longitudinal row of four large, rectangular foveae medially on dorsum. Forewing (Fig. 1.1) with apical segment of Rs and basal segment of Cu1 present, spectral; veins M+Cu and Cu1 aligned; basal section of M nearly equal in length to 1cu-a. Metasoma elongate, subcylindrical. Female ovipositor barely longer than half body length, male genitalia directed downward.

Description.—Female. Body minutely shagreened except posterior part of vertex minutely punctate and propodeum rugose; moderately to densely pubescent, with pale short setae, except antennae nearly bare. Measurements as given in Table 1.

Head. Eyes oval, one-third higher than long, with short dispersed setae; posterior orbits with narrow groove and sharp carina;

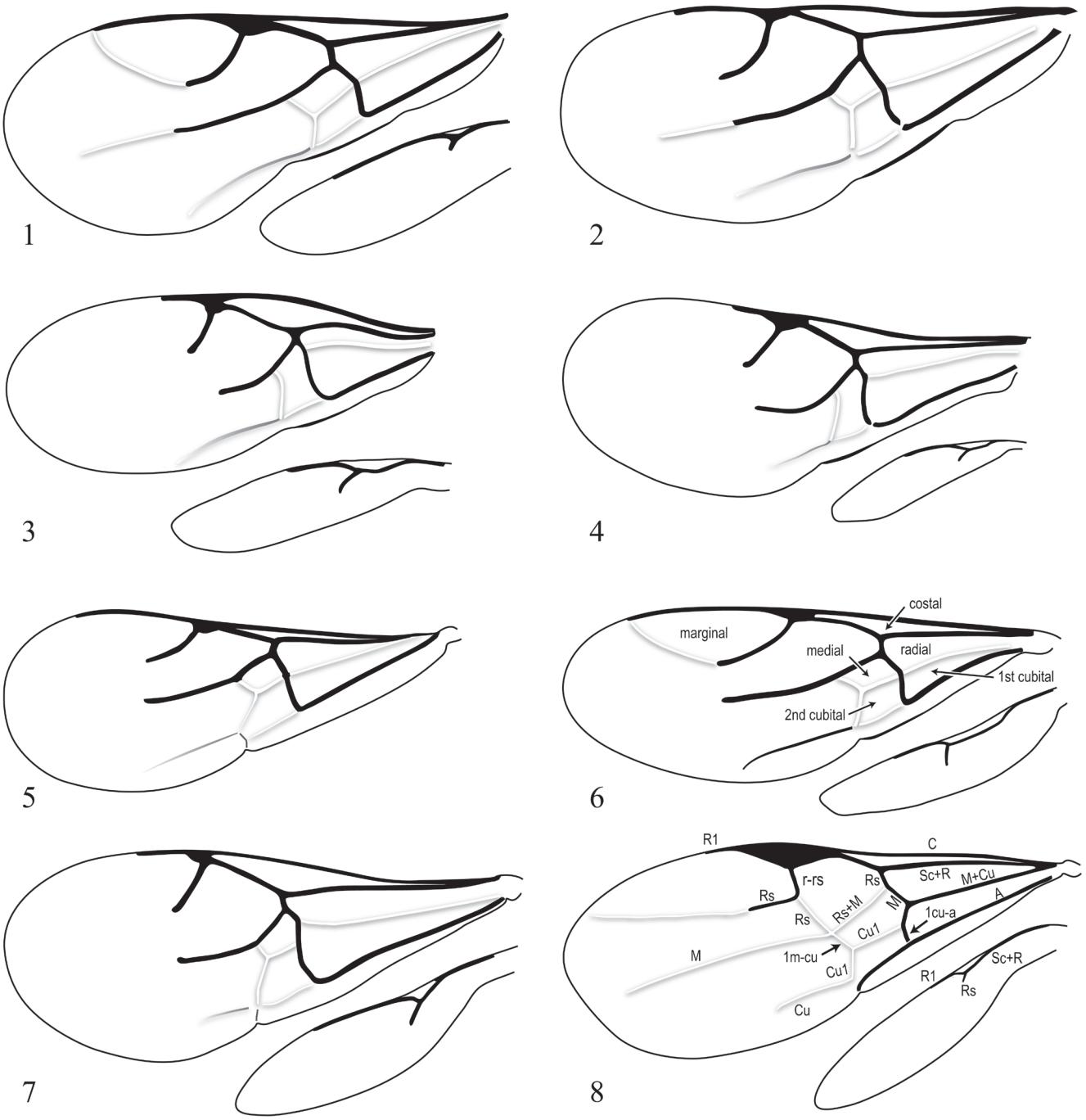

Figure 1. Variation in wing venational pattern of Cretodinapsini (wings not at same scale); *1*, *Prodinapsis succinalis*, MfN-MB.I-5446; *2*, *P. minor*, female, GZG-BST-6480; *3*, *P. pumilio* n. sp., female, SIZK-K-3258; *4*, *P. janzeni* n. sp., male, KU-NHM-ENT B-128; *5*, *P. oesiensis* n. sp., male, MNHN-PA-48; *6*, *Ukrainosa prolata* n. gen. and sp., female, SIZK-K-7046, with cells labeled; *7*, *Rubes bruesi* n. gen. and sp., female, KU-NHM-ENT B-129; *8*, *Cretodinapsis caucasica* Rasnitsyn (adapted from Rasnitsyn, 1977), with venational traits labeled.

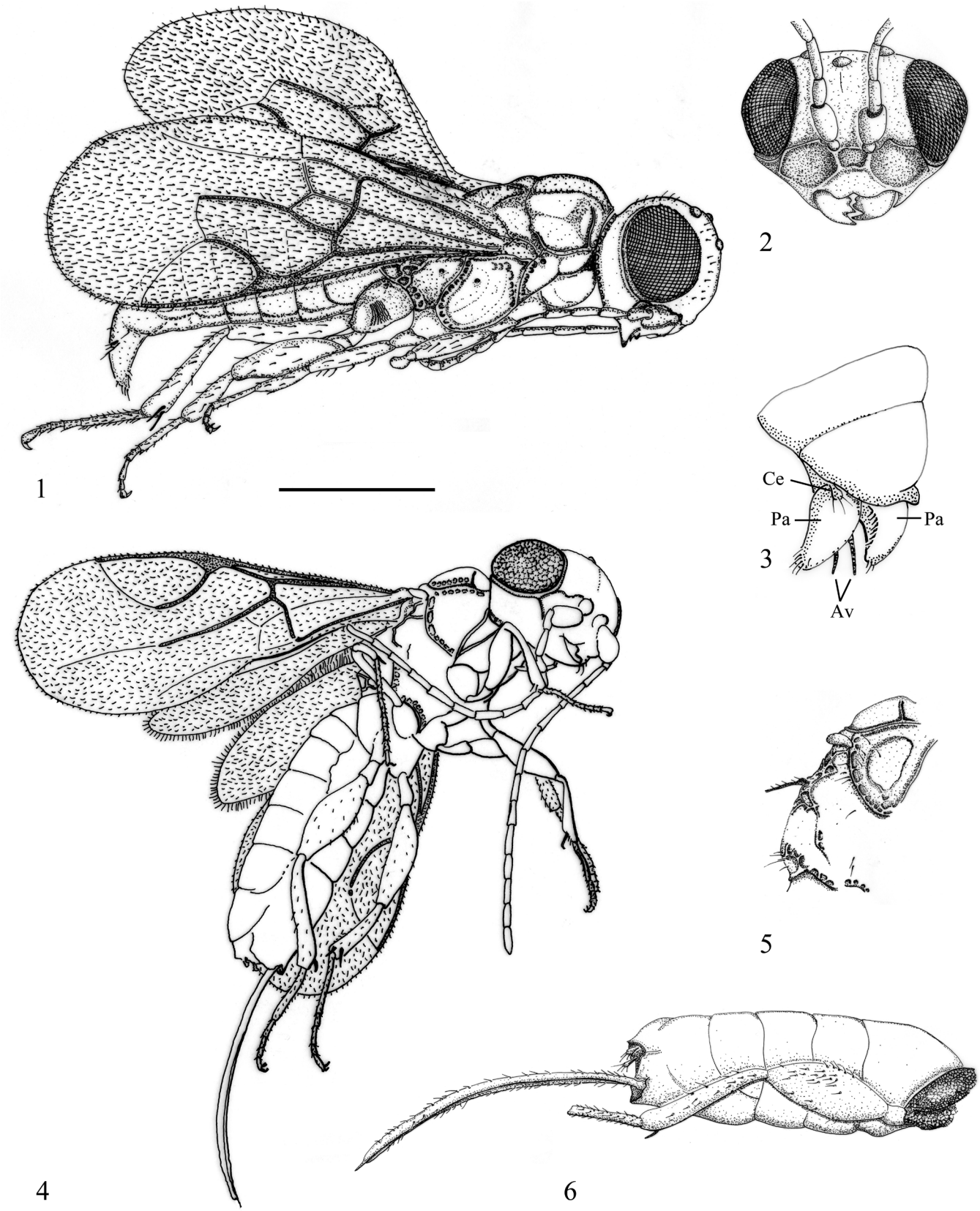

Figure 2. *Prodinapsis succinalis* Brues; *1*, male, habitus, MfN-MB.I-5440; *2*, head in frontal view, male, MfN-MB.I-5651; *3*, genitalia in laterodorsal view, male, KU-NHM-ENT B-115; *4–6*, female, MfN-MB.I-5446; *4,* habitus; *5*, mesosoma in lateral view; *6*, metasoma in lateral view (scale bars: *1*, *4–6* = 0.5 mm; *2–3* = 0.25 mm). See p. 3 for explanation of abbreviations.

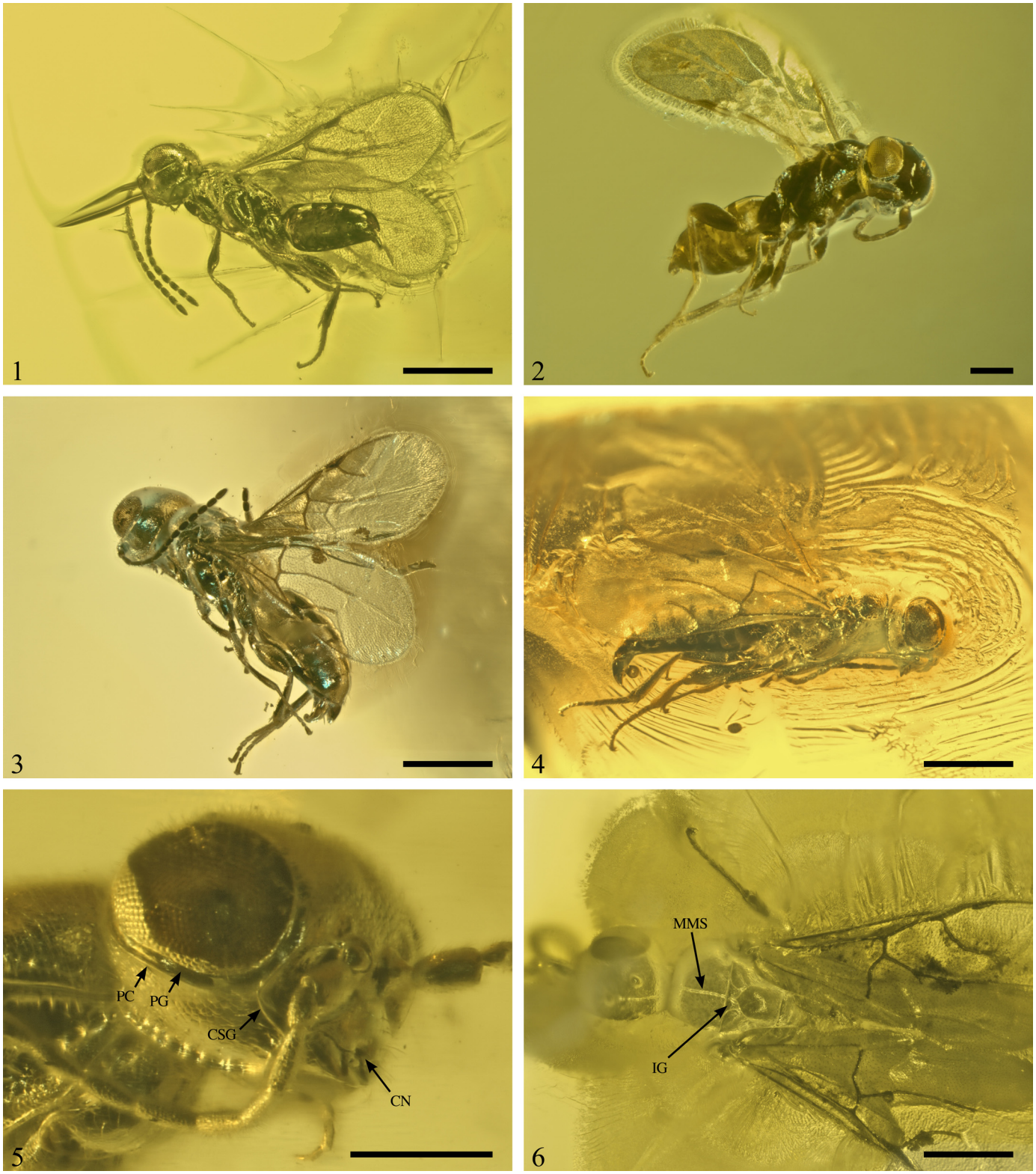

Figure 3. Various male representatives of *Prodinapsis succinalis* Brues; *1*, neotype, habitus, KU-NHM-ENT B-113; *2*, habitus, KU-NHM-ENT B-114; *3*, habitus, KU-NHM-ENT B-115; *4*, habitus, MfN-MB.I-5440; *5*, GZG-BST-26981, detail of head; *6*, KU-NHM-ENT B-124, details of head, mesosoma, and forewings in dorsal view (scale bars: *1–4, 5* = 0.25 mm; *6* = 0.5 mm). See p. 3 for explanation of abbreviations.

Table 1. Variation in sizes and structures as observed on studied specimens of Cretodinapsini (*Prodinapsis*, *Ukrainosa*, and *Rubes);* lengths are given in mm; symbols: √ = sparsely setose; √√ = conspicuously setose; x = absent; – = not visible or measurable. See p. 3 for explanation of abbreviations.

Specimen number	Sex	BL	AL/BL	ML/BL	FWL	FWL/HL	VMP	PGW	FWRs	FWCu1	HL/HW	OL/BL
***P. succinalis* Brues**												
MfN-MB.I-5446	F	2.20	0.66	0.50	1.60	4.00	√	0.018	spectral	spectral	–	0.46
KU-NHM-ENT-B-123	F	2.62	0.80	0.43	2.10		√	0.019	spectral	spectral	–	0.48
KU-NHM-ENT-B-136	F	3.76	0.69	0.50	2.62	4.22	√	0.040	spectral	spectral	0.62	0.41
KU-NHM-ENT-B-138	F	2.50	0.64	0.48	1.60	3.48	√	0.020	spectral	spectral	0.72	0.43
KU-NHM-ENT-B-139	F	2.80	0.66	0.45	2.00		√√	0.025	spectral	spectral	–	0.57
KU-NHM-ENT-B-140	F	4.00	–	0.51	3.12		√√	–	spectral	spectral	–	0.56
JVC-307	F	2.44	0.82	0.41	2.00	3.84	√	0.038	spectral	spectral	–	0.41
MfN-MB.I-5440	M	2.00	–	0.48	1.56	4.33	√	0.018	spectral	spectral	–	
MfN-MB.I-5650	M	2.75	0.62	0.45	2.00	4.00	√√	0.030	spectral	spectral	0.63	
MfN-MB.I-5651	M	2.25	0.98	0.39	1.80	3.91	√	0.025	nebulous	nebulous	0.64	
GZG-BST-26981a	M	2.20	0.68	0.36	1.85	3.85	√√	0.025	spectral	spectral	–	
GZG-BST-26981b	M	–	–	–	–	–	√√	–	spectral	spectral	–	
GZG-BST-6498	M	1.45	0.62	0.41	1.30	4.26	√√	–	spectral	spectral	–	
SIZK-UA-881	M	1.60	0.75	0.44	1.40	–	–	–	x	–	–	
SIZK-K-7092a	M	1.82	0.69	0.48	1.64	4.37	√	0.015	spectral	spectral	0.64	
RMRS-Ip253/13614	M	2.00	–	–	–	–	–	–	spectral	spectral	–	
JVC-248	M	1.90	0.61	0.42	1.60	4.16	√√	0.019	spectral	nebulous	–	
KU-NHM-ENT-B-113	M	1.40	0.61	0.39	1.30	4.26	√√	0.015	spectral	spectral	–	
KU-NHM-ENT-B-114	M	1.72	–	0.40	1.40	4.11	√	0.025	spectral	spectral	0.65	
KU-NHM-ENT-B-115	M	1.72	0.55	0.44	1.30	3.25	√	0.025	spectral	spectral	0.69	
KU-NHM-ENT-B-116a	M	1.60	0.58	0.43	1.20	3.50	√√	0.018	spectral	spectral	–	
KU-NHM-ENT-B-116b	M	1.60	0.56	0.41	1.20	3.50	√√	0.018	spectral	spectral	–	
KU-NHM-ENT-B-117	M	1.95	0.56	0.48	–	–	√√	–	spectral	spectral	–	
KU-NHM-ENT-B-119	M	2.15	0.67	0.44	1.68	4.20	√√	0.031	spectral	spectral	0.67	
KU-NHM-ENT-B-121	M	2.05	0.78	0.39	1.88	4.27	√√	–	spectral	spectral	0.69	
KU-NHM-ENT-B-122	M	2.40	0.69	0.42	1.70	3.50	√	0.025	spectral	spectral	0.69	
KU-NHM-ENT-B-124	M	3.20	0.51	0.50	2.00	3.70	√√	0.012	spectral	spectral	0.68	
KU-NHM-ENT-B-127	M	3.12	0.66	0.41	2.20	3.66	–	–	nebulous	spectral	0.75	
KU-NHM-ENT-B-134	M	1.85	0.61	0.48	1.60	4.70	√√	0.019	spectral	spectral	0.63	
***P. minor* Brues**												
GZG-BST-6480	F	2.00	0.45	0.45	1.72	5.05	x	x	x	spectral	0.43	
JVC-282	M	2.45	–	0.46	1.80	5.29	√√	0.025	spectral	nebulous	0.52	
JVC-294	M	2.00	0.70	0.50	1.60	5.00	–	–	spectral	spectral	–	
KU-NHM-ENT-B-111	M	1.80	0.64	0.44	1.65	5.33	√√	0.021	spectral	spectral	0.56	
***P. pumilio* Perrichot & Perkovski n. sp.**												
SIZK-K-3258	F	1.38	0.65	0.52	0.95	3.45	x	x	x	x	0.50	0.35
***P. janzeni* Perrichot n. sp.**												
KU-NHM-ENT-B-128	M	1.40	1.11	0.38	1.28	4.57	√	x	x	x	0.52	
KU-NHM-ENT-B-126	M	2.00	0.95	0.38	1.40	2.80	√	x	x	x	0.71	
KU-NHM-ENT-B-133	M	1.00	1.05	0.42	1.00	3.84	x	x	x	x	0.59	
SIZK-K-27	M	1.70	1.03	0.41	1.60	4.00	x	x	x	x	0.57	
***P. oesiensis* Perrichot n. sp.**												
MNHN-PA-48	M	1.85	0.68	0.49	1.30	5.00	√	x	x	spectral	0.50	
***Ukrainosa prolata* Perrichot & Perkovsky n. sp.**												
SIZK-K-7046	F	2.80	0.77	0.50	2.10	3.68	√√	x	spectral	spectral	0.55	1.00
***Rubes bruesi* Perrichot n. sp.**												
GZG-BST-3132	F	1.75	0.69	0.34	1.40	3.50	x	x	x	spectral	0.57	0.42
KU-NHM-ENT-B-112	F	1.80	0.69	0.44	1.44	3.42	√	x	x	spectral	0.64	0.36
KU-NHM-ENT-B-118	F	2.25	0.64	0.51	1.60	4.00	x	x	x	spectral	0.48	0.29
KU-NHM-ENT-B-120	F	1.40	0.61	0.36	1.12	2.80	x	x	x	spectral	0.63	0.57
KU-NHM-ENT-B-125	F	1.52	0.72	0.43	1.20	3.15	x	x	x	spectral	0.68	0.36
KU-NHM-ENT-B-129	F	2.25	0.64	0.38	1.68	3.50	√	x	x	spectral	0.60	0.28
KU-NHM-ENT-B-135	F	2.30	0.61	0.43	1.70	3.36	√	x	x	spectral	0.57	0.22

