Geologica Acta, Vol.2, Nº1, 2004, 37-43
Available online at www.geologica-acta.com

The oldest fossil Tingidae from the Lowermost Eocene amber of the Paris Basin (Heteroptera: Cimicomorpha: Tingoidea)

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

ABSTRACT

The oldest accurate tingid bug, *Parazetekella eocenica* n. gen., n. sp., is described from the Lowermost Eocene amber of the Paris basin. Within the present state of knowledge on the tingid systematic and phylogeny, it probably belongs to the Phatnomatini and shows some superficial similarities with the Neotropical genus *Zetekella* DRAKE 1944. The two Lower Cretaceous 'tingid' genera *Golmonia* POPOV 1989 and *Sinaldocader* POPOV 1989 are considered as Heteroptera *incertae familiae* n. sit.

KEYWORDS **Heteroptera. Tingidae. Taxonomy. Cretaceous. Lowermost Eocene. Amber. France.**

INTRODUCTION

The Tingoidea are not very frequent in the fossil record. After Golub and Popov (1998, 1999, 2000a, b, c), no more than 23 species are known. We add the following citations to those of these authors: Lutz (1984) cited the Tingidae from the Oligocene lacustrine outcrop of Céreste (Vaucluse, France). Barrón et al. (1997) listed the Tingidae among the Miocene entomofauna of Izarra (Álava, Spain). Golub (2001) described the new tingine genus and species *Archepopovia yurii* from the Baltic amber.

Popov (1989) attributed two Lower Cretaceous genera to the Tingidae. We consider them as very dubious (see discussion below). Thus the oldest accurate record of the family Tingidae is from the Upper Eocene Baltic amber, even if the oldest known Vianaididae is Upper Cretaceous.

Drake and Ruhoff (1965) divided the Tingidae into the 3 subfamilies Vianaidinae, Tinginae and Cantacaderinae. Lis (1999) divided the Tingoidea into Vianaididae, Tingidae and Cantacaderidae. She excluded the 'Phatnomini' *sensu* Drake and Ruhoff (1965) from the 'Cantacaderidae' and considered them as a subfamily 'Phatnomatinae' of the 'Tingidae'. Alternatively, Froeschner (1996, 2001) divided the Tingoidea into Vianaididae and Tingidae, this family being subdivided into 'Tinginae' and 'Cantacaderinae' (= Cantacaderini + 'Phatnomatini' nom. amend.). Golub (2001) followed the same classification, even if he maintained the name 'Phatnomini'. Guilbert (2001) also contradicted Lis' analysis, with the 'Cantacaderinae' (= Cantacaderini + Phatnomatini) falling as a subgroup of a paraphyletic group 'Tinginae'. Thus, this analysis puts in doubt the 'traditional' subdivision of 'Tingidae' into 'Tinginae' and 'Cantacaderinae'. But it would need confirmation because Guilbert represents the Cantacaderinae by only 2 *Cantacader* spp. and one *Phatnoma* sp. After this rapid overview, it appears that the phylogenetic relationships between the main groups of Tingoidea are still badly established and not really consensual. We provisionally follow in this paper the traditional classification of Drake and Ruhoff (1965).

© UB-ICTJA

We describe a new Tingidae from the Lowermost Eocene amber of the Paris basin, representing the oldest accurate record of the family.

SYSTEMATIC PALAEONTOLOGY

Order: Hemiptera LINNAEUS, 1758
Suborder: Heteroptera LATREILLE, 1810
Family: Tingidae LAPORTE, 1832
Subfamily: Cantacaderinae STAL, 1873
Tribe: Phatnomatini DRAKE and DAVIS, 1960

GENUS ***Parazetekella*** n. gen.

Type species: *Parazetekella eocenica* n. sp.

Diagnosis: Collar well defined, transverse and well separated from pronotum by a deep furrow; pronotal disc with a broad punctuation and with three carinae; scutellum nearly completely hidden under pronotum; paranotum very broad, rounded, extending anteriorly to level of eyes, with 5 rows of broad areolae; clavus large, clearly separated from mesocorium by a clear commisura; costal area with a web of strong veins separating small groups of areolae, and very broad, broader than subcostal and discoidal areas; sutural area broad; stenocostal area absent. Gender female.

