

Phylogeny of Cantacaderinae (Heteroptera: Tingidae) revisited after the description of a new genus and new species from New Caledonia

ERIC GUILBERT

Muséum National d'Histoire Naturelle, Département de Systématique et Evolution, UMR 7205 CNRS, CP50, 57 rue Cuvier,
75005 Paris, France; e-mail: guilbert@mnhn.fr

Key words. Heteroptera, Tingidae, Cantacaderinae, description, New Caledonia, new genus, new species, phylogeny, systematics, taxonomy

Abstract. A new genus and new species of Cantacaderinae (Heteroptera: Tingidae) is described, *Caledoderus monteithi*. A key to genera is provided. The phylogenetic relationships among the Cantacaderinae, including this new genus and species, are revisited. The results are congruent with previous studies. However, the Ceratocaderini is a sister group of Carldrakeaninae and not Cantacaderini, even if only weakly supported by the analysis. Therefore, the status of Ceratocaderini and Cantacaderini is maintained, whereas Carldrakeanini stat. nov. is reduced to tribal level and they are all included in the Cantacaderinae.

INTRODUCTION

The Cantacaderinae Stål is considered to be a subfamily of the Tingidae by most authors (Froeschner, 1996; Golub, 2001; Guilbert, 2001, 2004). However, Lis (1999) reconsidered the phylogeny of the family and raised Cantacaderinae to family level. She proposed a new systematic organization of the group, splitting it into two subfamilies: Carldrakeaninae Lis and Cantacaderinae, and dividing the latter into two tribes, Ceratocaderini Lis and Cantacaderini sensu Lis. The Phatnomatini Drake and Davis were excluded from the Cantacaderinae and their position remains controversial (Guilbert, 2001, 2004; Schuh et al., 2006).

In this paper, a new genus and species are described from New Caledonia. A key to genera of Cantacaderinae is provided and the relationships within the Cantacaderinae are studied using a phylogenetic analysis based on morphology. In this analysis, I follow the taxonomic results of Schuh et al. (2006) and consider Cantacaderinae to be a subfamily of Tingidae.

MATERIAL AND METHODS

The description of the new genus and new species is based on four specimens collected in New Caledonia by G. Monteith: two males and a female collected at 5070 m up the northern slope of Pic d'Amoa (20°58'S, 165°17'E); one male collected 10th November, 2001 using a Berlese funnel and sieved litter from the rainforest; one male collected 10th–11th November, 2001 using a trap baited with human dung; one female on 23th November, 2003 – 30th January 2004, using a flight interception trap; and a fifth instar collected at 1000 m on the summit of Aoupinié (21°11'S, 165°16'E) on 20th October 2004 by G. Monteith, by fogging trees and logs with pyrethrum. All measurements are in millimetres (mm).

Specimens were imaged by CT scanning at the AST-RX MNHN computed tomography facility in Paris, using a v|tome|x L 240 from GE Sensing & Inspection Technologies phoenix|x-ray. CT parameters for adults specimens were 25 kV, 550 µA, 3000 projections, exposure time 1000 ms, fast|scan

mode. The voxel size was 0.0036 mm for a total of 1558 slices along the transverse axis of the specimen. CT parameters for larval specimens were 28 kV, 450 µA, 3000 projections, exposure time 1000 ms, fast|scan mode. The voxel size was 0.0029 mm for a total of 1396 slices along the transverse axis of the specimen.

“Phoenix datos|x” (®GE Sensing & Inspection Technologies phoenix|x-ray, Release 2.0; license UMS 2700 CNRS-MNHN, Paris) was used to reconstruct a virtual stack of slices in transverse, coronal and sagittal planes. VGStudio Max (®Volume Graphics, Release 2.1; license UMS 2700 CNRS-MNHN, Paris) was used to complete visualization and 3D rendering.