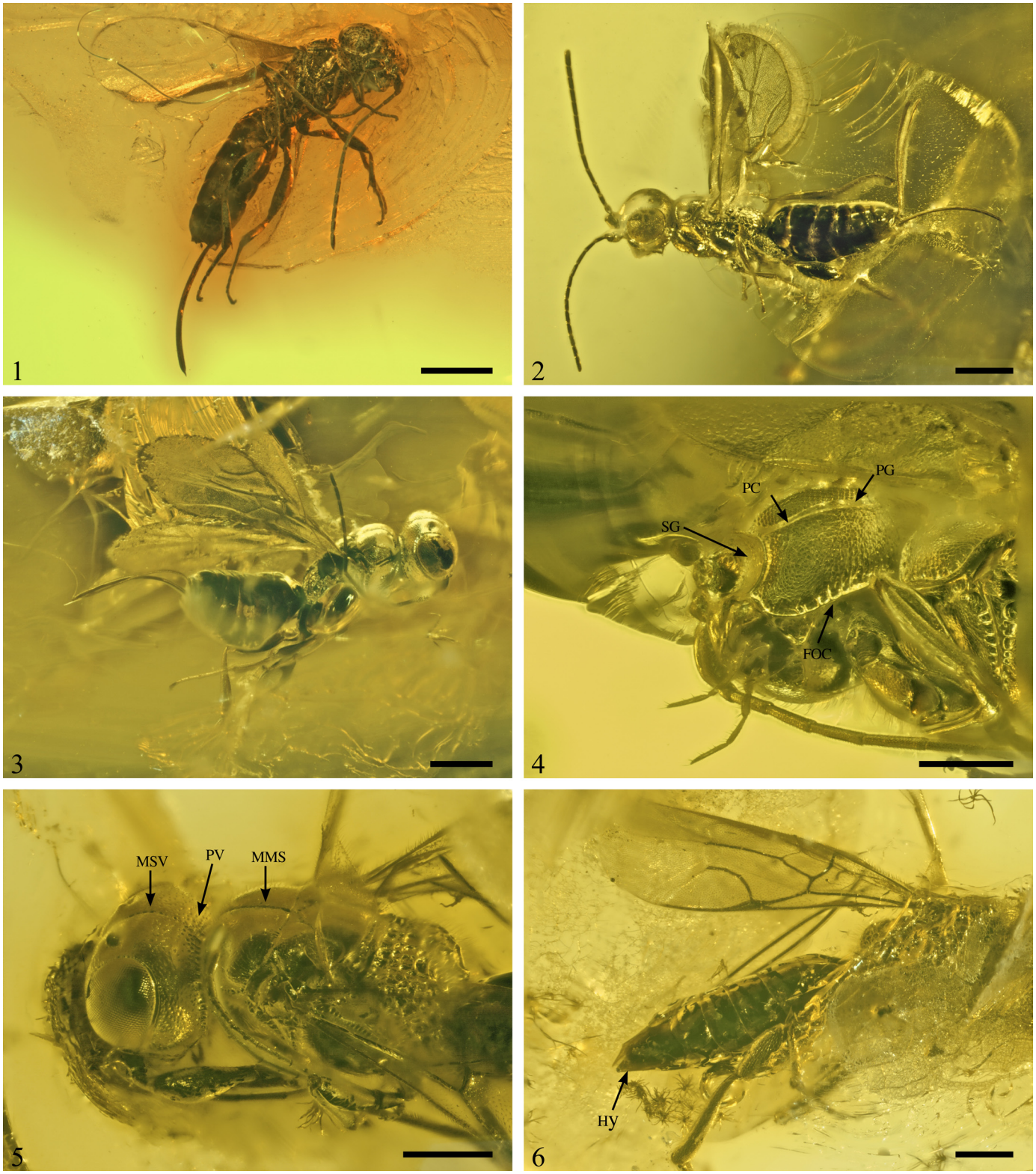

Figure 4. Various female representatives of *Prodinapsis succinalis* Brues; *1*, habitus, MfN-MB.I-5446; *2*, habitus, KU-NHM-ENT B-138; *3*, habitus, JVC-307; *4*, habitus, KU-NHM-ENT B-123, detail of head in lateral view; *5*, head and mesosoma in laterodorsal view, KU-NHM-ENT B-140; *6*, forewing and metasoma in lateral view, KU-NHM-ENT B-140 (scale bars: *1–3, 5–6* = 0.5 mm; *4* = 0.25 mm). See p. 3 for explanation of abbreviations.

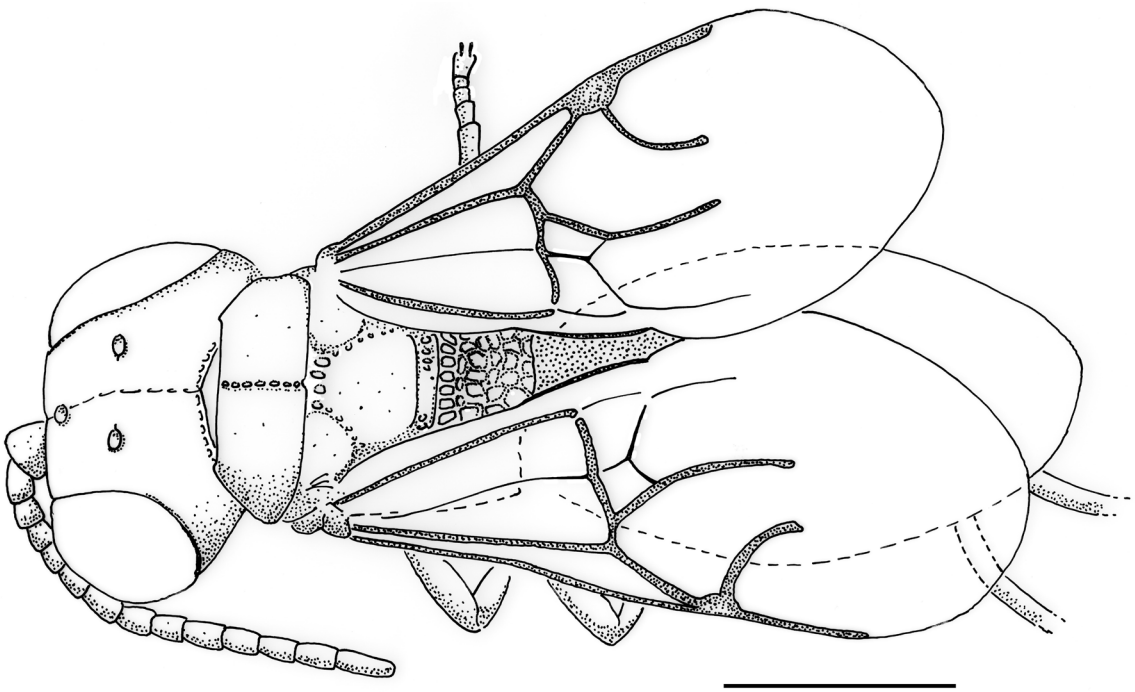

Figure 5. *Prodinapsis minor* Brues, habitus of female neotype, GZG-BST-6480, Eocene Baltic amber (scale bar: 0.5 mm).

small punctures posteriorly on vertex gradually enlarging toward occipital margin; antennae more than two-thirds body length, not extending beyond apex of metasoma, inserted at a distance of clypeus; scape about two-thirds as broad as long, more than twice as long as pedicel; pedicel scarcely twice as long as broad; flagellomeres I–IV subequal in length, about six times as long as broad, V–VIII and apical one about five times as long as broad, IX–XI about three times as long as broad; mandibles small, with three teeth increasing in size from base to apex.

Mesosoma. Mesoscutum about twice as broad as long; propodeum with small, irregular areolae on each side of the median longitudinal foveae; pleural margins foveolate.

Wings. Hyaline, without infumate banding pattern. Forewing broadly rounded at apex, scarcely extending beyond metasoma; vein R1 long; r-rs with apex nearly aligned with that of tubular segment of M; apical segment of Rs spectral, reaching wing margin; M+Cu, Cu1, 1m-cu, and A distally of 1cu-a spectral, Cu nebulous to spectral, almost reaching wing margin. Hind wing venation reduced to Sc+R, R1, and Rs, with Rs reaching middle of wing.

Legs. Metacoxa with anterodorsal part rugose, medial part often with a strigate patch laterally (also in males, see Fig. 2.1); metatibial setae prone, metabasitarsomere with a preening brush of stiff setae along inner margin, its length subequal or slightly longer than combined length of tarsomeres II–V; pretarsal claws curved, simple, as long as arolium.

Metasoma. Elongate, about half body length; cerci bearing six to ten very fine setae; hypopygium moderately large, extending backward for a short distance; ovipositor exserted for less than half body length.

Comment.—Males are very similar but usually smaller, and they differ by the following characters: vertex not punctate posteriorly; antennae with flagellomeres distinctly setose, shorter (I–IV about twice as long as broad, V–IX about two-thirds as broad as long, apical one the longest, more than twice as long as broad); propodeum without median line of large foveae. The genital appendages are rather large, with parameres bearing a fringe of fine setae at apex and along inner margin (Fig. 2.3).

PRODINAPSIS MINOR Brues, 1933

Figures 1.2, 5, 6.1–6.4

Prodinapsis minor Brues, 1933, p. 23, pl. 3,*9* (holotype, female, in former Königsberg collection, without reference number provided and presumed destroyed).

Type material.—Neotype (designated herein) female, specimen GZG-BST-6480, in Baltic amber from Samland Peninsula, upper Eocene, with old collection number Z2853 engraved on the amber piece.

Other material examined.—Specimen KU-NHM-ENT B-111, one male; specimen JVC-282, one male; JVC-294, one male; in Eocene Baltic amber.

Diagnosis.—Very similar to *P. succinalis* but female without postorbital groove, with only a small carina; antennae much shorter, less than half body length, with flagellum compact and noticeably thickened toward tip; toruli in contact with clypeus; face without depression between subantennal grooves; a small carina dorsally of subantennal grooves; clypeus with anterior margin not bilobed in female, convex; metasoma cylindrical, moderately elongate.

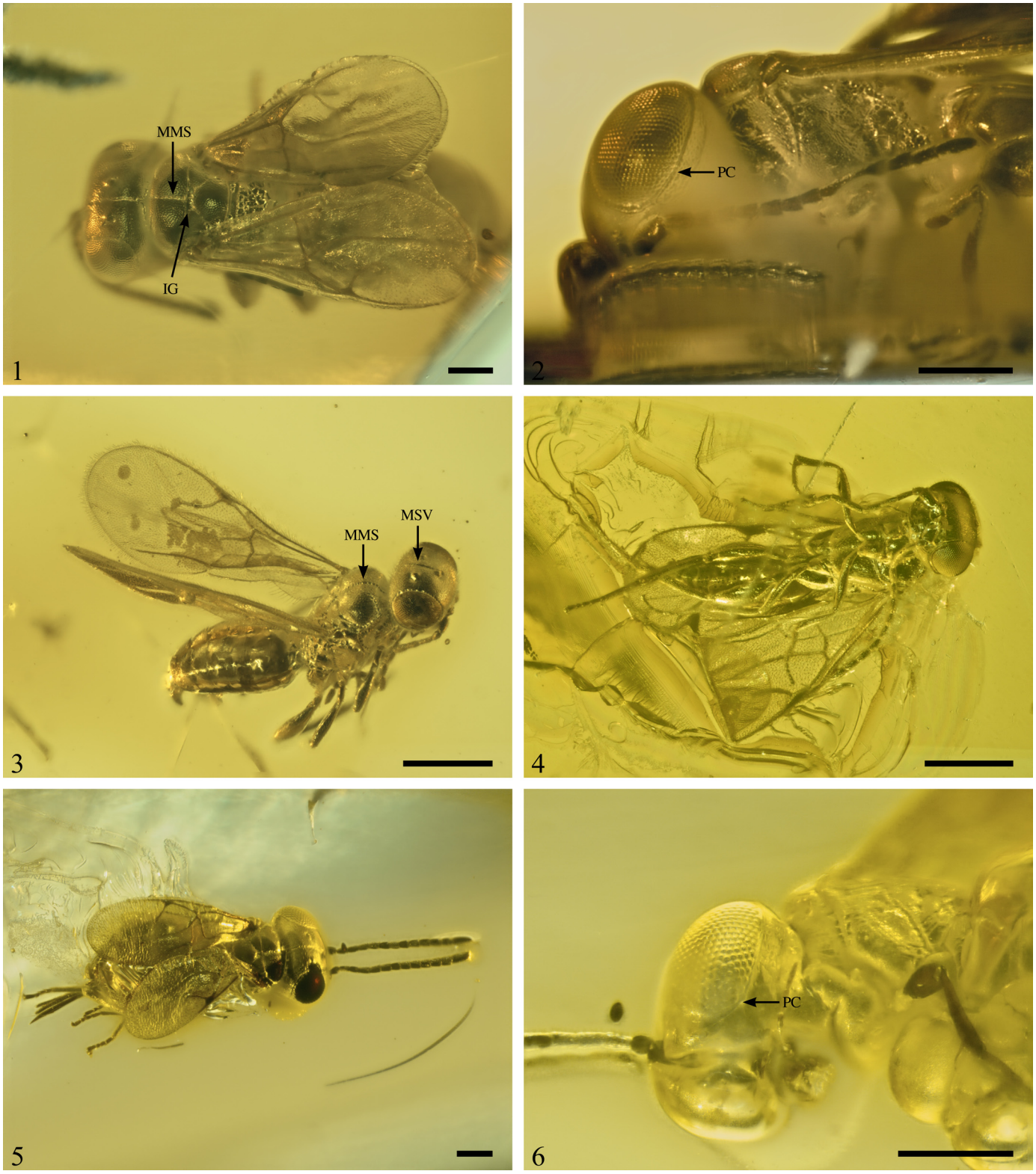

Figure 6. *1–4*, *Prodinapsis minor* Brues, Eocene Baltic amber; *1–2*, neotype, female, GZG-BST-6480; *3*, male, JVC-282; *4*, male, KU-NHM-ENT-B-111; *5–6*, *Prodinapsis pumilio* n. sp., holotype, female, SIZK-K-3258, Eocene Rovno amber, Ukraine (scale bars: *1–2, 5–6* = 0.25 mm; *3–4* = 0.5 mm). See p. 3 for explanation of abbreviations.

Description.—Female. Body minutely shagreened except propodeum, entirely bare; ventral and right lateral views mostly obscured by milky coat. Measurements as given in Table 1.

Head. Eyes oval, one-third higher than long, bare; posterior orbit of eyes raised by a weak carina, without groove (Fig. 6.2); well-impressed median line on vertex extending from median ocellus to occipital carina. Antennae inserted close to each other just above clypeus; scape globular, excavated at apex for reception of pedicel, about twice as long as pedicel; flagellomeres compact, subcylindrical (Fig. 5), nearly equal in length to pedicel; FI–FVII slightly longer than thick, FVIII–FXI scarcely longer than thick, FXII the longest, about twice as long as thick; mandibles small, with three teeth, other mouthparts hidden by milky occlusion.

Mesosoma (Fig. 5, 6.1). Median mesoscutal sulcus and inner axillar grooves crenulate; axillae not meeting at inner angle, separated by four shallow foveae; metanotum not foveate medially; propodeum minutely areolate-rugose; mesopleuron foveolate along anterior, dorsal, and posterior margins.