Etymology: After its close similarities with the modern genus *Zetekella*.

Parazetekella eocenica n. sp.
Figures 1 to 3

Material: Holotype specimen PA 2443, mounted in Canada balsam, in collection De Ploëg and Indivision Langlois-Meurine, deposited in Muséum National d'Histoire Naturelle, Paris. Specimens collected in Le Quesnoy

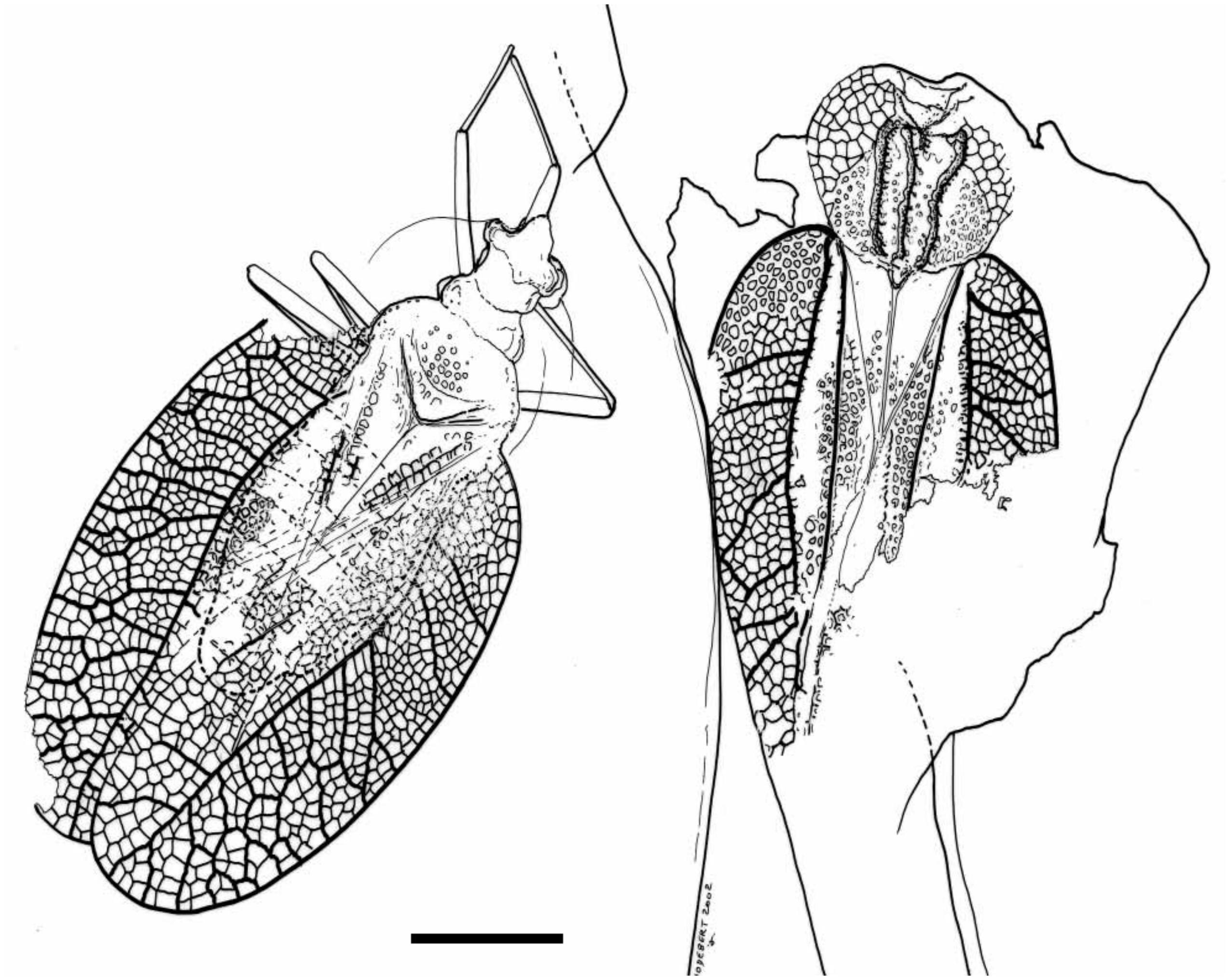

FIGURE 1 ***Parazetekella eocenica*** **n. gen., n. sp., holotype specimen PA 2443, reconstruction. As dorsal surface of pronotum was removed during the collect, it is figured separately. Scale bar: 1 mm.**