Phylogenetic analysis

The phylogenetic analysis is based on the Schuh et al. (2006) character and taxa matrix, following Lis (1999) (i.e., 23 taxa corresponding to the 12 known genera of Cantacaderini, and 11 out group taxa). Among the out group taxa, *Phatnoma* Fieber and *Zetekella* Drake belong to the tribe Phatnomatini; *Agramma* Stephens, *Corythucha* Stål and *Tingis* Fabricius the Tingini Laporte; *Annomatocoris bolivianus* Schuh, Cassis & Guilbert the Vianaoidinae Kormilev; *Xylastodoris* Barber and *Onymocoris* Drake & Slater, both Thaumastocoridae, *Myiomma* Puton, *Psallops* Usinger and *Plagiognathus* Fieber are all Miridae. The new genus described here and *Afghanoderus* Lis are included in the sample of taxa analyzed in this paper. The two known fossil genera of Cantacaderinae were not included in the analysis because data on many of their characters are not available. Fifty characters of the Schuh et al. (2006) character set were used (Appendix 1). Characters 21 and 40 included in the Schuh et al. (2006) analysis were not used because character 21 is the same as character 19 and character 40 is not informative. Characters are treated as non-additive, as in Lis (1999), whereas multistate characters were treated as additive in Schuh et al. (2006). The data matrix was analysed by parsimony, using a heuristic search, multi TBR + TBR, 1000 iterations and two starting trees, using Nona (Goloboff, 1998) through a Winclada interface (Nixon, 2002). A bootstrap analysis was performed to test the robustness of the nodes with 1000 iterations. The matrix and characters are presented in Appendix 1.

RESULTS

Caledoderus gen. n.

Type species: *Caledoderus monteithi* sp. n., here designated.

Diagnosis

Body wide, shiny, glabrous, uniformly brown.

Head long, slightly punctate on dorsal surface, armed with pairs of frontal and jugal tubercles; first two antennal segments not surpassing apex of head; bucculae long, extending in front of clypeus, parallel and not in contact; rostrum long, reaching the eighth abdominal tergite.

Pronotum trapezoidal, not extending posteriorly, tubercle on scutellum exposed, not lobed laterally, pentacarinate; distinct median and lateral carinae along entire length of pronotum; supra-humeral carinae short, joining lateral carina before half the length of pronotum; paranota narrow, with a row of very small areolae.

Hemelytra large, sharply widen, with round areolae of regular size over the entire surface; stenocostal vein present dorsally and ventrally, stenocostal and hypocostal areas with one row of areolae; costal area wide and of the same size all along hemelytra; clavus, discoidal and sub-costal areas not delimited by boundary veins; sutural area small and narrow.

Etymology. The name refers to New Caledonia where the specimens were collected, “Caledo-” and to the ending of Cantacaderinae, the sub-family to which this new genus belongs “-der”, “-us” gender masculine.

Comments. The genus has a stenocostal vein visible on both sides, which characterizes the Cantacaderinae (sensu Lis, 1999). It also has a prominent tubercle visible on the scutellum, which characterizes the Ceratocaderini (sensu Lis, 1999); however, the pronotum is not extended posteriorly. On this basis, this genus is assigned to the tribe Ceratocaderini, despite the pronotum not extending posteriorly and members of the tribe rarely possessing a pentacarinate pronotum.

Caledoderus monteithi sp. n.

(Figs 1–2)

Material examined. Holotype: 1 ♂, New Caledonia, Pic d’A-moa, N slopes, 10.x.2001, G. Monteith, OM Berlese 1050, 20°58’S, 165°17’E, rainforest, 500 m, sieved litter. Paratypes: 1 ♂, New Caledonia 8688, 20°58’S, 165°17’E, 500 m, Pic d’A-moa, N slopes, 10.–11.xi.2001, trap baited with human dung, G. Monteith; 1 ♀, New Caledonia 11482, 20°58’S, 165°17’E, 500 m, Pic d’A-moa, N slopes, 27.x.2003–30.i.2004, G. Monteith, flight int. trap. Other material: 1 fifth instar, New Caledonia, 11665, 21°11’S, 165°16’E, Aoupinié summit, 100 m, 20.x.2004, G. Monteith, pyrethrum, trees & logs.

Adult (Fig. 1)

Body wide, shiny, glabrous, uniformly brown; legs long and slender, tarsi much longer than wide. Body length 4.84; width 3.20.

Head much longer than wide, with two pairs of short, blunt, erect tubercles, a frontal and a jugal pair, jugal tubercles slightly longer than frontal tubercles; clypeus long and narrow; antennal process short and spiny;

