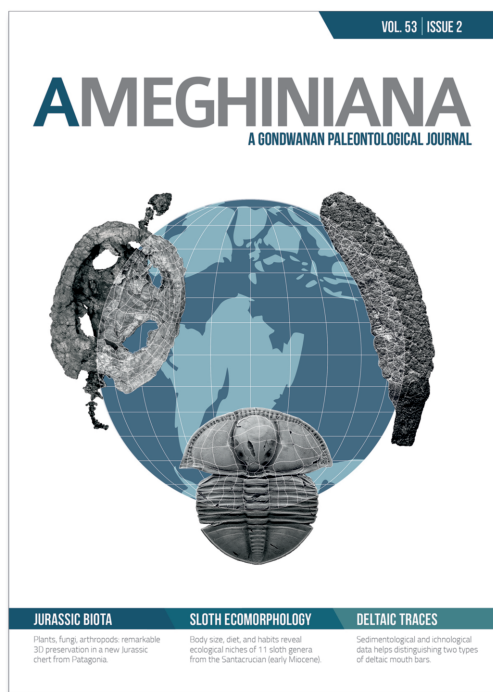




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FIRST FOSSIL RECORD OF PARASITIC FLAT-BARK BEETLE (COLEOPTERA: PASSANDRIDAE) FROM THE EOCENE OF PATAGONIA, ARGENTINA

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FIRST FOSSIL RECORD OF PARASITIC FLAT-BARK BEETLE (COLEOPTERA: PASSANDRIDAE) FROM THE EOCENE OF PATAGONIA, ARGENTINA

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Abstract. *Catogenus punctatus* sp. nov. is the first fossil species described of the family Passandridae (Coleoptera: Cucujoidea) worldwide. The specimen was collected from the Río Pichileufú fossil-bearing strata, Huitrera Formation, Río Negro, Argentina.

Key words. Passandridae. Middle Eocene. Huitrera Formation. Argentina.

Resumen. PRIMER REGISTRO FÓSIL DE ESCARABAJOS PLANOS DE LA CORTEZA (COLEOPTERA: PASSANDRIDAE) DEL EOCENO DE PATAGONIA, ARGENTINA. *Catogenus punctatus* sp. nov. es la primera especie fósil de la familia Passandridae (Coleoptera: Cucujoidea) descripta en el mundo. El espécimen fue extraído de los estratos fosilíferos de Río Pichileufú, en la Formación Huitrera, Río Negro, Argentina.

Palabras clave. Passandridae. Eoceno medio. Formación Huitrera. Argentina.

THE family Passandridae "the parasitic flat bark beetles" comprises a small group of beetles containing nine genera and about 150 extant species distributed worldwide except in the west Palearctic Region and in New Zealand (Thomas, 2002). The adults live under bark and in the tunnels of wood-boring insects and may be attracted to light at night. The larvae are ectoparasitic on the larvae and pupae of wood-boring insects, including the families Bostrichidae, Cerambycidae, Curculionidae (including Scolytinae and Platypodinae), and Hymenoptera (Burckhardt and Ślipiński, 2003).

Passandrids have been historically treated as a subfamily of Cucujidae (Casey, 1884; Bruch, 1914; Hetschko, 1930; Blackwelder, 1945), but Crowson (1955) recognized them as a distinct family. Systematics within the family were treated by Ślipiński (1987, 1989), Burckhardt and Ślipiński (1991, 1995, 2003), and Ivie and Ślipiński (2005).

Fossil record of Passandridae and related families (Cucujidae; Laemophloeidae; Silvanidae)

A number of fossil insects within the Cucujidae (*sensu lato*) and other related families were mentioned and/or described in the literature (Appendix 1). Carpenter (1992) cited only *Lithocoryne gravis* Scudder, 1900 (Coleoptera: Cucujidae), and included "*Laemophloeus*" and "*Pediacus*" among the recent genera of Coleoptera with doubtfully assigned species, but the fossil species in these genera are not cited (Appendix 1). Carpenter (1992, p. 332) also attributed the record of *Laemophloeus* from the Eocene of Wyoming to Scudder (1890), but Scudder did not include any *Laemophloeus* in the text, except that he listed *Laemophloeus* in the alphabetical index on page 50, which deals with arachnids, probably a printing error. Later, this genus was not cited by Scudder (1891) in his index of fossil insects, nor in his systematic list of the non-rhynchophorous Cenozoic Coleoptera of North America (Scudder, 1900).

Most of the references cited by Spahr (1981a) are also cited by Carpenter (1992) but others are not (Heer, 1859; Klebs, 1910; Handlirsch, 1925; Jeannel, 1942; Bachofen-Echt, 1949). Poinar (1992), based on Spahr (1981b), mentioned that representatives of Cucujidae (*sensu lato*) of the genera *Cucujus* Fabricius, 1775; *Passandra* Dalman, 1817 and *Silvanus* Latreille, 1804, occurred in Baltic amber (30–50 Ma). Cucujidae (*sensu lato*) in Dominican amber (15–20 Ma) was cited by Poinar (1992) without more details, but no records of Cucujoidea were included among the described taxa from Dominican amber (Arillo and Ortuño, 2005).

