# The oldest palm bug in the Lowermost Eocene amber of the Paris Basin (Heteroptera: Cimicomorpha: Thaumastocoridae)

## A. NEL, A. WALLER and G. DE PLOËG

Laboratoire d'Entomologie and CNRS UMR 8569, Muséum National d'Histoire Naturelle 45 rue Buffon, F-75005 Paris, France. Nel E-mail: anel@mnhn.fr

#### $\dashv$ ABSTRACT $\vdash$

The oldest fossil Thaumastocoridae, Protodoris minusculus n. gen., n. sp. is described from the Lowermost Eocene amber of Paris basin (France). Its phylogenetic affinities are discussed. This discovery indicates the presence of a very warm climate for the Paris basin during the Lowermost Eocene.

KEYWORDS | Insecta. Heteroptera. Thaumastocoridae. Protodoris minusculus n. gen., n. sp. French amber.

#### INTRODUCTION

The Thaumastocoridae is a small true bug family with 6 extant genera and only 3 described fossil species from the Dominican and Baltic ambers (Poinar and Santiago-Blay, 1997; Bechly and Wittmann, 2000; Slater and Baranowski, 2000). The fossil described herein is the oldest known member of this family. The Thaumastocoridae were supposed to have a relictual Gondwanian distribution, after the extant record in Australia, South India, South America, Cuba and Florida (Schuh and Slater, 1995). The present discovery supports the hypothesis of Bechly and Wittmann (2000) that 'the Gondwanian pattern of distribution (of Thaumastocoridae) is just an artefact of extinction due to climatic changes in the Tertiary.'

#### SYSTEMATIC PALEONTOLOGY

Order: Hemiptera LINNAEUS, 1758 Suborder: Heteroptera LATREILLE, 1810 Family: Thaumastocoridae KIRKALDY, 1907

#### GENUS Protodoris n. gen.

Type species: Protodoris minusculus n. sp.

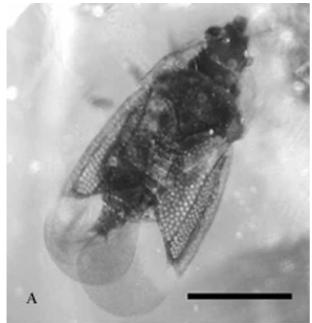
Diagnosis: Thaumastocorid genus characterized as follows: no lobate appendage at the apex of fore tibia; compound eyes not protuberant; large ocelli on a line between bases of compound eyes; antenniferous tubercles apparently not strongly protuberant; no pulvilli attached to tarsal claws; apex of corium not extending near hemelytra apex; hemelytral clavus with 4-5 rows of areolae in broadest part; membrane large, without veins except for a small vein stub; veins on corium not forming cells; broad thoracic paranota with 3 irregular rows of small areolae; lateral margin of pronotum convex; tarsal segments linear, not ellipsoidal.

Etymology: After Proto and doris in reference to its strong similarities with the extant genus *Xylastodoris*.

Protodoris minusculus n. sp.

Figures 1 and 2

| 51 | © UB-ICTJA



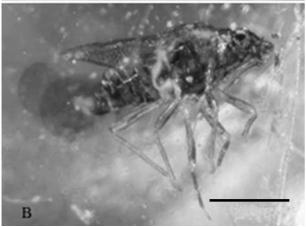


FIGURE 1 *Protodoris minusculus* n. gen., n. sp., holotype specimen PA 86 (1/2). A) Photograph of dorsal view. B) Photograph of ventro-lateral view. Scale bar: 0,5 mm.

*Material*: Holotype specimen PA 86 (1/2), mounted in Canada balsam, paratype specimen PA 7024 (1/4), with three Hymenoptera: Chalcidoidea. Collection De Ploëg and Indivision Langlois-Meurine, housed in Muséum National d'Histoire Naturelle, Paris. Specimens collected in Le Quesnoy all bear the letter PA for Paris (meaning Paris Basin), the following number is the ordinal number in the collection.

*Locality deposit*: Le Quesnoy, Chevrière, region of Creil, Oise department, France.

*Geological age*: Lowermost Eocene, Sparnacian, level MP7 of the mammal fauna of Dormaal. We have demonstrated that the amber is autochthonous and very different

from the Baltic amber in age, chemical composition and origin (Feugueur, 1963; De Ploëg et al., 1998; Nel et al., 1999; Nel et al., 2004).

Etymology: After the very small size of this species.

Diagnosis: That of the genus.

Description Dorsal surface of body and hemelytra finely to rather coarsely lacy, veinlets forming limits of areolae slightly raised; total body length, 1.36 mm; maximal width, 0.6 mm (holotype), 1.5 mm long and 0.6 mm wide (paratype).