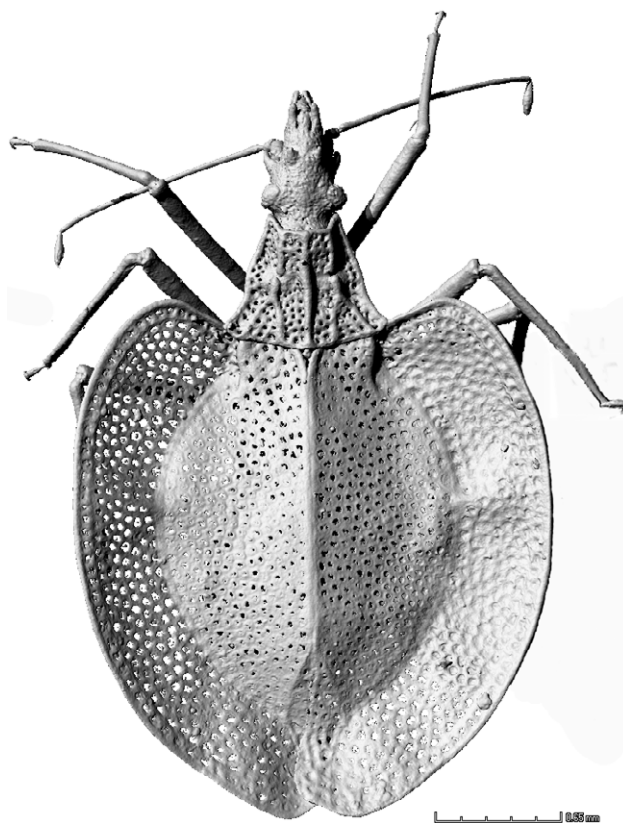


Fig. 1. *Caledoderus monteithi* sp. n., adult, dorsal habitus.

antennae long and slender, first two segments short, not surpassing apex of head, third the longest, fourth short, oblong and densely pilose. Antennal segment measurements, I, 0.20; II, 0.12; III, 1.76; IV, 0.24; bucculae long and narrow, mostly three areolae wide, wider in posterior half, extending in front of clypeus, apex ending abruptly, almost parallel and not in contact; rostrum long reaching subgenital plate or eighth abdominal tergite.

Pronotum trapezoidal, widening posteriorly, punctate, pentacarinate; median carina large, raised, with one areola in the middle; lateral carinae smaller than median one, raised but without areolae, interrupted near calli, present on collar; suprahumeral carinae only present on posterior half of pronotum, joining lateral carinae before calli and forming a “Y” with lateral carinae; collar slightly raised; posterior margin almost straight, not elongate posteriorly along carinae, exposing scutellum tubercle; paranota present all along pronotum and narrow, wider opposite calli; with one row of tiny areolae on anterior two thirds, ridge-like on posterior third; sulcus narrow, meso- and metasternal laminae short, raised, with one row of areolae of moderate size; metepisternal gland orifice crevice-like.

Hemelytra wide, broadly rounded, widening at base, with small, regular, rounded areolae; veins R, M and Cu almost invisible, except very base of R+M and apex of R+M+Cu; Stenocostal area developed ventrally and dorsally, with one row of areolae; costal area wide, six to eight areolae across; hypocostal area narrow, with one row of small areolae; discoidal and sub-costal areas fused into a single area, 14 areolae across at widest part; sutural

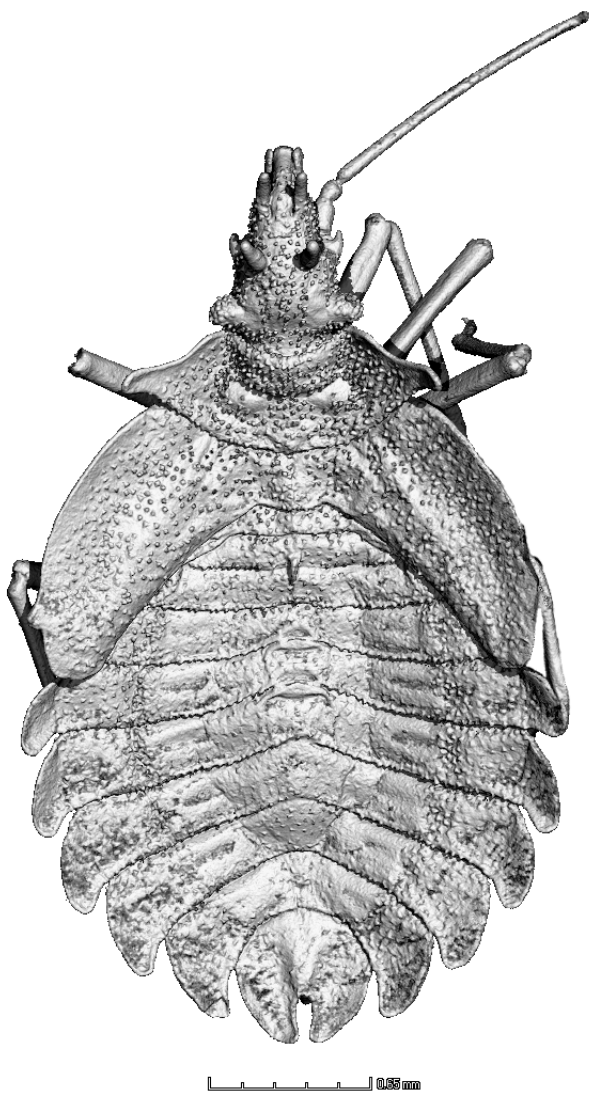


Fig. 2. *Caledoderus monteithi* sp. n., fifth instar, dorsal habitus.

area very short and narrow, three areolae across at widest part.