According to Burckhardt and Ślipiński (2003), some instances of Old and New World vicariations indicate that the age of the genera within Passandridae post-dates the complete separation of Africa and South America.

Hitherto no formal description of a fossil Passandridae is recorded in the literature (Appendix 1). Until 2000, no fossil insects referable to Cucujoidea were described from the Cenozoic of South America (Petrulevičius and Martins-Neto, 2000).

The study of materials from the fossil-bearing strata of the Huitrera Formation, Río Negro (Argentina), dated as middle Eocene (Wilf *et al.*, 2005 and references therein), sheds light on a well preserved specimen of Passandridae. Therefore, the main purposes of the present contribution are: 1) to describe, for the first time, a fossil Passandridae; 2) to establish the taxonomic affinities of this fossil species with extant taxa; 3) to evaluate the paleoecological implications of this fossil species.

MATERIALS AND METHODS

The specimen studied in this contribution was collected by one of us (J.C.). Originally it was partly covered, and was prepared with a thin needle. Drawings were made with camera lucida adapted to a stereoscopic microscope, and photographs were taken with a Canon EOS 50D camera using slanted light (front and side) in order to highlight the structures relief. All images have been edited and digitized using open-source software.

Measurements were made using a filar micrometer as follows: length, from apical margin of the clypeus to apex of elytra; head width, across eyes; head length from anterior margin of the clypeus to posterior margin of transverse occipital groove; antennal length, along straight from the base

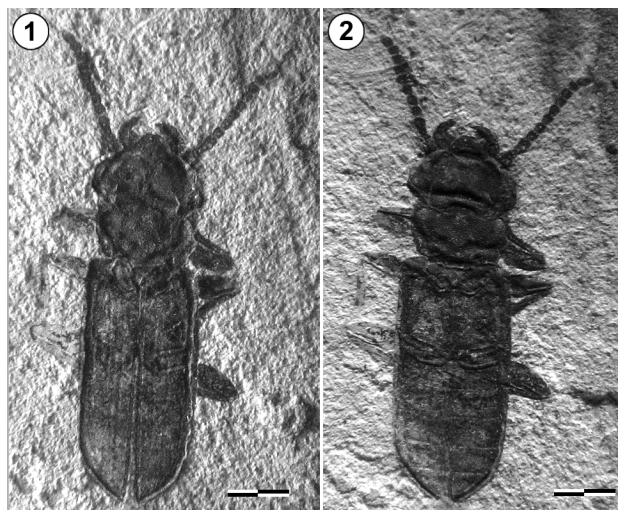


Figure 1. *Catogenus punctatus* sp. nov. General aspects. 1, slanted light highlighting the dorsal structures; 2, slanted light highlighting the ventral structures. Scale bars= 2 mm.

of scape to the extreme tip of last antennomere; pronotal length, straight from anterior to posterior margin; pronotal width, across widest point; elytral length, along the suture including scutellum.

The specimen was compared with extant taxa present in Argentina and adjacent countries housed in the collection of the last author (O.D.) in the Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires. The morphological terminology adopted here is mainly that of Ślipiński (1989).

SYSTEMATIC PALEONTOLOGY

Orden COLEOPTERA Linnaeus, 1758

Suborden POLYPHAGA Emery, 1886

Superfamily CUCUJOIDEA Latreille, 1802

Family PASSANDRIDAE Erichson, 1845

Genus *Catogenus* Westwood, 1830

Type species. *Cucujus rufus* Fabricius, 1798.

† *Catogenus punctatus* sp. nov.

Figures 1–4

Derivation of name. The name refers to the densely punctuated pronotum of the specimen.

