

PHYLOGENY AND CLASSIFICATION OF CANTACADERINI [= CANTACADERIDAE STAT. NOV.] (HEMIPTERA: TINGOIDEA)

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Abstract. — The tribe Cantacaderini (sensu Froeschner 1996) was studied morphologically and phylogenetically, and its systematic position within Tingidae *s. lato* was estimated. The cladistic analysis at the tribal level within Tingidae *s. lato* has shown the subfamily Cantacaderinae is a polyphyletic taxon; moreover, it identified the tribe Phatnomatini (sensu Froeschner 1996) as a sister group of the subfamily Tinginae, while the tribe Cantacaderini (sensu Froeschner 1996) as an evolutionary lineage is quite separate from Phatnomatini (both have hitherto been united within Cantacaderinae). A new classification of the superfamily Tingoidea is proposed, that includes its division into three families, i.e. the Cantacaderidae (new family status), the Tingidae with two subfamilies, Phatnomatinae (new subfamily status) and Tinginae, and the Vianaididae.

On the basis of the cladistic analysis at the generic level, the Cantacaderidae is divided into two subfamilies, i.e. Cantacaderinae Stål (*sensu novo*) and Carldrakeaninae *subfam. nov.*; moreover, the former was proved to consist of two tribes, namely Cantacaderini *s. str.* and Ceratocaderini *trib. nov.* The ancestral area for the whole family was estimated, and its historical biogeography was also discussed.

Furthermore, diagnostic characters for the family, subfamilies, tribes and all the genera, with a list of their species (including data on type material and distribution) are presented. Lectotypes are designated for *Piesma tingidoides* Spinola, 1852, *Cantacader attenuatus* Distant, 1902, *Cantacader lethierryi* Scott, 1874, and *Cantacader uniformis* Distant, 1902.



Key words. — Hemiptera, Heteroptera, Tingoidea, Cantacaderidae, Tingidae, taxonomy, classification, phylogeny, historical biogeography, new status, new taxa.

INTRODUCTION

The cimicomorphan family Tingidae due to the lacy appearance of hemelytra of its representatives is known under the common name of "lace bugs". It is also the character for an easy distinguishing the tingids from other Cimicomorpha, but it can not be treated as the autapomorphy for the family, since the same type of wing modification is known in some other families (including pentatomorphan Piesmatidae).

No one has studied Tingidae phylogenetically and the extent of the taxon varies among modern authors. Drake and Davis (1960) considered it as a family with three subfamilies: Cantacaderinae, Tinginae and Vianaidinae; it was treated in the same way in the World catalogue of Drake and Ruhoff (1965). Štys and Kerzhner (1975), based on Pendergrast's (1957) and Scudder's (1959) studies on genitalia of the Heteroptera regarded the taxon as a superfamily (Tingoidea) with two families: Tingidae and Vianaididae. This arrangement was then followed by Popov (1981), and recently by Froeschner (1996) in his revision of the lace bugs

genera of the World. It is also accepted herein as a base for the phylogenetic studies, since relationships of Tingidae *s. lato*, Thaumastocoridae and Miridae (sometimes held together within the superfamily Miroidea) seems to be still unclear (Schuh and Štys 1991).

According to recent paper of Froeschner (1996) the family Tingidae *s. stricto* is divided into two subfamilies, i.e. Cantacaderinae and Tinginae. The former included three tribes (Popov 1989, Froeschner 1996): two recent – Cantacaderini and Phatnomatini, and one fossil – Golmoniini.

To date, studies on Cantacaderini and Phatnomatini have been restricted mainly to descriptions of new taxa; representatives of both tribes have rarely been revised at species level. Moreover, their morphology has never been compared, and no attempt to find homologous structures was undertaken (it caused many misinterpretations in external and internal morphology leading to wrong determination of taxa).

At present, the tribe Cantacaderini is represented by ten genera and 54 species distributed in all zoogeographical

regions of the World except Nearctics (Froeschner 1996, B. Lis 1997a, 1997b, 1999a, 1999b), while the Phatnomatini by 26 genera and 82 species, known from all regions but Palaearctics, Nearctics and New Zealand (Froeschner 1996).

The third tribe Golmoniini was erected for a fossil species *Golmonia pater* Popov, described from the Lower Cretaceous of Mongolia (Popov 1989). Nevertheless, the venation of hemelytron and the head shape suggest the taxon has nothing to do with Tingidae (Cantacaderinae); it seems rather to be allied to Thaumastocoridae (B. Lis, unpublished data). Due to the uncertain position of that tribe, and incompleteness of morphological data, Golmoniini was excluded from the present phylogenetic analysis.

The most recent paper on the subfamily Cantacaderinae (Froeschner 1996) presented only an outline of its morphology, short diagnosis and keys to tribes, genera and some species, and summarized distribution of included taxa.

The aim of the present paper was (1) to study the morphology of the Cantacaderini in detail, (2) to give a full list of characters connected with wings modification, (3) to unify the nomenclature of certain parts of a body and to homologize certain structures, (4) to analyze phylogenetically the Tingidae *s. stricto* in order to find out relationships between its tribes, (5) to analyze relationships between genera within the tribe Cantacaderini, and (6) to estimate the ancestral area for the Cantacaderini and briefly discuss its historical biogeography.

SYSTEMATIC POSITION OF CANTACADERINI

Cantacaderini and Phatnomatini have always been grouped together to constitute the subfamily Cantacaderinae on the basis of the following characters (Drake and Davis 1960, Drake and Ruhoff 1965, Froeschner 1996): head elongated between antennae with apex always surpassing the second antennal segment (Fig. 13); bucculae either long and broad, joined together before head apex, or shorter, with apices recurved inwards and enclosing lateral surfaces of clypeus (Figs 13, 15, 16); pronotum short, its posterior margin never strongly triangularly produced to cover clavus (Figs 8, 54); the latter well developed (Figs 20, 54), sometimes fused with the discoidal area (Fig. 45); scutellum present, either well visible (Figs 43, 54) or covered by the posterior margin of pronotum (Figs 8, 53); abdominal sterna II and III (visible I and II) fused.

The subfamily Cantacaderinae was regarded as well defined, natural and valid group (Froeschner 1996), representing the oldest living forms of the whole family Tingidae; moreover, the tribe Cantacaderini was considered to be the most primitive tingids only on the basis of the presence of stenocostal area, not found in other taxa of Tingidae.

When we take the characters regarded so far as distinctive and common for both Cantacaderini and Phatnomatini into account, we may notice that some of them occur also in the subfamily Tinginae. For instance, a head elongated between the antennae is characteristic also for representatives of *Biskria* Puton, *Dictyonota* Curtis, *Ypsotingis*

Drake (to give only some examples), and a head with the apex surpassing the second antennal segment can be found not only in Cantacaderinae, but also in *Dictyonota pakistana* Drake and Maldonado. The latter character regarded up to date as common for all the taxa belonging to Cantacaderinae does not occur in *Cantacader* Amyot and Serville, *Ceratocader* Drake and *Pseudophatnoma* Blöte, where the head is relatively short, and only bucculae are strongly anteriorly produced to surpass the second antennal segment (Figs 47, 50, 52).

On the other hand, there are some characters found in many representatives of the subfamily Tinginae, as well as in those representing the tribe Phatnomatini, but not known in the tribe Cantacaderini at all (i.e. moderately long bucculae with anterior apices recurved inwards and not reaching the head apex, or elongated bucculae joined together along dorsal margins of their anterior part). Moreover, the feature considered so far as the most characteristic for the whole subfamily Tinginae (i.e. clavi covered by strongly produced triangular posterior margin of pronotum) is not found in some taxa of that subfamily, for instance in *Derephysia cristata* (Panzer), in the genus *Campylosteira* Fieber, or *Kalama* Puton.

At present, only two characters, namely well developed clavi and fused abdominal sterna II and III can be regarded as common for all the representatives of both Cantacaderini and Phatnomatini (without judging their phylogenetic significance).

MATERIAL AND METHODS

Material

The study was based on approximately 1000 adult specimens (mainly undetermined or wrongly identified) borrowed from various institutions and private collections all over the world. Additionally, the type material for 21 species of Cantacaderini was examined.

The following abbreviations are used to indicate the collections where the specimens are held (mostly after Aukema and Rieger 1995).

AMNH	-	American Museum of Natural History, New York, USA;
BMH	-	Bernice P. Bishop Museum, Honolulu, Hawaii, USA;
BMNH	-	The Natural History Museum, London, Great Britain;
BL	-	Author's collection, Department of Zoology, University of Opole, Opole, Poland;
EH	-	E. Heiss collection, Tiroler Landesmuseum, Innsbruck, Austria;
HNHM	-	Hungarian Natural History Museum, Budapest, Hungary;
ISNB	-	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;
JP	-	J. Péricart collection, Montereau, France;

- MCSN – Museo Civico di Storia Naturale “Giacomo Doria”, Genova, Italy;
- MNHN – Muséum National d’Histoire Naturelle, Paris, France;
- MHNG – Muséum d’Histoire Naturelle, Geneva, Switzerland;
- MRAC – Musée Royal de l’Afrique Centrale, Tervuren, Belgium;
- MVMA – Museum of Victoria, Abbotsford, Victoria, Australia;
- MZLU – Museum of Zoology, Lund University, Sweden;
- NHMW – Naturhistorisches Museum Wien, Vienna, Austria;
- NHRS – Naturhistoriska Riksmuseet, Stockholm, Sweden;
- NKUM – Nankai University, Department of Biology, Tianjin, China;
- NMBZ – National Museum, Bulawayo, Zimbabwe;
- NMSA – Natal Museum, Pietermaritzburg, Republic of South Africa;
- NSMT – National Science Museum (Natural History), Tokyo, Japan;
- PPRI – Plant Protection Research Institute, Pretoria, South Africa;
- QMBA – Queensland Museum, South Brisbane, Australia;
- REL – R. E. Linnavuori, Somersoja, Finland (belongs to AMNH);
- RMNH – Nationaal Natuurhistorisch Museum, Leiden, The Netherlands;
- SAM – South Australian Museum, Adelaide, Australia;
- TMP – Transvaal Museum, Pretoria, Republic of South Africa;
- USNM – National Museum of Natural History, Washington D.C., USA;
- ZMAN – Zoölogisch Museum, University of Amsterdam, Amsterdam, The Netherlands;
- ZMAS – Zoological Institute RAS, St. Petersburg, Russia;
- ZMHB – Zoologisches Museum, Humboldt Universität, Berlin, Germany;
- ZMPA – Museum and Institute of Zoology PAS, Warsaw, Poland;
- ZSMC – Zoologische Staatssammlung, München, Germany.