Fifth instar (Fig. 2)

Body ovate, wide, flat, shinny, glabrous, covered with very small star-like protuberances on the dorsum, brown with small reddish patches on abdominal tergites, hemelytral pads, pronotum and apex of cephalic tubercles. Body length 3.88; width 2.32.

Head longer than wide, with two pairs of straight, blunt, erect tubercles, a frontal and a jugal pair; antennal processes short and spiny, antennae long and slender; antennal segment measurements: I, 0.16; II, 0.12; III, 1.36; IV, 0.24; clypeus narrow; bucculae long, slightly extending in front of clypeus, apex sub-parallel and not joined; rostrum long, reaching ninth abdominal tergite.

Pronotum short and wide, extended laterally though narrow, lateral pads slightly raised and with round apex.

Hemelytral pads wide and rounded, with a short, lateral and flat protuberance on apical third.

First abdominal tergite with a short median tubercle directed posteriorly. Fourth to ninth abdominal tergites extend laterally with a wide, rounded, flat protuberance, which is slightly raised.

Etymology. This new species is named in honour of Dr Geoff Monteith (Queensland Museum, Brisbane) who has provided the author with many specimens of Tingidae, including this new species.

Comments. This genus differs from all other genera of Cantacaderinae by the hemelytra being without distinct central veins. It resembles *Nectocader* Drake and *Teratocader* Drake in having wide hemelytra. It also resembles *Ceratocader* Drake, *Allocader* Drake and *Australocader* Lis in the wide costal area and the absence of a distinct scutellum. It is pentacarinata and the suprahumeral carinae join the lateral carinae as in *Cantacader*, however, not at the calli but at a more posterior position.

The larva described here was not collected together with the adults. However, Mont Aoupinié is close to Pic d'Amoa. It is expected to belong to the new species due to its general habitus, which do not correspond to any other known New Caledonian species of Tingidae (see Guilbert, 2008).

Key to genera

Lis (1999) and Froeschner (1996) have already provided keys to the genera of Cantacaderinae. Therefore, a new key, which includes *Afghanoderus* and *Caledoderus*, is proposed on the basis of these former keys. I did not modify the key to Carldrakeanini of Lis (1999) as no new genus was added to the tribe.

- 1 Scutellum entirely covered by the pronotum. Cantacaderini Stål 2
- Scutellum with a distinct tubercle posteriorly. 5
- 2 Paranotum strongly sinuate, margin forming triangular projection anterolaterally and at mid-length. *Pseudophatnoma* Blöte
- Paranota sinuate or not, never forming large triangular projections. 3
- 3 Paranota bilobed, costal area wide, widening abruptly at base, with 15–16 rows of areolae at apex of clavus. *Teratocader* Drake
- Paranota straight, not bilobed, costal area narrower, with at least 10 rows of areolae at apex of clavus. 4
- 4 Costal area present only in the basal and apical parts of hemelytra; subcostal area divided into two parts by an additional longitudinal vein. *Afghanoderus* Lis
- Costal area present along entire length of hemelytra; subcostal area not longitudinally divided. *Cantacader* Amyot and Serville
- 5 Costal area narrow, with at least one row of areolae; steno-costal area developed only ventrally. Carldrakeanini stat. nov. (see Lis, 1999)
- Costal area wide; stenocostal area developed ventrally and dorsally. *Ceratocaderini* Lis 6
- 6 Pronotum with five carinae. 7
- Pronotum with three carinae. 8
- 7 Suprahumeral carinae connected anteriorly to lateral carinae; hemelytra without the main veins visible. *Caledoderus* gen. nov.