Type material. Julián Corsolini leg., labeled "*Catogenus puncta-*

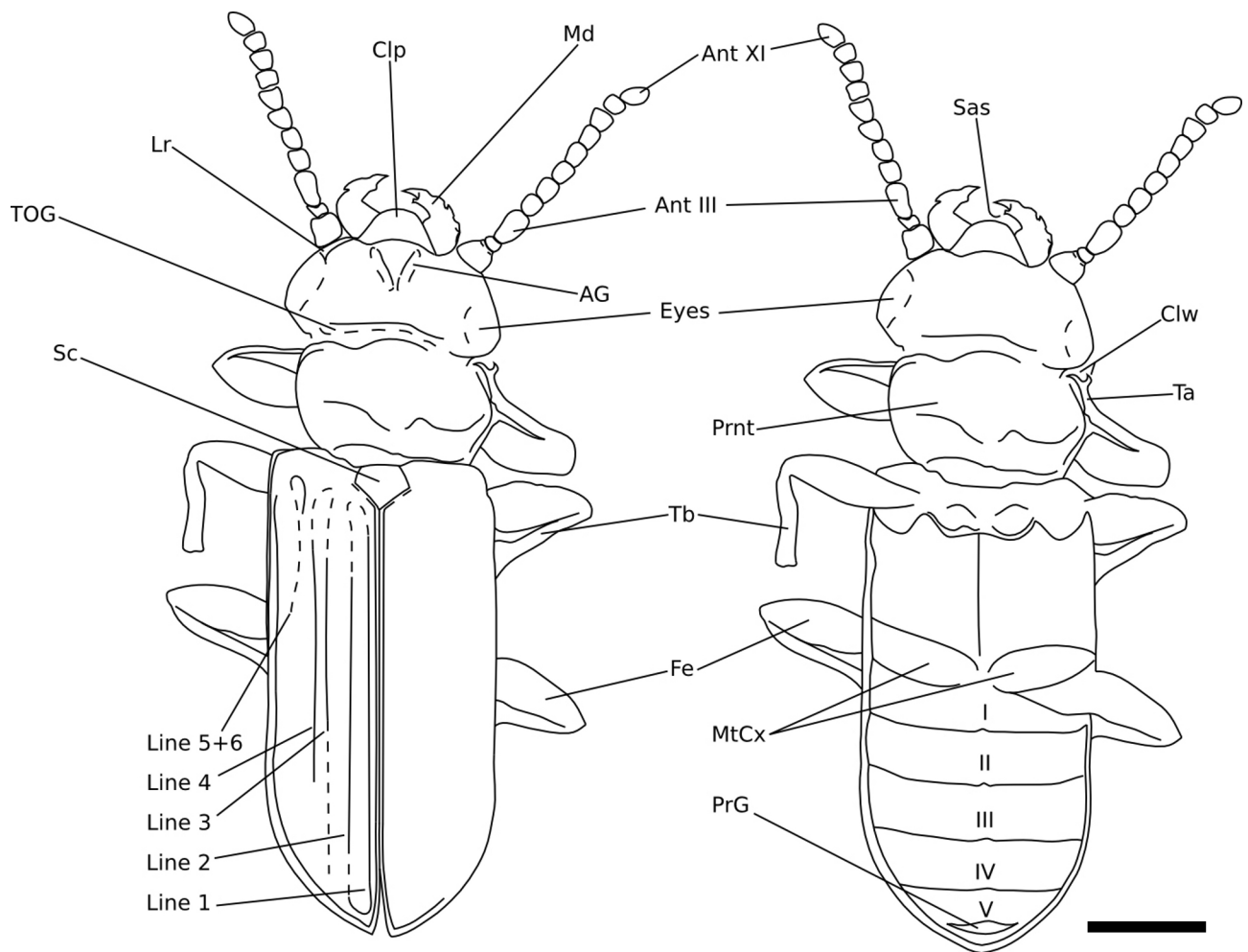


Figure 2. Camera lucida drawing of *Catogenus punctatus* sp. nov. **Abbreviations:** AG, admedial grooves; Ant, antennomere; Clp, clypeus; Clw, claws; Fe, femorae; Lr, lateral ridge; Md, mandible; MtCx, metatoracic coxae; PrG, preapical groove; Prnt, pronotum; Sas, subapical structure; Sc, scutellum; Ta, tarsus; Tb, tibiae; TOG, transverse occipital groove. Scale bar = 2mm.

tus / Ramírez, Corsolini / and Di Iorio, sp. nov. / Holotypus", # 1158, deposited in the Museo del Lago Gutierrez "Dr. Rosendo Pascual", Villa Los Coihues, San Carlos de Bariloche, Río Negro, Argentina.

Type-locality. Argentina, Río Negro, near Estancia Don Hipólito, 41° 09' 26.06" S, 70° 49' 57.11" W, about 60 km east from San Carlos de Bariloche.

Type-stratum and age. Río Pichileufú fossil-bearing strata, Huitrera Formation, middle Eocene, 47.46 ± 0.05 Ma, based on $^{39}\text{Ar}/^{40}\text{Ar}$ dating of sanidine phenocrystals from stratigraphically related tuffs (Wilf *et al.*, 2005).

Description. Adult stage. Body length 11.75 mm. Color uniformly brown; dorsal surface densely punctuated. Head transverse (Fig. 1), length 3.95 mm, width 4.15 mm; admedian grooves shallow and barely developed; transverse oc-

cipital groove clearly defined (Fig. 2); lateral ridge visible only in the anterior portion; eyes very large, lateral, rounded, exceeding the lateral margins of the head (Figs. 1–2). Antennae stout, 4.95 mm long, 11-segmented, inserted in front of the eyes (Figs. 1–2); antennomere III longest, IV–X subequals, and XI slightly asymmetrical and distally pointed (Fig. 3). Clypeus wide, subtriangular and prominent between mandibles (Figs. 1–2, 4). Mandibles large and inwardly curved (Figs. 1–2), the base three times wider than the distal portion with a subapical structure in the incisor edge of the right mandible (probably product of deformation). Pronotum transverse (Figs. 1–2), length 2.85 mm, width 3.05 mm, densely and regularly punctuated; anterior angles obtuse; lateral margins entirely visible, slightly constricted in the posterior portion.

