

LUTETIACADER, A PUZZLING NEW GENUS OF CANTACADERID LACE BUGS (HETEROPTERA: TINGIDAE) FROM THE MIDDLE EOCENE MESSEL MAAR, GERMANY

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Abstract: A new genus of cantacaderid lace bugs, *Lutetiacader* gen. et sp. nov., is described from the lower Middle Eocene of Messel Quarry, Germany. It clearly belongs to the cantacaderid lineage of Tingidae, and is the second known fossil genus of the tribe Cantacaderini (after *Paleocader* Froeschner). It appears to be most similar to extant species of the genera *Nectocader* Drake (Brazil) and *Teratocader* Drake

(Malay Peninsula). *Lutetiacader* occupies a central position with respect to the geographical gap between the ranges of these two extant genera. Its biogeographical significance is discussed.

Key words: Heteroptera, Tingidae, Cantacaderinae, *Lutetiacader petrefactus*, historical biogeography, Eocene, Messel.

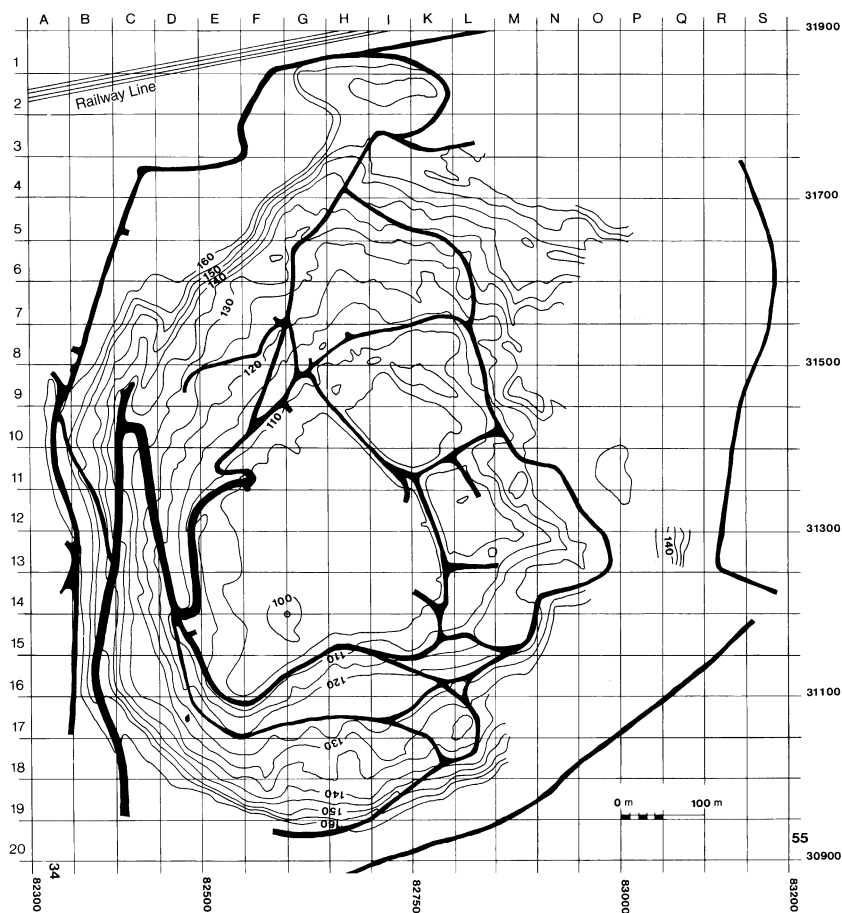
TINGIDS have puzzled entomologists for decades and prompted considerable debate. Phylogenetic relationships among the main groups of Tingoidea are poorly understood and consensus has not been reached. Lis (1999a) undertook a cladistic analysis of Tingoidea and the genera of the Cantacaderini based on 26 characters. She divided the Tingoidea into Vianaididae, Tingidae and Cantacaderinae, and suggested that the Cantacaderini are an independent family and the Phatnomini have subfamily status. In a more recent study, Guilbert (2001) was critical of the characters analysed by Lis, and carried out a new analysis based on 85 characters from 55 taxa. He recognized the Cantacaderinae (= Cantacaderini + Phatnomini) as a subgroup of the paraphyletic group Tinginae. However, this study is not appropriate to provide a solution to this problem, as the Cantacaderinae is under-sampled compared with the study of Lis (1999a). In this study I follow the classification of Froeschner (1996, 2001) with the Tingidae divided in two subfamilies: Cantacaderinae and Tinginae. The former includes three tribes: Cantacaderini, Phatnomini and Golmoniini(?). The latter includes the tribes Ypsotingini, Tingini and Litadeini.