All material available to the study was listed under respective species in the “Material examined” section; number of specimens, acronyms of collections, type data (HT – holotype, PT – paratype, ST – syntype, LT – lectotype) were given in parentheses.

Beside it, following specimens were studied during the morphological and phylogenetic analysis: *Cantacaderini*: *Cantacader* spp. (3 ex., BMNH; 25 ex. NSMT; 3 ex., MNHN; 97 ex., BMH; 10 ex., NHMW; 1 ex., ZMAN; 4 ex., MZLU; 2 ex., ZMAS; 3 ex., EH; 43 ex., HNHM; 1 ex., REL; 5 ex., ZMPA; 7

ex., JP; 4 ex., BL); Phatnomatini: *Phatnoma costalis* Distant (2 ex., MZLU; 1 ex., NHMW); *P. laciniatum* Fieber (1 ex., MZLU; 1 ex., MNHN); *P. veridica* Drake and Maa (1 ex., ZSMC); *Phatnoma* sp. (3 ex., HNHM; 1 ex., MNHN; 11 ex., BMH); *Cnemidrus typicus* Distant (50 ex., BMH); *Gonycentrum coronatum* (Fieber) (6 ex., MZLU); *Microcader unicostatus* Péricart (8 ex., HNHM); *Microcader thai* Péricart (3 ex., BMH); *Indocader loebli* Péricart (5 ex., HNHM; PT, EH); *Eocader vergrandis* Drake and Hambelton (PT, HNHM); *Ulmus drakei* (Schouteden) (1 ex., HNHM); *U. eteosus* (Drake) (1 ex., MNHN); *U. testudineatus* Distant (1 ex., HNHM); *Taphnoma tuberculum* (Jing) (1 ex., NKUM); Tingini: *Tingis cardui* (Linnaeus) (4 ex., BL); *Acalypta gracilis* (Fieber) (2 ex., BL); *Dictyla echii* (Schrank) (4 ex., BL); *Dictyla humuli* (Fabricius) (1 ex., BL); *Agramma femorale* Thomson (11 ex., BL); *Lasiantha capucina* (Germar) (7 ex., BL); *Stephanitis oberti* (Kolenati) (2 ex., BL); *Campylosteira verna* (Fallén) (2 ex., BL); *Galeatus affinis* (Herrich-Schaeffer) (2 ex., BL); *Orotingis intermedius* B. Lis (3 ex., ZSMC); *Copium clavicorne* (Linnaeus) (2 ex., BL); *Habrochila* sp. (1 ex., NMSA); *Belenus dentatus* (Fieber) (1 ex., ZMAS); Ypsotingini: *Dictyonota strichnocera* Fieber (3 ex., BL); *Dictyonota fuliginosa* A. Costa (1 ex., BL); *Kalama tricornis* (Schrank) (2 ex., BL); *Derephysia foliacea* (Fallén) (2 ex., BL); *Derephysia cristata* (Panzer) (2 ex., BL); Litadeini: *Litadea delicatula* China (2 ex., BMNH).

Methods

Morphology. In order to examine characters that might be used for diagnosing the genera, as well as for further phylogenetic analysis I have tried to study the types of all the type-species for each genus of Cantacaderini. Only in three cases (genera *Allocader*, *Pseudophatnoma*, *Cyperobia*) the type material of the type-species were not available, and the studies were based on non-type material of the type-species (*Cyperobia*) or the type material of non type-species (*Allocader*, *Pseudophatnoma*). Specimens were analysed and illustrated with use of the Olympus SZH-10 stereomicroscope and Biolar microscope. Illustration of the same body parts in different taxa were made to the same scale. In some cases specimens were dissected and their structures (genitalia, antennae, legs, wings) were placed on glycerine slides for further examination.

Phylogenetic analysis. Two analyses were done; the first one in a broad context to confirm (or falsify) the preliminary hypotheses about the monophyly of Cantacaderini and to find out relationships among the tribes of Tingidae. The second analysis was performed at the generic level, to investigate an internal phylogeny of the tribe Cantacaderini.

Cladistic analyses were undertaken using the computer software Hennig86 ver. 1.5 (Farris 1988). The final cladograms and the mapping of characters were produced using Clados (Nixon 1992).

MORPHOLOGY

Head

In species of Cantacaderini head is elongated in its preocular part (Fig. 8), with apex distinctly surpassing second antennal segment (*Nectocader*, *Teratocader*) (Figs 49, 53), or it may be shorter (*Cantacader*, *Ceratocader*, *Pseudophatnoma*) with long bucculae surpassing second antennal segment (Figs 47, 50, 52). Head length is probably connected with the length of rostrum; in species with extremely long rostrum (*Allocader leai*, *Teratocader*) head is elongated, especially in its clypeal part. The same situation was observed in the subfamily Tinginae, namely in the tribe Ypsotingini (genus *Ypsotingis*).

Eyes in species of Cantacaderini are relatively large, located laterally in the posterior part of head, usually near the anterior edge of the collar. Ocelli are always absent.

Representatives of Tingidae are characterized by the presence of 2–9 cephalic dorsal spines (sometimes totally absent, e.g., in *Dietyla echii*). According to Froeschner (1996), they can be divided into two groups: paired and unpaired spines. Paired spines consist of the jugal pair, the frontal pair and the occipital pair (Fig. 13); the unpaired spines, located in the midline, include the dorsomedial spine, the clypeal spine, and sometimes one additional spine located between the frontals (e.g., in *Ulmus* sp. – Fig. 13).

Members of the Cantacaderini have always only two pairs of cephalic spines (the anterior and the posterior), and their location is very characteristic for this tribe (Fig. 10).

When comparing the location of cephalic spines in Cantacaderini with the Froeschner's scheme (1996), it is very difficult to estimate whether the anterior pair in the Cantacaderini relates to the jugal pair or to the frontal pair in the Froeschner's scheme, because their location may be the same as for the former (e.g., in *Cyperobia* – Fig. 43) or for the latter (e.g., in *Cantacader* – Fig. 50). Therefore, the anterior pair of cephalic spines in Cantacaderini should be called the jugo-frontal spines.

The posterior pair of spines may also be located in the same place as the frontal ones of the Froeschner's scheme (e.g., in *Nectocader* – Fig. 49), or it may be placed more posteriorly, almost between the eyes (e.g., in *Pseudophatnoma* – Fig. 52); therefore, the posterior pair of spines in Cantacaderini should be called the preocular spines.

The third pair of spines in the Froeschner's scheme (the occipital pair) occurring in both Tinginae and Phatnomatini is absent in Cantacaderini at all, as well as the unpaired spines do.

It is very probable, that anterior and posterior pairs of spines in Cantacaderini are indeed homologous to the jugal and frontal spines in Tinginae and Phatnomatini, and we can observe a set of transformations concerning placement of the paired spines (from typical location in *Cyperobia* to the arrangement seen in *Cantacader*, where the posterior pair of spines is located between the eyes, and the anterior pair only somewhat more anteriorly to the posterior one).

A position change of cephalic spines in Cantacaderini was probably caused by abbreviation of the posterior head part, especially that between the eyes and the preocular pair of spines.

Cephalic spines in Cantacaderini may be adherent to the head surface (e.g., *Cantacader afzelii*), or they may be raised up (e.g., *Cantacader quadricornis*, *Ceratocader armatus*). Their length and shape vary in species; they may be very long (e.g., *Cantacader subtilis*) or quite short and tubercle-like (e.g., *Allocader leai*), stout (e.g., *Ceratocader armatus*) or slender (e.g., *Cantacader afzelii*).

Head surface in Cantacaderini is usually finely punctate, or occasionally granulate (e.g., *Stenocader tingidoides*). Bucculae (two longitudinal laminae lying on the ventral head surface) are well developed, areolate (usually composed of 3–4 rows of areolae), and elongate (usually surpassing the head apex) (Fig. 9). They form an anterior part of median trough for labium; their apices may be rounded or angularly curved, usually placed close to or even touch each other.

Antennae are 4-segmented in Tingidae; there are additional intersegment between segment III and IV in all Tingidae, except the Cantacaderini.

Antennae in Cantacaderini are usually long and slender; the second segment is shorter than the first, the third usually very long and thin, fourth more or less short bearing sparse long, protruding hairs, especially well visible in its apical half (Fig. 10). Remaining segments usually bears no pilosity, though sometimes (*Cantacader afzelii*) also the third segment bears short, sparse hairs, evenly spaced along its length.

The length of third antennal segment shows sometimes infraspecific differences connected with sexual dimorphism, e.g., *Cantacader afzelii* – 1.75–1.83 mm in males, 1.01–1.13 mm in females, *C. tenuipes* – 1.92–2.06 mm in males, 1.43–1.54 mm in females, *C. quadricornis* – 1.20–1.65 mm in males, 1.00–1.30 mm in females. Moreover, differences connected with sexual dimorphism concern sometimes also the pilosity of third antennal segment, i.e. males of the genus *Cantacader* bear numerous, fine, flattened hairs (well visible under the magnification of 480x), but this type of pilosity is absent from females.