Scutellum pentagonal, well developed. Elytra 7.80 mm length, lateral margins parallel, posterior external margin rounded (Fig. 1); humeral carina not evident; lines 1–4 completely grooved, line 5 evident only in the basal portion, line 6 joined to line 5 behind the shoulder; interval sculpture not evident. Legs stout (Figs. 1–2); femorae swollen and tibiae slender; no spurs or spines shown. Tarsus of the right prothoracic leg visible bearing two subequal claws. Metacoxae separated (Fig. 2), metasternite suture underlies the elytral junction and not visible. Abdomen with five subequal sternites (Fig. 2); sutures between sternites straight (Fig. 2); last sternite with a preapical groove poorly developed.

TAXONOMIC DISCUSSION

Affinities with Cucujidae. The related family Cucujidae is characterized by having the tarsi usually 5-5-4 segmented in males, sometimes 4-4-4 in both sexes; the tarsomeres II

and III not lobed below, the tarsomere I shorter than IV; the front coxal cavities usually open or narrowly closed behind; and the antennae usually filiform (Crowson, 1967).

The genus *Cucujus* (type-species *Cucujus clavipes* Fabricius, 1775), *sensu* Lee and Satô (2007), may be separated from the fossil specimen by the large head, transverse, often distinctly triangular with well-developed temples; antennae with 11 antennomeres, filiform to nearly moniliform, laterally inserted, insertion hidden; pronotum quadrate, usually smaller than the head (except *Cucujus chinensis* Lee and Satô, 2007), without anterior angles, laterally margined, dentate or denticulate, disc usually with depressions (without depressions in *Cucujus mnischevi* Grouvelle, 1874 and *C. chinensis*); scutellum pentagonal; elytra irregularly punctate, not striated; scutellary striole absent.

Nevertheless, some characters are shared between *C. punctatus* sp. nov. and *Cucujus*: body elongate, parallel-sided

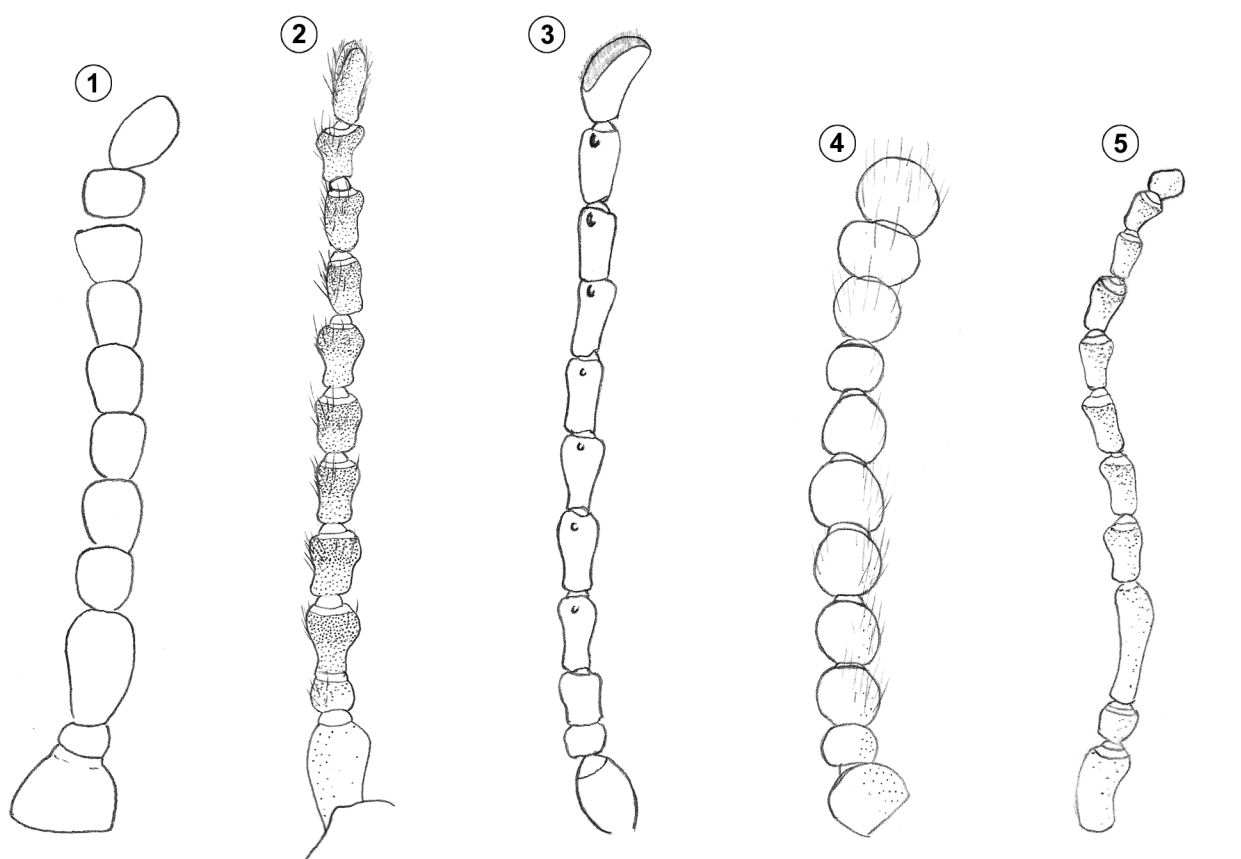


Figure 3. Antennae. 1, *Catogenus punctatus* sp. nov.; 2, *Catogenus castaneus*; 3, *Passandra fasciata*; 4, *Taphroscelidia semicastanea*; 5, *Palae-tes freyreissi*. Scale bars= 1 mm.