Studies of recent material have focused on amber fossils (Baltic and Dominican amber) (Golub and Popov 1998, 2000a, 2002; Golub 2001; Heiss 2002) and several Oligocene–Miocene fossil sites in Russia, Spain and France (Golub and Popov 2000b; Wappler 2004). To date nearly 40 fossil species of Tingoidea have been described

or recorded (Wappler 2003), spanning more than 120 million years of geological history (e.g. Popov 1989; Golub and Popov 1998, 1999, 2000a–c, 2002, 2003; Golub 2001; Wappler 2003, 2004; Nel *et al.* 2004). Most of these have been described from numerous Cenozoic localities in Western Europe. Until now only a few indisputable Mesozoic fossils have been described (Popov 1989; Golub and Popov 1999, 2000c, 2003). Present knowledge about the evolution of the major groups Tingoidea (Tingidae + Vianaididae) is hampered by the scarcity of well-preserved Mesozoic fossils.

The present paper reports an interesting and unexpected new genus and species of the cantacaderid lineage of Tingidae (a cryptic cimicomorphan group of Heteroptera) from the finely laminated organic-rich sediments ('oil-shales') of Messel. It is noteworthy because the general habitus of *Lutetiacader* gen. et sp. nov. (i.e. its very broad costal area) is superficially similar to taxa that are today distributed in Brazil (*Nectocader* Drake) and on the Malay Peninsula (*Teratocader* Drake). It may help to shed light on the biogeographical history of this special group of cryptic cimicomorphan Heteroptera.

The family Tingidae is readily recognizable because of the highly ornamented wings and a hood-like structure covering the head. The adults are usually small (2–8 mm), rectangular and with an overall flattened appearance. The wings are held flat over the insect in rest, with the wing tips and outer margins extending beyond



TEXT-FIG. 1. Topographic map of the Messel maar (from Schaal and Möller 1991). Numbers represent altitude above sea level in metres; the thick lines represent paths through the pit. The specimen of *Lutetiacader petrefactus* was collected in grid square G 8/9.

the perimeter of the body. The tops of the front wings, head and thorax are membranous, composed of many raised ridges, which give a lace-like appearance (hence the common name 'lace bug').

Today lace bugs comprise over 2100 species in about 300 genera found in all major zoogeographical regions (Drake and Ruhoff 1965; Froeschner 1996). They are exclusively plant feeders, and although more species are found on herbaceous plants, the most common species occur on the foliage of trees and shrubs.

MATERIAL AND METHODS

The fossil described in this paper is deposited in the collections of the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main (SMF). The specimen was studied by immersing the slab in glycerine, which is also used to prevent oxidation. All measurements were made using an ocular micrometer, with structures measured as preserved. The terminology for wing venation and morphology was taken from Froeschner (1996). The insects of the Messel Formation were

embedded in soft, finely laminated, organic-rich clays that have been strongly compressed during diagenesis ('oil-shales') (Text-fig. 1). Therefore, they are preserved as compression fossils with only minor relief (e.g. Lutz 1990; Schaal and Ziegler 1992). Biostratigraphically, Messel represents European Mammal Reference Level MP 11. Recently, $^{40}\text{Ar}/^{39}\text{Ar}$ dating of basalt fragments from the diatreme breccia underlying the lake sediments revealed an age of approximately 47.8 Ma (D. F. Mertz, pers. comm. 2004).