Labium (rostrum) in Cantacaderini are four-segmented; it is usually long, reaching III or IV abdominal segment, sometimes even the first genital segment (*Teratocader*); in some cases it surpasses only the posterior margin of metasternum (*C. attenuatus*).

Thorax

Pronotum in all Cantacaderini is rather uniform, and divided into a collar (anterior part), paranota (lateral parts), and a disc (remaining part) (Fig. 8).

Pronotal disc is convex in macropterous forms of Cantacaderini (Fig. 8), while it is almost flat in forms with shortened wings (Fig. 51). It usually has five carinae, the median carina, a pair of long lateral carinae, and a pair of more or less developed suprahumeral carinae (Fig. 8). The

latter is characteristic only for some representatives of the tribe Cantacaderini, and occurs neither in Phatnomatini nor in Tinginae. In some cases pronotal disc bears only three (median and lateral) carinae (e.g., *Allocader*, *Cantacader hulstaeri*) or a single median carina (e.g., *Cantacader bomansi*).

Carinae themselves can be low and stout (*Cantacader afzelii*), or high and laminated (*Cantacader tenuipes*). Within the same species, they are usually lower in forms with shortened wings than those in macropterous forms.

A collar in Cantacaderini always bears three carinae (Fig. 8) – the median carina (being a prolongation of the pronotal median carina), and two lateral carinae (a character not found in Tinginae) separated from discal lateral carinae by calli (smooth, sometimes shining, usually depressed, transverse furrows – Fig. 45). A collar can sometimes be elongated and inflated anteriorly to form a well visible hood (Fig. 47).

Paranota are the expansions of lateral pronotal margins; they may be narrow and almost carinated (*Allocader* – Fig. 45, *Cyperobia* – Fig. 43), or broad and expanded (Figs 47, 52, 53). Cells (areolae) of paranota in Cantacaderini are of the same (or almost the same) size and colour as the areolae of pronotal disc, contrary to Phatnomatini and Tinginae, where the cells on paranota are usually lighter and larger than those on pronotal disc (that is often black and shining). Paranotal margins in Cantacaderini can be straight, sinuate or even dentate.

Posterior margin of pronotum in Cantacaderini can be almost straight (*Cyperobia* – Fig. 43) or elongated along either the lateral carinae (*Ceratocader* – Fig. 47) or the median carina (*Cantacader* – Fig. 50). In the latter case, scutellum is usually totally covered by the posterior margin of pronotum (Figs 50, 53), in other cases at least the posterior part of scutellum is visible (Figs 43, 45, 47).

Scutellum when visible, is usually flat (*Pseudophatnoma* – Fig. 52), or bears a tubercle in its posterior part (*Australocader* – Figs 14, 46).

Ventrally, the thoracic sterna in Cantacaderini may be smooth and shiny, punctured or with areolae of the same type as those on hemelytra. All epimera and episterna are developed in a form of lobes covering lateral surfaces of coxae. The pleural suture between each epimeron and episternum is present, and bears a lobe-like, recurved process in many representatives of Cantacaderini.

Each sternum has ventrally a pair of laminae forming a narrow channel for labium (often called the rostral groove) when in repose (Fig. 9). Sternal laminae can be low and carinated, or high with rows of areolae.

The metathorax bears ventrally a single pore (the ostiolar opening) on either side, accompanied by peritreme. It is crevice-like and placed close to the lateral margin of metasternum in Cantacaderini (Figs 9, 14), in contrary to Phatnomatini and Tinginae, where it is either funnel-like or developed as an apically closed loop and placed closer to coxae, or totally indistinct (Tinginae: *Ypsotingini*).

Wings

The forewings (mesothoracic wings) in Tingidae are modified into lace-like or reticulate hemelytra (Fig. 8), with the membrane of the same structure as in the corium (known as the sutural area in Tingidae).

A partly membranous sutural area occurs in most genera of Cantacaderini; it is particularly well visible in macropterous form of *Cyperobia caretorum*, where the membranous part occupies nearly half of the sutural area. It is possible that most species of the Australian genera (*Allocader*, *Australocader*, *Ceratocader*, *Carldrakeana*) have well developed (at least partly) membranous sutural area, but they are known by now only by forms with shortened wings, where sutural area is greatly reduced.

The clavi are well developed in Cantacaderini and Phatnomatini, but they are fused with mesocorium in forms with shortened wings. In Tinginae clavi are reduced and depressed below surface of the mesocorium, because they are covered by strongly produced triangular posterior margin of pronotum, that may impede spreading of the forewings.

Three main veins divide hemelytron into costal, subcostal, discoidal and sutural areas in Tinginae and Phatnomatini (Fig. 19); one another vein and additional area (i.e. stenocostal area) occur in Cantacaderini (Fig. 20).

The first main vein (called in all Heteroptera subcosta or costa+subcosta – see Schuh and Slater 1995), is thickened ventrally into the hypocostal lamina (or hypocosta). The vein hitherto called the hypocosta in all Tingidae (Drake and Davis 1960, Péricart 1983) appeared to be the true subcosta (or Sc+C), while the structure known in all Tingidae as the hypocostal area so far should be in fact called the hypocosta (or hypocostal lamina) (Figs 9, 14).

Thus, the vein lying along the outer margin of hemelytron in Tingidae (considered previously as the subcosta by Drake and Davis 1960, and Péricart 1983) might be regarded as a separate costal vein. Nevertheless, as confirmed by Betts (1986), the subcosta (or Sc+C) is the most external true vein in Heteroptera, therefore the vein lying along the outer margin of hemelytron in Tingidae should be actually regarded as a thickening of the outer margins of the most external areolae, and is not homologous to any vein in heteropteran forewing (moreover it is more or less developed, sometimes even hardly visible, that supports my hypothesis it is not a true vein).

The area called the costal area in Tingidae (sometimes greatly reduced or absent) is probably only a lateral expansion of the subcosta (or vein C+Sc – Fig. 19).

The position of the remaining veins (R+M and Cu) is the same as it was presented by Drake and Davis (1960).

In Cantacaderini the hypocosta is interrupted near its base by a trough, that is delimited by a pair of elevated crossveins leading from near apex of ostiolar canal. This elevation of adjacent veins continues along the ventral surface of costal area to set off a single row of areolae (i.e. stenocostal area) in most genera of Cantacaderini (Fig. 9).

According to Froeschner (1996) the stenocostal area serves as a trough to convey the scent-gland fluid to the costal area for evaporation. This hypothesis seems to be reasonable, especially with respect to genera with very broad costal area (e.g., *Nectocader*), where the scent-gland fluid outflow may be impeded.

In my opinion development of the stenocostal area is connected with specific structure of the peritreme and ostiolar pore. The orifices are directed upward and they are covered by the hypocostal lamina, and therefore the latter must be interrupted at the level of ostiolar pore. Three levels of complication of the ostiolar-stenocostal system presented by Froeschner (1996) pointed out that development of this structure was probably an introduction to expansion of the costal area in Cantacaderini.

According to Froeschner (1996) stenocostal area in the genus *Carldrakeana* is developed only as a trough across the hypocosta between two thickened, subbasal veins just opposite the apex of the peritreme, while the costal area is reduced, bearing only 1–2 rows of areolae. Analysing the ventral venation of the hemelytron I have found, that stenocostal area in *Carldrakeana* is normally developed (with one row of areolae), but the costal area is developed as a very thick and convex vein (*C. engista* – Fig. 38), sometimes with areolae, that divided this vein into two more veins (*C. socia*, *C. tindalei*). The outer one might be homologous to the true costal vein (since it has separated from the subcostal vein, or more frankly Sc+C) but, due to its ventral location and specific direction (parallel to outer margin of hemelytron, and near its base abruptly turned inward and joined with an inferior edge of the hypocosta) it may be an additional vein not homologous to any other vein in Heteroptera.

In the next stages of development of the ostiolar-stenocostal system in Cantacaderini, we can observe a gradual expansion of the costal area, and upcurving of the stenocostal area.

If we accept this way of evolution of the ostiolar-stenocostal system, it should be pointed out that the costal area of Cantacaderini is not homologous to the costal area of Tinginae and Phatnomatini (since it developed secondarily); the latter should be regarded as homologous to the stenocostal area of Cantacaderini (its primary location in genus *Carldrakeana* corresponds to location of the costal area in former groups).

It can not certainly be also excluded, that the absence of the costal area in *Carldrakeana engista* has appeared secondarily, as an adaptation for living among mosses and lichens; moreover, we can not eliminate the hypothesis that evolution of the ostiolar-stenocostal system has led from forms with broad costal area to those with narrow (or even absent) costal area.

Hindwings (metathoracic wings) in Tingidae are rather uniform in respect to their venation (Drake and Davis 1960, Davis 1961, Péricart 1983).

Main differences in the posterior wing venation within Tingidae concern the shape and position of radial (R),

cubital (Cu) and median (M) veins. Veins R and M lie almost parallel to each other in Cantacaderini (Fig. 21), while do not in Phatnomatini and Tinginae (Figs 22, 23). Moreover, the anterior part of M (cross-vein) is placed perpendicularly to both R and Cu in Cantacaderini (Fig. 21), while it is oblique in Phatnomatini and Tinginae (Figs 22, 23). The latter type of posterior wing venation (especially the shape of R) is found also in some other families of Cimicomorpha, e.g. Joppeicidae and Thumastocoridae (see Davis 1961, Schuh and Slater 1995).

Though a general pattern of the venation in posterior wings in Phatnomatini is the same as in Tinginae (Fig. 22, 23), it should be noticed that in some representatives of the former (e.g., *Phatnoma*, *Gonycentrum*) there exists an additional structure that resembles hamus occurring in other Cimicomorpha. This structure diverges from Cu in its basal part (Fig. 22); its location is very unique among Cimicomorpha, since normally hamus appears in the mid-length of Cu. Therefore, this structures found in Phatnomatini is called here "pseudohamus".