Wings (Fig. 1.2). Membrane hyaline, without infumate banding pattern. Forewing not extending beyond apex of metasoma; vein R1 moderately long; apical segment of Rs absent; veins M+Cu, Cu1, 1m-cu, and distal part of A spectral; basal section of M nearly equal to 1cu-a; M+Cu and Cu1 aligned; Cu nebulous, almost reaching wing margin. Hind wing vein Rs barely approaching middle of wing.

Legs. Protibia without visible apical stout spines; metacoxa with anterodorsal surface conspicuously rugose; length of metabasitarsomere subequal to combined length of tarsomeres II–V; tarsomeres V of all legs with two median stiff setae apically; pretarsal claws curved, simple, as long as arolium.

Metasoma. Short, less than half body length; ovipositor only partly preserved.

Comment.—Brues (1933) mentioned that he could not find any rationale for distinguishing between males of *P. succinalis* and *P. minor*. Indeed, during the present study, and despite a careful morphometric comparison of 25 specimens (Table 1), I failed to find features that would allow the confident distinction of the two species. No male has antennae with flagellomeres compact and thickened toward apex, nor posterior orbits with groove absent and carina reduced, as in females of *P. minor*. Three specimens are tentatively assigned herein to *P. minor* on the basis of the forewing length (FWL) relative to the head length (HL), the only apparent morphometric character that allows the discrimination of two groups and matches that of the females (see Table 1): a *succinalis*-group with 3.5<FWL/HL<5; and a *minor*-group with FWL/HL≥5.

PRODINAPSIS PUMILIO
Perrichot & Perkovsky, new species

Figures 1.3, 6.5, 6.6, 7

Type material.—Holotype female, specimen SIZK-K-3258, in upper Eocene Rovno amber.

Type locality.—Klesov, Rovno region, Ukraine.

Etymology.—From the Latin *pumilio* meaning dwarf, or pygmy, in reference to the very small size of the species.

Diagnosis.—Antennae with flagellum broadened toward tip; posterior orbits without groove, with a very weak carina diverging from eye posteroventrally (Fig. 6.6, 7.2); longitudinal median sulcus on vertex finely impressed. Mesoscutum very short (Fig. 7.1); mesoscutal groove and inner axillar grooves finely crenulate; axillae scarcely meeting at inner angles; metanotum not foveate medially; propodeum with a transverse row of foveae along anterior margin, remaining part irregularly areolate-rugose. Forewing extending only slightly beyond metasoma (Fig. 7.1); apical segment of Rs absent; basal section of M very short, branching from M+Cu proximad to Rs+M; basal segment of Cu1 absent (Fig. 1.3). Metasoma longer than mesosoma; ovipositor short.

Description.—Female. Body minutely shagreened except propodeum; mostly bare, in ventral view largely hidden by bubbles and milky coat. Measurements as given in Table 1.

Head. Eyes oval, higher than long, bare; longitudinal median sulcus on vertex extending from median ocellus to occipital margin. Antennae two-thirds body length, with flagellum gradually thickened toward tip; pedicel the shortest segment, less than twice as long as thick; FI–FIV subequal in length, at least twice as long as thick; FV–FXI shorter, less than twice as long as thick; FXII the longest. Toruli, face, and clypeus hidden by air bubble and milky occlusion; mandible small; maxillary palps 5-segmented.

Mesosoma. Mesoscutum three times wider than long, with weak lateral carina along vertical anterior portion; axillae meeting at inner angles anteriorly to axillar grooves for a very short distance; metanotum not foveate medially.

Wings. No visible infumate pattern. Forewing with pterostigma very short; vein R1 short, not extending beyond apices of r-rs and M; 1m-cu, distal segment of Cu1, and A distally of 1cu-a spectral; Cu nebulous for a short distance. Hind wing vein Rs reaching middle of wing (Fig. 1.3).

Legs. Protibia with short apical stout spines; metabasitarsomere as long as combined length of following tarsomeres, with a preening brush of very short, stiff setae along inner margin.

Metasoma. Moderately elongate oval, dilated dorsoventrally by bubbles; about half body length; segments I–IV subequal in length, V–VII decreasing in length; ovipositor exserted for a short distance, about one-third body length (Fig. 7.2).

Comment.—Brues (1933) distinguished *P. succinalis* from *P. minor* based, in females, on larger body size and antennae and a sharp posterior orbital carina separated from compound eyes by a distinct groove. This new species is closely similar to *P. minor* in the proportions of antennae relative to the body and the weak ocular carina. It is less than 1.40 mm in length, however, while females of *P. minor* range between 1.60 and 2.00 mm (2.30 to 4.00 mm for *P. succinalis*). It differs from both species by its forewing venation with the basal segment of M being very short and the

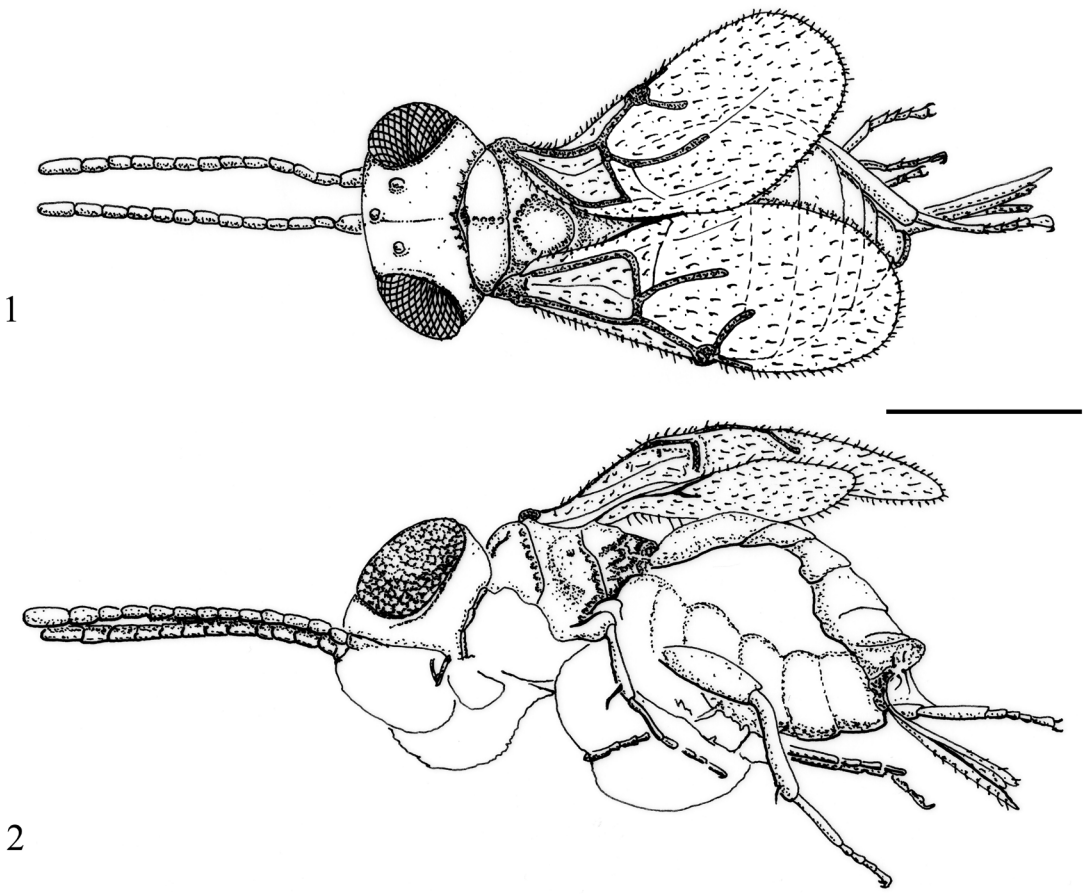

Figure 7. *Prodinapsis pumilio* n. sp., holotype, female, SIZK-K-3258, Eocene Rovno amber, Ukraine; habitus in dorsal (*1*) and lateral (*2*) views (scale bar: 0.5 mm).

basal part of vein Cu1 being absent and by the axillae meeting at inner angles.

PRODINAPSIS JANZENI
Perrichot, new species
Figures 1.4, 8, 9

Type material.—Holotype male specimen KU-NHM-ENT B-128; paratypes male specimens KU-NHM-ENT B-126, B-133, in upper Eocene Baltic amber from Samland Peninsula; paratype male specimen SIZK-K-27, in upper Eocene Rovno amber from Klesov, Ukraine.

Etymology.—The species name is in honor of Jens-Wilhelm Janzen, former owner of the Baltic amber type material.

Diagnosis.—Posterior orbits of eyes without groove, only raised by a small carina; inner orbits finely crenulate; antennae as long as or longer than body, with flagellum filiform; subantennal grooves with a faint dorsal carina, separated by shallow depression medially on face; clypeus with anterior margin bilobed; forewing extending beyond apex of metasoma, with apical segment of Rs and basal segment of Cu1 absent; basal section of M very short, branching from spectral M+Cu proximad to fork of Rs and Rs+M; metasoma compact; genitalia small, projected downward.

Description.—Male. Body minutely shagreened except pronotum; pubescence barely visible, on frons; vertex, eyes, and mesosoma with scattered, very short pale setae. Measurements as given in Table 1.

Head. Eyes oval, about one-third higher than long; posterior orbits raised by small carina; inner orbits irregularly and finely crenulate (Fig. 8); longitudinal median sulcus on vertex distinct, extending from median ocellus to occipital margin; antennae extending slightly beyond apex of metasoma, filiform (Fig. 8, 9.1–9.6); scape and pedicel less than twice as long as broad; pedicel the shortest segment; flagellomeres cylindrical, scarcely one-third as broad as long, densely covered by short setae, with multiporous plates elliptical, prominent; FIV and FXII the longest, nearly four times as long as broad; other flagellomeres subequal in length; toruli each connected to clypeus by a short, sharp carina, forming a shallow median depression above clypeus; subantennal grooves deep, with a faint dorsal carina; clypeus about one-third wider than long; mandibles with three small teeth increasing in size from base to apex; maxillary palps with segments greatly increasing in length from base to apex.

Mesosoma. Mesoscutum short, 0.4 times as long as wide; median mesoscutal sulcus and inner axillar grooves crenulate; triangular axillae separated at inner angles by small foveae; propodeum areolate-rugose (Fig. 8, 9.1).

Wings (Fig. 1.4). Hyaline, without infumate banding pattern. Forewing broadly rounded at apex; pterostigma reduced; R1 short;

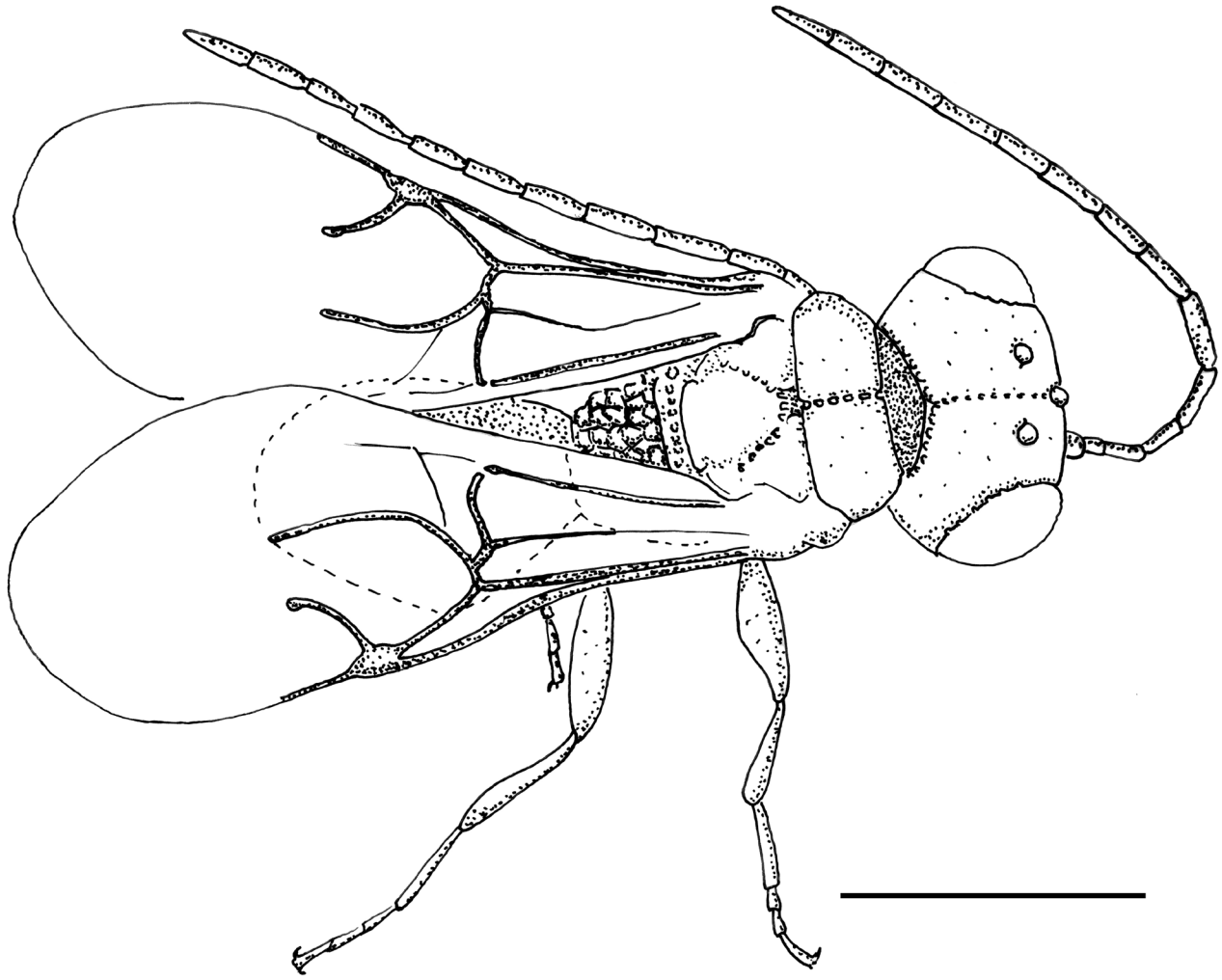

Figure 8. *Prodinapsis janzeni* n. sp., holotype, male, KU-NHM-ENT B-128, Eocene Baltic amber; habitus in dorsal view (scale bar: 0.5 mm).

vein r-rs not conspicuously curved toward wing tip, with apex nearly aligned with that of tubular segment of M; M+Cu, 1m-cu, apical segment of Cu1, and A distally of 1cu-a spectral; Cu nebulous for a short distance. Hind wing with vein Rs straight, reaching middle of wing.

Legs. Protibia without apical stout spines; anterodorsal surface of metacoxa minutely rugose; metabasitarsomere subequal in length to combined length of tarsomeres II–V; metabasitarsomere with a preening brush of stiff setae along inner margin; pretarsal claws simple, curved, as long as arolium.

Metasoma. Compact, less than half body length, nearly as broad as long; genitalia with small parameres and spinelike valves of aedegus projecting downward (Fig. 9.3).

Comment.—It is observed in *P. succinalis* that most males are smaller than females (Table 1). Therefore, the smaller size of the present specimens, together with a small posterior ocular carina, could indicate males of *P. minor* or even *P. pumilio*. But they differ from females of *P. minor* by the forewing with basal section of M being very short and a single medial cell, and from both species by very long antennae. They are thus attributed to a new, distinct species.

PRODINAPSIS OESIENSIS
Perrichot, new species

Figures 1.5, 10, 11.1–11.4

Type material.—Holotype male, specimen MNHN-PA-48, in lower Eocene (Ypresian) French amber.

Type locality.—Farm Le Quesnoy, Chevrière, near Creil, Oise department, France.

Stratigraphic horizon.—Lowermost Eocene, Ypresian, ca. 53 Ma, level MP7 of the mammal fauna of Dormaal (Nel & others, 1999).

Etymology.—The specific epithet refers to Oesia, the Latin name of the Oise river, which gave its name to the French department from where the fossil specimen originates.

Diagnosis.—Easily distinguished from other species by the absence of median depression on face, the clypeus not being bilobed, the absence of crenulation on median mesoscutal sulcus and inner axillar grooves, a bifoveate groove crossed by small longitudinal ribs between axillae, the anterior margin of propodeum with a transversal row of deep foveae, and the male genitalia with large parameres strongly deflected forward.