SYSTEMATIC PALAEOLOGY

Suborder HETEROPTERA Latreille, 1810

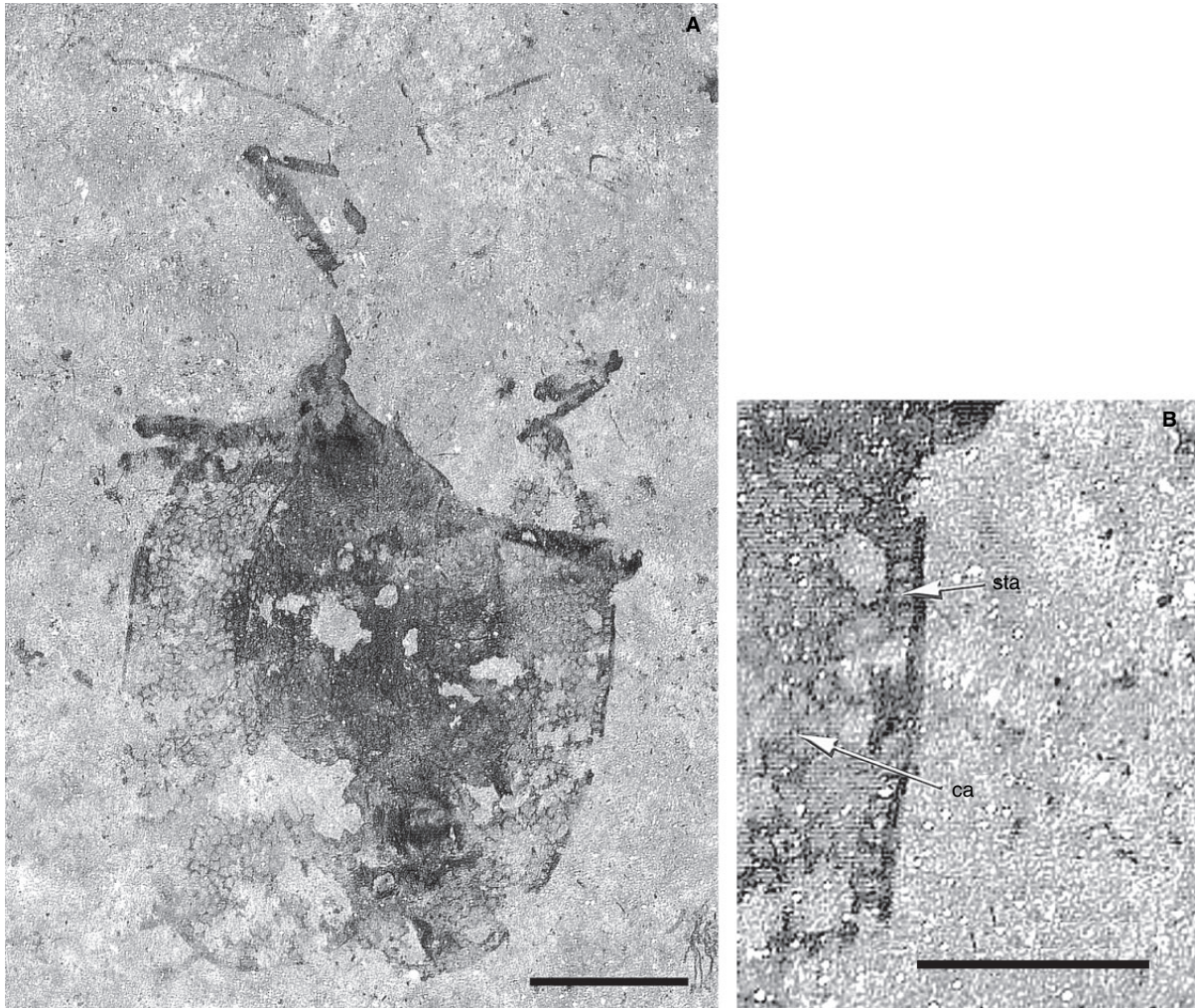
Family TINGIDAE Laporte, 1833

Subfamily CANTACADERINAE Stål, 1873

Tribe CANTACADERINI Stål, 1873

Genus LUTETIACADER gen. nov.

Derivation of name. A combination of *Lutetia* (from Lutetian, a stage of the Middle Eocene), plus the non-descriptive fragment



TEXT-FIG. 2. *Lutetiacader petrefactus*, SMF MeI 11781, holotype. A, whole specimen, dorsoventrally compressed. Scale bar represents 1 mm. B, detail of hemelytra with structure of stenocostal area. Scale bar represents 0.5 mm. Abbreviations: ca, costal area; sta, stenocostal area.

-cader from the generic name *Cantacader*, denoting another generic type in the taxon containing *Cantacader*. Gender masculine.

Type and only known species. *Lutetiacader petrefactus* sp. nov.

Diagnosis. As for the type and only known species.

Lutetiacader petrefactus gen. et sp. nov.

Text-figures 2–3

Derivation of name. A combination of the Greek and Latin words *petr*, rock or stone, and *faci*, appearance, with reference to the preservation of this species.

Holotype. Incomplete individual, head not preserved, pronotum partly missing, tarsomeres of all legs completely missing,

dorsoventrally compressed; coll. Forschungsinstitut Senckenberg (SMF), Frankfurt am Main (Germany), specimen SMF MeI 11781.

Locality and horizon. Messel Quarry near Darmstadt (Hesse, Germany). Messel Formation; 1.70–2.40 m above marker horizon α , grid square G 8/9. Known only from the lower Middle Eocene (Lower Lutetian, ELMA Geiseltalian, MP 11).

Diagnosis. Large specimen, c. 4.1 mm; body oblong-oval; antennae long and slender; pronotal disc with three carinae, posterior margin straight; scutellum exposed; paranotum narrow; hemelytra broad, finely areolated, and distinctly subdivided by raised veins into costal (broader than subcostal and discoidal areas), subcostal, discoidal and sutural areas; stenocostal area present, uniseriated; legs long, slender; gender female.

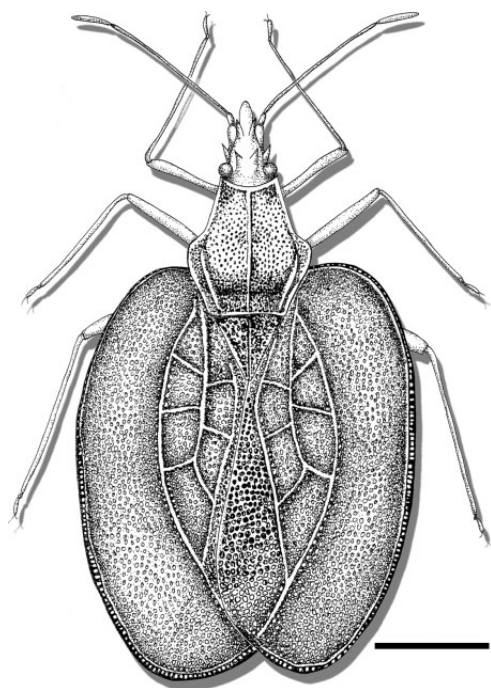
Description. Macropterous form. Total body length 4.1 mm, body width (across hemelytra on the level of the apex of clavus) 3.09 mm, length of hemelytron 3.53 mm, length of discoidal area 1.61 mm, width of stenocostal area 0.07 mm.