all bear the letter PA for 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 (Nel et al., 1999).

Etymology: After the Eocene age of the type outcrop.

Diagnosis: That of the genus.

Description: Body 4.62 mm long; head 0.58 mm long and 0.58 mm wide; eyes fully developed, 0.14 mm wide, with a normal number of ommatidia; eyes 0.30 mm apart; antennae missing; nearly all anterior part of head missing, with dorsal ornamentation unknown; nevertheless, head much produced in front of eyes; ocelli not preserved, if present; rostrum 0.96 mm long, ending midway between pro- and mesothoracic coxae; bucculae well developed with 2 rows of areolae.

Thorax: collar well defined, transverse, 0.68 mm wide and 0.26 mm long, wider than head, and well separated from pronotum by a deep furrow; pronotal disc 0.44 mm long, 1.10 mm wide, transverse, high, pronotal disc with a broad punctuation, with a median and 2 lateral carinae, all raised, median one highest; a broad and large triangular posterior scutellum, 0.20 mm long and 0.60 mm wide, covered with small punctuations, nearly completely hidden under pronotum; paranota very broad, reflexed, extending anteriorly to level of eyes, 0.42 mm wide, with 5 rows of wide areolae; metapleural ostiolar canal slightly arcuate, non branching and nearly vertical.

Hemelytra: completely developed, 3.34 mm long, 1.22 mm wide; all surface covered by areolae; areolae very small to large, the largest being rather regular; clavus large, 0.30 mm wide and 0.70 mm long, completely visible, clearly separated from mesocorium by a clear commisura; presence of a faint vein ACu on corium along clavus; costal area very broad, 0.78 mm wide, showing 10-12 rows of areolae separated in small groups by a web of strong veins; subcostal area narrower, 0.26 mm wide, with 3 strong transverse veinlets; discoidal area narrower than subcostal area, 0.24 mm wide, with 2-3 rows of areolae; sutural area broad, 0.64 mm wide, with 5 rows of areolae with same structure as for costal area; stenocostal area absent.

Hind wing: well developed, partly visible under hemelytra.

Legs: apices partly missing; trochanters not fused with femora; all legs long and slender, prothoracic femora 0.84 mm long.

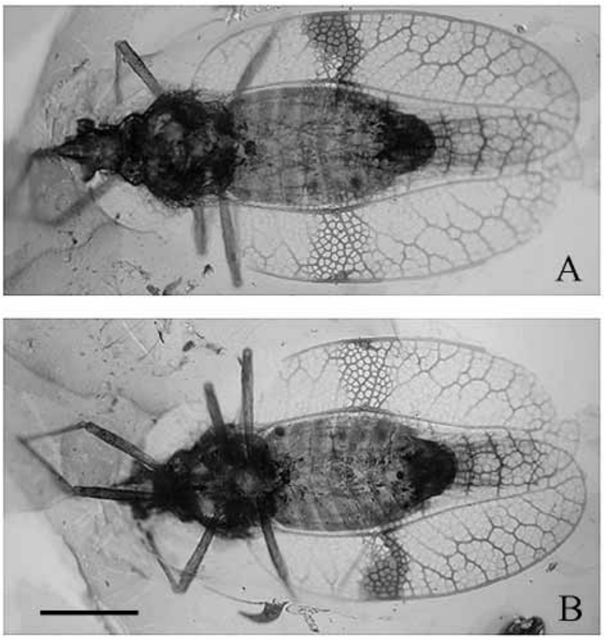

FIGURE 2 **Photography of *Parazetekella eocenica* n. gen., n. sp., holotype specimen PA 2443. A) Dorsal view. B) Ventral view. Scale bar: 1 mm.**

Abdomen 1.84 mm long and 1.08 mm wide; only sternites 2 and 3 fused ('visible abdominal segments I and II fused', Froeschner, 1996), 'separation' between them being distinctly less indicated than between other sternites; tergites and paratergites not visible (*sensu* Péricart, 1983); genitalia poorly visible.