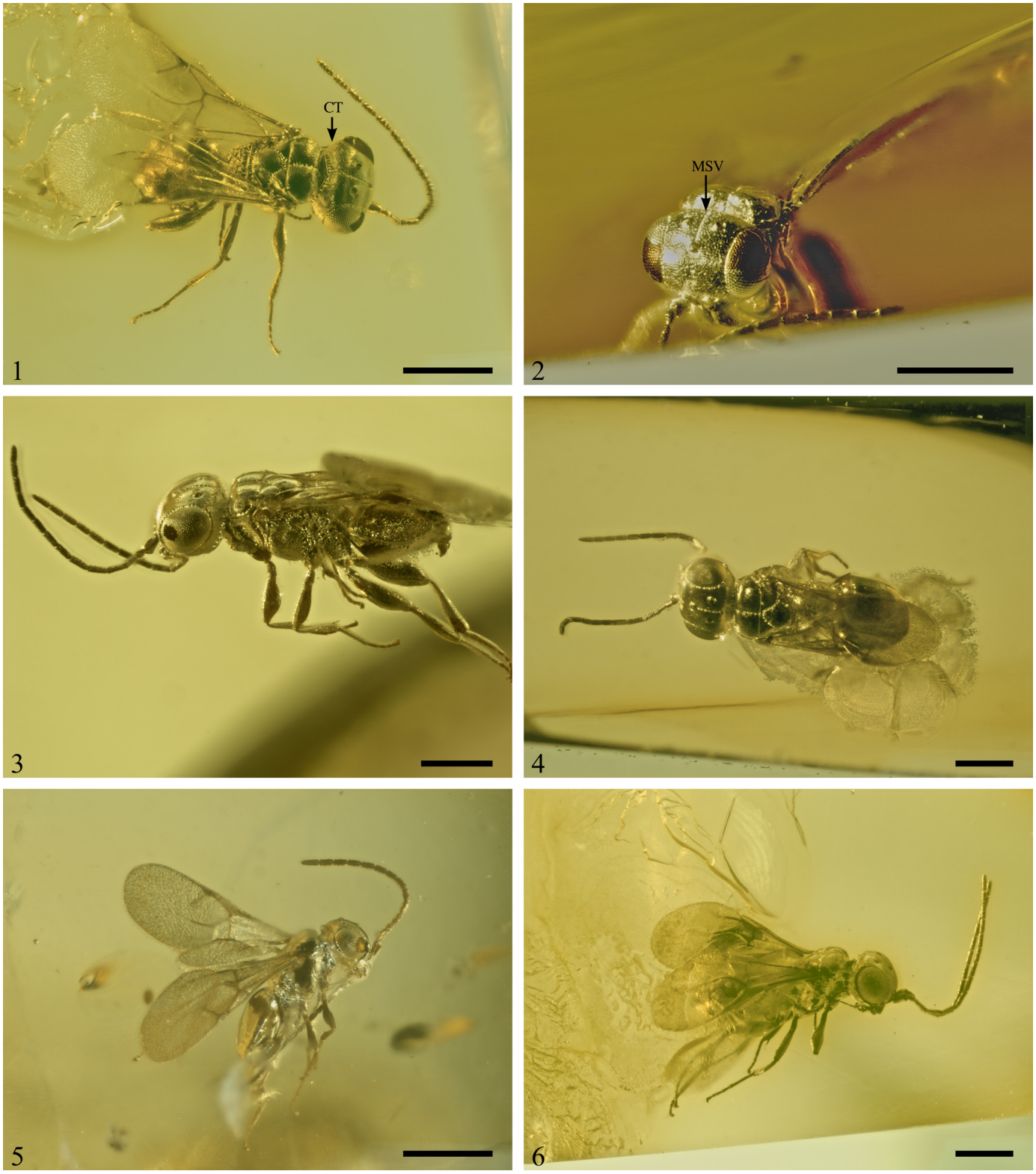

Figure 9. Various male representatives of *Prodinapsis janzeni* n. sp., Eocene Baltic and Rovno amber; *1–2*, holotype, KU-NHM-ENT B-128, habitus in dorsal view (*1*) and head in frontal view (*2*); *3–4*, paratype, KU-NHM-ENT B-126, habitus in lateral (*3*) and dorsal view (*4*); *5*, paratype, KU-NHM-ENT B-133, habitus in lateral view; *6*, paratype, SIZK-K-27, habitus in lateral view (scale bars: 0.5 mm). See p. 3 for explanation of abbreviations.

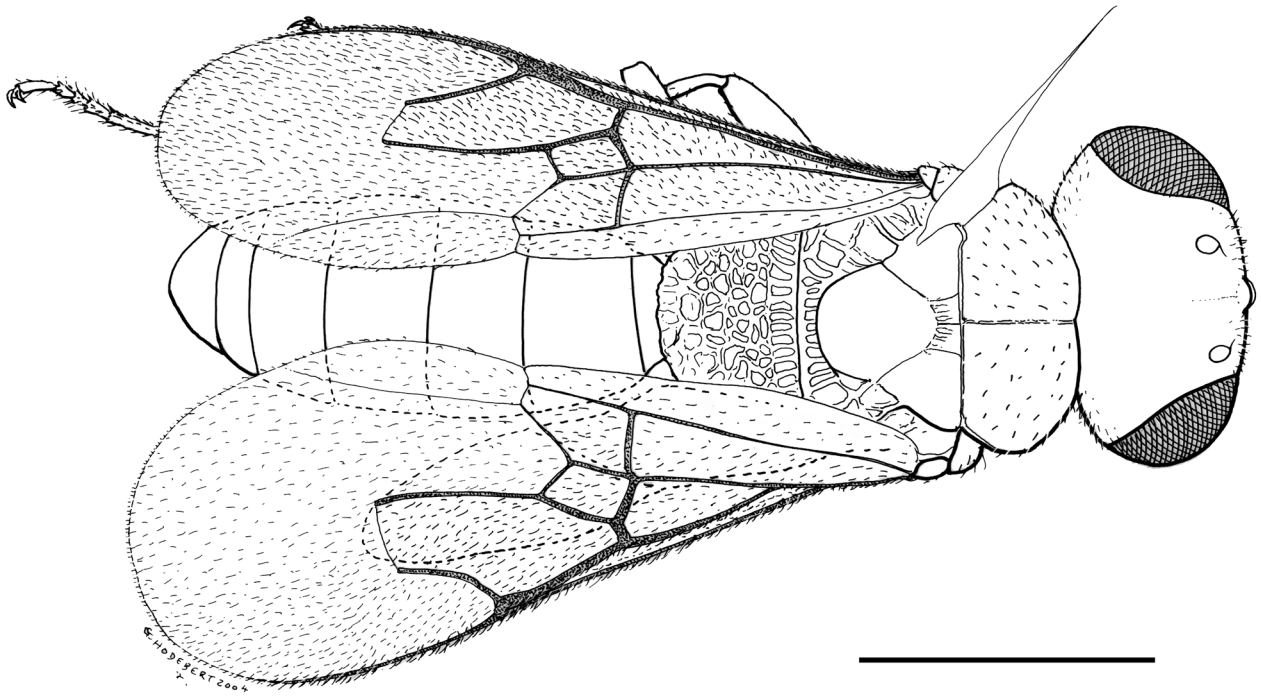

Figure 10. *Prodinapsis oesiensis* n. sp., habitus, female holotype, MNHN-PA-48, Eocene amber, Oise, France (scale bar: 0.5 mm). Drawing courtesy of G. Hodebert, MNHN.

Description.—Male. Body minutely shagreened except pronotum and propodeum; head and mesoscutum covered by sparsely scattered short setae, antennae and legs densely covered by short setae; metasoma bare. Measurements as given in Table 1.

Head. Eyes oval, higher than long, apparently bare; posterior orbits raised by a weak carina, without groove; vertex with a short, only finely impressed longitudinal median sulcus extending from median ocellus slightly posterior to lateral ocelli (Fig. 10, 11.3, 11.4); antennae filiform, about two-thirds body length; scape globular, about twice as long as pedicel (Fig. 11.3); flagellomeres cylindrical, with short setae and elliptical multiporous plates, FII–FIV and FXII twice as long as thick, subequal to scape length, FI and FV–FXI nearly equal in length, less than twice as long as thick; face without deep median depression between subantennal grooves; only a weak dorsal carina visible dorsally of subantennal grooves; clypeus with anterior margin convex, bearing a fringe of erect setae; mouthparts not visible, hidden by milky occlusion.

Mesosoma (Fig. 10, 11.4). Mesoscutum nearly half as long as wide; median mesoscutal sulcus and inner axillar grooves not crenulate; inner angles of axillae separated by a large bifoveate groove crossed by small longitudinal ribs; metanotum in dorsal view entirely foveate, with posterior edge straight; propodeum with a transverse row of deep rectangular foveae along anterior margin, otherwise densely areolate-rugose, with scattered stiff setae on declivity.

Wings (Fig. 1.5). No visible infumate pattern. Forewing broadly rounded at apex, not extending beyond metasoma; vein R1 long; r-rs distinctly curved toward wing tip, apical segment of Rs absent; apices of veins Rs and M nearly aligned; veins M+Cu, Cu1, 1m-cu, and distal part of A spectral; basal section of M long, subequal to 1cu-a; M+Cu and Cu1 aligned. Hind wing with three visible hamuli.

Legs. Protibia with a fringe of apical stout spines and long curved spur; meso- and metatibial spurs short and straight; metacoxa large, minutely rugose; metatibia as long as combined length of tarsomeres, covered by prone setae; metabasitarsomere with a preening brush of short, stiff setae along inner margin; pretarsal claws simple, curved.

Metasoma. Elongate, about half body length, subcylindrical; genitalia with large parameres and spinelike valves of aedegus strongly curved forward (Fig. 11.2); inner margin of parameres with short setae.

Comment.—The new fossil is identical to all *Prodinapsis* species in most characters, including the longitudinal median sulcus on vertex, a weak ocular carina, wing venation, a straight fore metapleural margin, and large axillae not meeting at inner angles. The most apparent difference is the absence of crenulation on the median mesoscutal sulcus and axillar grooves. Among species of *Prodinapsis*, it differs from *P. succinalis* by the anterior margin of clypeus not being bilobed, the absence of median depression on face between subantennal grooves, and the absence of posterior orbital groove. It is more similar to *P. minor* in these characters, but it differs by having longer antennae, a shorter median line on vertex, and entirely foveate metanotum.

Genus UKRAINOSA
Perrichot & Perkovsky, new genus

Type species.—*Ukrainosa prolata* n. sp., by designation and monotypy herein.

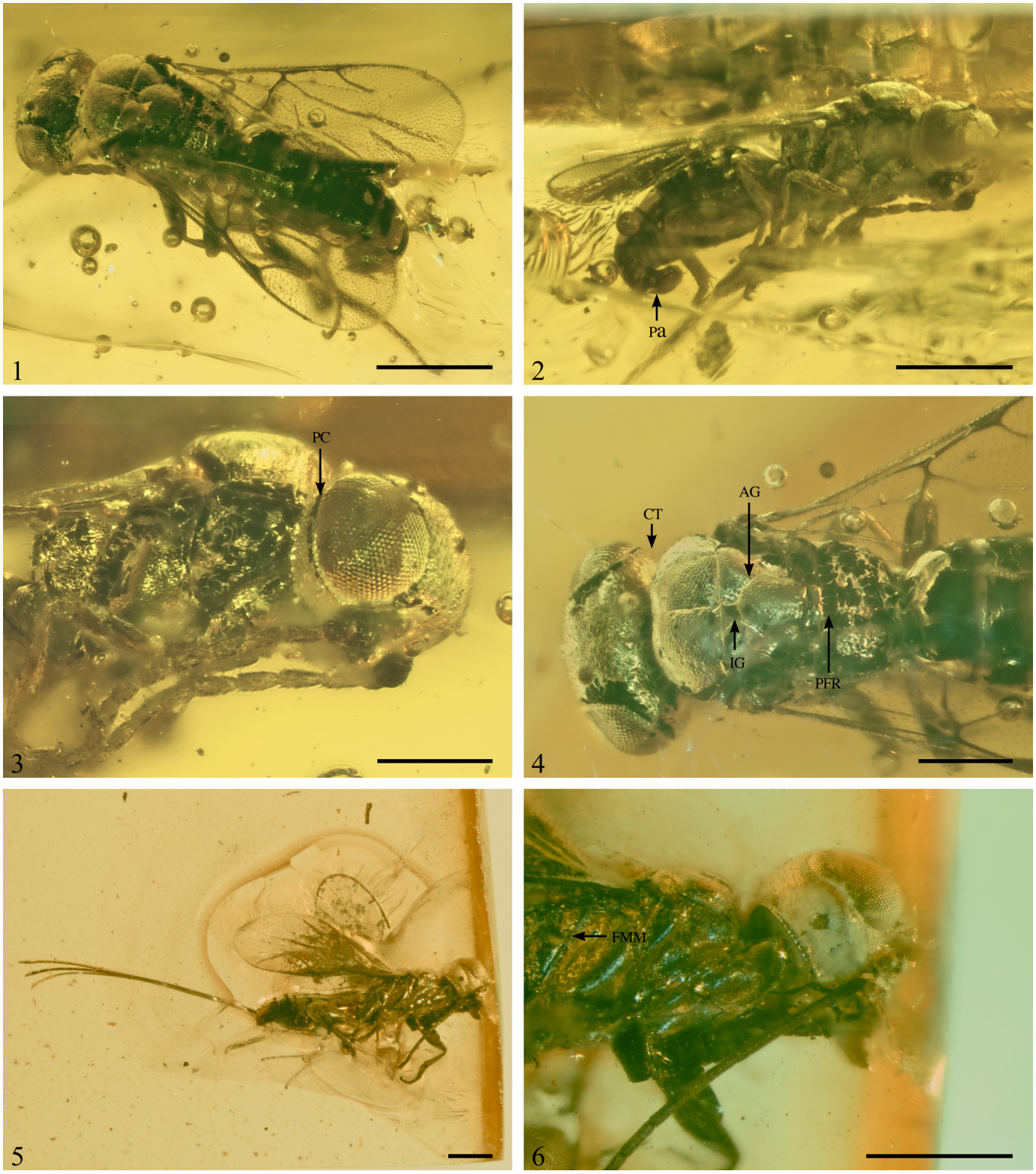

Figure 11. *1–4*, *Prodinapsis oesiensis* n. sp., holotype, male, MNHN-PA-48, Eocene amber, Oise, France; habitus in dorsal (*1*) and lateral (*2*) views; detail of head and mesosoma in lateral (*3*) and dorsal (*4*) views; *5–6*, *Ukrainosa prolata* n. gen. and sp., holotype, female, SIZK-K-7046, Eocene Rovno amber, Ukraine; habitus (*5*) and detail of head and mesosoma (*6*) in lateral view (scale bars: *1*, *2*, *5*, *6* = 0.5 mm; *3–4* = 0.25 mm). See p. 3 for explanation of abbreviations.

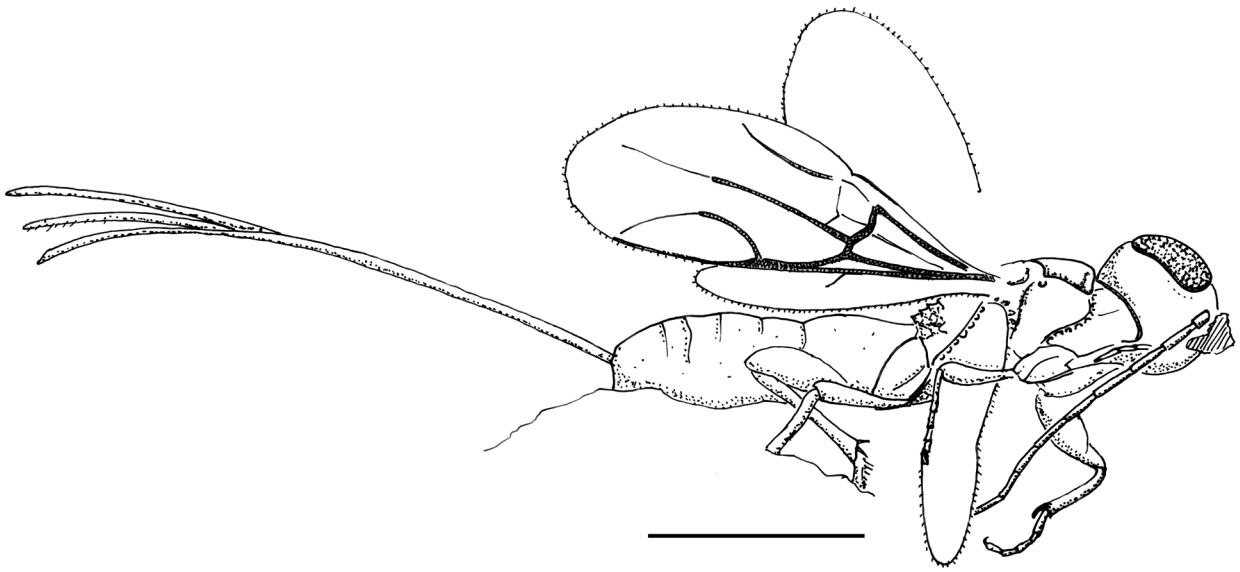

Figure 12. *Ukrainosa prolata* n. gen. and sp., habitus, female holotype, SIZK-K-7046, Eocene Rovno amber, Ukraine (scale bar: 1 mm).

Etymology.—The new genus-group name is a combination of Ukraine, the country from which the specimen originates, and the Ukrainian word *osa* meaning wasp.

Diagnosis.—Head scarcely wider than mesosoma, with posterior orbits smooth, without groove or carina; vertex with a faint longitudinal median sulcus; occipital carina minutely foveate; antennae with flagellomeres much longer than broad, cylindrical, flagellomeres II–IV being longest; apical flagellomere obtusely pointed at apex; subantennal grooves deep, with a broad dorsal carina; clypeus bilobed; maxillary palps 5-segmented, labial palps 3-segmented. Mesoscutum moderately elongate, with anterolateral carina present; median mesoscutal sulcus and inner axillar grooves deeply crenulate; axillae widely separated at inner angles by foveae; metanotum entirely foveate medially; propodeum with a transverse row of small, deep foveae anteriorly, remaining part areolate-rugose; mesopleuron with anterior, dorsal, and posterior margins foveate; fore metapleural margin straight. Forewing extending moderately beyond apex of metasoma; wing venation identical to that of *P. succinalis* except Cu long and tubular on forewing. Hind legs stout; metacoxa large, smooth; protibia with a fringe of apical stout spines and a long, curved spur; meso- and metatibiae with one and two short straight spurs, respectively; basitarsomeres of all legs with a brush of stiff setae along inner margin. Metasoma cylindrical, elongate; hypopygium large, protruding backward; ovipositor long, well exserted.

Comment.—The new genus is very similar to *Prodinapsis* in most features, but differs by the absence of postocular groove and carina and the forewing vein Cu being tubular for a long distance.

UKRAINOSA PROLATA
Perrichot & Perkovsky, new species

Figures 1.6, 11.5, 11.6, 12

Type material.—Holotype female, specimen SIZK-K-7046, in upper Eocene Rovno amber from Klesov, Ukraine.

Etymology.—The specific epithet is based on the Latin *prolatus* meaning elongate and refers to the general aspect of the specimen with an elongate metasoma and ovipositor.

Diagnosis.—As for genus.

Description.—Female. Body minutely shagreened; head (including eyes) and mesosoma uniformly covered by short, pale setae. Measurements as given in Table 1.