Antennae long and slender, probably four-segmented, fourth segment darker, pale brown; length of segments 3–4: 1.42 mm, 0.29 mm.

Pronotal disc poorly preserved; most structures are only visible as impressions on the slab; disc with three carinae; lateral carinae on the collar particularly weakly developed, not reaching the middle of pronotal disc. Posterior edge of pronotum straight; scutellum exposed, with prominent tubercle in its apical part. Paranota rather narrow.

Hemelytra very broad, abruptly dilating from bases; finely areolated, irregular. Stenocostal area uniseriate, areolae small, almost rectangular (its areolae clearly differ in shape and size from those of the costal area). Costal area bearing 11 rows of areolae in the middle part and about 14 rows of areolae in the posterior part. Subcostal area with three transverse veins. Discoidal area divided into three smaller areas by two transverse veins. Sutural area narrow.

Legs long, slender; femora with brownish patches in its distal part. Tibia elongated. Tarsi unknown.



TEXT-FIG. 3. Reconstruction of *Lutetiacader petrefactus*; scale bar represents 1 mm. [Unfortunately the head of the holotype is not preserved, so important taxonomic features, particularly the position and length of head spines, is highly hypothetical in the reconstruction. In general, the heads of Cantacaderini possess the following characters: (1) head prolonged in its preocular part; (2) head surpassing second antennal segment; (3) eyes relatively large; (4) anterior and posterior pairs of spines normally developed. Hence, the reconstruction of the head is based on the purported close affinities of *Lutetiacader* to the extant genera *Nectocader* and *Teratocader*.]

Remarks. Guilbert (2001) characterized the Cantacaderini by the following autapomorphies: (1) stenocostal area present; (2) occipital spines inserted in front of the eyes. Character state (1) is clearly visible in *Lutetiacader* gen. nov. (Text-fig. 2B) and unequivocally places it in the tribe Cantacaderini (Drake and Ruhoff 1965; Péricart 1983). Character (2) cannot be accurately observed in *Lutetiacader*, and consequently it shares only one potential synapomorphy of the Cantacaderini (*sensu* Guilbert 2001).

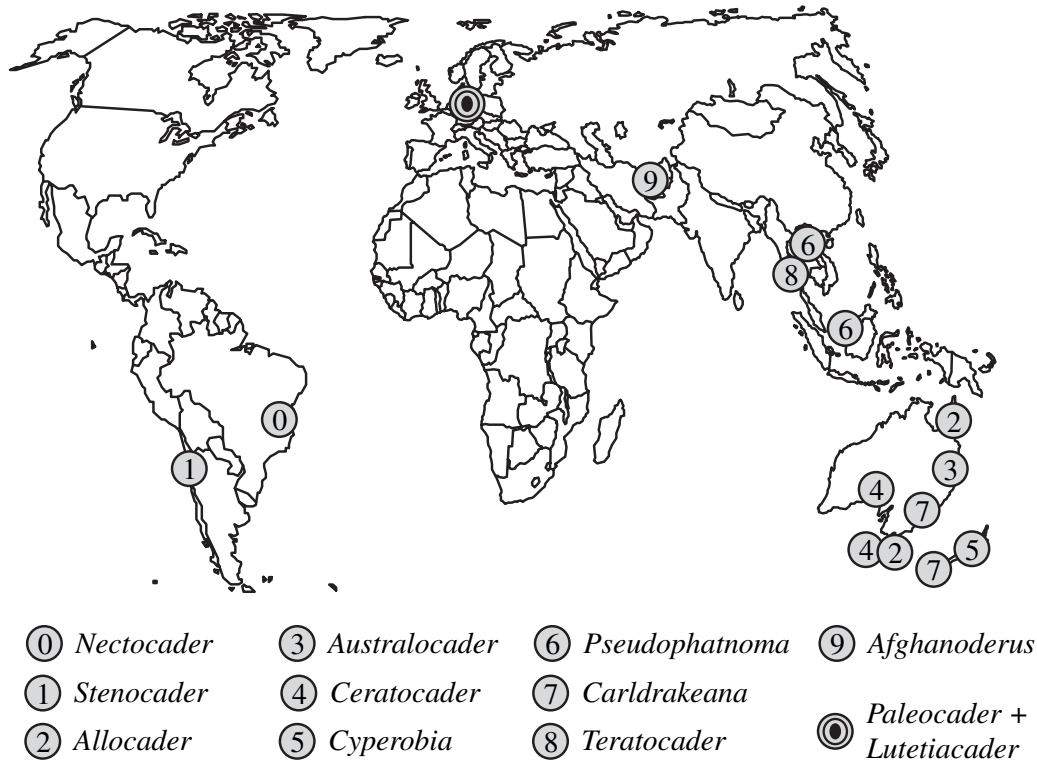
The current classification of this tribe contains 11 extant genera (Drake and Ruhoff 1965; Froeschner 1996; Lis 1999a) and one extinct genus (Froeschner 1996). Characters of the fossil *Lutetiacader* suggest it is most closely related to the genera *Nectocader* Drake, 1928 and *Teratocader* Drake, 1950; all three have very broad hemelytra, abruptly dilating from their bases, with more than ten rows of areolae in the costal area, and the stenocostal area is developed dorsally and ventrally (*Carldrakeana*, *Stenocader* and *Cyperobia* have only a ventrally developed stenocostal area, and their areolae are of the same shape and size as those of the costal area) (Text-fig. 2B). The new genus differs from *Nectocader* in having a three-carinated pronotum, a costal area bearing about 14 rows of areolae in the posterior part and a subcostal area with three transverse veins (not two). It can be distinguished from *Teratocader* because it has a three-carinated pronotum and lacks a totally exposed scutellum.