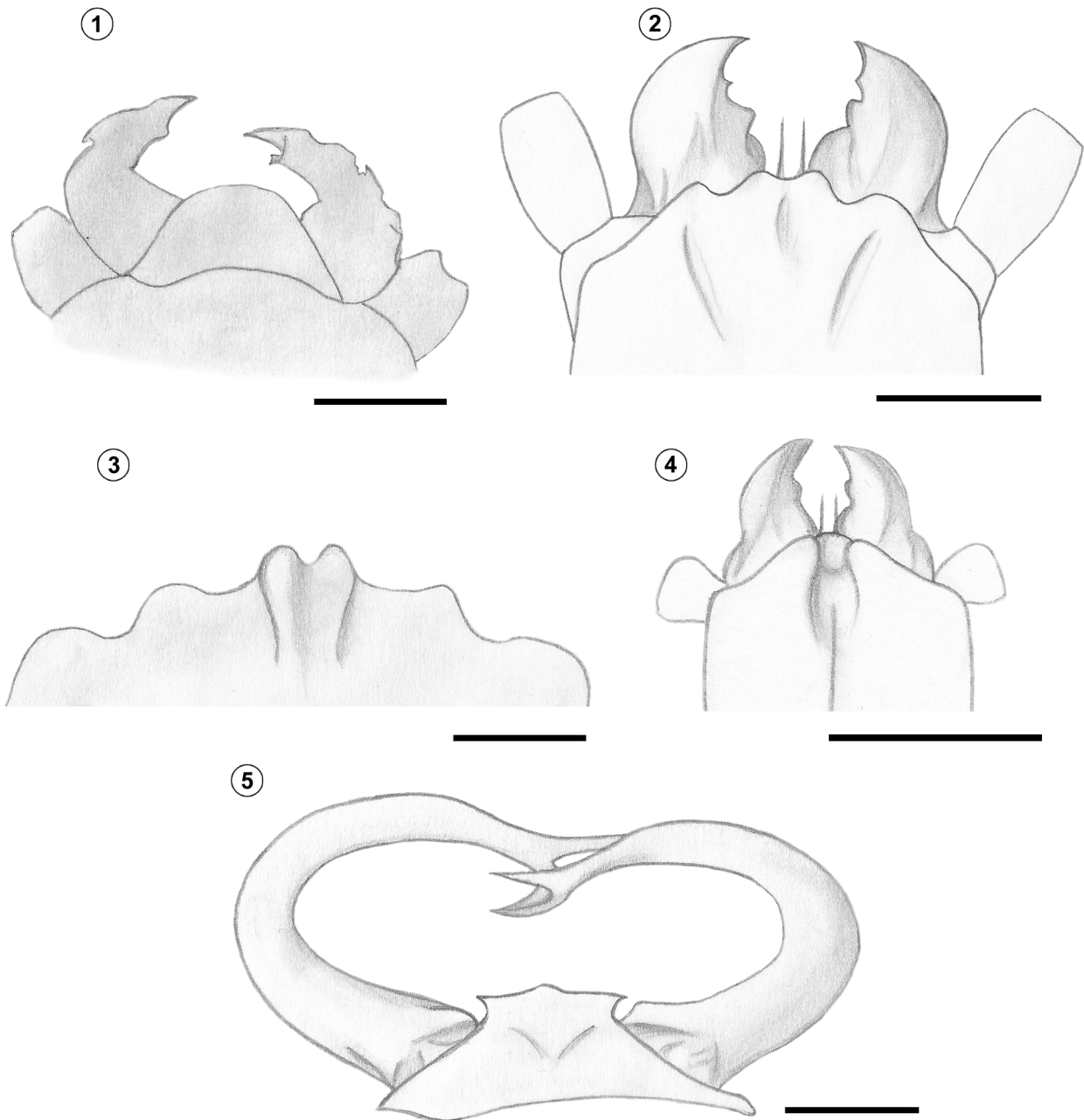


Figure 4. Clypeus. 1, *Catogenus punctatus* sp. nov.; 2, *Catogenus longicornis*; 3, *Passandra fasciata*; 4, *Taphrosclidia semicastanea*; 5, *Palaestes freyreissi*. Scale bars= 1 mm.