Legs

Three pairs of legs in Cantacaderini are developed almost typically as in other tingids. Sometimes, tibiae are very long and slender (Fig. 50), for instance in some species of the genus *Cantacader*, where additionally they are longer and stouter in males than in females.

The most important difference between Cantacaderini and other tingids (Phatnomatini and Tinginae) concerns the trochanter. Its distal part is totally fused with proximal part of femur in Cantacaderini (though sometimes a trace of junction is visible), while it is quite free and normally functionable in Phatnomatini and Tinginae. Tarsi are two-segmented in all taxa.

Abdomen

Pregenital abdomen in Cantacaderini is composed of segments II–VII in females, and II–VIII in males (first visible adominal segment consists of segment II, and greatly reduced segment I).

The abdominal segments II–III are fused in both Cantacaderini and Phatnomatini, but segments II–IV (*Campylosteira*, *Tingis*), or even II–VI (*Stephanitis*) are fused in Tinginae (Drake and Davis 1960, Péricart 1983, Froeschner 1996).

The spiracles (II–VIII) are placed ventrally (Fig. 9). The small, smooth area (a muscle attachment scar) are placed near each spiracle.

Each pregenital segment in Tingidae and Phatnomatini consists of sternite, tergite and two lateral sclerites on either body side. These lateral sclerites are placed dorsally, between tergites and sternites, and they were called inner and outer laterotergites (or paratergites) (Drake and Davis 1960, Péricart 1983). Each pregenital segment in Cantacaderini is composed of sternite, tergite, and a single lateral sclerite placed between them on either body side.

According to Sweet (1996) lateral abdominal sclerites should be called epipleurites (sclerites placed dorsally), and hypopleurites (sclerites placed ventrally and bearing spiracles). The presence of two pleural sclerites on either body side, which are placed dorsally, is characteristic for Leptopodomorpha and Pentatomomorpha; the presence of dorsally placed epipleurites, and ventrally placed hypopleurites, which together form connexivum, is characteristic for Cimicomorpha (Sweet 1996). The hypopleurites may be fused with sternites in Gerromorpha (Sweet 1996), but we can observe the same process in some cimicomorphan groups (e.g., in Miridae, Anthocoridae, and probably in Tingidae).

The structure of pregenital segments in Tinginae and Phatnomatini (that is comparable to that found in the pentatomomorphan and leptopodomorphan groups) might developed in four different ways: (1) by separation of inner lateral sclerites from tergites, (2) by partition of epipleurites, (3) by development of the additional sclerites in pleural membrane between epipleurites and tergites, (4) in the same way as in Pentatomomorpha (by development of so called "turned over connexivum" – see Sweet 1996), but the spiracles originated primarily on sternites (not on hypopleurites).

The double set of lateral plates in Tinginae and Phatnomatini (inner lateral plates in Phatnomatini may be differently sclerotized) originated most probably by the development of additional sclerites in the pleural membrane occurring between tergites and epipleurites (Figs 26, 27); moreover, hypopleurites fused with sternites and formed the ventral plate of each segment (Fig. 27).

The inner lateral sclerites are totally absent in Cantacaderini (Figs 24, 25); nevertheless, the possibility of desclerotization of these sclerites can not be excluded in this group. Such a situation makes the very flat cantacaderid abdomen more elastic, and enables females to fill it with eggs.

The number of sensory pits, their shape and structure, as well size of nodules (small tubercles), that occur on the surface of the abdominal terga in Tingidae, were occasionally used to find differences between subfamilies, tribes, genera and species of the family (Duarte Rodrigues *et al.* 1982). Unfortunately, those studies (Duarte Rodrigues *et al.* 1982) were based only on the single species of Cantacaderinae (namely *Cantacader tenuipes*, representing Cantacaderini), and eight species of Tinginae (tribes Tingini and Ypsotingini); no taxon of Phatnomatini was examined.

The absence of sensory pits in Cantacaderinae, and nodules which diameter is considerably smaller than a distance between them (vs. the presence of sensory pits in Tinginae, and larger nodules with diameter notably larger than a distance between them) were the main differences between both subfamilies reported by the authors (Duarte Rodrigues *et al.* 1982).

During examination of these structures in Phatnomatini (*Cnemidrus typicus*) I have found them similar to those occurring in Ypsotingini (Duarte Rodrigues *et al.* 1982). I have confirmed the presence of about 20 sensory pits on

either side, and the presence of big nodules in diameter larger than a distance between them. Additionally, the size of sensory pits and nodules is nearly the same, and a single sensory pit is associated with only one nodule; these characters were found previously only in Tinginae (Duarte Rodrigues *et al.* 1982).

Female genital segments are formed by several genital plates. The first is a subgenital plate (rhomboid or rounded) placed medially, beneath the VII sternite; it forms the base of ovipositor (Fig. 41). The eighth sternite is composed of two sclerites, each consisting of the gonocoxopodite I (valvifer) and laterotergite VIII fused together (Fig. 41).

The apodeme (distinct, thickened ridge serving for the attachment of muscles) is located ventrolaterally, between gonocoxopodite I and laterotergite VIII. It is well developed in Cantacaderini (Fig. 28), while usually strongly reduced in both Tinginae and Phatnomatini (Figs 29, 30).

Segment IX (Fig. 41) is developed as two large plates (laterotergites IX) that cover gonocoxopodites II and the ovipositor (Figs 28, 29, 30). Gonopods are very weakly sclerotized (nearly membranous) in Cantacaderini, and considerably more sclerotized in Tinginae and Phatnomatini.

The ovipositor in all Tingidae is elongate and it consists of gonapophyses I and II (Figs 28, 29, 30). The distal parts of gonapophyses (I and II) are serrate, since the eggs are deposited in a plant tissue.

The vagina (genital chamber) is large and sacciform in Cantacaderini (Fig. 31); a single ring sclerite (sometimes very large and massive, e.g., in *Allocader cordatus*) is present posteriorly in dorsal wall of vagina. The rudimentary median spermatheca is present, and it probably consists of the distal flange pump and small spermathecal bulb (e.g., in *Allocader cordatus*). The bases of the lateral oviducts are bulbous, and most probably serve as the sperm-storage organs.

The vagina in Tinginae and Phatnomatini is rather small and narrow (Figs 32, 33); a single, delicate ring sclerite may be present posteriorly at the dorsal wall of vagina; rudimentary spermatheca is absent. The vagina continues as a short common oviduct, then divides into two lateral oviducts. At the bases of lateral oviducts, the paired sperm sacs (pseudospermathecae) are present; they are joined together bearing a common duct in Phatnomatini (Fig. 32), or separated from each other with two (sometimes very short) independent ducts in Tinginae (Fig. 33).

The number of ovarioles is seven in Tinginae and Phatnomatini, and five in Cantacaderini.

The male ninth abdominal segment (pygophore) in Tingidae is not deeply telescoped into the abdominal segment VIII (Figs 26), but in some genera of Cantacaderini (e.g., *Cantacader* and *Pseudophatnoma*) the pygophore is really penetrating into the preceding segment, thus it is located between posteriorly elongate laterotergites VIII (Fig. 24). The opening of the pygophore is dorsally covered by a proctiger (small, quadrate sclerite) bearing the anus; the proctiger is accompanied by hooklet-like, directed backwards parameres on either side (Fig. 24).

The structure of the phallus in studied groups of Tingidae is rather uniform (Figs 34, 35, 37); the most distinctive feature of tingid phallus is the presence of endosomal diverticula (paired, sac-like extension of the ejaculatory duct).

The endosomal wall in Tinginae and Phatnomatini bears various large sclerites (Figs 35, 37). The latter are absent in Cantacaderini, where only in some genera the endosomal wall is almost evenly furnished with numerous, minute, conical protuberances (Fig. 34).

Other details of male and female genitalia in Tingidae were presented by Scudder (1959), Drake and Davis (1960), and Lee (1969), and are not repeated here.

Characters connected with wings modification

Differences shown by macropterous and brachypterous individuals of the same species in Tingidae are so important, thus deserving a separate description.

Wing modifications in Tingidae have been categorized so far into three types (all definitions after Slater 1975): macropterous (clavus and corium distinct, membrane well developed, hind wings elongate), submacropterous (clavus and corium distinct, membrane of forewings reduced leaving posterior abdominal segments exposed, hind wings either slightly reduced or elongate), and brachypterous (forewings reduced, not covering abdominal terga VI and VII, clavus and corium fused or not, but elements recognizable, hind wings reduced but usually not flap-like). Sometimes, the fourth form (subbrachypterous) was also recognized (see Péricart 1983).

Forms regarded hitherto as brachypterous in Tingidae do not correspond exactly to the above definition, since their hemelytra cover the whole abdomen or usually even are longer than the latter. It would be better to define these forms as coleopterous (according to the terminology of Slater 1975).

Below I present a list of characters (based on my own studies) defining the coleopterous forms in Cantacaderini (it can also be useful in Phatnomatini and Tinginae), that supplemented the general definition of Slater (1975). The "coleopterous" condition of hemelytra is defined by three characters:

1. clavo-corial suture absent, clavus and corium indistinguishable fused (Fig. 43);
 2. sutural area reduced (Fig. 43), sometimes to the degree when hemelytra in repose do not touch each other along posterior margins;
 3. hind wings absent or reduced;
- and are always accompanied by following other characters:
4. body length reduced about 15–20% in comparison to macropterous forms;
 5. apical parts of costal area narrower than in macropterous forms due to a reduction of areolae size (not areolae number), making the anterior margin of hemelytra more rounded than in macropterous individuals;
 6. pronotal disc flattened (Figs 45, 51), making paranota (if

present) visually broader than in macropterous individuals;

7. pronotal carinae stouter than in macropterous forms. Such characters as a body colouration, the shape of head, antennae and legs, as well as a number of areolae in costal, subcostal and discoidal areas do not change in coleopterous forms when comparing to macropterous individuals of the same species.