The extinct genus *Paleocader* was described by Froeschner (1996) for the fossil species *P. avitus* (Drake), *P. strictus* Golub and Popov, and *P. quinquecarinatus* (Germar and Berendt) from Baltic amber. *Lutetiacader* differs from *Paleocader* because it has the following characters: (1) only three distinctly elevated carinae; (2) posterior margin of pronotum straight; (3) subcostal area with at least three distinctly elevated crossveins.

DISCUSSION

Fossils may provide important clues to past distributions that enable us to choose among equally plausible biogeographical hypotheses. When plotted on palaeogeographical reconstructions at a given geological time, the fossil record may also suggest possible pathways of dispersal or vicariance events of the past. Below I discuss the distribution of fossil Tingidae, in particular Cantacaderinae, in a historical biogeographical context.

It seems reasonable from such a perspective that the Tingoidea as a whole are quite an ancient group. They probably arose and became differentiated rapidly during the Early to mid Cretaceous (Golub and Popov 2003; Nel *et al.* 2004), with subsequent diversification within each lineage in the early Cenozoic. Most species of the world



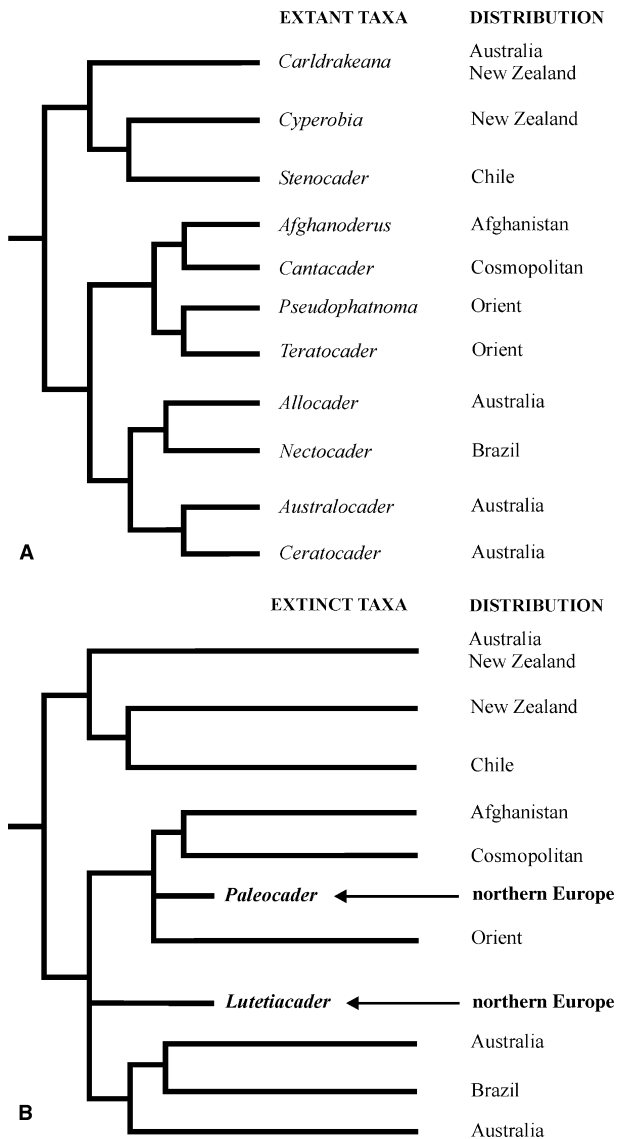
TEXT-FIG. 4. Present distribution of extant and extinct genera of Cantacaderini (without *Cantacader*) (Froeschner 1996; Lis 1999a).

TABLE 1. Distribution of extant and extinct Cantacaderini by zoogeographical regions based on Drake and Ruhoff (1965), Froeschner (1996) and Lis (1997a, b, 1999a, b, 2001a, b) (numbers = totals of genera and species).