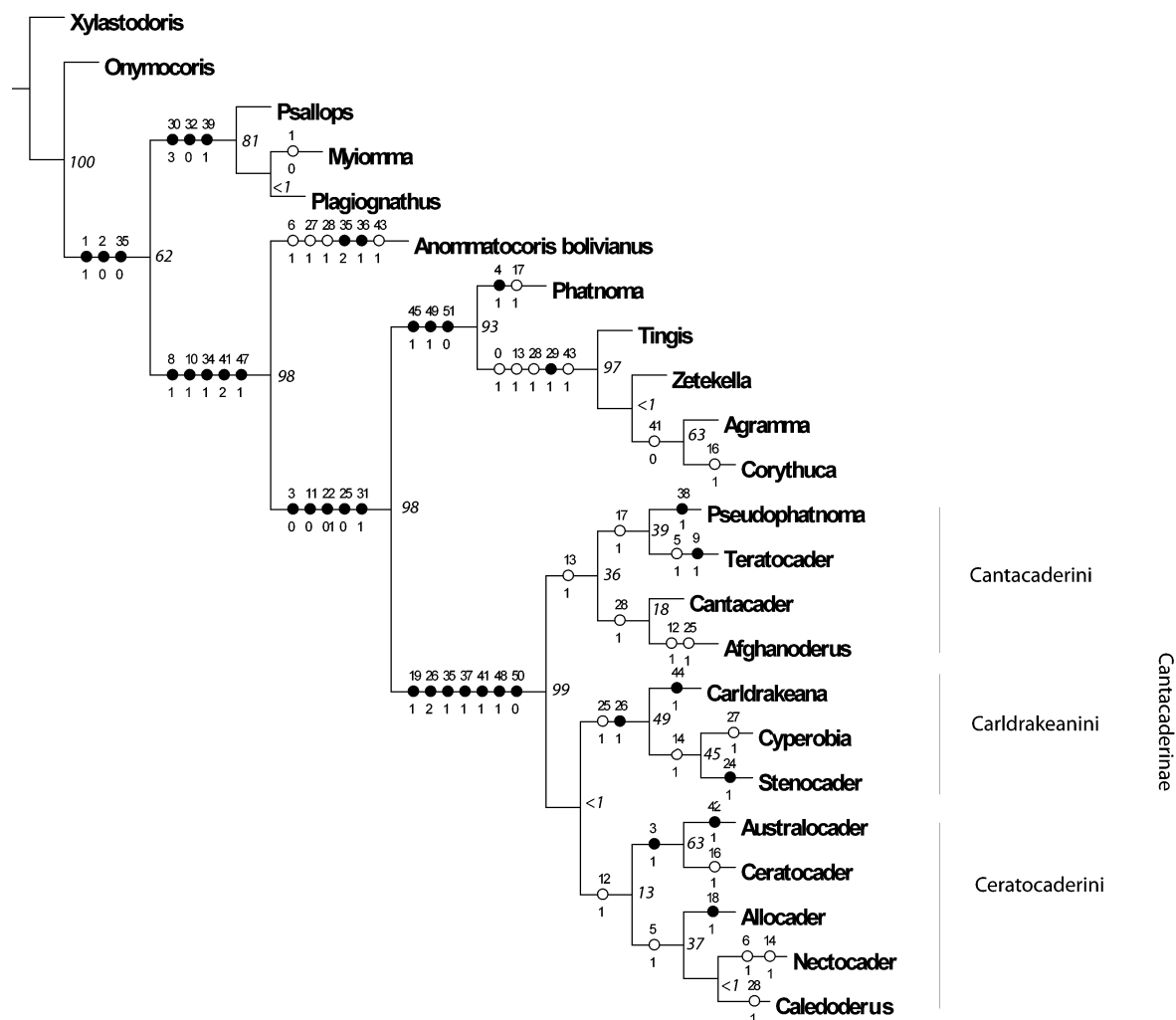


Fig. 3. Most parsimonious cladogram of the Cantacaderinae. Solid black circles represent non-homoplasious acquisition of a state; white circles indicate homoplasious acquisition of a state; bootstrap values at each node are in italics.

- Suprahumeral carinae not in contact with lateral carinae; hemelytra with the usual veins distinctly present. *Nectocader* Drake
- 8 First visible abdominal sternite with two median laminae. *Australocader* Lis
- First visible abdominal sternite without median laminae. 9
- 9 Paranota with six to eight spines; anterior margin of pronotum forming a hood. *Ceratocader* Drake
- Paranota without spines, anterior margin of pronotum not forming a hood. *Allocader* Drake