Head (Fig. 11.6). Hypognathous, about half as long as high; eyes oval, less than half longer than high; ocelli in a large triangle; longitudinal median sulcus on vertex faintly impressed, barely extending beyond lateral ocelli. Antennae about three-quarters body length, with very short setae; scape one-third longer than broad, twice as broad as pedicel; pedicel the shortest segment, about twice as long as broad; flagellomeres I, V–IX, and XII three times longer than broad, II–IV four times longer than broad, X–XI twice as long as broad; torulus separated from clypeus by a short longitudinal carina; clypeus three times wider than long; mouthparts not visible by preservation.

Mesosoma. Mesoscutum about one-third mesosomal length; mesothoracic spiracle small, entirely surrounded by pronotal cuticle. Fore metapleural margin straight (Fig. 11.6).

Wings (Fig. 1.6). No visible infumate pattern. Forewing with apical segment of Rs, M+Cu, 1m-cu, Cu1, and A distally of 1cu-a spectral; Cu tubular, long, approaching wing margin. Hind wing venation reduced to Sc+R, R1, and Rs, with Rs reaching middle of wing.

Legs. Metabasitarsomere as long as combined length of following tarsomeres; pretarsal claws simple, curved.

Metasoma. First tergum the longest, following ones gradually decreasing in length; cerci small, spatulate, with a tuft of long, fine setae; ovipositor as long as body length.

Genus RUBES Perrichot, new genus

Type species.—*Rubes bruesi* n. sp., by designation and monotypy herein.

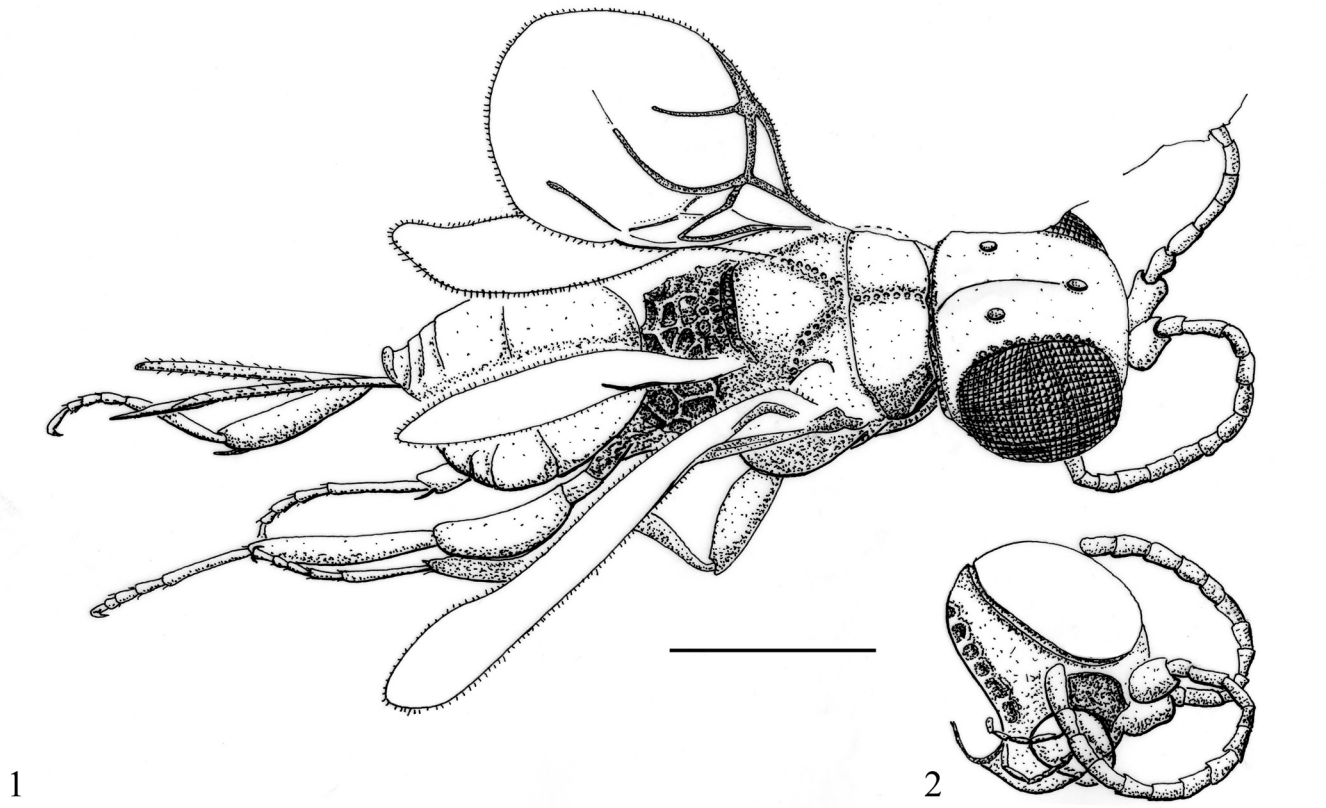

Figure 13. *Rubes bruesi* n. gen. and sp., female paratype, GZG-BST-3132, Eocene Baltic amber; *1*, habitus in laterodorsal view; *2*, head in lateroventral view (scale bar: 0.5 mm).

Etymology.—The new genus-group name is an anagram of Brues (Charles T.), as an acknowledgement of his contribution to the study of fossil hymenopterans.

Diagnosis.—Head distinctly wider than mesosoma, with large prominent oval eyes covering length of head, transversely narrowed immediately behind eyes; inner orbits irregularly crenulate, posterior orbits with only a small carina; toruli almost touching; antennae gradually broadened toward apex, with flagellomeres compact; ocelli in a very large triangle; distinct longitudinal median sulcus on vertex posterior to central ocellus, and on face anterior to central ocellus; clypeus projecting downward, not bilobed. Mesoscutum short, with anterolateral carina present; median mesoscutal sulcus and inner axillar grooves punctate; axillae separated anteromedially by faint foveae; propodeum areolate-rugose. Forewing with veins r-rs and M short; apical segment of Rs absent; veins M+Cu, 1m-cu, Cu1, and A distal of 1cu-a spectral, others tubular; a prebasal (proximal) segment of Cu1 present, aligned with 1cu-a, resulting in a pentagonal medial cell. Legs with metacoxa dorsally rugose; tibial spur formula 1-1-2. Metasoma compact, nearly as wide as long; ovipositor less than half body length.

Comment.—This fossil has some general similarities with *Maimetsha,* but it differs by its reduced number of antennomeres and its forewing venation lacking the basal and apical segments of Rs (thus excluding it from the tribe Dinapsini). It is tentatively placed in the tribe Cretodinapsini on the basis of the longitudinal median sulcus on vertex (possible synapomorphy of the tribe, according to Shaw, 1990b). The postorbital carina is present as in Dinapsini, however without an orbital groove, thus it is more similar to that observed in *Prodinapsis*.

RUBES BRUESI Perrichot, new species

Figures 1.7, 13, 14

Type material.—Holotype female, specimen KU-NHM-ENT B-129. Paratype females, specimens KU-NHM-ENT B-112, B-118, B-120, B-125, B-135, GZG-BST-3132; all preserved in upper Eocene Baltic amber from Samland Peninsula.

Etymology.—The species name is in honor of Charles T. Brues for his contribution to the knowledge of Megalyridae.

Diagnosis.—As for genus.

Description.—Female. Body densely shagreened except propodeum and tarsomeres, sparsely covered by very short, pale setae except on metasoma, and longer pale setae on legs and propodeum. Measurements as given in Table 1.

Head. Wider than long, as wide as high, with anterior and posterior margins nearly parallel as viewed dorsally (Fig. 14.1, 14.2, 14.4); eyes very large, covering all the sides of head, sparsely covered by very short, pale setae; inner orbits minutely crenulate, posterior orbits raised by a small carina but without groove (Fig. 13.1); subantennal groove present, without dorsal carina (Fig. 13.2); toruli closer to each other than to eye margins; antennae

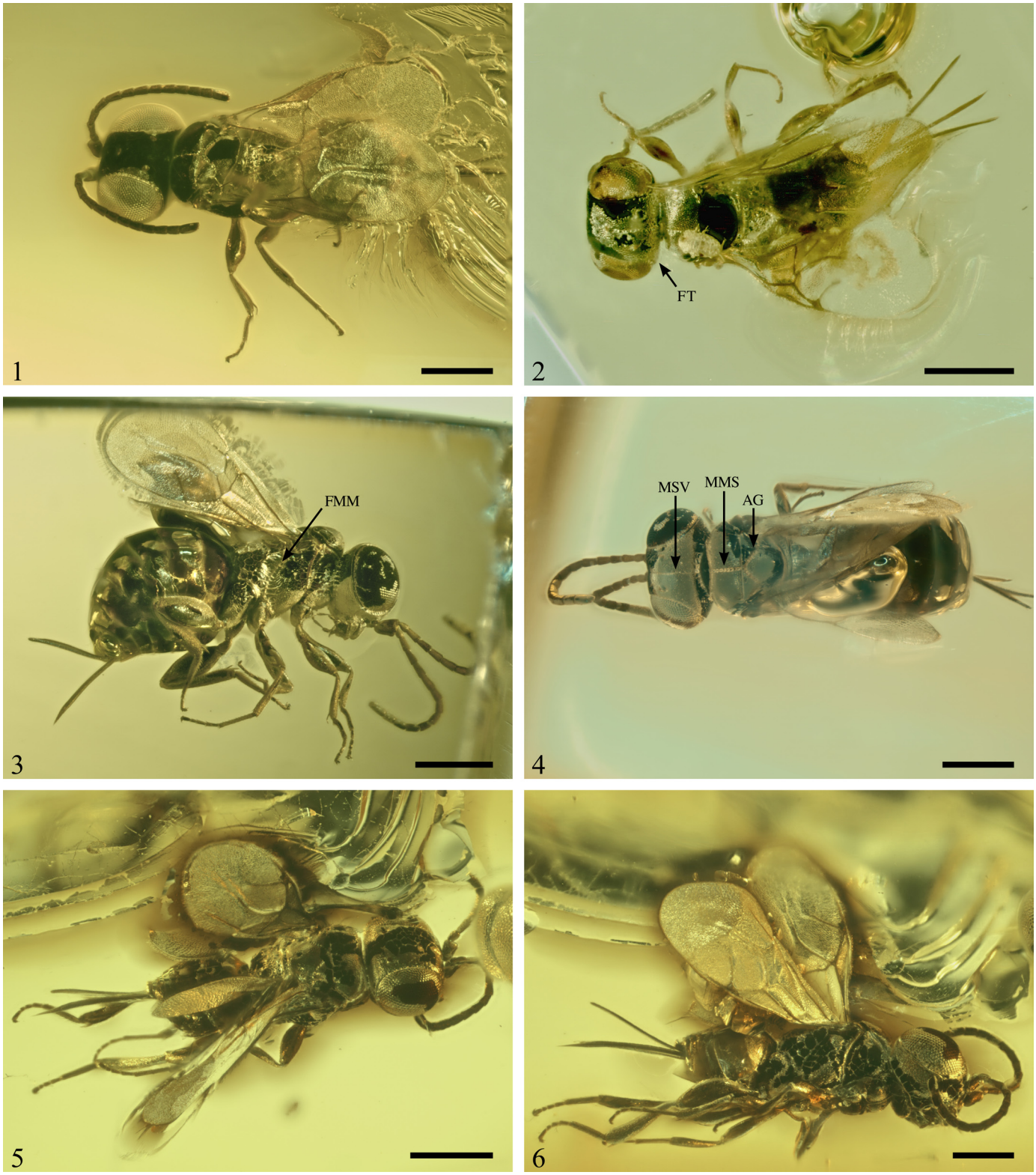

Figure 14. *1–6*, Various female representatives of *Rubes bruesi* n. gen. and sp., Eocene Baltic amber; *1*, holotype, KU-NHM-ENT B-129; *2*, paratype, KU-NHM-ENT B-120; *3–4*, paratype, KU-NHM-ENT B-118; *5–6*, paratype, GZG-BST-3132 (scale bars: 0.5 mm). See p. 3 for explanation of abbreviations.

less than two-thirds body length, with antennomeres cylindrical, compact (Fig. 13.2, 14.1, 14.3), covered by very short, barely visible setae; scape less than twice as long as broad; pedicel the shortest segment, half as long as scape, nearly as long as broad; apical flagellomere the longest, not acute apically, about twice as long as broad; other flagellomeres gradually shortened and broadened from base to apex, with small, multiporous plates rounded; ocelli widely separated, lateral ones closer to eye margins than to each other; vertex with a distinct longitudinal median sulcus extending from central ocellus to occipital margin (Fig. 13.1, 14.4); occipital carina bordered by a row of small to large foveae; clypeus and mouthparts conspicuously protruding downward; anterior margin of clypeus not bilobed; mandibles small, largely hidden by clypeus when closed, with one small basal and two larger apical teeth; labial palps short, with three nearly equal segments, maxillary palps long, with five segments gradually increasing in length.

Mesosoma. Mesoscutum short, about three times wider than long, with anterolateral carina along vertical anterior portion, median mesoscutal sulcus punctate; large triangular axillae connected anteriorly, separated from scutellum by punctate grooves (Fig. 13.1, 14.4); metanotum narrow, with a transverse row of small foveae medially and larger foveae laterally, with posterior edge nearly straight; propodeum areolate-rugose; mesothoracic spiracle very small, entirely surrounded by pronotal cuticle; fore metapleural margin slightly sinuate, anteriorly bordered by a row of small foveae.

Wings. Membrane hyaline. Forewing with only very short, fine marginal setae; pterostigma much reduced, only swelling at r-rs junction; apices of veins r-rs and M nearly aligned; apical segment of Rs absent; basal segment of M short, about half length of 1cu-a; veins M+Cu, 1m-cu, Cu1, and A distal of 1cu-a spectral; a prebasal (proximal) segment of Cu1 present, aligned with 1cu-a, resulting in a pentagonal medial cell. Hind wing venation reduced to Sc+R, R1, and Rs, with Rs reaching middle of wing (Fig. 1.7).

Legs. Slender, sparsely setose, with femora swollen (Fig. 14.3). Protibia with small, apical, stout spines and one long, curved spur; meso- and metatibiae with one and two straight spurs, respectively; metacoxa large, with dorsal surface areolate-rugose; metabasitarsomere longer than combined length of those that follow, with a ventral row of short, comblike spines; pretarsal claws small, simple.

Metasoma. Compact, shorter than mesosoma, nearly as wide as long; first tergum the longest; following one gradually decreasing in size; cerci very small, with long apical setae; ovipositor less than half body length, mostly straight (Fig. 13.1, 14.3, 14.5, 14.6).

Tribe MEGAZARINI Perrichot, new tribe

Type genus.—*Megazar* n. gen., by designation herein.

Diagnosis.—Head hypognathous, globular; eyes large, oval, posterior orbits without groove or carina; vertex with or without longitudinal sulcus. Antennae long, with 14 segments, flagellum filiform; scape moderately long, pedicel very short, flagellomeres cylindrical, elongate; subantennal groove shallow, without dorsal carina; mandibles broad and short, with four teeth; occipital carina present, foveate or not. Pronotum with anteromedial part moderately high as viewed from side, weakly visible dorsally; mesoscutum very large, nearly half length of mesosoma, with parapsides present; median mesoscutal sulcus not crenulate; axillae large, for a short distance connected anteriorly at inner angles; inner axillar grooves deep, crenulate or not; propodeum carinate, with sharp angle between dorsum and declivity to form a nearly vertical posterior surface; mesothoracic spiracle not surrounded by pronotal cuticle posteriorly; fore metapleural margin sinuate. Forewing with marginal and submarginal cells closed by tubular veins, medial cell small, basal segment of Rs very long, vein M+Cu tubular, and apical segments of M and Cu nebulous or tubular, nearly reaching wing margin. Hind wing venation reduced to Sc+R. Hind leg much stouter than fore and midlegs; metacoxa very large, not rugose; metatrochanter, metafemur, and metatibia with row of comblike spines along inner margin; first two metatarsomeres with preening brush of stiff setae along inner margin; tibial spurs thick. Metasoma elongate, cylindrical, with large tergum 7 and sternum 6 (hypopygium); small spatulate cerci; ovipositor well exserted, at least half body length.

Comment.—The new tribe is immediately distinctive from all other megalyrid tribes by its mandibular form, the mesothoracic spiracle being free posteriorly, the large mesoscutum having parapsides, the forewing vein M+Cu being tubular, the basal segment of Rs very long, the marginal cell enclosed and narrow, the hind wing venation reduced to Sc+R, and the hind leg with comblike spines on trochanter, femur, and tibia. This tribe comprises the genera *Megazar* n. gen. and *Megalava* n. gen. and is known from the mid-Cretaceous (Albian) of France and Spain.

Genus MEGAZAR Perrichot, new genus

Type species.—*Megazar elegans* n. sp., by designation and monotypy herein.

Etymology.—Combination of the suffix *Mega-,* in reference to the family Megalyridae, and the name of the Lebanese paleoentomologist Dany Azar, in acknowledgement of his contribution to the study of French amber insects.