Discussion: According to the key of Drake and Ruhoff (1965), *Parazetekella* n. gen. falls into the ['Tinginae' + 'Cantacaderinae'], rather than into the 'Vianaidinae', because of: 'normally developed eyes'; 'scutellum very small'; 'ostiolar canal simple'; 'only abdominal sternites 2 and 3 fused'. Note that Golub and Popov (2000a) attributed the Cretaceous genus *Vianagramma* to the Vianaididae, on the sole basis of the presence of a Y-shaped ostiolar canal and despite its large eyes and a relative uncertainty concerning the fusion of the abdominal sternites 2 to 5.

According to Drake and Ruhoff (1965) and Péricart (1983), the clavus completely visible of *Parazetekella* n. gen. suggests an attribution to the 'Cantacaderinae' (= Cantacaderidae + Tingidae: Phatnomatinae *sensu* Lis, 1999). *Parazetekella* n. gen. falls into the 'Cantacaderinae' (= Cantacaderini + Phatnomatini) because of the same character of the clavus plus 'sternites 2 and 3 fused only' (Froeschner, 1996, p. 4). Note that Golub (2001) indicated that 'a well developed clavus is characteristic not only of the Cantacaderini and Phatnomini, but also of many Tinginae'.

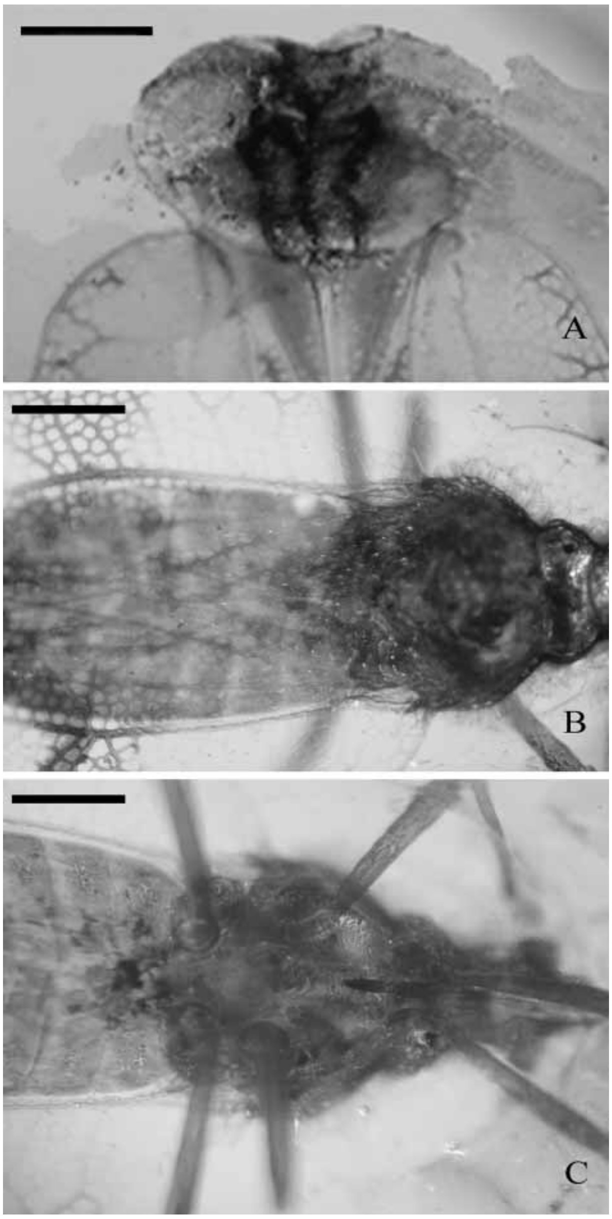

FIGURE 3 **Photography of *Parazetekella eocenica* n. gen., n. sp., holotype specimen PA 2443. A) Detail of pronotum. B) Detail of clavus. C) Detail of rostrum. Scale bar: 0.5 mm.**