Taxon	Neotropical	Palearctic	Oriental	Ethiopian	Madagascan	Australian	New Zealand	Oceania
Cantacaderinae								
Cantacaderini	2, 2	4, 11	3, 13	1, 19	1, 1	5, 10	2, 2	1, 3
<i>Afghanoderus</i> (1)		1						
<i>Allocader</i> (3)						3		
<i>Australocader</i> (1)						1		
<i>Cantacader</i> (42)		7	10	19	1	2		3
<i>Carldrakeana</i> (3)						2	1	
<i>Ceratocader</i> (2)						2		
<i>Cyperobia</i> (1)							1	
† <i>Lutetiocader</i> (1)		1						
<i>Nectocader</i> (1)	1							
† <i>Paleocader</i> (2)		2						
<i>Pseudophatnoma</i> (2)			2					
<i>Stenocader</i> (1)	1							
<i>Teratocader</i> (1)			1					

fauna are represented in the tropics and subtropics. The fossil genera *Paleocader* (Baltic amber) and *Lutetiocader* (Messel maar, lower Middle Eocene) are the oldest reliable fossil members of the tribe Cantacaderini, setting the

minimum age of this tribe at 50–45 Ma. However, since their sister group, the Phatnomini, are possibly as old as 120 Ma (see Appendix), the Cantacaderinae (= Cantacaderini + Phatnomini; *vide* Guilbert 2001, for phylogenetic



TEXT-FIG. 5. Taxon-area cladograms for the genera of Cantacaderini. Geographical distributions superimposed upon the cladogram of relationships between genera. A, taxon-area cladograms for extant genera (redrawn from Lis 1999a). B, the same with extinct genera included (distribution in bold type).

relationships) may have originated during the Late Cretaceous (Nel *et al.* 2004) or even earlier.

Thus, tropical and subtropical lace bugs persisted into at least the early Cenozoic in Europe but perhaps were only relict and eventually became extinct during the climatic changes marking the Eocene/Oligocene transition (Prothero and Berggren 1992, Prothero 1994; Golub and Popov 1999). It is evident that the subfamily was more or less globally distributed in the past and has undergone significant extinctions. The broader distribution and climatic range of extinct lace bug lineages are probably

linked. In particular those lace bug lineages not already adapted to colder climates in the early Cenozoic, especially most of the Cenozoic Cantacaderinae, would have faced rapid extinction. The global climate in the Cretaceous and early Cenozoic was warmer than at present. For at least the first 10 myr of the Eocene, the bulk of the Earth had climates with winter temperatures much higher than today (Greenwood and Wing 1995; Mai 1995; Collinson and Hooker 2003; Svenson *et al.* 2004). The postulated extinction at the Eocene/Oligocene transition (e.g. Prothero and Berggren 1992, Prothero 1994) left the colder-adapted lineage of the Tingidae free to diversify in the temperate habitats of the Northern Hemisphere during the latest Palaeogene and Neogene, thereby giving us the present distribution of the Cantacaderinae (Golub and Popov 1999; Wappler 2004). Most probably a replacement of the tingid fauna took place in Eurasia during the Neogene and Pleistocene (Golub and Popov 1999; Nel *et al.* 2004). This region was occupied by Tinginae, while the once-dominant Cantacaderinae were confined almost exclusively to the tropics and subtropics (Péricart 1983; Péricart and Golub 1996; Golub and Popov 1999; Lis 1999a; Golub 2001).

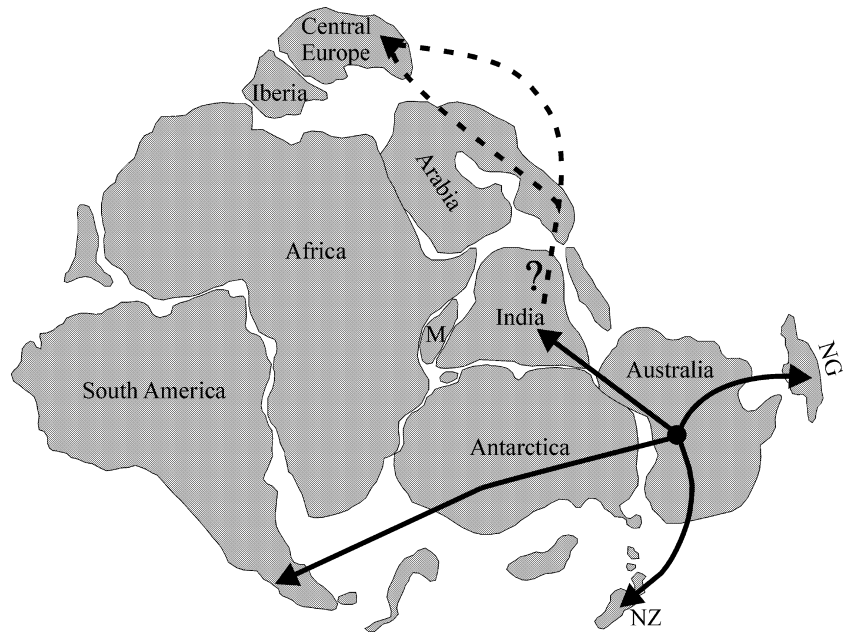
HISTORICAL BIOGEOGRAPHY

Historical biogeography is the study of patterns of spatial distribution of organisms explained by their evolutionary history. According to the dispersal model certain geographical areas were originally devoid of organisms and later colonized from some source area, whereas the vicariance model presumes that the organisms evolved *in situ*. Fossil locality data may provide important biogeographical information. When a fossil species can be placed in a monophyletic clade that also comprises extant species, the distribution of the fossil species can be compared with the known distribution of extant species belonging to the same clade. There are two possible implications of such comparisons:

1. If the fossil locality is within the distribution range of the extant clade members, it confirms that the distributional area of the taxon has persisted through geological time and the present distribution of the taxon is not necessarily an effect of recent dispersal from another area.
2. If the fossil locality is outside the distributional range of the extant clade members, it indicates that the taxon once had a wider distribution and has now disappeared in some part of its former distributional area.