Diagnosis.—Head globular, without longitudinal sulcus on vertex; eyes very large, posterior orbits without groove or carina; antennae long, with scape globular and flagellomeres elongate; mandibles broad and short, rectangular, with four teeth. Mesoscutum very large, more than half length of mesosoma dorsally, with faint parapsides present; median mesoscutal sulcus and inner axillar grooves smooth; axillae broader than long, shortly connecting at inner angles; propodeum carinate, with posterior portion nearly vertical; mesothoracic spiracle not surrounded by pronotal cuticle posteriorly; fore metapleural margin distinctly sinuate. Forewing with vein M+Cu tubular; basal segment of M very short; vein Rs present between r-rs and Rs+M to form a large submarginal cell; apical segment of Rs tubular, without elbow indicating former insertion of vein r-m; marginal cell narrow; presence of a short prebasal segment Cu1 between M+Cu and 1cu-a, forming a small pentagonal medial cell; apical segments of M and Cu nebulous, reaching wing margin. Hind wing venation reduced to Sc+R. Hind leg very stout; protibia with a fringe of apical stout spines and one long and curved spur, meso- and metatibiae with two straight long spurs; metacoxa very large, not rugose; hind leg with row of comblike spines along inner margin of trochanter, femur, and tibia, a

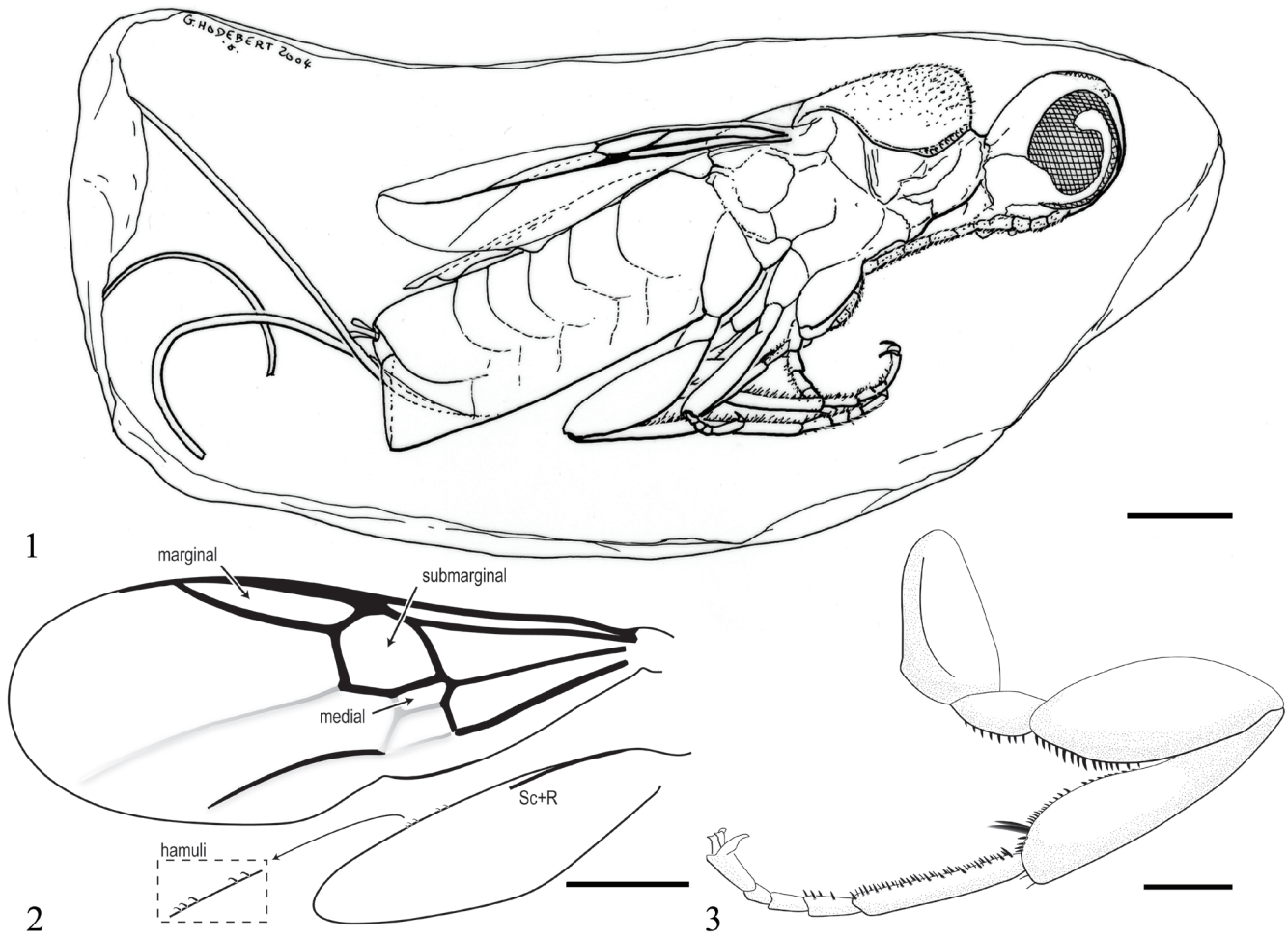

Figure 15. *Megazar elegans* n. gen. and sp., holotype, female, MNHN-CDL-2.11, Cretaceous (upper Albian) amber, Charentes, France; *1*, habitus (drawing courtesy of G. Hodebert, MNHN); *2*, wings; *3*, left hind leg (scale bars: *1* = 0.5 mm; *2–3* = 0.25 mm).

preening brush of stiff setae along inner margin of tarsomeres I–II. Metasoma elongate, with large hypopygium protruding backward; ovipositor well exserted, at least half body length.

Comment.—Shaw (1988) proposed the recent Megalyridae to be a monophyletic group on the basis of two synapomorphies, viz. a reduced hind wing venation and the mesothoracic spiracle being completely surrounded by pronotal cuticle (see also Gibson, 1985, for this last character). However, the new fossil is the first megalyrid ever known to possess a spiracle not surrounded by pronotal cuticle posteriorly. It also displays unusual mandibles with four teeth, while most megalyrids have only three, except *Carminator,* which has five teeth. In addition, the new fossil has parapsides, which are absent in all other megalyrids. Nevertheless, the new genus can be included in Megalyridae as it has 14-segmented antennae inserted below the level of the eyes, subantennal grooves present, median mesoscutal sulcus present, a swollen metafemora, and wing venation rather similar to that of the Dinapsini. Unlike the three dinapsine genera *Dinapsis, Neodinapsis,* and *Ettchellsia*, however, the new genus has no postorbital carina and dorsal carina of subantennal grooves, and its forewing has a tubular vein M+Cu and a narrow marginal cell closed by a tubular vein Rs without elbow, reminiscent of the lost vein r-m. These unique characters preclude an assignment to any of the existing tribes and justify the new tribe.

MEGAZAR ELEGANS Perrichot, new species

Figures 15, 16.1–16.4

Type material.—Holotype female, specimen MNHN-CDL-2.11 (coll. Arnaud), originally in a piece of amber with 45 various arthropod inclusions, now isolated and embedded in Canada balsam (see Néraudeau and others, 2008, fig. 3A).

Type locality.—Cadeuil, Charente-Maritime, southwestern France.

Stratigraphic horizon.—Lower Cretaceous, uppermost Albian, level A1b (*sensu* Néraudeau & others, 2008).

Etymology.—The specific epithet is the Latin adjective *elegans* and refers to the elegant position of preservation of the specimen.

Diagnosis.—As for genus.

Description.—Female. Body moderately setose, with setae short and fine, except stouter on antennae and longer on pronotum; surface sculpturing not visible.

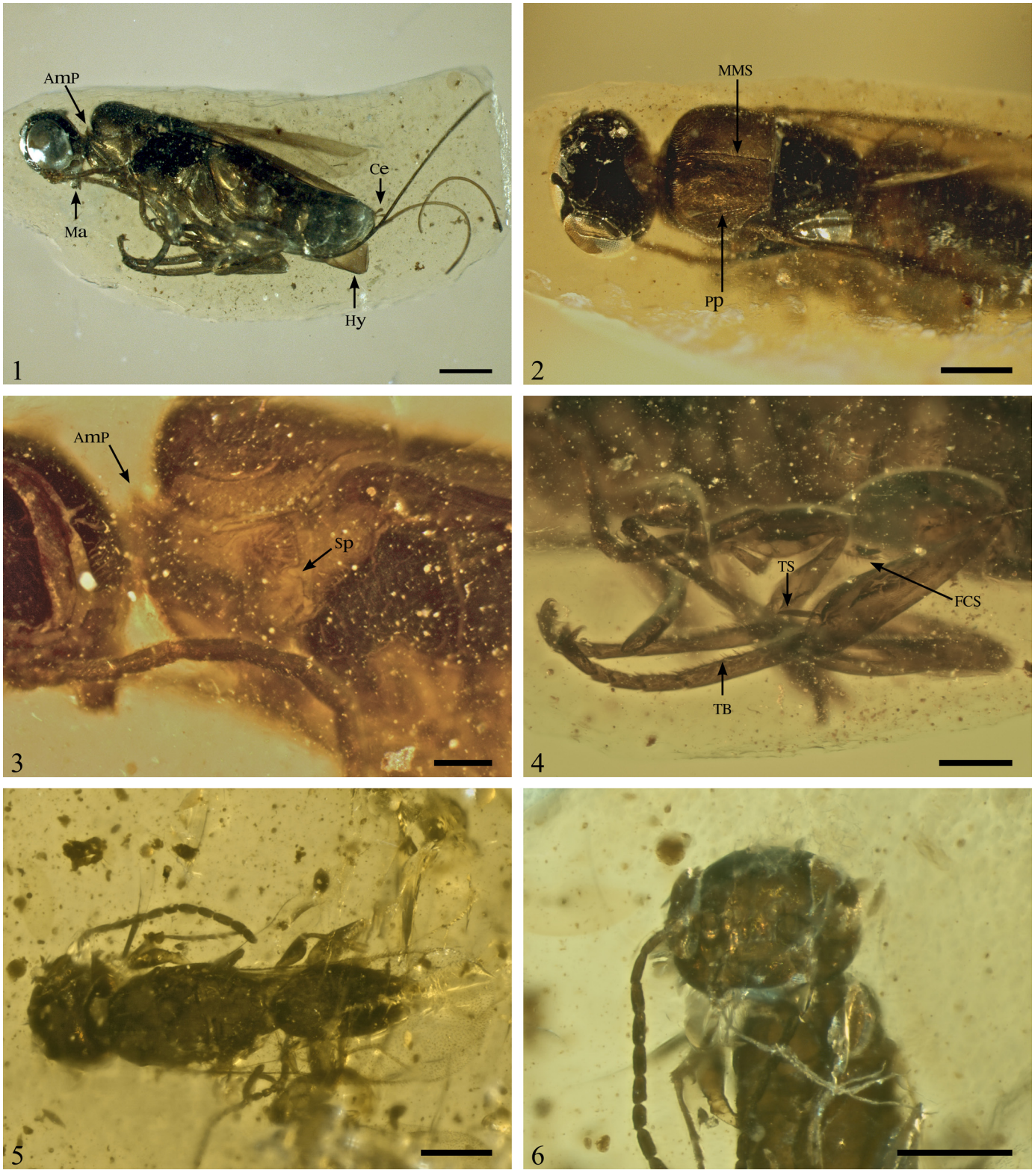

Figure 16. *1–4*, *Megazar elegans* n. gen. and sp., holotype female, MNHN-CDL-2.11, Cretaceous (lower Albian) amber, Charentes, France; *1*, habitus in dorsal view; *2*, head and mesosoma in dorsal view; *3*, anterior part of mesosoma in lateral view; *4*, hind legs; *5–6*, *Valaa delclosi* n. gen. and sp., holotype male, MCNA-12578a, Cretaceous (lower Albian) amber from Álava, Spain; *5*, habitus in dorsal view; *6*, detail of head in ventral view (scale bars: *1–2* = 0.5 mm; *3–5* = 0.25 mm). See p. 3 for explanation of abbreviations.

Head. One-third broader and higher than long, slightly broader than mesosoma. Eyes oval, very high (Fig. 15.1, 16.1), sparsely setose; posterior orbit of eyes without groove or carina; ocelli equidistant, forming a large triangle; no longitudinal median sulcus on vertex; occipital carina weak, not margined by foveae. Antennae long, more than half body length, inserted below ventral margin of eyes; scape short, globular; pedicel the shortest segment, a quarter longer than thick; flagellomeres elongate, cylindrical (Fig. 16.3), densely covered by very short, stout setae, with rounded multiporous plates; FI, FIII–FIV, FXII subequal in length, about three times as long as thick; FII, FV–FXI shorter, about twice as long as thick. Distance between toruli equivalent to distance between torulus and eye; subantennal grooves shallow, without dorsal carina; clypeus with anterior margin convex, simple; mandibles rectangular, endodont, with 4 teeth increasing in size toward posterior margin (Fig. 16.1); maxillary palps 5-segmented, labial palps 3-segmented.

Mesosoma. Pronotum weakly visible dorsally, medially moderately high as viewed laterally (Fig. 16.1, 16.3); hind lateral margin of pronotum with circular notch around spiracle, making it free posteriorly (Fig. 16.3); mesoscutum only slightly broader than long, more than half mesosomal length dorsally, with anterior and lateral margins foveate, without anterolateral carina; parapsides very faintly impressed, widely separated from median mesoscutal sulcus, long but not reaching anterior mesoscutal margin (Fig. 16.2); median mesoscutal sulcus and axillar grooves smooth; axillae broader than long, meeting at inner angles anteriorly; propodeum carinate, with dorsum short, declivity nearly vertical; mesopleuron apparently not foveate posteriorly; fore metapleural margin sinuate (Fig. 15.1).

Wings. Membrane hyaline. Forewing not extending beyond sixth metasomal segment; pterostigma small, vein R1 long, marginal cell narrow (Fig. 15.2); Rs present between r-rs and Rs+M, straight and tubular; apical segment of Rs tubular, reaching wing margin; basal segment of M very short, apical part of M reaching wing margin, nebulous; presence of a short prebasal segment of Cu1 between M+Cu and 1cu-a; medial cell small, pentagonal; 1m-cu, second and third portions of Cu1, distal portion of M, and A distally of 1cu-a nebulous; Cu reaching wing margin, tubular. Hind wing venation reduced to Sc+R diverging from wing margin for a short distance, other veins absent. Five distal hamuli, the two most proximal ones somewhat distant from other three.

Legs. All tibiae distinctly thickened apically, tip about twice as broad as base, with short apical stout spines; all but apical tarsomeres with two or three apical stiff setae; metacoxa without sculpturing on dorsal surface; one or two rows of comblike spines on inner margin of metatrochanter, metafemur, and metatibia (Fig. 15.3, 16.4); preening brush of stiff setae on tarsomeres shorter than comblike spines, not aligned in rows; metafemur almost half as broad as long in its middle part; metatarsomeres II–IV gradually decreasing in length, with IV only slightly longer than thick; apical tarsomere about as long as second one; pretarsal claws long and curved, simple.

Metasoma. Cylindrical elongate, half body length; first segment the broadest; first and sixth tergites the longest, subequal in length, other tergites gradually decreasing in length (Fig. 15.1, 16.1); cerci spatulate; ovipositor with only right sheath completely preserved, about half body length; sheath with microscopic transverse striations, with small perforations at apex; hypopygium well developed.

Measurements (in mm). Body length 3.50; head length 0.62, width 0.92, height 0.67; antennae length ~1.90; scape length and width 0.12, pedicel length 0.10, width 0.08; mesosoma length 1.25; forewing length 2.10; metasoma length 1.63, height 0.65, maximal width 0.87; ovipositor sheath external length ~1.70.

Genus MEGALAVA Perrichot, new genus

Type species.—*Megalava truncata* n. sp., by designation and monotypy herein.

Etymology.—Combination of the suffix Mega-, in reference to the family Megalyridae, and Álava, name of the Spanish province from which the amber containing the specimen originates.

Diagnosis.—Distinctive from *Megazar* in having a longitudinal median sulcus on vertex, occipital carina being foveate, the inner axillar grooves broadly crenulate, and the forewing with the medial cell being rectangular instead of pentagonal, with M and Cu entirely tubular. The eyes are also slightly smaller and the antennal scape thinner than in *Megazar*. The mesothoracic spiracle is considered herein to be free posteriorly, although it is not possible to ascertain this character very confidently.

MEGALAVA TRUNCATA Perrichot, new species

Figure 17

Material.—Specimen MCNA-9416, in Cretaceous Spanish amber.

Type locality.—Amber geological site Peñacerrada 1, near Moraza, Basque-Cantabrian province, Spain.

Stratigraphic horizon.—Escucha Formation, Lower Cretaceous, lower Albian.

Etymology.—The specific epithet is from the Latin *truncare* (truncated), in reference to the incomplete preservation of the specimen.

Diagnosis.—As for genus.

Description.—Sex unknown. Metasoma, left fore and mid legs not preserved. Ventral structures barely visible, obscured by detritus.

Head. Shorter than wide and high, broader than mesosoma. Eyes large, higher than long, not pubescent; postorbital margin without groove, foveae, or carina (Fig. 17.1, 17.2). Lateral ocelli closer to inner eye margin than to each other; vertex with a longitudinal median sulcus extending from median ocellus to level of posterior margin of eyes; occipital margin raised by a small carina, with a row of small foveae. Antennae long, with 14 segments, inserted below level of ventral margin of eyes; toruli slightly closer to each other than to eyes; pedicel half as long as scape, scarcely longer than broad; flagellomeres cylindrical, first and apical ones subequal in length, more than twice as long as broad, intermediate ones shorter, nearly equal to scape in length. Clypeus and mouthparts poorly visible, except maxillary palps 5-segmented.