Phylogenetic analysis

The phylogenetic analysis provide a single tree of 81 steps, CI = 77, RI = 91 (Fig. 3). The topology is similar to those obtained by Schuh et al. (2006) and Lis (1999) with few differences. *Anommatocoris bolivianus* is basal and a sister group to all the other Tingidae. *Phatnoma* is basal and a sister group to the Tingini represented by *Tingis*, *Zetekella*, *Agramma* and *Corythucha*. Note that *Zetekella* belongs to the Phatnomatini and is represented here as a sister group of *Tingis*. The clade (Phatnomatini + Tingini) is a sister group to the clade grouping all the Cantacaderinae (sensu Schuh et al., 2006). The Cantacaderinae are divided into two main clades: that called “Cantacader-

ini” by Lis, and a second clade representing Carldrakeaninae plus Ceratocaderini sensu Lis. Here, the Ceratocaderini were found to be a sister group of Carldrakeaninae, whereas Lis (1999) found that they were a sister group of the Cantacaderini in the Cantacaderinae.

Afghanoderus is a sister genus of *Cantacader*, as suggested by Lis (2001).

The Ceratocaderini are divided into two clades: *Australocader* + *Ceratocader* and *Allocader* + *Caledoderus* + *Nectocader*. *Caledoderus* gen. nov. is a sister genus of *Nectocader* in the Ceratocaderini.

The bootstrap values are high for the basal nodes separating the taxa at higher levels. The node leading to the Cantacaderinae is strongly supported (99%). However, most of the apical nodes in the Cantacaderinae are weakly supported, with bootstrap values lower than 50%, particularly the node leading to the Carldrakeanini sister group of the Ceratocaderini and the node leading to *Nectocader* sister genus of *Caledoderus* (both being around 1%).

The different groups within the Cantacaderinae are supported mostly by homoplasious character states. The Cantacaderini are supported by a scutellum covered by the pronotum (char. 21) and a pronotum elongate along

median carina (char. 13). Both characters are shared with the Tinginae. The Carldrakeanini share a narrow costal area with no, or only a single row of areaolae (char. 24) with *Afghanoderus*. They are also characterized by a ventrally developed stenocostal region (char. 25). The Ceratocaderini share an elongated pronotum along the lateral carinae (char. 12) with *Afghanoderus*. Also, the Cantacaderini have a pronotum elongated along median carina, including *Afghanoderus*. The pronotum elongation has been coded as elongated along median carina and lateral carinae for *Afghanoderus* because of the ambiguity of the character.

Afghanoderus is a sister of *Cantacader* on the basis of the discoidal area lacking transverse veins (char. 27), a character also shared with *Caledoderus*.

The group *Allocader* + *Caledoderus* + *Nectocader* is supported by a clypeus clearly surpassing the apex of the jugo-frontal spines (char 5), a character shared with *Teratocader*. However, no autapomorphy characterizes *Caledoderus* as a sister of *Nectocader*.

DISCUSSION

The phylogenetic analysis presented here provides a single tree where the groups defined by Lis (1999) are validated as such in the Cantacaderinae. However, the relationships between these groups differ from the analysis of both Lis (1999) and Schuh et al. (2006). Here, I present results that the Carldrakeaninae are a sister group of the Ceratocaderini, whereas they were a sister group of the Cantacaderini in Lis' study. However, the bootstrap values indicate that the relationships between these taxa are weakly supported. As the characters used are the same in both analyses, this result is directly due to the introduction of the new genera *Afghanoderus* and *Caledoderus*. The introduction of new species or genera could again change the topology of the relationships within Cantacaderinae. Therefore, if the results presented here invalidate the composition of the two subfamilies defined by Lis (1999), Carldrakeaninae and Cantacaderinae, but are not strongly supported, I would propose keeping the two tribes Ceratocaderini and Cantacaderini as defined by Lis and changing the status of Carldrakeaninae to tribal level, with all of them in the Cantacaderinae, as a subfamily in the family Tingidae, as suggested by Schuh et al. (2006):

Cantacaderini, including *Cantacader*, *Pseudophatnoma*, *Teratocader* and *Afghanoderus*;

Ceratocaderini, including *Allocader*, *Australocader*, *Ceratocader*, *Nectocader* and *Caledoderus* gen. nov.;

Carldrakeanini stat. nov., including *Carldrakeana*, *Cyperobia* and *Stenocader*.

ACKNOWLEDGEMENTS. The author is grateful to G. Monteith (Queensland Museum) for the loan of numerous specimens of Tingidae from New Caledonia, including the new genus and species described in this paper; T. Henry (USDA, Smithsonian Institution), U. Kodandaramaiah (Stockholm University) and M. Moir (University of Melbourne) for their helpful comments on the manuscript. This study was supported by the ANR Program BioNéoCal. I also thank F. Goussard and B. Mora (MNHN, Paris) for providing CT scans and 3D renderings that were pro-

duced using the AST-RX computed tomography facility (UMS 2700 CNRS-MNHN, Paris).