(Figs. 1–2), strongly flattened dorsoventrally; head densely punctate; antennae with 11 antennomeres, without a distinct club, antennomere III longest (Fig. 3); mandibles large, robust; abdomen with five visible sterna (Fig. 2), sutures entire. Some other characters are also shared with the cucujid beetle *Palaestes freyreissi* (Fig. 5): the third antennomere longer than the scape and all remaining articles (Fig. 3), and the clypeus broadly projected between mandibles (Fig. 4).

These characters are probably plesiomorphic in a phylogenetic line leading from Cucujidae to Passandridae.

Affinities with Silvanidae. The family Silvanidae was separated from Cucujidae by the tarsi 5-5-5 segmented in both sexes; the tarsomere III distinctly lobed below; the tarsomere IV shorter than I; the front coxal cavities broadly closed behind; and the antennae usually clubbed. The genus *Silvanus* (type-species *Ips unidentata* Olivier, 1789) may be

distinguished by the scape broader than segments 2 to 8; the prothorax longer than broad, with the anterior angles of pronotum poorly to strongly developed, and the lateral margins finely serrated with 15–20 denticles, each bearing a seta, and the elytra with nine rows of punctures forming striae (Halstead, 1973).

The characters related to coxal cavities and tarsi are not visible in the fossil specimen, except the clearly visible antennae that are not clubbed (Fig. 3). Therefore, the fossil specimen does not belong to Silvanidae, which also have a different prothoracic shape (Halstead, 1973).

Affinities with Passandridae. Passandridae were first separated by Crowson (1967) from all other families of Cucujoidea Section I in a key based on the confluent gular sutures; the tarsi 5-5-5 segmented in both sexes, with the tarsomere I usually small, none of the segments lobed below; the maxillae usually concealed by outgrowths of head-capsule (in ventral view); the front coxal cavities small and rounded, open to almost closed behind; the front coxae strongly transverse but with outer parts enclosed; the middle coxal cavities externally closed by meeting of meso- and metasterna; the antennae rarely clubbed, usually somewhat moniliform; the metaendosternite of hylecoetoid type, with narrow stalk and anterior tendons close together.

According to Burckhardt and Ślipiński (2003), Passandridae are also recognizable by their large mandibles with exposed articulations (visible in the fossil specimen), with a single apical tooth and rarely with smaller, blunt, subapical tooth on the incisor edge (the first state visible); strongly unequal tibial spurs (not visible); heavily sclerotized body (visible); externally reduced labrum (not visible); stout antennae (visible), 11-segmented (visible), without distinct club (visible), usually with marginal keel along external edge of the terminal antennomere (not visible); latero-dorsal antennal insertion, under front ridges in front of eyes (visible); very short clypeus, narrow and prominent between mandibles (this last state visible); frons and vertex with at least lateral ridge (visible), usually with admedian carinae or grooves (visible); eyes large, lateral (visible), without interfacettal setae (not visible); prothorax with complete or almost complete and smooth lateral edges (not visible); pronotum often with incomplete or complete sublateral (paramarginal) line or ridge (not visible); metacoxae transverse, narrowly separated (visible); wings always present

(not visible); legs stout (visible in part), femora swollen (visible), tibiae with sharp but smooth external edges (partially visible), usually with pointed or hooked outer apical angles (not visible); apical tibial spines strongly unequal (not visible); tarsi (only visible the foretarsi with the apical segment bearing two subequal claws) and claws (visible); abdomen of five ventrites (visible), freely movable (not visible); functional spiracles on segments 1 to 7 (not visible); ventrite 1 subequal to 2 (visible); last ventrite often with preapical groove (visible) [most ventral characters enumerated by Burckhardt and Ślipiński (2003) were omitted here].

Regrettably, ventral characters relative to gular sutures, coxal cavities and tarsi are not visible in the fossil specimen, except the clearly visible antennae somewhat moniliform (Figs. 1–3) as in Passandridae. Because of the other visible characters of Passandridae listed above, and its general aspect (Figs. 1–2, 5), the fossil specimen is here assigned to this family. Among the characters that Burckhardt and Ślipiński (1991, 1995, 2003), and Ślipiński (1987, 1989) used to define the genus *Catogenus*, the following ones are recognizable in the fossil specimen: head with admedian grooves never reaching occipital grooves; antennomeres lacking ventral impressions or grooves; last antennomere asymmetrical and distinctly keeled apically; sublateral lines on pronotum almost absent or vestigial; elytral line 1–4 well-developed and deeply grooved; last abdominal ventrite with preapical groove. Because of that, we assign the fossil specimen to this genus.

Catogenus punctatus sp. nov. can be recognized by the following combination of characters: dorsal surface densely punctured; antennomere III longest (Fig. 3); clypeus wide, subtriangular, projected between mandibles (Figs. 1–2, 4); elytral lines 1–4 completely grooved and 5–6 joined behind the shoulder, and only recognizable in the proximal portion. It resembles *Catogenus asper* (Ślipiński, 1989), *Catogenus castaneus* (Perty, 1834), and *Catogenus cylindricollis* (Lacordaire, 1854) (Fig. 5) by having the elytral lines 5 and 6 joined behind the shoulder, not evident in the distal portion, the humeral carina barely developed, and the head with the median line feeble. However, it can be separated from *C. cylindricollis* by its shorter and anteriorly close admedian grooves, from *C. asper* by the well developed occipital groove (Fig. 2), and from *C. castaneus* by the shape and size of the clypeus (Fig. 4).