The present distribution of the genera that belong to the monophyletic cantacaderid group (Lis 1999a; Golub 2001), which consists of the extant *Afghanoderus*, *Allocader*, *Australocader*, *Carldrakeana*, *Ceratocader*, *Cyperobia*,

TEXT-FIG. 6. Hypothetical ancestral area and main migrational paths of Cantacaderini in Gondwana; M, Madagascar; NG, New Guinea; NZ, New Zealand.



Nectocader, *Pseudophatnoma*, *Stenocader*, *Teratocader* and the fossil *Paleocader* and *Lutetiocader* (excluding *Cantacader*), is rather disjunct (Text-fig. 4). Today the Cantacaderini are distributed in all geographical regions that include at least one modern member of this tribe, except in the Nearctic (Table 1). *Cantacader* is restricted to the Old World. Of the other 11 genera, two are confined to the Neotropics, and two occur only in the Oriental Region. Cantacaderid genera are most abundant in the Australo-New Zealand complex, where species of six (of 11) extant genera occur (Drake and Ruhoff 1965; Froeschner 1996; Lis 1997a, b, 1999a, b, 2001a, b).

Based on a cladistic analysis of relationships between genera, Lis (1999a) applied various analytical tools to study the distribution of extant genera of Cantacaderini. When superimposed upon a cladogram of generic relationships, the occurrence of *Carldrakeana* in the Australo-New Zealand complex, *Stenocader* in Chile, and the vicariant distribution of the sister taxa *Pseudophatnoma*/*Teratocader* (Malayan Archipelago) and *Nectocader* (Brazil), suggests that the ancestors of the tribe were cosmopolitan (Text-fig. 5A). The addition of fossil genera classified in this tribe (Text-fig. 5B) provides further support for this hypothesis. Despite the geographical bias in the fossil record, the data suggest that Paleogene Europe was inhabited by a rather diverse fauna of cantacaderid lace bugs (Wappler 2003; Nel *et al.* 2004; see Appendix), in particular by the tribes Phatnomini and Cantacaderini. Today the latter is represented in Europe only by *Cantacader quadricornis* (Le Peletier and Serville) and *C. laticollis* Horváth of the cosmopolitan *Cantacader* (Froeschner 1996; Lis 1999a).

Migratory paths

I limit the description of possible migratory paths to the fossil genera of cantacaderid lace bugs, *Lutetiocader* and *Paleocader*, and the general habitus of superficially similar extant taxa, *Nectocader* and *Teratocader*. Based on all previous data, it can be assumed that the Cantacaderini originated about 140–120 Ma in a region that today belongs to the Australo-New Zealand complex (Text-fig. 6). This is mainly based on the fact that New Zealand was the first terrain to separate from Gondwana (Windley 1995). *Carldrakeana* occurs only in New Zealand and Australia. Since a close connection between Antarctica and South America persisted at least until 50 Ma (Windley 1995), *Nectocader*, which is closely related to three Australian genera (*Allocader*, *Australocader*, *Ceratocader*) (Lis 1999a), could reach the South American continent. The absence of these, or related, genera in Africa suggests that the westward migration of Cantacaderini from Australia began not earlier than 110 Ma, when Africa began to separate from South America (Petters 1991). Taxa that are distributed on the Asian continent most probably migrated there via the Indian subcontinent. All the genera known from Asia represent a single evolutionary line (Lis 1999a); moreover, *Teratocader* and *Pseudophatnoma* show close affinities to Australian genera and probably also to the South American *Nectocader*. *Paleocader* most probably radiated first in Asia, since that region was more or less isolated from Europe by the Turgai Sea during the Jurassic and Cretaceous (Briggs 1995). The beginning of a regression at about 50 Ma (Mai 1995;

Manchester 1999; Rögl 1999) enabled *Paleocader* to migrate to and radiate in Europe. Similar paths must be postulated for *Lutetiocader*. At present both genera represent the northern off-shoot of the European Cantacaderini line.

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APPENDIX

Taxonomic catalogue of fossil cantacaderid lace bugs

The following preliminary catalogue attempts to summarize the named species of cantacaderid lace bugs. Names are in taxonomic order. (†) indicates an extinct taxon.

Suborder Heteroptera Latreille, 1810

Infraorder Cimicomorpha Leston, Pendergrast and Southwood, 1954

Family Tingidae Laporte, 1833

Subfamily Cantacaderinae Stål, 1873

Tribe Golmoniini Popov, 1989

†*Golmonia* Popov, 1989, p. 172. Type species: *Golmonia pater* Popov, 1989, monobasic and original designation.