PHYLOGENETIC ANALYSIS

Because of uncertain position of Cantacaderini to other tingids it was decided to conduct two analyses; the first one to find out relationships among the tribes of Tingidae, and the second to investigate an internal phylogeny of the tribe Cantacaderini.

The first analysis included all the tribes of Tingidae, as proposed by Drake and Ruhoff (1965), and the family Vianaididae for outgroup comparison; a total of 23 characters were selected. The second analysis included all known genera of Cantacaderini, and two other tingid genera – *Tingis* (subfamily Tinginae) and *Phatnoma* (tribe Phatnomatini) as the outgroup for the analysed tribe; a total of 26 characters were selected. The characters were analysed using "ie*" option in Hennig86.

All characters were divided usually into two, sometimes three or four states; the character states were used to construct the data matrix (Table 1, 2). In order to avoid misinterpretation of multistate characters polarity (Forey *et al.* 1992), states were treated as unordered and unweighted (option "cc-"). Moreover, the successive weighting procedure was also performed, but it produced exactly the same cladograms as the standard procedures.

Characters for the analysis at the tribal level within Tingidae

0. head: distinctly projecting in front of eyes, surpassing antennal segment 1 (0); short, not surpassing antennal segment 1 (1);
1. clypeal spine: absent (0); present (1);
2. bucculae: short, not surpassing head apex (0); elongate, buccal laminae contact each other by their dorsal margins in front of clypeus (1); bucculae distinctly projecting in front of the head (they may touch each other in their apical parts) (2);
3. antennal segment 2: distinctly shorter than antennal segment 3 (0); subequal to antennal segment 3 (1);
4. posterior margin of pronotum: straight (0); slightly prolonged backward, rounded (1); distinctly prolonged backward, forming triangular process (2);
5. number of pronotal carinae: none (0); 1–3 (1); 5 (2);
6. lateral carinae on collar: absent (0); present (1);
7. hemelytra: punctate (0); tiny areolate (areolae small, rather irregular) (1); areolate (areolae differ in their size, sometimes they are very large, and quite regular) (2);
8. costal area: absent (0); present (1);

9. stenocostal area: absent (0); present (1);
10. membrane in macropterous form: normally developed (0); rudimentary or absent (1);
11. trochanter: free (0); fused with femur (1);
12. scent gland opening (ostiolar pore): peritreme developed as an apically closed loop (0); peritreme crevice-like, ostiolar pore directed upward (1); peritreme T-shaped, evaporating area very large (2); absent (3);
13. medial vein in hindwings: acutely connected with cubitus (0), developed as a perpendicular vein to cubitus (1);
14. apodeme between laterotergite VIII and gonocoxopodite I: completely developed and functioning as a muscle connection (0); rudimentary (1); absent (2);
15. pregenital abdominal segments: only II and III fused (0); II, III, and IV (or more) fused (1);
16. clavus: normally developed (0); weakly developed than mesocorium and depressed below its surface (1);
17. second tarsal segment: normally developed (0); rounded and strongly convex (1);
18. pseudospermatheca (sperm sac): absent (0); present (1);
19. abdomen: with a simple set of lateral sclerites (0); with a double set of lateral sclerites (1);
20. rudimentary spermatheca: present (0); absent (1);
21. gonoplares: strongly sclerotized (0); weakly sclerotized or membranous (1);
22. vagina (genital chamber): small (0); spacious, sac-like (1).

Characters for the analysis at the generic level within Cantacaderini

0. costal area: broad (more than 2 areaolae in its median part) (0); narrow (none or 1 areola in its median part) (1);
1. tubercles on the second abdominal sternum: absent (0); present (1);
2. stenocostal area: absent (0); developed only ventrally (1); developed ventrally and dorsally (2);
3. pronotum: not elongated along lateral carinae (0); elongated along lateral carinae (1);
4. pronotum: not elongated along the median carina (0); elongated along the median carina (1);
5. lateral margins of hemelytra: normally developed (0); serrate (1);
6. lateral margins of pronotum: straight (0); bisinuated (1);
7. veins R+M and Cu in basal part of hemelytron: separated from each other (0); fused (1);
8. lateral margins of paranota: without teeth (0); with a single tooth (1); with 6–8 teeth (2);
9. spines on head: straight (0); clearly broadly upcurved (1);
10. carinae on the second abdominal sternum: absent (0); present (1);
11. hood in anterior part of pronotum: absent (0); present (1);
12. femur: without spur (0); with apical spur (1);
13. discoidal area: with transverse veins (0); without transverse veins (1);

14. paranotum: unilobed (0); bilobed (1);
15. scutellum: with a distinct tubercle in its posterior part (0); without tubercle, or covered by posterior margin of pronotum (1);
16. rostrum: short, not reaching genital segment (0); long, reaching genital segment (1);
17. margins of bucculae: without pilosity (0); with short stiff hairs (1);
18. clypeal spine: absent (0); present (1);
19. trochanters: not fused with femora (0); fused with femora (1);
20. scent gland peritreme: developed as an apically closed loop (0); crevice-like (1);
21. lateral carinae on collar: absent (0); present (1);
22. pseudospermatheca: absent (0); present (1);
23. gonoplares: strongly sclerotized (0); membranaceous (1);
24. paranota: horizontally to pronotal disc (0); strongly reflected upwards (1);
25. clypeus: short, reaching at best apical ends of jugo-frontal spines (0); long, clearly surpassing apical ends of jugo-frontal spines (1);

Results

Tribal level. As a result of the analysis only a single tree was obtained (Fig. 1) of 33 steps, CI=90 and RI=70.

The resulted tree shows that Cantacaderini are a group supported by seven synapomorphies in characters 2, 4, 5, 6, 9, 11, 13, and identifies it as a sister group of the remains of tingids. Furthermore, the results of this analysis also show that Phatnomatini clearly are a part of Tingidae and that there is no justification for uniting them with Cantacaderini within the subfamily Cantacaderinae (sensu Froeschner, 1996), that appeared during present studies to be polyphyletic. Therefore, it is proposed herein to raise Cantacaderini to the family level – Cantacaderidae *stat. nov.*

Moreover, Phatnomatini and Tinginae are held together as sister taxa based on the hemelytra with areolae of different sizes (# 7), the presence of pseudospermatheca (# 18), and the peculiar, double set of lateral sclerites between abdominal terga and sterna (# 19). These characters can also be regarded as synapomorphies for the Tingidae *sensu novo*.

Recently described (from the Baltic amber) fossil genus *Tingicader* Popov (1998) that, according to this author (Popov 1998) occupies an intermediate position between Phatnomatini and Tinginae, also supports the close relationship of these two high-level taxa.

As we can see from the cladogram the monophyletic Tingidae *sensu novo* are divided into two sister groups – Phatnomatini (sensu Froeschner 1996) and Tinginae. It is proposed herein to raise the former to a subfamily level – Phatnomatinae *sensu novo* characterised by the presence of the clypeal spine (# 1).

The monophyly of Tinginae is supported by the posterior margin of pronotum distinctly prolonged backward, forming triangular process (# 4), and the absence of claval suture,

that is connected with a reduction of clavi (#16). The internal relationships within the Tinginae should be regarded as preliminar (many studies need to be done before a satisfactory tribal classification can be presented within Tinginae).

Generic level. This analysis resulted in six cladograms (Figs 2A–2F); only one tree was completely resolved (Fig. 2A) and this was selected to present the relationships among the studied taxa ($L=34$, $CI=82$, $RI=77$). The incompletely resolved consensus tree (Fig. 2G) was also excluded from consideration.

The cladogram (Fig. 2A) shows that the family Cantacaderidae can be divided into two monophyletic sister groups – Carldrakeaninae *subfam. nov.* (synapomorphy in character 0), and Cantacaderinae *sensu novo* (synapomorphy in character 2).

Carldrakeaninae *subfam. nov.* includes three most primitive cantacaderid genera and is characterised by a narrow costal area and the stenocostal area developed only ventrally. The second subfamily (Cantacaderinae *sensu novo*) contains seven genera held together on the basis of broad costal area and the stenocostal area well developed ventrally and dorsally.

Furthermore, the results of the analysis show that Cantacaderinae *sensu novo* includes two distinct evolutionary lineages.

The first monophylum (Cantacaderini *sensu novo*) grouped the genera with pronotum elongated along the median carina (# 4) and flat scutellum bearing no tubercle, or covered by posterior margin of pronotum (# 15). The programme treated these characters as homoplasies, since similar states appear in Tinginae; one can assume that in some cases a parallel evolution took place in Tingidae and Cantacaderidae, making their representatives superficially similar.

The second monophyletic group (Ceratocaderini *trib. nov.*) is supported by the synapomorphy in character 3 (pronotum elongated along lateral carinae), and it is hypothesized as the sister group of Cantacaderini *sensu novo*.

Classification of Tingioidea. Prevailing studies aimed to clarify the relationships between Tingidae (*sensu* Froeschner 1996) and other cimicomorphan high-level taxa (Drake and Davis 1960, Schuh and Štys 1991, Schuh and Slater 1995) did not result in unquestionable placement of the family within any superfamily of Cimicomorpha.

Representatives of Tingidae (*sensu* Froeschner 1996) have many characters in common with different taxa in five out of seven cimicomorphan superfamilies (B. Lis, unpublished); the family is similar to Reduvioidea (the same type of scent glands, paired pseudospertmatheca), to Joppeicoidea (the same shape of antennae and their segments proportions, the vein R+M in hemelytron raised and keel-like), to Miroidea (the absence of ocelli, four-segmented rostrum), to Naboidea (the structures of external female genitalia), and to Velocipedoidea (the presence of costal area in hemelytron).