REFERENCES

- FROESCHNER R.C. 1996: Lacebug genera of the world, I: Introduction, Subfamily Cantacaderinae (Heteroptera: Tingidae). *Smiths. Contrib. Zool.* **574**: 1–43.
- GOLOBOFF P. 1998: *Nona, version 2.0*. Fundación e Instituto Miguel Lillo, Miguel Lillo 205, 4000 S.M. de Tucumán, Argentina.
- 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). *Mitt. Geol.-Palaötol. Inst. Univ. Hamburg* **85**: 263–276.
- GUILBERT E. 2001: Phylogeny and evolution of exaggerated traits among the Tingidae (Cimicomorpha, Heteroptera). *Zool. Scr.* **30**: 313–324.
- GUILBERT E. 2004: Do larvae evolve the same way as adults in Tingidae (Insecta: Heteroptera)? *Cladistics* **20**: 139–150.
- GUILBERT E. 2008: New Caledonian Tingidae (Insecta: Heteroptera): new species and new records. In Grandcolas P. (ed.): *Zoologia Neocaledonica 6. Biodiversity studies in New Caledonia. Mém. Mus. Natn. Hist. Nat.* **197**: 63–78.
- LIS B. 1999: Phylogeny and classification of Cantacaderini [= Cantacaderidae stat. nov.] (Hemiptera: Tingidae). *Ann. Zool. (Warszawa)* **49**: 157–196.
- NIXON K.C. 1999: *Winclada (beta) ver. 0.9.9*. Ithaca, NY.
- SCHUH R.T., CASSIS G. & GUILBERT E. 2006: Description of the first recent macropterous species of Vianaidinae (Heteroptera: Tingidae) with comments on the phylogenetic relationships of the family within the Cimicomorpha. *J. N. Y. Entomol. Soc.* **114**: 38–53.
- WAPPLER T. 2006: *Lutetiocader*, a puzzling new genus of cantacaderid lace bugs (Heteroptera: Tingidae) from the middle Eocene Messel Maar, Germany. *Palaeontology* **49**: 435–444.

Received June 10, 2011; revised and accepted September 8, 2011

APPENDIX 1. The 23 taxa and 52 morphological characters included in the phylogenetic analysis.

- 0 – head distinctly projecting in front of eyes, surpassing antennal segment 1 (0); short, not surpassing antennal segment 1 (1);
- 1 – ocelli present (0); absent (1);
- 2 – mandibular plates not enlarged (0); enlarged, extending to apex of clypeus (1);
- 3 – spines on head straight (0); broadly upcurved (1); absent (2);
- 4 – clypeal spine absent (0); present (1);
- 5 – clypeus short, reaching at most to apex of jugo-frontal spines, if spines present (0); long, clearly surpassing apex of jugo-frontal spines (1);
- 6 – margins of bucculae without pilosity (0); with short, stiff setae (1);
- 7 – anterior length of bucculae short, not surpassing apex of head (0); bucculae in contact along dorsal margin anterior to clypeus (1); distinctly projecting in front of head, sometimes in contact (2);
- 8 – posterior length of bucculae short to moderately long, never reaching prosternum (0); elongate, extending from clypeus to prosternum (1);
- 9 – labium short, not reaching genital segment (0); long, reaching genital segment (1);
- 10 – labial groove on thoracic sternum absent (0); present (1);

- 11 – antennal segment II distinctly shorter than antennal segment III (0); sub equal to antennal segment III (1);
 12 – pronotum not extended posteriorly along lateral carinae (0); extended posteriorly along lateral carinae (1);
 13 – pronotum not extended posteriorly along median carina (0); extended posteriorly along median carina (1);
 14 – lateral margins of pronotum straight (0); bsinuate (1);
 15 – lateral margins of paranota without teeth (0); with a single tooth (1); with 6 to 8 teeth (2);
 16 – hood on anterior part of pronotum absent (0); present (1);
 17 – paranotum unilobed (0); bilobed (1);
 18 – paranota parallel to pronotal disc (0); strongly reflected upwards (1);
 19 – lateral carinae on collar absent (0); present (1);
 20 – number of pronotal carinae, none (0); 1 to 3 (1); 5 (2);
 21 – scutellum with a distinct tubercle posteriorly (0); covered by pronotum (1); relatively large, triangular (2);
 22 – costal vein extending to apex of corium (0); extending to apex of membrane (1);
 23 – lateral margins of hemelytra normally developed (0); serrate (1);
 24 – costal area broad, more than 2 areolae wide medially (0); narrow, none or one areola wide medially (1); absent (2);
 25 – stenocostal area absent (0); developed only ventrally (1); development ventrally and dorsally (2);
 26 – veins r+m and cu in basal part of hemelytron separate from one another (0); fused (1);
 27 – discoidal area with transverse veins (0); without transverse veins (1);
 28 – clavus normally developed (0); weakly developed and depressed below level of mesocorium (1);
 29 – hemelytra (punctuation) punctate (0); with small irregular areolae (1); with large areolae (2); impunctate (3);
 30 – membrane in macropterous form normally developed (0); rudimentary or absent (1);