Head: dorsum of head capsule without trichobothrium-like setae; compound eyes normal, with many ommatidia but not strongly protuberant; width between compound eyes, 80 \_m; 2 rather large and well separated ocelli, positioned on line connecting base of compound eyes; antennal segments 1 and 2 short and broad, segment 2 slightly longer than segment 1; segments 3 and 4 three times longer than basal segments, elongate, subequal, and bearing long setae; head prognathous, with large mandibular plates that are not surpassing the anteclypeus; bucculae broad but short and not protruding below or before the head, buccular bridge absent; labium inserted on ventral surface of head, rather long, reaching bases of hind coxae, 4-segmented, labial segment 1 long and slender.

Thorax: no visible channel of metathoracic scent gland; no anterior pronotal carina; paranota well developed, 0.08 mm wide, with 3 irregular rows of small areolae; lateral margin of pronotum convex; disc of pronotum flat, anteriorly produced, punctured, no collar; no visible callosities; hind pronotal margin slightly concave, not triangularly prolonged backwards; mesoscutellum large, well visible, not hidden under the pronotum, with a mucronate projection in its apical part and a row of very small spines along its lateral margins.

Forewings: macropterous; costal fracture absent; hemelytral clavus well-developed, with 4-5 rows of areolae in its broadest part; clavo-corial suture present; hyaline membrane large, without any vein and any areola, but with a small vein stub; border between corium and membrane nearly straight, corium not extending toward wing apex; corium with only one longitudinal convex vein, not divided into cells; hemelytra broadly overlapping; hemelytra areolae small and rather regular, of the same size and covering all surface except membrane area; subcostal area with 2-3 rows of areolae.

Hindwing: not visible under the hemelytra, although the abdomen is clearly visible.

Legs: tarsal claw with no basal tooth; pulvilli absent; tarsi 2-segmented, the second tarsomere being the longest, tarsal segments linear, not ellipsoidal; no lobate apical appendage on the tibiae.

Abdomen: no abdominal trichobotria; abdominal spiracle 1 present near dorsal margin of sternite; spiracles 2 to 7 ventral; ventral laterotergites not visible, probably fused with the sternites; genital appendages hardly visible, but symmetrical, thus it is probably a female specimen.

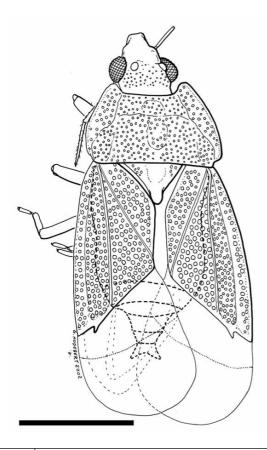


FIGURE 2 | Protodoris minusculus n. gen., n. sp., holotype specimen PA 86 (1/2), general habitus. Scale bar: 0,5 mm.

Discussion: The presence of distinct clavus, corium and membrane is a synapomorphy of the Panheteroptera (Wheeler et al., 1993). The Pentatomorpha should be excluded because of the absence of trichobotria on the abdominal sternites but two genera of Piesmatidae have also completely lost their trichobotria (Stys and Davidova-Vilimova, 2001, p. 123). The Piesmatidae can be excluded because of the absence of the pulvilli in *Protodoris* n. gen. (Wheeler et al., 1993).

Within the Cimicomorpha, *Protodoris* n. gen. shares with the Thaumastocoridae the buccular bridge absent and membrane with no cells (plus tarsi 2-segmented,

mandibular plates greatly enlarged, labial segment 1 long, abdominal spiracle 1 present, abdominal trichobotria absent) (Slater and Drake, 1958; Schuh and Stys, 1991). It differs from this family in the presence of a vein stub in the membrane but this character is homoplastic within the clade 'Miriformes' *sensu* Schuh and Stys (1991).

The Thaumastocoridae are currently divided into two subfamilies Thaumastocorinae Kirkaldy, 1907 and Xylastodorinae Barber, 1920. Heiss and Popov (2002) recently transferred the subfamily Thaicorinae Kormilev, 1969 (one extant genus Thaicoris KORMILEV 1969) from the Piesmatidae into the Thaumastocoridae. The Thaumastocorinae are characterized by the presence of a lobate appendage at the apex of fore tibia and the compound eyes strongly protuberant (Schuh and Stys, 1991; Bechly and Wittmann, 2000). Both these autapomorphies are absent in Protodoris n. gen. The Xylastodorinae would be characterized by two possible autapomorphies: 'loss of both parameres' and 'conspicuously projecting antenniferous tubercles' (Slater and Brailovsky, 1983; Bechly and Wittmann, 2000). The antenniferous tubercles of Protodoris n. gen. seem to be not strongly protuberant, and its male genital structures are unknown. The Xylastodorinae are also 'characterized' by: 'presence of pulvilli attached to the tarsal claws' and 'apex of corium extending near hemelytra apex' (Slater and Drake, 1958; Schuh and Slater, 1995). Both these character states are not present in *Protodoris* n. gen. but their polarities are not determined.