At the present state of our knowledge it seems to be more

reliable to return to the previous conception of the separate superfamily Tingioidea (Pendergrast 1957, Scudder 1959, Štys and Kerzhner 1975, Popov 1981), that was accepted also recently by Froeschner (1996). The main synapomorphy for that taxon grouped Vianaididae, Cantacaderidae and Tingidae is the presence of endosomal diverticula, not found in any other cimicomorphan family.

On the basis of all these facts, I suggest the following classification of the superfamily Tingioidea:

Superfamily Tingioidea

Family Cantacaderidae Stål, 1873 (*stat. nov.*)

Subfamily Cantacaderinae Stål, 1873 (*sensu novo*)

Subfamily Carldrakeaninae *subfam. nov.*

Family Tingidae Laporte, 1832 (*sensu novo*)

Subfamily Phatnomatinae Drake and Davis, 1960 (*stat. nov.*)

Subfamily Tinginae Laporte, 1832

Family Vianaididae Kormilev, 1955

Nevertheless, more investigations are necessary to construct the final cladistic hypotheses concerning a systematic position of Tingidae and related families (Vianaididae, Cantacaderidae) within all Cimicomorpha.

HISTORICAL BIOGEOGRAPHY

The analysis leading to estimation of the date and place of origin of Cantacaderidae, and their most probably migratory paths was based on the present distribution of its taxa, the palaeontological data, and the ancestral area analysis.

Geographic distribution. The distribution area of Cantacaderinae includes all biogeographic regions except the Nearctic (Figs 6, 7). The most species rich genus *Cantacader* Amyot and Serville is restricted to the Old World; it is known from the Oriental (9 species), Australian (5 species), Afrotropical (20 species), and Palaearctic (3 species) Regions (Fig. 4), where it reaches 45°N latitude.

Stenocader Drake (known only from Chile) and *Nectocader* Drake (recorded from Brasil) are confined to the Neotropics, and are the only two genera known to occur there (Fig. 3).

The Australian Region is the most abundant in cantacaderid genera, where species of six of the ten genera are distributed (Fig. 6), namely *Allocader* Drake (Australia, Tasmania, Lord Howe Island), *Australocader* B. Lis (Australia), *Carldrakeana* Froeschner (Australia, Tasmania, New Zealand), *Ceratocader* Drake (Australia, Tasmania), *Cyperobia* Bergroth (New Zealand), and *Cantacader* Amyot and Serville (Australia, New Guinea, Bismarck Archipelago).

The Oriental Region (Fig. 6), besides the genus *Cantacader* Amyot and Serville, has two more genera, *Pseudophatnoma* Blöte (Riau Archipelago, Borneo, Laos) and *Teratocader* Drake (Malay Peninsula).

Palaeontological data. The oldest fossils with no doubts belonging to the Cantacaderidae come from the oligocene Baltic amber, and are represented by one genus (*Paleocader* Froeschner) with three species, *P. avitus* (Drake),

P. quinquecarinatus (Germar and Berendt) and *P. strictus* Golub and Popov. The genus shows all the characters of Cantacaderidae, namely the pronotum with five carinae, the presence of lateral carinae on pronotal collar, typically placed cephalic spines and well developed stenocostal area. The absence of tubercle on the scutellar apex indicates a relationship to *Cantacader*, *Pseudophatnoma* and *Teratocader*.

On the other hand, the oldest representative of Tingidae (*sensu novo*), *Sinaldocader drakei* Popov, that was described from Lower Cretaceous of Mongolia (Popov 1989), shows two characters (structure of pronotum, and the absence of stenocostal area) which allow to place it within Phatnomatinae (*sensu novo*).

Ancestral area analysis. The estimation of the ancestral area for the Cantacaderidae was based on the Bremer's method (Bremer 1992). The area cladogram for the family (Fig. 5) was constructed by replacing the terminal taxa in Fig. 2A cladogram by their distribution area.

The total distribution area of the family was divided for the purpose of the present paper into following areas: Palaearctics (PAL), Africa (AFR), Orient (without both Indochinese and Malayan Peninsula, and without Malayan Archipelago) (IND), area including Indochinese and Malayan Peninsula, and Malayan Archipelago (MAL), New Guinea (NG), Australia (AUS), New Zealand (NZ), and Neotropics (NEO).

Application of Bremer's method for Cantacaderidae area cladogram resulted in different numbers of gains and losses for certain areas (Table 3). For all areas, except New Zealand (NZ) and Australia (AUS), the number of losses exceeds the number of gains. For New Zealand both numbers equal, while only for Australia the number of gains exceeds the number of losses, and the probability that Australia was included in the ancestral area is the highest.

Therefore, I conclude that the ancestral area for the family Cantacaderidae was smaller than the present day area of distribution, and it included Australian continent.

Origin of the family and its migratory pathes. Basing on all the previous data I assume that the family Cantacaderidae originated most probably about 140 MYBP, in the early Cretaceous, on the territory that at present belongs to Australian continent, when it was included in the Gondwana.

The estimation of the date of origin is based on the fact, that New Zealand was the first land to separate from the main masses of Gondwanaland, and about 125 MYBP it was isolated from it wide enough to make the migration of animals between New Zealand and Gondwana impossible (Briggs 1995). Since representatives of *Carldrakeana* occur in New Zealand and Australia, it is clear that the genus must have originated before New Zealand separated from Gondwana, and thus the history of the whole family has begun earlier, at the time when Gondwana started to breakup.

On the other hand, *Cyperobia* (the genus endemic to New Zealand) originated later, most probably in the Cretaceous (97–66 MYBP), when the first sedges (its host plants) have evolved.

Since a close connection between Antarctica and South America existed at least till 50 MYBP (Stanley 1986), it enabled *Stenocader* (the genus closely allied to both *Carldrakeana* and *Cyperobia*) to reach South American continent; the same migratory path was shared also by South American genus *Nectocader*, closely related to three Australian genera (*Allocader*, *Australocader*, *Ceratocader*). The absence of those or related genera in Africa (located between South America and the remaining parts of Gondwanaland) suggests that the westward migration of Cantacaderidae from Australia initiated not earlier than 110 MYBP, when Africa started to separate from South America (Sclater 1977).

Since at present, Cantacaderidae are distributed also in the Asian continent, they migrated there most probably with the Indian subcontinent. The latter, occurred between Africa, Antarctica and Australia in the main block of Gondwana, started to separate at first from Australia about 125 MYBP (Keast 1981); most probably it was the time when Cantacaderidae have migrated from its place of origin (Australia) to the Indian subcontinent.

After first slow period of separation of Indian subcontinent from other parts of Gondwanaland, about 80 MYBP it moved rapidly northward (Keast 1981). Then, about 65 MYBP (the beginning of the Cenozoic) India have come in close contact with Sundaland (a continental block including present lands of Java, Sumatra, Borneo, Malaya and Indochina and forming at that time the nucleus of Southeast Asia), and then it collided with the main Asian continent (Keast 1981). It was the beginning of migration of Cantacaderidae at first to Sundaland, and then to continental Asia (Fig. 6).

At present, all the genera known from Asia represent the same single evolutionary line; moreover, *Teratocader* and *Pseudophatnoma* (having representatives on the territory of previous Sundaland) show close affinities to Australian genera (i.e. very broad costal area).

Cantacader, belonging to the same evolutionary lineage as the two previous genera, is the most abundant cantacaderid genus, that has also the widest area of geographic distribution of its species.

The genus has firstly radiated in Asia, that was since middle Jurassic separated from Europe by the Turgai Sea; its regression (Briggs 1995) about 35 MYBP (late Eocene/early Oligocene) enabled some species of *Cantacader* to migrate and radiate in Europe. The fossil genus *Paleocader*, represented by three species known from the Baltic amber, is dated back to the same period when *Cantacader* has radiated in Europe, and both genera seem to be very closely related. Most probably *Paleocader* represented the northern off-shot of the European Cantacaderidae line.

Gradual global climatic changes (cooling and drying) in Europe and Asia caused a major migration of high-latitude taxa of Cantacaderidae to lower latitudes, at least down to surpass the latitude 45°N.

About 20 MYBP (early Miocene) initial contact has been made between the Sundaland and the New Guinean margin

of Australia (Keast 1981); then by 10 MYBP (late Miocene) the leading edge of Australia has collided with the Sundaland (Keast 1981), and enabled representatives of *Cantacader* (occurring at that time in Sundaland) to colonize Australian landmasses.

About 15 MYBP Africa has contacted both, Europe and Asia (Briggs 1995), and Cantacaderidae migrated to colonize northern Africa via Gibraltar, and its tropical regions via Arabian Peninsula (Fig. 7). These migratory paths are consistent with the present distribution of some species, i.e. *Cantacader quadricornis* and *C. laticollis*, both known only from southern Europe and northern Africa, and *C. tenuipes* known from Arabian Peninsula and tropical Africa.

It is also worth to mention that at the same time (early Cretaceous), when the very first Cantacaderidae appeared in East Gondwana, the representative of Phatnomatinae (Tingidae), i.e. *Sinaldocader drakei* (Popov 1989), already lived in the present territory of Mongolia. In addition, this fact supports also the phylogenetic analysis and allows to treat cantacaderids as evolutionary line quite separate from phatnomatids and the rest of Tingidae.

TAXONOMY

Family Cantacaderidae Stål, stat. nov.

Cantacaderaria Stål, 1873: 116.

Cantacaderinae: Drake et Ruffhoff, 1965: 22.