Mesosoma. Pronotum short medially although anteromedial part slightly visible dorsally, with posteromedial part moderately high as viewed laterally (Fig. 17.2). Mesoscutum slightly longer

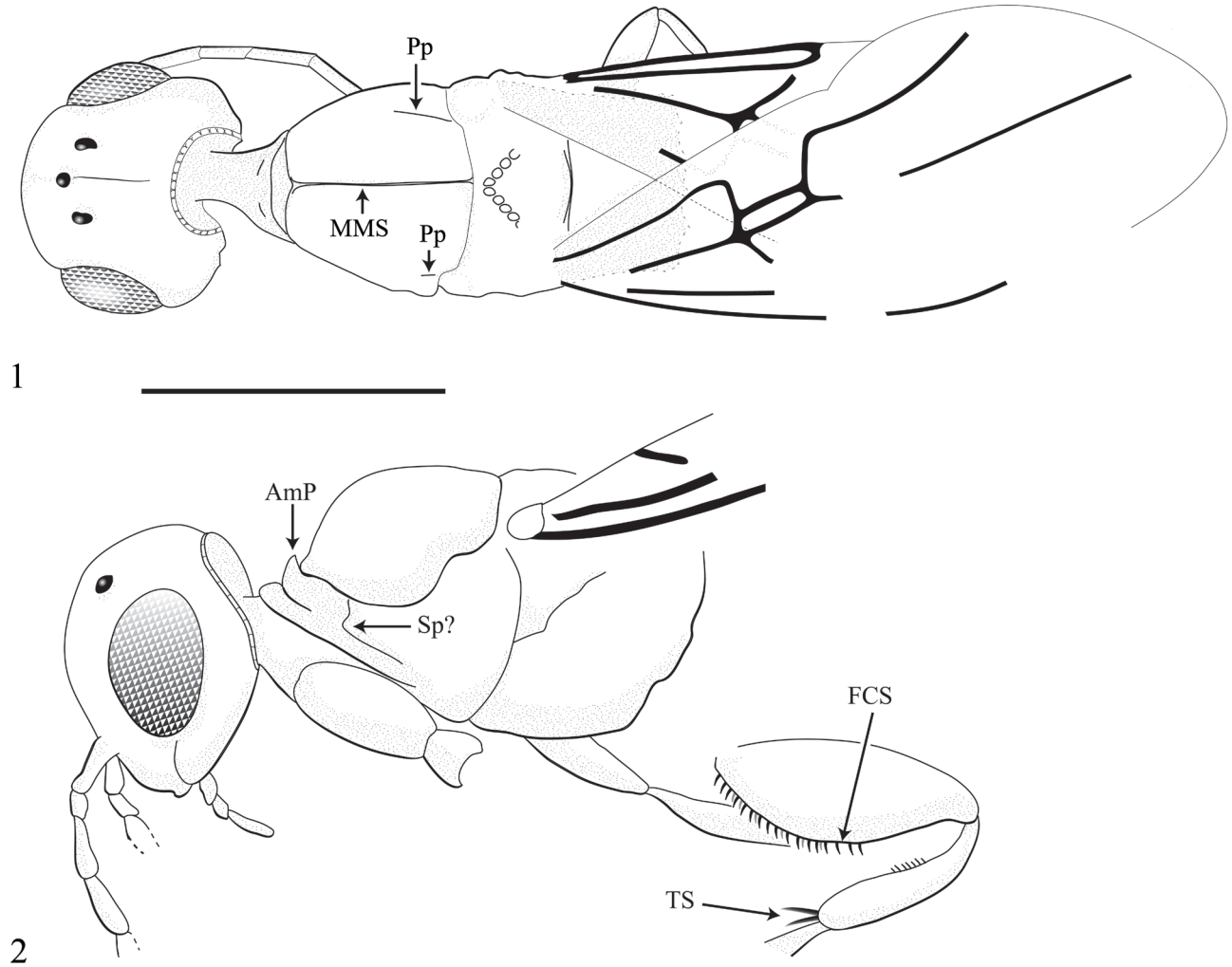

Figure 17. *Megalava truncata* n. gen. and sp., MCNA-9416, Cretaceous (lower Albian) amber, Álava, Spain; habitus in dorsal (*1*) and lateral (*2*) view (scale bar: 0.5 mm). See p. 3 for explanation of abbreviations.

than broad, not abruptly truncate anteriorly, without anterolateral carina, with posterior margin not straight dorsally; median mesoscutal sulcus deep, not crenulate (Fig. 17.1); faint parapsides present, widely separated from median mesoscutal sulcus. Axillae large, anteriorly slightly meeting at inner angles, with inner grooves broadly crenulate. Propodeum carinate, with sharp angle between dorsum and declivity to form an almost vertical posterior surface (Fig. 17.2). Pronotal spiracle hardly visible by preservation, possibly free posteriorly, as the pronotal cuticle seems to make a notch along posterior margin (Fig. 17.2); mesopleuron with a row of small foveolae along posterodorsal margin. Fore metapleural margin apparently sinuate.

Forewings hyaline; pterostigma, vein r-rs and apical part of Rs not preserved; M+Cu tubular, aligned with Rs+M (Fig. 17.1); medial cell subrectangular, very small, entirely closed by tubular veins, with M and 1m-cu very short; distal segments of M and Cu tubular, reaching wing margin. Hind wings not visible.

Legs. Fore legs poorly preserved; protibia with two short apical spurs; hind leg stout, with large coxa; metafemur swollen, with at least two rows of short, comblike spines along inner margin (Fig. 17.2); metatibia with two short apical spurs, with a few visible stout spines along inner margin; pretarsal claws small, simple.

Measurements (in mm). Head length 0.30, width and height 0.40; antennae length 0.80; mesosomal length 0.72, maximal width 0.36; forewing length ~1.10.

Comment.—Although incomplete, this fossil shows characteristic features of the Megalyridae with the 14-segmented antennae inserted below eyes, the mesoscutum with a deep median mesoscutal sulcus, and the hind legs with swollen femora. Critical characters like the complete wing venation are missing, but it is very similar to *Megazar* in its overall aspect. Indeed, the two fossil specimens are the only ones with such a preening or grooming device on the hind legs.

Tribe DINAPSINI Waterston, 1922
Genus VALAA Perrichot, new genus

Type species.—*Valaa delclosi* n. sp., by designation and monotypy herein.

Etymology.—The genus-group name is an anagram of Álava, name of the Spanish province from which the amber containing the specimen originates.

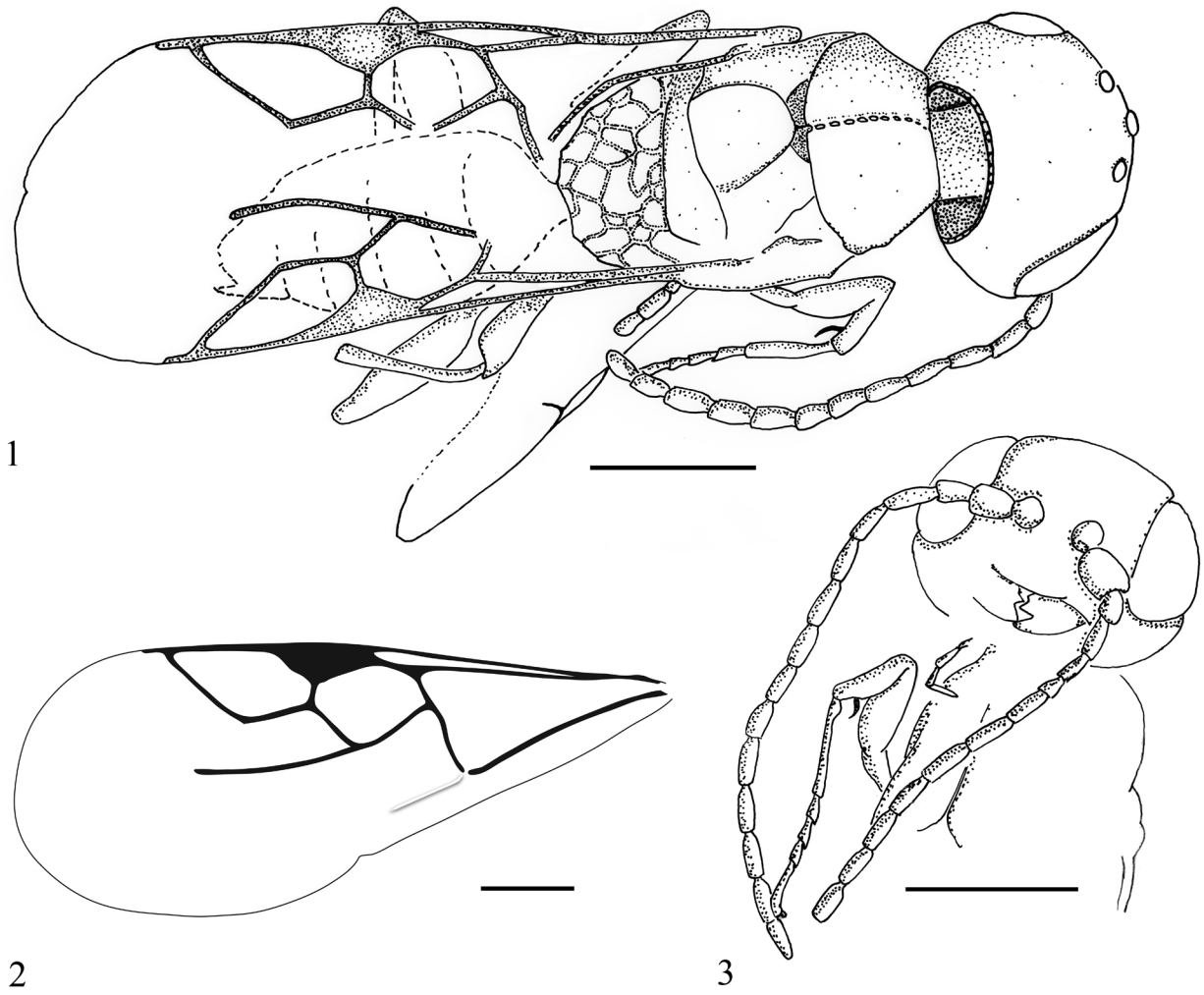

Figure 18. *Valaa delclosi* n. gen. and sp., holotype male, MCNA-12578a, Cretaceous (lower Albian) amber, Álava, Spain; *1*, habitus; *2*, forewing with cells labeled; *3*, detail of head and right fore leg in ventral view (scale bars: *1*, *3* = 0.5 mm; *2* = 0.25 mm).

Diagnosis.—Head hypognathous, wider than long, without longitudinal median sulcus on vertex; eyes large, oval; posterior orbits without groove or carina; antennae filiform, with 14 segments, flagellomeres elongate, cylindrical; subantennal groove shallow, without dorsal carina; clypeus transverse, much wider than high, anterior margin convex, simple; mandibles short, endodont, with three large teeth increasing in size from base to apex. Mesoscutum moderately large, with a small anterolateral carina; median mesoscutal sulcus minutely crenulate (Fig. 18.1); axillae not connected at inner angles, separated by two shallow triangular foveae, with inner edges separated from scutellum by smooth grooves; propodeum irregularly carinate; mesopleuron with posterior margin foveate; fore metapleural margin straight. Forewing extending beyond metasoma, with venation identical to that of *Neodinapsis*. Fore and midlegs slender, hind legs moderately stouter; all legs with tibiae shorter than combined length of tarsomeres; protibia with fringe of apical stout spines and one long and curved spur, meso- and metatibiae with one and two straight, short spurs, respectively; metacoxa not rugose; metabasitarsomere with short, stiff setae along inner margin. Metasoma compact, oval, with acute tip.

Comment.—The absence of longitudinal sulcus on the vertex and the forewing venation with tubular basal and apical segments of Rs strongly indicate affinities with the Dinapsini. The forewing venation is remarkably similar to that of *Neodinapsis* but, as for *Megazar* n. gen. described above, the new genus differs from it and all other extant genera of this tribe by the absence of a foveate-reticulate sculpture on the head and mesosoma, the absence of postorbital groove and carina, and the absence of dorsal carina on subantennal grooves.

VALAA DELCLOSI Perrichot, new species

Figures 16.5–16.6, 18

Type material.—Holotype male, specimen MCNA-12578a, in a piece of Spanish Cretaceous amber with two Hymenoptera: Falsiformicidae (larger, 12578b) and Chalcidoidea (smaller, 12578c).

Type locality.—Amber geological site Peñacerrada 1, near Moraza, Basque-Cantabrian province, Spain.

Stratigraphic horizon.—Escucha Formation, Lower Cretaceous, lower Albian.

Etymology.—The species name is in honor of the Spanish paleoentomologist Xavier Delclòs who facilitated access to the

material, and for his contribution to the knowledge of Spanish amber.

Diagnosis.—As for genus.

Description.—Male. Body without apparent pubescence.

Head. Shorter than broad and high, slightly broader than mesosoma; eyes bare, higher than long; ocelli in a large triangle; small occipital carina present, finely foveolate (Fig. 18.1); antennae moderately elongate (Fig. 18.3), about 0.75 times body length; scape less than twice as long as broad; pedicel the shortest segment, about twice as long as broad; all flagellomeres nearly subequal in length, 2.5 times longer than broad; apical flagellomere acute at tip; distance between toruli subequal to distance between torulus and eye; clypeus about four times wider than long.

Mesosoma. Pronotum not visible dorsally. Mesoscutum less than twice as broad as long, with a short carina along each anterolateral corner; propodeum with fine carinae arranged irregularly (Fig. 18.1); lateral parts of mesosoma barely visible.

Wings. No visible banding pattern. Forewing broadly rounded at apex (Fig. 18.2); pterostigma broad and short, with marginal and submarginal cells closed by tubular veins; veins M+Cu, Cu1, 1m-cu, and A distally of 1cu-a absent; vein R1 long, extending beyond Rs; r-rs short, branching into Rs proximad to level of apical midlength of pterostigma; Rs tubular between Rs+M and r-rs, straight; apical segment of Rs entirely tubular, with a distinct elbow, curving toward anterior margin of wing; M long distal of Rs+M. Hind wing vein Rs short, not reaching middle of wing (Fig. 18.1).

Legs. Metabasitarsomere the longest, combined length of metatarsomeres II–IV about 1.7 times length of apical tarsomere.

Metasoma. Compact, slightly shorter than mesosoma, less than half body length; genitalia barely visible by preservation, apparently reduced.

Measurements (in mm). Body length 1.13; head length 0.31, width 0.44, height 0.38; antennae length 0.87; mesosoma length 0.59, maximal width 0.38; mesocutum length 0.20, width 0.34; forewing length 1.12; metasoma length 0.50, maximal width 0.25.

Tribe UNCERTAIN
Genus MEGALLICA Perrichot, new genus

Type species.—*Megallica parva* n. sp., by designation and monotypy herein.

Etymology.—Combination of the suffix Mega- in reference to the family Megalyridae, and the Latin *Gallica*, meaning from France, country from which the specimen originates.

Diagnosis.—Body small. Head without postocular carina or orbital row of foveae, with a weak longitudinal median sulcus on vertex; occipital carina very weak; antennae about half body length, with all but apical segments nearly equal in length; pedicel and flagellomeres scarcely twice as long as thick, apical flagellomere about twice as long as thick; subantennal grooves shallow; clypeus simple, mandibles with three teeth. Median mesoscutal sulcus and axillar inner grooves crenulate; axillae not connected, separated by two large triangular foveae; pronotum areolate-rugose. Forewing with pterostigma much swollen at junction with r-rs; vein Rs beyond r-rs elbowed, entirely tubular to form a fully closed radial cell [2R1]; Rs segment between Rs+M and r-rs present as a short tubular stub not reaching Rs+M, no medial cell; veins M+Cu and A distal of 1cu-a spectral. Legs slender; protibia without apical stout spines, with one long curved spur; meso- and metatibiae with two short straight spurs; metacoxa scarcely larger than others, metafemur swollen; metabasitarsomere short, with a preening brush of stiff setae along inner margin. Metasoma elongate oval, slightly longer than mesosoma. Male genitalia reduced.

Comment.—This genus is easily distinguishable from all other megalyrids by its unique forewing venation with a broad pterostigma, the radial cell being closed, the short stub of Rs present between Rs+M and r-rs but not reaching Rs+M, and the absence of medial cells (Dinapsini-like venation pattern), combined with the presence of a longitudinal median sulcus on vertex. This last character was a possible synapomorphy of the Cretodinapsini, according to Shaw (1990b), but the monophyly of this tribe has not been demonstrated and a sulcus on vertex is also found in *Megalava,* which belongs in the new tribe Megazarini. The configuration of the forewing venation, with the radial vein present, even if not complete basally, supports affinities with the Dinapsini. The posterior orbital carina, another putative synapomorphy of this tribe, is not present in the new fossil, but Shaw (1990b) indicated that this character is homoplastic. The new genus strengthens the possibility that the presence of this carina is not a synapomorphy for this tribe. Therefore, the new genus cannot be placed confidently in any existing tribe.

MEGALLICA PARVA Perrichot, new species

Figures 19, 20.1–20.2

Type material.—Holotype male, specimen MNHN-ARC-362.2, originally in a piece of amber with two Diplopoda belonging to Synxenidae, now isolated and embedded in a polished block of epoxy resin.

Type locality.—Font-Benon quarry, Archingeay-Les Nouillers, in Charente-Maritime, France.

Stratigraphic horizon.—Lower Cretaceous, uppermost Albian, level A1sl2 (*sensu* Néraudeau & others, 2002).

Etymology. From the Latin *parvus* meaning small, in reference to the minute size of the species.

Diagnosis.—As for genus.

Description.—Body mostly bare, minutely shagreened except pronotum.