In two partial phylogenetic analyses, Lis (1999) characterized the ‘Cantacaderidae’ by the following synapomorphies: (1) ‘stenocostal area present’ (see Froeschner, 1968 for definition). This character is always absent in the ‘Tingidae’ *sensu* Lis, 1999). Guilbert (2001) indicated that the ‘presence of a stenocostal area’ is an autapomorphy of the ‘Cantacaderini’. Golub and Popov (1998, 1999) noted that the ‘Cantacaderini’ have ‘a complex ostiolar-stenocostal system’, i.e. ‘separation of stenocostal area … by veins C and Sc’, unlike the ‘Phatnomini’ (= ‘Phatnomatinae’ *sensu* Lis, 1999); (2) ‘trochanter fused with femora’; (3) ‘peritreme of scent gland crevice-like’; (4) ‘lateral carinae of collar present’; (5) ‘gonoplacs membranaceous’; (6) ‘pseudospermatheca absent’. The character states (1) and (2) are absent in *Parazetekella* n. gen. The character (3) cannot be accurately observed in *Parazetekella* n. gen. The characters (5) and (6) are not visible in *Parazetekella* n. gen. Thus, *Parazetekella* n. gen. has none of the potential synapomorphies of the ‘Cantacaderidae’ *sensu* Lis (1999). On the contrary, *Parazetekella* n. gen. would share with the ‘Tingidae’ *sensu* Lis (1999) (incl. ‘Phatnomatinae’) the character ‘areolae differ in their size, sometimes they are very large and quite regular’.

In Guilbert’s (2001) analysis, the monophyly of the Cantacaderinae is supported by the following character states: (1) ‘first two antennal joints not surpassing front of head’; (2) ‘a visible clavus’; (3) ‘lack of a hind pronotal process’; (4) ‘presence of two more carinae on pronotum’; (5) ‘rounded costal area’. Character state (1) is unknown in *Parazetekella* n. gen. Character state (2), shared by *Parazetekella* n. gen., is homoplastic (one reversal). Character state (3), not shared by *Parazetekella* n. gen., is also homoplastic (one reversal and convergently present in the tinginae *Holophygdon nishidae*, after Guilbert, 2001). Character (4), not shared by *Parazetekella* n. gen., is unknown in the chosen out groups. Thus, its polarisation is made after the tree topology itself. Character (5) is curiously labelled because if a vein can be sinuate, straight or rounded, it is not so for an area.

Golub (2001) proposed, in a non-phylogenetic analysis, one ‘synapomorphy’ for the Cantacaderinae (= Cantacaderini + Phatnomatini), i.e. ‘presence of several or many additional elevating cross veins on the hemelytra’. This character seems to be present in *Parazetekella* n. gen., although the cross-veins look differently organised in *Parazetekella* n. gen. and *Cantacader*, but its polarity and value has not been tested through a phylogenetic analysis. The same author also contradicted the polarity of the character state ‘a visible clavus’ proposed by Guilbert (2001), as he indicated that this character is plesiomorphic, but without supporting this assumption through a phylogenetic analysis.

In conclusion, *Parazetekella* n. gen. shares one potential synapomorphy with the Cantacaderinae (= Cantacaderini + Phatnomatini). But this character is subject to homoplasy because it is also present in some Tinginae: ‘a visible clavus’ (Golub 2001). It has not the synapomorphies of the ‘Cantacaderini’ *sensu* Guilbert (2001), nor the synapomorphies of the ‘Cantacaderinae’ *sensu* Lis (1999) (character states absent or unknown).

After Drake and Ruhoff (1965) and Froeschner (1996), it would fall into the Phatnomatini after the absence of the stenocostal area, but Guilbert (2001) considered this character state as a plesiomorphy. After Lis (1999) and Golub (2001), the unique synapomorphy of the Phatnomatini would be the presence of the clypeal spine, but this character is unknown in *Parazetekella* n. gen.