- 31 – membrane with closed cells (0); without closed cells (1);
 32 – medial vein of hind wing acutely connected with cu (0); perpendicular to cu (1);
 33 – ostiole of metathoracic glands absent or posterior on metepisternum (0); anterior on metepisternum (1);
 34 – scent gland peritreme developed as an apically closed loop or absent (0); crevice-like (1); T-shaped (2); absent (3);
 35 – evaporative area of metathoracic glands absent to moderately developed, never covering entire metepisternum (0); covering entire metepisternum (1);
 36 – trochanters not fused with femora (0); fused with femora (1);
 37 – femur without apical spur (0); with apical spur (1);
 38 – meso- and metafemoral trichobothria absent (0); 3 or more present on meso- and metafemora (1);
 39 – parempodia well developed, setiform (0); greatly reduced (1); absent (2);
 40 – carinae on abdominal sternum II absent (0); present (1);
 41 – pregenital abdominal segments only II and III fused (0); II, III, IV, or more fused (1);
 42 – tubercles on abdominal sternum II (Lis 2-1) absent (0); present (1);
 43 – abdomen with a simple set of lateral sclerites (0); with a double set of lateral sclerites (1);
 44 – apodeme between laterotergite VIII and gonocoxopodite I completely developed and functioning as a muscle connection (0); rudimentary or absent (1);
 45 – female abdominal sternum VII simple (0); with posterior medial projection (1);
 46 – gonopods strongly sclerotized (0); membranous (1);
 47 – pseudospermatheca absent (0); present (1);
 48 – rudimentary spermatheca present (0); absent (1);
 49 – vagina (genital chamber) small (0); spacious, sac-like (1);

Characters	01234567891111111111222222222233333333334444444444 0123456789012345678901234567890123456789
<i>Xylastodoris</i>	-012--00000100000--0021020000001-0300000000--0001-
<i>Onymocoris</i>	-012--00000100000--0020020000001-0300000000--0001-
<i>Myiomma</i>	100200000001-00-0--0020020000300-00000100000-00011
<i>Psallops</i>	110200000001-00-0--0020020000300-00000100000-00011
<i>Plagiognathus</i>	110200000001-00-0--0020020000300-00000100000-00011
<i>Anommatocoris bolivianus</i>	010200101011000-0--0021020110001?12100020100210?11
<i>Agramma</i>	1100000110100100000011-00001121-010000000101110110
<i>Corythuca</i>	1100000110100100100011-00001121-010000000101110110
<i>Tingis</i>	1100000110100100000011-00001121-010000020101110110
<i>Zetekella</i>	1100000110100100000011-00001121-010000020101110110
<i>Phatnoma</i>	0100100110100000010010-00000021-010000020001110110
<i>Afghanoderus</i>	0100000210101100000121-01201011-111010010000011001
<i>Allocader</i>	0100010210101000001120-00200011-111010010000011001
<i>Australocader</i>	0101000210101001000120-00200011-111010011000011001
<i>Caledoderus</i>	0100010210101000000120-00201011-111010010000-11001
<i>Cantacader</i>	0100000210100100000121-00201011-111010010000011001
<i>Carldrakeana</i>	0100000210100000000120-01100011-111010010010011001
<i>Ceratocader</i>	0101000210101002100120-00200011-111010010000011001
<i>Cyperobia</i>	0100000210100010000120-01110011-111010010000011001
<i>Nectocader</i>	0100011210101010000120-00200011-111010010000011001
<i>Pseudophatnoma</i>	0100000210100100010121-00200011-111011010000011001
<i>Stenocader</i>	0100000210100010000120-11100011-111010010000011001
<i>Teratocader</i>	0100010211100100010121-00200011-111010010000011001