Head. One-third broader than long, slightly broader than maximum width of mesosoma (Fig. 19.1, 20.1, 20.2). Eyes bare, large; orbital margins without groove or raised carina; lateral ocelli widely separated, closer to inner orbit of eyes than to each other; vertex with a fine, impressed median line extending from median ocellus to occipital margin; occipital margin raised by a very weak carina, without foveae. Antennae about half body length, inserted below level of ventral margin of eyes, distance between toruli larger than distance between torulus and eye; scape short, globular; pedicel ovoid, less than twice as long as thick; flagellomeres cylindrical, scarcely half as broad as long, subequal in length to pedicel except apical one longer; subantennal grooves present but shallow, without dorsal carina; clypeus with anterior margin

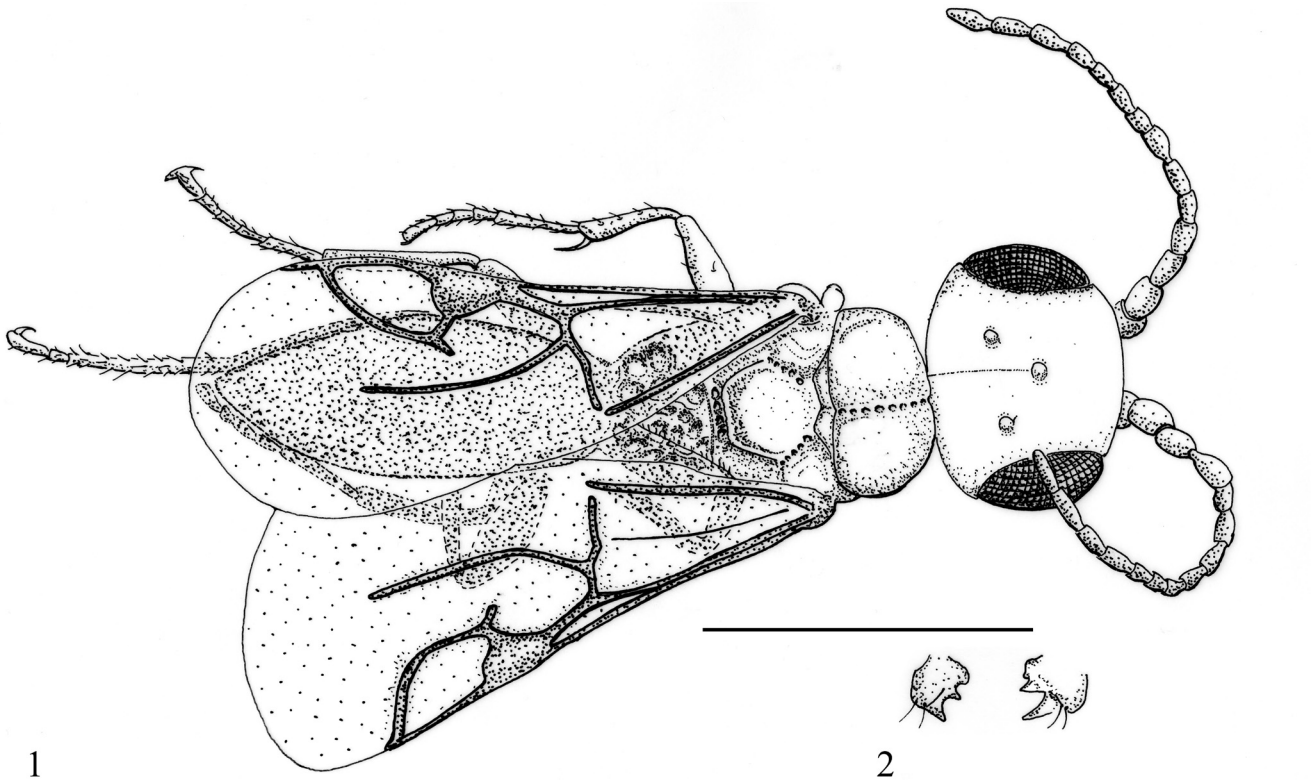

Figure 19. *Megallica parva* n. gen. and sp., holotype male, MNHN-ARC-362.2, Cretaceous (upper Albian) amber, Charentes, France; *1*, habitus; *2*, detail of mandibles in ventral view (scale bar: 0.25 mm).

convex, not bilobed; mandibles short, with three teeth increasing in size from base to apex (Fig. 19.2).

Mesosoma. Pronotum not visible dorsally; mesoscutum less than twice as long as broad, with anterior portion subvertical, without visible anterolateral carina; median mesoscutal sulcus and axillar inner grooves crenulate (Fig. 19.1, 20.2); large triangular axillae not meeting at inner angles, separated by two triangular foveae; metanotum with a transverse row of small foveae dorsomedially; propodeum finely carinate; mesopleuron with posterodorsal margin foveolate.

Wings. No visible infumate pattern. Forewing not extending beyond metasoma (Fig. 19.1); pterostigma broadly swelling at junction with r-rs; R1 long, extending beyond apical segment of Rs; Rs between Rs+M and r-rs present as a short, tubular stub branching from r-rs proximad to midlength of pterostigma, not reaching Rs+M; apical segment of Rs with a slight but distinct elbow, tubular, reaching wing margin to form a closed marginal cell; vein 1cu-a distinctly longer than basal segment of M; veins 1m-cu and Cu1 absent; veins M+Cu and A spectral distal of 1cu-a. Hind wing barely visible, venation apparently reduced to Sc+R, R1, and Rs.

Legs. Hind leg moderately stouter than others; metacoxa not rugose on dorsal surface; metafemur swollen; all tarsomeres with short apical stout setae; metabasitarsomere scarcely longer than combined length of tarsomeres II–IV; apical tarsomere as long as combined length of tarsomeres III–IV; pretarsal claws very small, curved, and simple.

Metasoma. Elongate oval, scarcely longer than mesosoma, in its median part nearly half as broad as long (Fig.20.1); segments nearly equal in length; genitalia barely visible.

Measurements (in mm). Body length 1.06; head length 0.22, width 0.34; antennae length 0.60; scape length/width 0.05/0.05; pedicel length/width 0.04/0.02; mesosoma length 0.40, maximal width 0.26; forewing length ~0.75; metasoma length 0.44, width 0.22.

Tribe MEGALYRINI Schletterer, 1889
Genus MEGALYRA Westwood, 1832
MEGALYRA BALTICA Poinar and Shaw, 2007

Figures 20.3–20.6

Megalyra baltica Poinar and Shaw, 2007, p. 65, fig. 1–4 (holotype female, in Baltic amber).

Material examined.—Female specimen KU-NHM-ENT B-137, in upper Eocene (Priabonian) Baltic amber.

Measurements (in mm). Body length 6.00; head length 0.78, width 1.47; ratio first/second flagellomeres length 0.80; mesosoma length 2.10; forewing length ~4.80; metasoma length 3.12; ovipositor length ~5.60.

Comment.—The new fossil matches almost perfectly the original description of *M. baltica* given recently by Poinar and Shaw (2007), including range sizes. The only visible differences are the forewing veins M+Cu, Cu1, 1m-cu, and distal segments of Rs and M being spectral instead of sclerotized. They also described

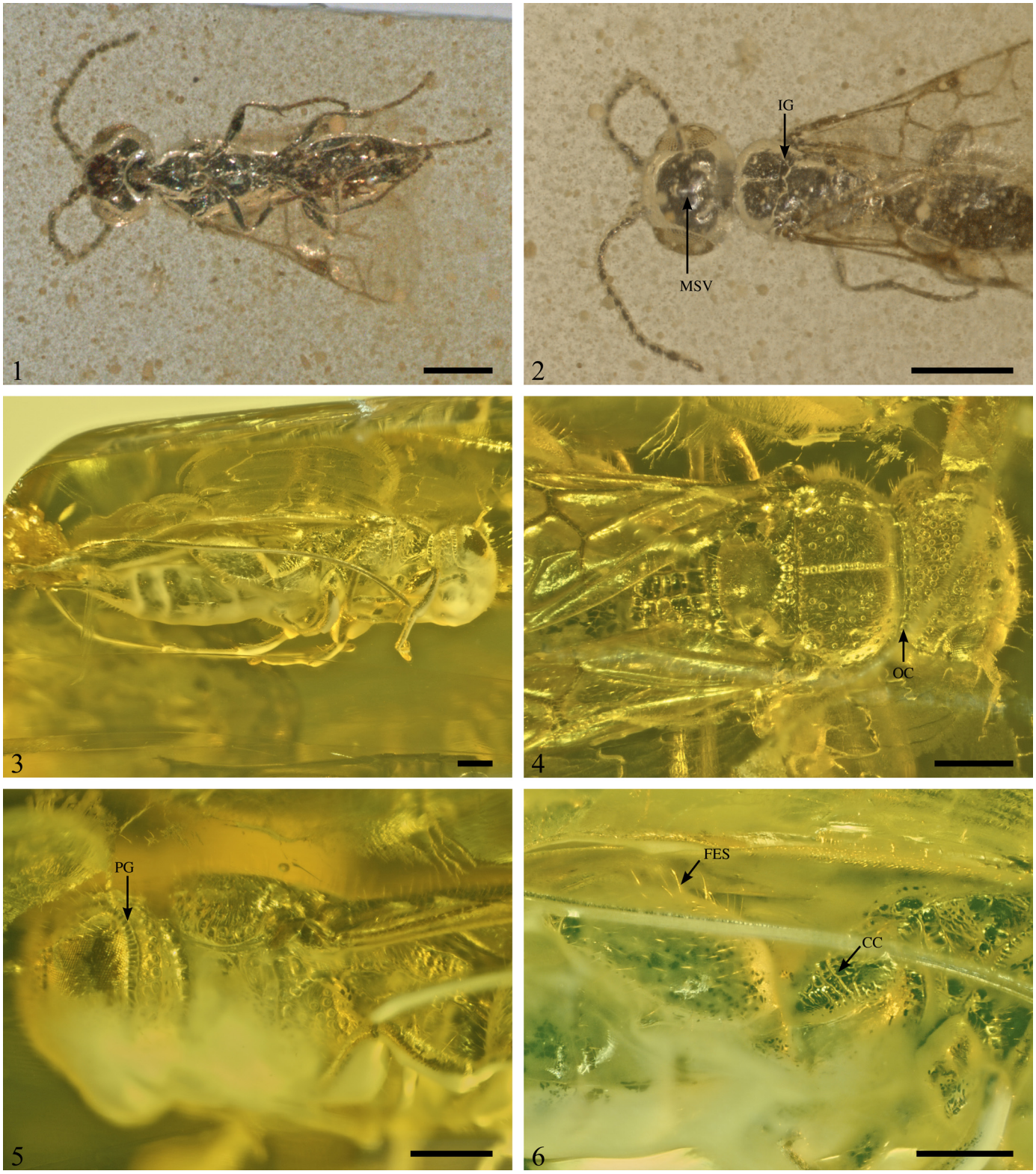

Figure 20. *1–2*, *Megallica parva* n. gen. and sp., holotype male, MNHN-ARC-362.2, Cretaceous (upper Albian) amber, Charentes, France; habitus in ventral view (*1*), detail of head, mesosoma, and forewings in dorsal view (*2*); *3–6*, *Megalyra baltica* Poinar & Shaw, female, KU-NHM-ENT B-137, Eocene Baltic amber; habitus in lateral view (*3*), head and mesosoma in dorsal (*4*) and lateral (*5*) views, right hind leg (*6*) (scale bars: *1–2* = 0.25 mm; *3–6* = 0.50 mm). See p. 3 for explanation of abbreviations.

the first flagellomere as being the longest, but it is not coherent with the ratio of the length of first flagellomere/length of second flagellomere of 0.70 that they give in the measurements section. On the new fossil, the first flagellomere is shorter than the subequal second to fourth flagellomeres, and the following ones are nearly equal to the first one. Finally, in the discussion, Poinar and Shaw (2007, p. 67) mentioned the character "anterolateral sharp spines on mesoscutum," a synapomorphy for *Megalyra* according to Shaw (1990a). Rather than "sharp spines," however, the terminology small projection is preferred (S. Shaw, personal communication, April 2009) as it is sometimes reduced as in *M. fasciipennis*. Indeed, only a very small anterolateral projection is visible dorsally on our specimen, and laterally this projection merely resembles the anterolateral carina that is visible in *Prodinapsis* or *Ettchellsia*. Some photographs (Fig. 20.3–20.6) give a few additional details present but not described nor visible in Poinar and Shaw's (2007) original account, such as the foveate occipital carina, the metacoxae with carinate sculpturing on dorsal surface, and the metafemora and metatibiae with long erect setae. All tarsomeres I–IV have a row of 5–6 apical spines on ventral surface (not figured herein).

DISCUSSION

The revised hierarchical classification of Megalyridae, including the new taxa described herein, is summarized in Appendix 1. The present study of several new fossils shows a few characters previously used as diagnostic within the family to be incorrect: the mesothoracic spiracle completely surrounded by the pronotal cuticle is not a synapomorphy of all Megalyridae, as shown by the condition in *Megazar* n. gen. (and probably *Megalava* n. gen.); and the putative synapomorphies proposed for separating the two tribes Dinapsini and Cretodinapsini are no longer supported, since *Megallica* n. gen. shows the combination of a forewing with vein Rs being tubular both basally and apically (synapomorphy of the Dinapsini according to Shaw, 1990b), and the presence of a longitudinal median sulcus on vertex (possible synapomorphy of the Cretodinapsini). A new phylogenetic analysis of morphological characters, including all fossil and extant megalyrids, is needed to clarify the definition of these two tribes and the internal classification of the family, which appears to be too finely split. In such an analysis, several groups should be combined for greater information on relationships.

It is noteworthy that all fossil megalyrids are known from regions where they are entirely absent today (see Appendix 1). This is arguably related to environmental changes in the last 20 million years, since they were present in tropical and equable climate forests (*sensu* Archibald & Farrell, 2003) of the northern hemisphere during the Cretaceous and Paleogene and are now mainly restricted to tropical and austral regions. Thus, climatic changes have had drastic consequences on their distribution.

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Appendix 1. Current hierarchical classification of Megalyridae; E = extant; F, † = fossil.

Classification	Temporal and spatial distribution
Megalyridae Schletterer, 1889	
Tribe †Cretodinapsini Rasnitsyn, 1977	
Genus †*Cretodinapsis* Rasnitsyn, 1977	
†*C. caucasica* Rasnitsyn, 1977	F: Cenomanian [Azerbaijan amber]
Genus †*Prodinapsis* Brues, 1923	
†*P. janzeni* Perrichot, new species	F: Eocene [Baltic, Rovno amber]
†*P. minor* Brues, 1933	F: Eocene [Baltic amber]
†*P. oesiensis* Perrichot, new species	F: Eocene [French amber]
†*P. pumilio* Perrichot & Perkovsky, new species	F: Eocene [Ukrainian Rovno amber]
†*P. succinalis* Brues, 1923	F: Eocene–Oligocene [Baltic, Saxonian amber]
Genus †*Rubes* Perrichot, new genus	
†*R. bruesi* Perrichot, new species	F: Eocene [Baltic amber]
Genus †*Ukrainosa* Perrichot & Perkovsky, new genus	
†*U. prolata* Perrichot & Perkovsky, new species	F: Eocene [Ukrainian Rovno amber]
Tribe Cryptalyrini Shaw, 1990b	
Genus *Cryptalyra* Shaw, 1987	
C. colombia Shaw, 2003	E: Colombia
C. depressa Azevedo & Tavares, 2006	E: Brazil
C. plaumanni Shaw, 1987	E: Brazil
Genus *Carminator* Shaw, 1988	
C. affinis Shaw, 1988	E: Malaysia
C. ater Shaw, 1988	E: Thailand
C. cavus Shaw, 1988	E: Taiwan
C. helios Mita, Terayama, & Yamane, 2007	E: Japan
C. japonicus Mita & Konishi in Mita & others, 2007	E: Japan
C. nooni Shaw, 1988	E: Papua New Guinea
Tribe Dinapsini Waterston, 1922	
Genus *Dinapsis* Waterston, 1922	
D. albicoxa Hedqvist, 1967	E: Madagascar
D. centralis Shaw & van Noort, 2009	E: Central African Republic
D. hirtipes Hedqvist, 1967	E: Madagascar
D. nubilus Hedqvist, 1967	E: Madagascar
D. oculohirta Hedqvist, 1967	E: Madagascar
D. seyrigi Hedqvist, 1967	E: Madagascar
D. turneri Waterston, 1922	E: South Africa
Genus *Neodinapsis* Shaw, 1987	
N. peckorum Shaw, 1987	E: Chile
Genus *Ettchellsia* Cameron, 1909	
E. philippinensis Baltazar, 1962	E: Philippines
E. piliceps Cameron, 1909	E: Borneo
E. sinica He, 1991	E: China
Genus †*Valaa* Perrichot, new genus	
†*V. delclosi* Perrichot, new species	F: Aptian–Albian [Spanish amber]
Tribe Megalyridiini Shaw, 1990b, nomen correctum	
Genus *Megalyridia* Hedqvist, 1959	
M. capensis Hedqvist, 1959	E: South Africa
Tribe Megalyrini Schletterer, 1889	
Genus *Megalyra* Westwood, 1832	
M. aquilonia Shaw, 1990a	E: Australia
M. australia Girault, 1925	E: Australia
†*M. baltica* Poinar & Shaw, 2007	F: Eocene [Baltic amber]
M. brevicauda Shaw, 1990a	E: Australia
M. caledonica Vachal, 1908	E: New Caledonia
M. candata Szépligeti, 1902	E: Australia
M. exigua Shaw, 1990a	E: Australia
M. fasciipennis Westwood, 1832	E: Australia
M. globula Shaw, 1990a	E: Australia
M. gnoma Shaw, 1990a	E: Australia
M. lilliputiana Turner, 1916	E: Australia
M. longiseta Szépligeti, 1902	E: Indonesia
M. minuta Froggatt, 1906	E: Australia

Appendix 1. *Continued.*

M. nanella Shaw, 1990a	E: Australia
M. plana Shaw, 1990a	E: Australia
M. pygmaea Shaw, 1990a	E: Australia
M. rieki Shaw, 1990a	E: Australia
M. rufipes Erichson, 1841	E: Australia
M. rufiventris Szépligeti, 1902	E: Papua New Guinea
M. sedlaceki Shaw, 1990a	E: Papua New Guinea
M. shuckardi Westwood, 1851	E: Australia
M. spectabilis Shaw, 1990a	E: Papua New Guinea
M. tawiensis Petersen, 1966	E: Philippines
M. testaceipes Turner, 1916	E: Australia
M. transversistriata Girault, 1925	E: Australia
M. troglodytes Naumann, 1987	E: Australia
M. viridescens Froggatt, 1906	E: Australia
M. wagneri Fahringer, 1928	E: Australia
Tribe †Megazarini Perrichot, new tribe	
Genus †*Megazar* Perrichot, new genus	
†*M. elegans* Perrichot, new species	F: Albian [French amber]
Genus †*Megalava* Perrichot, new genus	
†*M. truncata* Perrichot, new species	F: Aptian–Albian [Spanish amber]
Tribe Rigelini Shaw, 1990b	
Genus *Rigel* Shaw, 1987	
R. chiliensis Shaw, 1987	E: Chile
Tribe incertae sedis	
Genus †*Megallica* Perrichot, new genus	
†*M. parva* Perrichot, new species	F: Albian [French amber]