Because of the incomplete state of preservation of the type specimen and the very preliminary present state of knowledge on the phylogeny of the Tingidae, *Parazetekella* n. gen. has a rather uncertain position within this family. Nevertheless, it is most probably related to the Phatnomatini.

Froeschner (1996) proposed a key of the modern genera of Phatnomatini. The spines of the head are important structures to separate the genera, but they are unknown in *Parazetekella* n. gen. Nevertheless, the modern genera *Astolophos* DISTANT 1904, *Cnemiandrus* DISTANT 1902, *Cyclotynaspis* MONTANDON 1892, *Daillea* PÉRICART 1991, *Distocader* FROESCHNER 1968, *Eocader* DRAKE and HAMBLETON 1934, *Etesinalda* FROESCHNER 1996, *Microcader* PÉRICART 1981, *Minitingis* BARBER 1954, *Oranoma* DRAKE 1951, *Phatnoma* FIEBER 1844, *Phatnocader* STUSAK 1976, *Plesionoma* DRAKE 1950, *Pullocader* PÉRICART 1991, *Thaicader* PÉRICART 1991 can be excluded because of the very broad and rounded paranota of *Parazetekella* n. gen. *Ulmus* DISTANT 1904 has no clear separation between clavus and mesocorium and narrower paranota. *Taphonoma* PÉRICART 1991 and *Pseudacalypta* PÉRICART 1983 have only one pronotal carina and a narrower paranotum. *Phatnomella* PÉRICART 1981 has paranota strongly angular anteriorly and extending over the head. *Indocader* PÉRICART 1981 has paranota distinctly undulate or bilobed and one pronotal carina. *Exulmus* FROESCHNER 1996 has paranota with a strong marginal sinuation subapically. *Alloeoderes* DRAKE 1961 has paranota with a broad lateral expansion making the thorax three times wider than the head. *Angiocader* DRAKE 1950 has paranota not anteriorly expanded near the eyes. *Sinalda* DISTANT 1904 (recent and fossil in Baltic amber, see Golub and Popov, 1998) has bilobed paranota, more expanded in the Baltic amber species *S. baltica* (DRAKE 1950) and *S. froeschneri* GOLUB and POPOV 1998 than in the modern species *S. elegans* DISTANT 1904. The genus *Afghanoderus* LIS 2001 has large paranota but with a strong anterior angle.

The two species of *Paraphatnomella* LIS 2000 have broad rounded paranota that extend to the level of the eyes, but with a small anterior lobe, unlike in *Parazetekella* n. gen. Furthermore, they have a relatively narrow costal area, with 2-3 rows of areolae, narrower than the discoidal area, unlike *Parazetekella* n. gen. (Lis, 2000).

The Neotropical genus *Zetekella* DRAKE 1944 (especially *Z. zeteki* DRAKE 1944) has a pronotum and paranota very similar to those of *Parazetekella* n. gen. This last genus mainly differs from it in its costal area distinctly wider than its discoidal area and divided into large groups of areolets by strong veinlets.

Among the fossil Phatnomatini, *Parazetekella* n. gen. differs from the genus *Intercader* GOLUB and POPOV 1998 (Upper Eocene Baltic amber) in its paranota extending to the level of eyes and its high pronotal carinae. The genus *Tingicader* GOLUB and POPOV 1998 (Upper Eocene Baltic amber) differs from *Parazetekella* n. gen. in its numerous spines on lateral margins of pronotum and hemelytra. The genus *Eocader* GOLUB and POPOV 2000 (Oligo-Miocene amber of Dominican Republic) has paranota distinctly less expanded than that of *Parazetekella* n. gen., with only one row of areolets in its posterior half. The genera *Miotingis* NEL 1992 (Upper Miocene, France) and *Sinaldocader* POPOV 1989 (Lower Cretaceous, Mongolia, East Siberia, Kazakhstan) have no visible paranota (Popov, 1989; Nel, 1992; Golub and Popov, 1999).