Furthermore, the Xylastodorinae have a very particular corium extending near hemelytra apex and divided into several cells, unlike Thaumastocorinae and Joppeicidae. Both these characters could be autapomorphies of the Xylastodorinae, but the Tingidae also have the corium divided into large cells and no membrane. Thus they could also be homoplastic within the Miriformes.

Protodoris n. gen. has none of the currently accepted autapomorphies of the Thaumastocorinae or of the Xylastodorinae. Nearly all its characters appear plesiomorphic relative to these two subfamilies. The only putative synapomorphy of Protodoris n. gen. with the xylastodorine genera Xylastodoris BARBER 1920 (Recent), Proxylastodoris HEISS and POPOV 2002 (fossil), and Paleodoris POINAR and SANTIAGO-BLAY 1997 (fossil) is the 'broad thoracic paranota', only present in these genera within the Thaumastocoridae, but clearly more developed in Paleodoris and Protodoris n. gen. The second extant and fossil xylastodorine genus Discocoris KORMILEV 1955 has not this structure (Barber, 1920; Drake and Slater, 1957; Poinar and Santiago-Blay, 1997; Slater and Baranowski, 2000). The ocelli of *Protodoris* n. gen. are aligned with the eyes as in Xylastodoris, other Thaumastocoridae and Joppeicidae, unlike what occurs in Pale*odoris*. This character state is probably plesiomorphic. Lastly, *Thaicoris* strongly differs from *Protodoris* n. gen. in its large and sharp anterior expansions of thorax and head (Heiss and Popov, 2002).

The relationship of *Protodoris* n. gen. within the Thaumastocoridae remains uncertain, even if it could be more closely related to the two genera *Xylastodoris* and *Paleodoris* than to any other genera.

Bechly and Wittmann (2000) included the only known Baltic amber palm bug in the genus Xylastodoris (X. gerdae) because 'it shares all six diagnostic characters' of the generic key proposed by Poinar and Santiago-Blay (1997). Nevertheless, they also indicated that its labium ('rostrum') 'reaches up to the posterior third of the metathoracic sternite'. This character does not agree with the description and diagnosis of the extant Xylastodoris luteolus BARBER 1920 that has a very short labium 'not reaching mid coxae' (Barber, 1920; Drake and Slater, 1957; Poinar and Santiago-Blay, 1997). After these authors, this character is one of the main differences between Xylastodoris, Paleodoris and Discocoris. Drake and Slater (1957) also used this character to separate the thaumastocorine genera. Although, this character seems to be rather homoplastic within the Thaumastocoridae, it is probably of great importance in the feeding habits of the various species. It clearly justifies a generic separation between X. luteolus and X. gerdae BECHLY and WITTMANN 2000, which has been proposed by Heiss and Popov (2002), who included *X. gerdae* in the new genus Proxylastodoris.

The present discovery suggests that the phylogenetic history of the Thaumastocoridae is much more complicated than suggested by the study of the few extant species. Also the numerous differences between *Discocoris* and *Proxylastodoris* suggest that many other extinct taxa were probably flourishing during the Early Cenozoic.

The extant Thaumastocoridae are strictly living under very warm seasonal climates, even if one species was probably introduced and adapted to the climate of Florida. Their presence in the Paris basin during the Lowermost Eocene supports the presence of such a palaeoclimate during this period in the area (Nel et al., 1999).

### **ACKNOWLEDGMENTS**

We thank the Lafarge-Granulat company for the help with the sampling of the fossil and the Langlois-Meurinne family for the authorization of working in their property. We also thank G. Hodebert (MNHN) for the realization of the habitus drawings and mounting of the figures.