Diagnosis. Head elongated in its preocular part, with two pairs of spines: anterior – jugo-frontal, and posterior – preocular; bucculae laminate, bearing 2–4 rows of areolae, extend distinctly beyond anterior apex of head; bucculae may converge and their apices may touch each other. Pronotum with five or three carinae (exceptionally with one carina); outer (suprahumeral) carinae rather short, at best reaching calli; inner carinae, interrupted on calli, extending from the anterior margin of collar to the posterior edge of pronotum; the latter more or less prolonged backward, pronotal disc hardly punctated or tiny areolated; paranota enlarged, areolated. Scutellum, visible or covered by the posterior margin of pronotum, sometimes with prominent outgrowth in the apical part. Hemelytra areolated, areolae small, irregular; clavi normally developed, clearly separated from mesocorium by commissura (macropterous form) or fused with mesocorium (coleopterous form); an additional vein continues along the outer edge of the ventral surface of costal area and forms so called stenocostal area, that is usually composed of the one row of areolae. The crevice-like ostiolar pore is located between mesepimeron and metepisternite at the edge of the hypocosta. Legs are rather slender, with two tarsal segments; distal part of trochanter is fused with femur.

The family is represented by two subfamilies.

Biology. Biology of Cantacaderidae is poorly known; most of the studied specimens were collected at light. Based on the available data, one can conclude that representatives of the family feed on the above ground parts of plants, but

host plants are known only for a few of them, e.g., *Vernonia* sp. for *Nectocader gounellei* Drake, *Carex* sp., *Cassinia leptophylla*, and *Celmisia spectabilis* for *Cyperobia carectorum* Bergroth, mosses and lichens for *Carl-drakeana tindalei* (Hacker) and *C. socia* (Drake and Ruhoff), *Polygonum* sp. for *Cantacader quadricornis* (Le Peletier and Serville).

A type of plant formations inhabited by certain species of Cantacaderidae may be correlated with their type of wing modifications, as it was observed in Tingidae (B. Lis 1998). One may assume that species represented mainly by macropterous forms (e.g., *Cantacader tenuipes*) lives and feeds on trees and bushes, while those represented predominantly by coleopterous individuals (e.g., *Cantacader quadricornis*) lives and feeds on low plants forming turfs (e.g., *Polygonum* sp.). When taking some other facts into account, it is also highly probable that at least some species (especially of the genus *Cantacader*) lives and feeds on grasses (in Africa cantacaderids are distributed mostly in savannah regions, most of species has protective ochreous body colour, and, as the most important, numerous specimens studied by me were covered with small fragments of grasses). The wing form may be associated in some cases with sex, e.g., females of *Stenocader tingidoides* (Spinola) are most probably always submacropterous, while males are only macropterous.

Life-cycles and larval stages of Cantacaderidae are also almost unknown. Up to date nymphs of only two species (i.e. *Cantacader quadricornis* and *C. lethierryi*) were described (Lee 1969, Putshkov 1974, Péricart 1983); the nymph of *Ceratocader armatus* (Hacker) is illustrated here (Fig. 48).

Key to subfamilies of Cantacaderidae

1. Stenocostal area developed only ventrally; its areolae of the same shape and size as those of costal area; posterior edge of pronotum almost straight (Fig. 42) Carldrakeaninae
- Stenocostal area developed dorsally and ventrally; its areolae clearly differs in shape and size from those of the costal area; posterior edge of pronotum prolonged backward (Fig. 50) Cantacaderinae

Subfamily Carldrakeaninae subfam. nov.

Diagnosis. Head elongated, especially between eyes and preocular spines; antennae located slightly ventrally, below the line drawn through the middle of eyes; antennal segments I and II very small; outer pronotal carinae rather short; paranota narrow; posterior margin of pronotum almost straight, scutellum visible. Hemelytra rather massive, their areolae small, veins thick; stenocostal area developed only ventrally, its areolae of the same sizes and shape as the others; costal area narrow (0–1 areola in the middle part).

The subfamily includes three genera.

Key to genera of Carldrakeaninae

- 1. Pronotum dorsally with one or three carinae; first visible abdominal sternite with two tubercles (Fig. 39) *Carldrakeana*
- Pronotum dorsally with five carinae; first visible abdominal sternite without tubercles 2
- 2. Lateral margins of paranota and hemelytra with irregular serrations (Fig. 44) *Stenocader*
- Lateral margins of paranota and hemelytra without serrations *Cyperobia*

Genus *Carldrakeana* Froeschner (Fig. 42)

Carldrakeana Froeschner, 1968: 250. Type species by original designation: *Phatnoma tindalei* Hacker, 1928.

Diagnosis. Head elongated, triangular, with two pairs rather short and blunt spines; preocular spines located near apex of the head, far from the eyes. Bucculae elongated, form narrow laminae, their rounded apices may touch each other beyond the tip of head. Rostrum reaching the middle of third abdominal segment. Posterior edge of pronotum straight; scutellum exposed, with prominent tubercle in its apical part; paranota rather narrow; pronotal disc with either a single (median) or three laminate carinae. Hemelytra convex, rather narrow; stenocostal area developed ventrally, with one row of areolae; costal area absent or developed as one row of areolae, costal areolae sometimes appear only at the basal and apical part of hemelytron; subcostal area with several transverse veins; discoidal area with two transverse veins, which divide discoidal area into three smaller areas. First visible abdominal sternite with two median tubercles, forming continuation of the rostral groove. Body length about 2.5 mm; known only by coleopterous forms.

List of species:

- 1. *Carldrakeana engista* (Drake and Ruhoff)
Gonycentrum engistum Drake and Ruhoff, 1961: 127, 1965: 33.
Carldrakeana engista: Froeschner 1968: 251.
Type material: Holotype female: [AUSTRALIA]: New Guinea [error!], Mt. Lamington (USNM).
Distribution: Australia.
Remarks: The type-locality (Mt. Lamington, Qld) was erroneously given in the original description (Drake and Ruhoff 1961) as a New Guinean locality; the mistake was repeated by subsequent papers (Drake and Ruhoff 1965, Froeschner 1968, 1996).

- 2. *Carldrakeana socia* (Drake and Ruhoff)
Gonycentrum socium Drake and Ruhoff, 1961: 128; 1965: 33.
Cyperobia carectorum: Woodward 1961: 156 [part].
Carldrakeana socia: Froeschner 1968: 251.
Type material: Holotype male: [AUSTRALIA]: Launceston, Tasmania (USNM).
Distribution: Australia (South Australia, Tasmania), New Zealand.
Material examined: 31 ex., HNHM.

- 3. *Carldrakeana tindalei* (Hacker)
Phatnoma tindalei Hacker, 1928: 177.
Sinalda tindalei: Hacker 1929: 333.
Gonycentrum tindalei: Drake and Ruhoff 1965: 34.
Carldrakeana tindalei: Froeschner 1968: 251.
Type material: Holotype: [AUSTRALIA]: Lofty Ranges, South Australia (SAM); Paratypes: [AUSTRALIA]: Myponga, Mount Lofty, Belgrave (BMNH, SAM, QMBA, USNM).
Distribution: Australia (South Australia, Victoria).
Material examined: 1PT, BMNH.

Genus *Cyperobia* Bergroth (Fig. 43)

Cyperobia Bergroth, 1926: 673. Type species by monotypy: *Cyperobia carectorum* Bergroth, 1926.

Diagnosis. Head strongly elongated, its apex reaching beyond the second antennal segment; cephalic spines short and blunt; preocular spines located far from the eyes, jugo-frontal spines located near the apex of head; bucculae prolonged, their apices rounded and touch each other near the tip of head; rostrum long, reaching the middle of fourth abdominale segment. Pronotal disc with five low carinae; lateral carinae on the collar particularly weakly developed; outer carinae short, not reaching the middle of pronotal disc; paranota narrow, carinate, slightly enlarged opposite the calli; the latter developed as the downfolded, rounded lobes; posterior margin of pronotum almost straight. Scutellum exposed, with strongly prominent tubercle in its apical part. Areolae of hemelytra small, but veins thick; stenocostal area well developed only ventrally; costal area narrow, uniseriate; subcostal area with 2–3 transverse veins; discoidal area divided into three smaller areas by two transverse veins; coleopterous forms with narrow sutural area; macropterous forms with rudimentary membrane that occupies one third of the sutural area. Body length: 3.7–4.2 mm.

List of species:

- 1. *Cyperobia carectorum* Bergroth
Cyperobia carectorum Bergroth, 1926: 674; Drake and Ruhoff 1965: 31; Štusák 1979: 143, 149.
Cyperobia correctorum [!]: Drake and Davis 1960: 29.
Type material: Holotype female: [NEW ZEALAND]: Gollan's Valley, Wellington, New Zealand (location unknown).
Distribution: New Zealand.
Material examined: 4 ex., BMNH; 1 ex., HNHM.

Genus *Stenocader* Drake and Hambleton (Fig. 44)

Stenocader Drake and Hambleton, 1944: 120. Type species by original designation: *Piesma tingidooides* Spinola, 1852.

Diagnosis. Head elongated, reaching second antennal segment; head surface granulate, bearing two pairs of semierect cephalic spines; preocular spines located far from eyes, at head mid-length. Bucculae reaching head apex, sometimes they may touch each other. Rostrum reaching

posterior margin of third abdominal segment (in submacropterous forms), or slightly longer, reaching middle of fourth abdominal segment (in macropterous forms). Pronotum with five carinae; outer carinae short, not reaching the middle of pronotal disc; paranota narrow, marginally serrate; the serration formed by irregular, subtriangular projections; posterior margin of pronotum straight. Scutellum exposed, with a small prominent tubercle in its posterior part. Hemelytra tiny areolate, marginally serrate. Stenocostal area not visible dorsally, but well developed ventrally; costal area bearing two rows of areolae at base, one row of areolae in the middle, and totally reduced in the posterior part of hemelytron; subcostal area wide, with 5–6 transverse veins; discoidal area divided by two transverse veins into three smaller areas; veins distinctly developed, almost laminate; sutural area with rudimentary membrane (in macropterous forms). Body length: 3.3–3.6 mm.