Among the other tingid fossil taxa, the general habitus of *Parazetekella* n. gen. is superficially similar to that of the Oligocene *Dictyla veterna* (SCUDDER 1890) (in Tingidae inc. sed., after Golub and Popov, 1999), i.e. a well-defined collar and a transverse pronotum. After the figure of *D. veterna* proposed in Drake and Ruhoff (1965, pl. 35), it has a large triangular structure between the hemelytra and the pronotum that could correspond either to a posterior pronotal process or to a clavus. If it is a clavus, then *D. veterna* has no posterior process. If it is a pronotal process, it is longer than in *Parazetekella* n. gen., and *D. veterna* has no visible clavus.

The Cantacaderinae genus *Golmonia* POPOV 1989 (Lower Cretaceous, Mongolia) (fossil tribe Golmoniini Popov, 1989) is based on a single hemelytra. It has a membrane without any areolae, unlike all other fossil and modern Tingidae. The Lower Cretaceous genus *Sinaldocader* POPOV 1989 also has a hemelytra membrane hyaline without any areolae (after the reconstruction proposed by Popov, 1989, figs. 4-5). Popov (1989) did not give any clear argument to support these attributions. Lis (1999, p.167) indicated that *Golmonia* 'seems rather to be allied to Thaumastocoridae', and that *Sinaldocader* 'shows two characters (structure of pronotum and the absence of stenocostal area) which allow to place it within Phatnomatinae (*sensu novo*)'. Golub (2001) indicated that both *Sinaldocader* and *Golmonia* 'have the major morphological specific features of Tingoidea – deep punctuation of very small cell structure of the surfaces and, at least in *G. pater*, an elongated head'. These characters are not unique to the Tingidae but can also be found in Piesmatidae, Berythidae, Thaumastocoridae, and many other families. Popov (2001) indicated that the presence of a 'developed sutural area and partly hyaline membrane with longitudinal veins of hemelytra allows to distinguish' these two families. Thus, *Sinaldocader* shows greater superficial similarity with the Piesmatidae than with the Tingidae. But because of the lack of information concerning the abdominal setae or the tarsal pulvilli, the attribution of these fossils to the Cimicomorpha rather than to the Pentatomomorpha cannot be supported. We consider that both *Golmonia* and *Sinaldocader* are Heteroptera *incertae sedis* n. sit.

The present discovery of a Lower Eocene European Tingidae that probably belongs to the Phatnomatini supports the remarks of Golub and Popov (1999) about the importance and diversity of the 'Cantacaderinae' among the tingid fauna of the European Paleogene. This group is now mainly tropical and subtropical. These changes are probably related to a leading role of the temperature degradation during the Neogene and Pleistocene.

Nevertheless, because of the lack of accurate and complete phylogenetic analysis of the recent Tingidae, it is not possible to infer any accurate palaeoclimatic information after the presence of fossil Tingidae in any outcrop (Nel, 1997).

The present discovery also supports the hypothesis of a division of Tingidae into the three main lineages Tinginae, Cantacaderini and Phatnomatini before the Lower Eocene, probably during the Upper Cretaceous.

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 drawing and mounting of the figures, and Dr Viktor Golub, Dr Eric Guilbert, and Dr Barbara Lis for their useful referee's comments.

REFERENCES

Barrón, L.E., Ortuño, V., Arillo, A., 1997. Estudio paleontológico del afloramiento Mioceno de Izarra (Alava, España). Estudios Museo Ciencias Naturales de Álava, 12, 5-15.

Drake, C.J., Ruhoff, F.A., 1965. Lacebugs of the World: a catalog (Tingidae). Bulletin of the United States National Museum, 243, 1-634.

Froeschner, R.C., 1968. Notes on the systematics and morphology of the lacebug subfamily Cantacaderinae (Heteroptera: Tingidae). Proceedings of the Entomological Society of Washington, 70, 245-254.

Froeschner, R.C., 1996. Lace bug genera of the World, 1: introduction, subfamily Cantacaderinae. Smithsonian Contribution to Zoology, 574, 1-41.