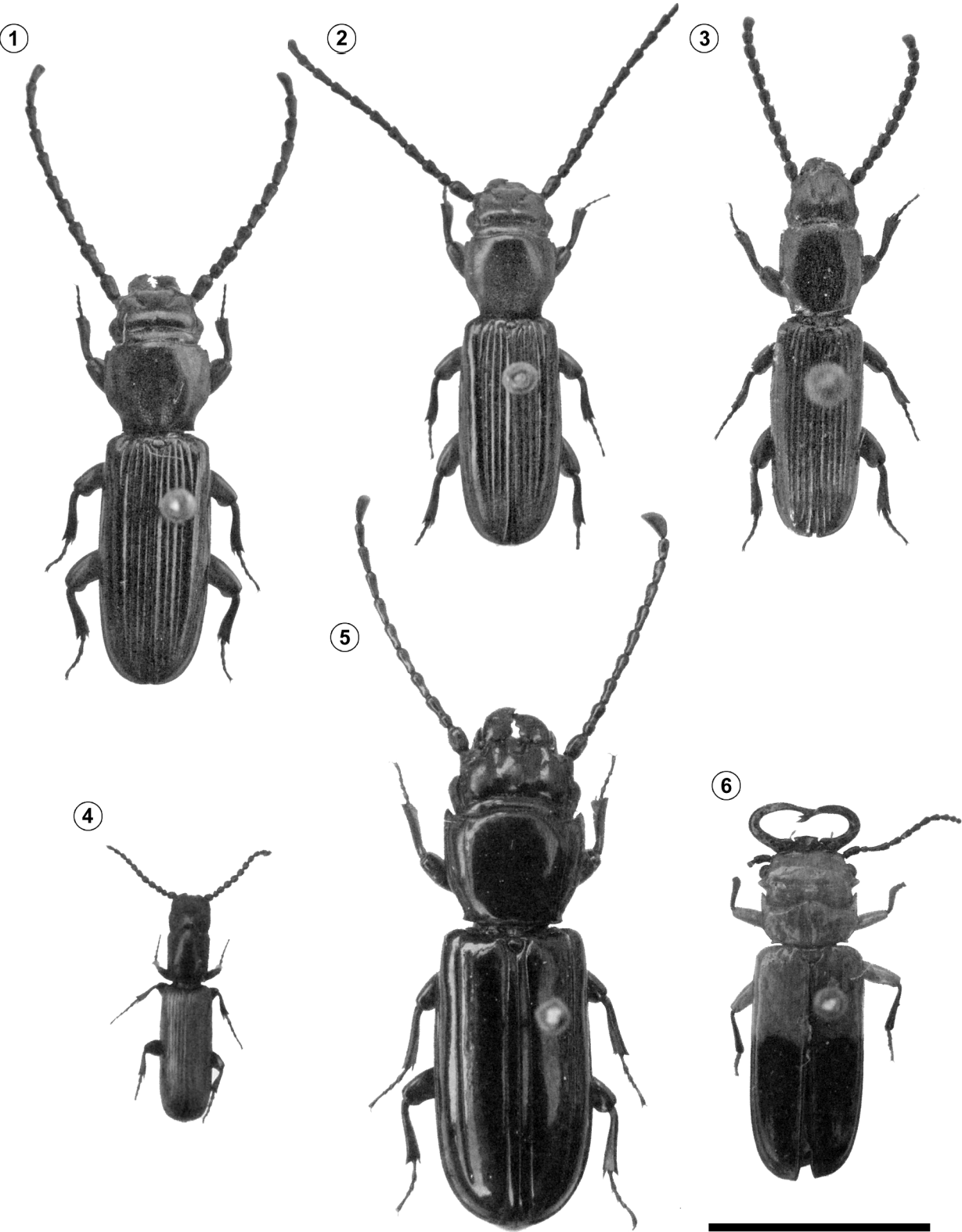


Figure 5. General aspects of Passandridae from Argentina. 1–2, *Catogenus longicornis*; 3, *Catogenus cylindricollis*; 4, *Taphrosclidia semicastanea*; 5, *Passandra fasciata*; 6, *Palaestes freyreissi* (Cucujidae). Scale bar= 5mm.

Paleoenvironmental conditions

The laminated tuffs and tuffaceous mudstones and sandstones of the Huitrera Formation occur interbedded with volcanic rocks (Báez and Pugener, 2003). These were originated by the extra-Andean magmatic arc during the Paleocene–Eocene (Melendi *et al.*, 2003) and interpreted as deposits in an ancient shallow lacustrine or swamp environment (Aragón and Romero, 1984).