Remarks. *Golmonia* is based only on a single hemelytra and shows characters unlike all other fossil and modern Tingidae (Golub and Popov 2004). Lis (1999a) considered that *Golmonia* is allied to Thaumastocoridae whereas Nel *et al.* (2004) considered it as Heteroptera *incertae sedis*.

†*Golmonia pater* Popov, 1989, p. 172; Lower Cretaceous, Bayan-Khongor Aimak, Mongolia.

Tribe Cantacaderini Stål, 1873

†*Lutetiacader* Wappler, herein. Type species: *Lutetiacader petrefactus* Wappler, monobasic and original designation.

†*Lutetiacader petrefactus* Wappler, herein; lower Middle Eocene (Lutetian), Messel, Germany.

†*Paleocader* Froeschner, 1996, p. 13. Type species: *Cantacader avitus* Drake, 1950, monobasic and original designation.

†*Paleocader avitus* (Drake, 1950), p. 161; Eocene, Baltic amber.

†*Paleocader quinquecarinatus* (Germar and Berendt, 1856), p. 23; Eocene, Baltic amber.

†*Paleocader strictus* Golub and Popov, 1998, p. 227; Eocene, Baltic amber.

Tribe Phatnomini Drake and Davis, 1960

Eocader Drake and Hambleton, 1934, p. 436. Type species: *Eocader vergrandis* Drake and Hambleton, 1934, monobasic and original designation.

†*Eocader babyrussus* Golub and Popov, 2000a, p. 166; lower Middle Miocene, Dominican amber, Hispaniola.

†*Exmesselensis* Wappler, 2003, p. 4. Type species: *Exmesselensis dissipinosus* Wappler, 2003, original designation.

†*Exmesselensis dissipinosus* Wappler, 2003, p. 6; lower Middle Eocene (Lutetian), Messel, Germany.

†*Intercader* Golub and Popov, 1998, p. 237. Type species: *Intercader weitschati* Golub and Popov, 1998, monobasic and original designation.

Remarks. *Intercader* is particularly noteworthy because of its position within the Cantacaderinae. Golub and Popov (1998) placed it with hesitation in the tribe Phatnomini, but it also shares some morphological features of the tribe Cantacaderini.

†*Intercader weitschati* Golub and Popov, 1998, p. 238; Eocene, Baltic amber.

†*Intercader velteni* Golub and Popov, 2002, p. 246; Eocene, Baltic amber.

†*Miotingis* Nel, 1992, p. 98. Type species: *Miotingis cantalensis* Nel, 1992, monobasic and original designation.

†*Miotingis cantalensis* Nel, 1992, p. 98; Upper Miocene, Murat, Cantal, France.

†*Parazetekella* Nel, Waller and De Ploëg, 2004, p. 38. Type species: *Parazetekella eocenica* Nel, Waller and De Ploëg, 2004, monobasic and original designation.

Remarks. Because of the incomplete state of preservation and the current uncertain status of the present preliminary state of Tingidae phylogeny, *Parazetekella* has a rather uncertain position within the family. Nevertheless, it is most probably related to the Phatnomini (Nel *et al.* 2004).

†*Parazetekella eocenica* Nel, Waller and De Ploëg, 2004, p. 38; lowermost Eocene (Sparnacian), Le Quesnoy, Oise department, France.

Sinalda Distant, 1903, p. 426. Type species: *Sinalda elegans* Distant, 1903, monobasic and original designation.

†*Sinalda baltica* (Drake, 1950), p. 153; Eocene, Baltic amber.

†*Sinalda froescheri* Golub and Popov, 1998, p. 235; Eocene, Baltic amber.

†*Sinaldocader* Popov, 1989, p. 168. Type species: *Sinaldocader drakei* Popov, 1989, monobasic and original designation.

Remarks. According to Lis (1999a) and Golub (2001) *Sinaldocader* shows major morphological features of the Tingioidea. However, Nel *et al.* (2004) considered that it shows greater superficial similarity to the Piesmatidae. Because of the incomplete preservation of this specimen it is better to consider this genus as Heteroptera *incertae sedis*.

†*Sinaldocader drakei* Popov, 1989, p. 169; Lower Cretaceous, Bayan-Khongor Aimak, Mongolia.

†*Tingicader* Golub and Popov, 1998, p. 239. Type species: *Tingicader cervus* Golub and Popov, 1998, monobasic and original designation.

Remarks. *Tingicader* occupies an intermediate position between the Tinginae and Cantacaderinae, in particular within the tribe Phatnomini (Golub and Popov 1998, p. 240).

†*Tingicader cervus* Golub and Popov, 1998, p. 240; Eocene, Baltic amber.

Weitschatiella Heiss, 2002, p. 222. Type species: *Weitschatiella elenae* Heiss, 2002, monobasic and original designation.

†*Weitschatiella elenae* Heiss, 2002, p. 223; Eocene, Baltic amber.