Froeschner, R.C., 2001. Lace bug genera of the World, 2: subfamily Tinginae: tribes Litadeini and Ypsotingini (Heteroptera: Tingidae). Smithsonian Contributions to Zoology, 611, 1-26.

Golub, V.B., 2001. *Archepopovia yurii* n. gen. n. sp. a new remarkable lace bug from Baltic amber, with some notes on phylogeny and classification of Tingidae (Heteroptera: Tingidae). Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, 85, 263-276.

Golub, V.B., Popov, Y.A., 1998. Cantacaderid lace bugs from the Baltic Amber (Heteroptera: Tingidae, Cantacaderinae). Mitteilungen aus dem Geologischen-Paläontologischen Institut der Universität Hamburg, 81, 223-250.

Golub, V.B., Popov, Y.A., 1999. Composition and evolution of Cretaceous and Cenozoic faunas of bugs of the superfamily Tingoidea (Heteroptera: Cimicomorpha). AMBA Projects Publications n°. AMBA/AM/PFCIM98/1.99, First Palaeoentomological Conference, Moscow 1998, Proceedings, 33-39.

Golub, V.B., Popov, Y.A., 2000a. A remarkable fossil lace bug from Upper Cretaceous New Jersey amber (Heteroptera: Tingoidea: Vianaididae), with some phylogenetic commentary. In Grimaldi, D.A. (ed.). Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey. Backhuys Publishers Leiden, 231-239.

Golub, V.B., Popov, Y.A., 2000b. New Cenozoic Lace Bugs (Heteroptera: Tingidae). Paleontological Journal, 34 (Suppl. 3), S.290-S.297.

Golub, V.B., Popov, Y.A., 2000c. New cantacaderid bugs from Dominican amber (Heteroptera: Tingidae: Cantacaderinae). Acta Geologica Hispanica, 35, 165-169.

Guilbert, E., 2001. Phylogeny and evolution of exaggerated traits among the Tingidae (Heteroptera: Cimicomorpha). Zoologica Scripta, 30, 313-324.

Lis, B., 1999. Phylogeny and classification of Cantacaderini (= Cantacaderidae stat. nov.) (Hemiptera: Tingoidea). Annales Zoologici, 49, 157-196.

Lis, B., 2000. *Paraphatnomella*, a new Oriental genus of Phatnomatinae with two new species (Hemiptera: Heteroptera: Tingidae). Genus, 11, 119-124.

Lis, B., 2001. *Afghanoderus mirabilis* gen. et sp. n. from Afghanistan (Hemiptera: Heteroptera: Cantacaderidae). Genus, 12, 23-27.

Lutz, H., 1984. Beitrag zur Kenntnis der Unteroligozänen Insektenfauna von Céreste (Süd-Frankreich). Documenta Naturae, 21, 1-26.

Nel, A., 1992. Nouveaux Tingidae fossiles du Cénozoïque de France (Heteroptera). Ecole Pratique des Hautes Etudes, Paris, Travaux du laboratoire de Biologie et Evolution des Insectes, 5, 97-104.

Nel, A., 1997. The probabilistic inference of unknown data in phylogenetic analysis. In: Grancolas, P. (ed.). The origin of Biodiversity in Insects: phylogenetic tests of evolutionary scenarios. Paris, Mémoires du Muséum national d'Histoire naturelle, 173, 305-327.

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, Paris, Sciences de la Terre et des Planètes, 329, 65-72.

Péricart, J., 1983. Hémiptères Tingidae euro-méditerranéens. Faune de France, Paris, Fédération Française des Sociétés de Sciences Naturelles, 69, 1-620.

Popov, Y.A., 1989. New fossil Hemiptera (Heteroptera, Coleorrhyncha) from the Mesozoic of Mongolia. Neues Jahrbuch für Geologie und Paläontologie, Monatshäfte, 166-181.

Popov, Y.A., 2001. Fossil Piesmatidae from Baltic amber (Heteroptera: Pentatomorpha: Piesmatidae). Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, 85, 211-220.

Manuscript received March 2002;
revision accepted April 2003.