# REFERENCES

- Barber, H.G., 1920. A new member of the family Thaumastocoridae. Bulletin of the Brooklyn Entomological Society, 15, 98-195.
- Bechly, G., Wittmann, M., 2000. Two new tropical bugs (Insecta: Heteroptera: Thaumastocoridae Xylastodorinae and Hypsipterygidae) from Baltic amber. Stuttgarter Beiträge zur Naturkunde, (B), 289, 11 pp.
- De Ploëg, G., Dutheil, D., Gheerbrant, E., Godinot, M., Jossang, A., Nel, A., Paicheler, J.-C., Pons, D., Rage, J.-C., 1998. Un nouveau gisement paléontologique 'Konservat-Lagerstätte' à la base de l'Eocène dans la région de Creil (Oise). In: The Palaeoecene/Eocene boundary in Europe: events and correlations. Symposium, Paris, Société Géologique de France, 108-110
- Drake, C.J., Slater, J.A., 1957. The phylogeny and systematics of the family Thaumastocoridae (Hemiptera: Heteroptera). Annals of the Entomological Society of America, 50, 353-370
- Feugueur, L., 1963. L'Yprésien du Bassin de Paris. Essai de Monographie stratigraphique. Mémoires pour servir à l'explication de la Carte Géologique Détaillée de la France, Paris, Publication du Ministère de l'Industrie, 568 pp.
- Heiss, E., Popov, Y.A., 2002. Reconsideration of the systematic position of Thaicorinae with notes on fossil and extant Thaumastocoridae (Hemiptera: Heteroptera). Polskie Pismo Entomologiczne, 71, 247-259.
- Kirkaldy, G.W., 1907. Memoir on a few heteropterous Hemiptera from Eastern Australia. Proceedings of the Linnean Society of New South Wales, 32, 762-788.
- Kormilev, N.A., 1955. Una curiosa familia de Hemipteros nueva para la fauna argentina *Thaumastotheriidae* (Kirkaldy), 1907. Revista de la Sociedad Entomologica Argentina, 18, 5-10.
- Latreille, P.A., 1810. Considérations générales sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides et des Insectes avec un tableau méthodique de leurs genres disposés en familles. Paris, ed. Schoell, 414 pp.
- Nel, A., De Plöeg, G., Dejax, J., Dutheil, D., de Franceschi, D., Gheerbrant, E., Godinot, M., Hervet, S., Menier, J-J., Augé, M., Bignot, G., Cavagnetto, C., Duffaud, S., Gaudant, J., Hua S., Jossang, A., de Lapparent de Broin, F., Pozzi, J.-P., Paicheler, J.-C., Bouchet, F., Rage, J.-C., 1999. Un gisement sparnacien exceptionnel à plantes, arthropodes et vertébrés (Éocène basal, MP7): Le Quesnoy (Oise, France). Comptes-Rendus de l'Académie des Sciences, Sciences de la Terre et des Planètes, 329, 65-72.
- Nel, A., De Ploëg, G., Millet, J., Menier, J.-J., Waller, A., 2004.
  The French ambers: a general conspectus and the Lowermost Eocene amber deposit of Le Quesnoy in the Paris Basin. Geologica Acta, 2, 3-8.
- Poinar, G.O.Jr., Santiago-Blay, J.A., 1997. *Paleodoris lattini* gen. n., sp. n., a fossil palm-bug (Thaumastocoridae, Xylosto-

- dorinae) in Dominican amber, with habits discernable by comparative functional morphology. Entomologica Scandinavica, 28, 307-310.
- Schuh, R.T., Slater, J.A., 1995. True bugs of the World (Hemiptera: Heteroptera). Classification and natural history. Comstock Publishing Associates, Ithaca and London, Cornell University Press, 336 pp.
- Schuh, R.T., Stys, P., 1991. Phylogenetic analysis of cimicomorphan family relationships (Heteroptera). Journal of New York Entomological Society, 99, 298-350.
- Slater, J.A., Baranowski, R.M., 2000. Discocoris dominicanus, a new species of palm bug from Dominican amber (Heteroptera: Thaumastocoridae). The Florida Entomologist, 83, 349-353.
- Slater, J.A., Brailovsky, H., 1983. The systematic status of the

- family Thaumastocoridae with the description of a new species of *Discocoris* from Venezuela. Proceedings of the Entomological Society of Washington, 85, 560-563.
- Slater, J.A., Drake, C.J., 1958. The systematic position of the family Thaumastocoridae. 10<sup>th</sup> International Congress of Entomology, Montréal, Proceedings, 1, 321-323.
- Stys, P., Davidova-Vilimova, J., 2001. A new genus and species of the Aphylidae (Heteroptera: Pentatomoidea) from Western Australia, and its unique architecture of the abdomen. Acta Societatis Zoologicae Bohemoslovacae, 65, 105-126.
- Wheeler, W., Schuh, R.T., Bang, R., 1993. Cladistic relationships among higher groups of Heteroptera: congruence between morphological and molecular data sets. Entomologica Scandinavica, 24, 121-137.

Manuscript received March 2002; revision accepted June 2002.