The Eocene paleoclimatic scenario inferred for the fossil-bearing locality suggests warm (estimated average annual temperature $19.2 \pm 2.4^\circ\text{C}$) and humid (average annual precipitation estimate 2000 to 2500 mm) conditions, supporting a diverse subtropical vegetation (Wilf *et al.*, 2005), and based on the evidence of plant/insect interactions also a diverse insect paleocommunity (Wilf *et al.*, 2010) in the north-western Patagonian region. A progressive temperature drop with an expansion of temperate to cold-temperate biomes characterized the middle Eocene–early Oligocene time interval (Romero, 1986; Barreda and Palazzesi, 2007). From the same fossil deposit, a flower of an Asteraceae plant was figured (Barreda *et al.*, 2010). Members of Asteraceae probably inhabited dry or transitional zones between humid and dry areas, as do the majority of current species (Barreda *et al.*, 2010).

Paleoecological aspects

Passandrid beetles are currently associated to a particular habitat (ecology-specific), *i.e.* wood infested by wood-boring beetles and their parasitic wasps, and not to a particular species of wood-boring beetles (species-specific). Even the same extant species may be found in very diverse habitats, ranging from desert areas to tropical rainforests, and also they are associated to different plants with different wood-boring beetles (Di Iorio pers. obs.). *Catogenus punctatus* sp. nov. provides relevant paleoecological information, as the presence of the host's larvae and the associated flora can be indirectly inferred. The wood-boring beetles and their parasitic wasps complex should have been present and well established to support the life cycle of *Catogenus punctatus* sp. nov. This encourages us to continue the taxonomic studies in order to increase the knowledge about the insect fauna, especially beetles, and to understand the ecological complexity of this middle Eocene Patagonian biome.

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APPENDIX 1

Cucujidae

Airaphilus denticollis Ermisch, 1942: 128; Spahr 1981b: 35 (cat.).

Cucujus [sp.]: Hope 1836: 141; Klebs 1910: 238; Bachofen-Echt 1949: 110; Larsson 1978: 160; Spahr 1981b: 35 (cat.; refs.).

Europs [sp.]: Klebs 1910: 238; Bachofen-Echt 1949: 110; Spahr 1981b: 35 (cat.; ref.).

Lithocoryne gravis Scudder, 1900: 83–84 (descr.), plate IX, fig. 4. Florissant, Colorado (Oligocene), one specimen, probable complete length 5.2 mm; Carpenter 1992: 308 (cat.; ref.).

Nausibius [sp.]: Klebs 1910: 238; Bachofen-Echt 1949: 110; Larsson 1978: 160; Spahr 1981b: 35 (cat.; refs.).

Parandrita vestita Scudder, 1890: 501–502 (descr., compared with *Parandrita cephalotes* LeConte), pl. 7, fig. 41. Green River, Wyoming (Oligocene), four specimens, Nos. 87, 83, 85, 95; Scudder 1891: 563 (cat.; ref.); Scudder 1900: 84 (ref.; distr.): **not cited by Carpenter (1992)**.

Pediacus periclitans Scudder, 1900: 82–83 (descr.), plate IX, fig. 7. Florissant, Colorado (Oligocene), one specimen, length 3.5 mm; Carpenter 1992: 332 (cat., only as *Pediacus*; ref.).

Platysus [sp.]: Klebs 1910: 238; Bachofen-Echt 1949: 110; Larsson 1978: 160; Spahr 1981b: 35 (cat.; refs.).

Passandridae

Hectarthrum [sp.]: Klebs 1910: 238; Spahr 1981b: 35 (cat.; ref.).

Passandra [sp.]: Menge 1856: 21. Prussian amber (Ligurian) [= Baltic amber from Samland Peninsula. Early Eocene to early Oligocene, according to Poinar 1992: 17, 19]; Motschulsky 1856: 28 (Collection Menge; list of genera); Heer 1859: 310; Scudder 1885: 800 (ref.); Scudder 1891: 563 (cat.); Handlirsch 1906–1908: 771; Klebs 1910: 238; Handlirsch 1925: 233; Bachofen-Echt 1949: 110; Spahr 1981b: 35 (cat.; refs.).

Passandridae: Jeannel 1942: 163; Jeannel 1949: 67; Žerichin [sic!, error by Zherikhin] and Sukačeva 1973: 19 [Russian amber]; Spahr 1981b: 35 (cat.; refs.).

Silvanidae

Pleuroceratos burmiticus Poinar, Kirejtshuk and Buckley, 2008: 250–257 (descr.; figs.). Burmese Amber (Cretaceous).

Silvanus (3 spp.): Menge 1856: 21. Prussian amber (Ligurian); Motschulsky 1856: 28 (Collection Menge; list of genera); Scudder 1885: 800 (ref.); Scudder 1891: 581 (cat.); Spahr 1981b: 35 (cat.; refs.).

Sylvanus?: Berendt 1845 (1854 ?). I: 56. Prussian amber (Ligurian); Scudder 1891: 586 (cat.).

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