Remarks. A sexual dimorphism in *Stenocader tingidoides* is strongly developed; males are macropterous, more slender than females; females have slightly shortened wings, but they are able to fly, and therefore are named submacropterous; they differ from males by considerably wider and more convex body. These two sexual forms were previously described under two different species, namely *Stenocader tingidoides* (females) and *Stenocader garmainii* (males).

List of species:

1. *Stenocader tingidoides* (Spinola)

Pisma tingidoides Spinola, 1852: 200; Stål 1873: 134.

Cantacader tingidoides Signoret 1863: 575.

Cantacader garmainii Signoret, 1863: 586; Stål 1873: 134.

Nectocader Garmaini [!]: Drake 1928: 42.

Nectocader tingitoides [!]: Drake 1928: 42; Monte 1937: 114.

Nectocader tingidoides: Monte 1942: 107.

Stenocader tingidoides: Drake and Hambleton 1944: 120; Drake 1950: 166;

Drake and Ruhoff 1965: 40.

Stenocader germani [!]: Drake 1950: 166.

Type material: Lectotype female (present designation) of *Pisma tingidoides*: [CHILE]: Chile (MNHN); 1 paralectotype: [CHILE]: Chile (MNHN). Syntyp(e) males of *Cantacader garmainii*: [CHILE]: Chili (location unknown).

Distribution: Chile.

Material examined: 1 ex., MNHN; 1 ex., ISNB; 2 ST (1 LT and 1 PLT), MNHN; 2 ex., HNHM.

Subfamily Cantacaderinae Stål sensu novo

Diagnosis. Head moderately elongated with apex not surpassing second antennal segment, or head with strongly elongated clypeus; antennal segments I and II relatively large; pronotum five- or three-carinate; paranota usually broad, sometimes reflected upward; posterior margin of pronotum prolonged backward along either median or lateral inner carinae; scutellum visible, either flat or with a tubercle in its posterior part, or scutellum sometimes totally covered by pronotum. Hemelytra delicate, clearly broadened in the basal part; stenocostal area developed dorsally and ventrally, its areolae clearly differ in shape and size from

those of the costal area; costal area broad (usually 4–5 areolae in its middle part).

Key to tribes of Cantacaderinae

1. Posterior margin of pronotum prolonged backward along lateral carinae; scutellum always visible, bearing prominent tubercle in its posterior part (Figs 46, 47)
 - Ceratocaderini
- Posterior margin of pronotum prolonged backward along median carina; scutellum either not visible or, without tubercle in its posterior part (Figs 50, 52)
 - Cantacaderini

Tribe Ceratocaderini trib. nov.

Diagnosis. Head relatively short, its apex not reaching beyond second antennal segment, or head long, with clypeus strongly elongated; pronotum tricarinate, rarely with five carinae; posterior margin of pronotum prolonged backward along inner lateral carinae; scutellum exposed, with tooth-like projection in its posterior part; hemelytra broadly rounded, dilated from base; stenocostal area developed dorsally and ventrally, composed of single row of regular, quadrate areolae; costal area wide, sometimes upcurved and strengthened by a thick, transverse vein in the middle.

Key to genera of Ceratocaderini

1. Pronotum with five carinae (Fig. 49) *Nectocader*
- Pronotum with three carinae (Fig. 45) 2
2. First visible abdominal sternite with two median carinae (Fig. 40) *Australocader*
- First visible abdominal sternite without median carinae
 - 3
3. Paranota with 6–8 long spines, anterior part of the median carina developed as a small hood (Fig. 47)
 - *Ceratocader*
- Paranota without spines, hood absent (Fig. 45)
 - *Allocader*

Genus *Allocader* Drake (Fig. 45)

Allocader Drake, 1950: 156. Type species by original designation: *Cantacader leai* Hacker, 1928.

Diagnosis. Head strongly elongated in preocular part, its apex reaching beyond second antennal segment; cephalic spines short and blunt, sometimes tuberculate; preocular spines placed distant from eyes, jugo-frontal spines located at the base of strongly elongated clypeus. Bucculae elongated, their apices rounded, reaching or slightly surpassing the head apex. Rostrum long, reaching the fifth abdominal segment. Pronotum narrow, tricarinate; carinae low and rather thick; paranota either laminate and recurved upward, or very narrow and almost carinate; posterior margin of pronotum almost straight, or slightly prolonged along lateral

carinae; scutellum exposed, with prominent tubercle posteriorly. Hemelytra broadly expanded at base, their margins widely rounded; costal area broad, bearing 5–9 areolae in the middle part; discoidal area with two, sometimes not clearly visible, transverse veins.

The genus is represented only by coleopterous forms. Body length: 3.0–9.0 mm.

List of species:

1. *Allocader cordatus* (Hacker)

Phatnoma cordata Hacker, 1927: 19.

Cantacader cordatus: Hacker 1928: 174.

Allocader cordata: Drake 1950: 156.

Type material: Lectotype female (designate by Cassis and Gross 1995: 398): [AUSTRALIA]: National Park, Queensland (QMBA).

Distribution: Australia (Queensland).

Material examined: LT, QMBA; 1 ex., HNHM.

2. *Allocader leai* (Hacker)

Cantacader leai Hacker, 1928: 176.

Allocader leai: Drake 1950: 156; Drake and Ruhoff 1965: 23.

Type material: Holotype male: [AUSTRALIA]: Hobart, Tasmania (QMBA).

Distribution: Australia (Tasmania).

3. *Allocader nesiotus* Drake and Ruhoff

Allocader nesiotus Drake and Ruhoff, 1962: 249, 1965: 23.

Type material: Holotype male: [AUSTRALIA]: Lord Howe Island (SAM).

Distribution: Australia (Lord Howe).

Genus *Australocader* B. Lis

(Fig. 46)

Australocader B. Lis, 1997: 211. Type species by original designation:

Australocader kerzhneri B. Lis, 1997.

Diagnosis. Head moderately long, reaching distal apices of the second antennal segments; cephalic spines massive, sharply ended, slightly recurved upward; preocular spines located nearby eyes, jugo-frontal spines located slightly in front of the preocular pair. Bucculae long, reaching beyond head apex, their apices angularly curved, touch each other in front of the head apex. Rostrum reaching the posterior edge of third abdominal segment. Pronotum tricarinate, carinae low and thick; paranota moderately wide, slightly upcurved, anterolaterally with a small, toothlike projection; posterior margin of pronotum prolonged backward along lateral carinae. Scutellum exposed, with prominent tubercle. Hemelytra broadly expanded at bases, margins widely rounded; costal area slightly upcurved, bearing 5–6 areolae in the middle part; subcostal area with a few transverse veins; discoidal area with not clearly visible transverse veins, that divided discoidal area into three smaller areas; sutural area narrow, with rudimentary membrane. The first visible abdominal sternite medially with two longitudinal carinae, each bearing one row of areolae, and forming a prolongation of the rostral groove. The ninth laterotergite

(females) with longitudinal concavity. Body length: 3.8–4.3 mm.

Species of the genus is known only by coleopterous forms, so far.

List of species:

1. *Australocader kerzhneri* B. Lis

Australocader kerzhneri B. Lis, 1997: 212.

Type material: Holotype female: [AUSTRALIA]: ACT, Canberra, Black Mt. (ZMAS).

Distribution: Australia (Canberra).

Material examined: HT, 3 PT, ZMAS.

Genus *Ceratocader* Drake

(Figs 47, 48)

Ceratocader Drake, 1950: 157. Type species by original designation:

Cantacader armatus Hacker, 1928.

Diagnosis. Head moderately long, its apex not surpassing the second antennal segment; dorsal surface armed with two pairs of upcurved spines, very stout basally and thin apically; preocular pair of spines located nearby eyes, jugo-frontal spines located close to the former. Bucculae very long, distinctly surpassing head apex, and touching each other apically. Rostrum reaching to posterior edge of metasternum. Pronotal disc slightly convex, with three laminate carinae. Anterior part of the median carina developed as small hood that is slightly prominent between eyes. Paranota moderately wide, with 6–8 spines; posterior margin of pronotum prolonged backward along lateral carinae. Scutellum exposed, with prominent tubercle in its distal part. Hemelytra widely expanded at bases, margins rounded; costal area broad, slightly upcurved, bearing 5 rows of areolae in the middle part; subcostal area with thick transverse vein at the apex of clavus, and with several indistinct transverse veins in its posterior part; discoidal area with two transverse veins that divided this area into three smaller areas; sutural area narrow, with rudimentary membrane along its inner edge. Body length: 3.5–4.5 mm.

All known species of the genus *Ceratocader* are represented only by coleopterous forms.

List of species:

1. *Ceratocader armatus* (Hacker)

Cantacader armatus Hacker, 1928: 174.

Ceratocader armatus: Drake 1950: 158 and 164; Drake and Ruhoff 1965: 29.

Type material: Holotype: [AUSTRALIA]: South Australia, Murray Bridge (SAM); Paratypes: [AUSTRALIA]: Murray Bridge (MVMA, SAM, QMBA, USNM).

Distribution: South Australia.

Material examined: 1 ex. imago, 1 ex. larva, HNHM; PT, MVMA.

2. *Ceratocader dentatus* (Hacker)

Cantacader dentatus Hacker, 1928: 175.

Ceratocader dentatus: Drake 1950: 158 and 164; Drake and Ruhoff 1965: 29.

Type material: Holotype: [AUSTRALIA]: Burnie, Tasmania (SAM).

Distribution: Australia (Tasmania).

Genus *Nectocader* Drake
(Fig. 49)

Nectocader Drake, 1928: 41. Type species by original designation: *Cantacader gounellei* Drake, 1923.

Diagnosis. Head long, distinctly surpassing second antennal segment; cephalic spines rather short and blunt, jugo-frontal spines located at the base of clypeus, preocular spines located anteriorly to eyes, on the line drawn through the base of antennal tubercles. Bucculae relatively low, slightly surpassing head apex; rostrum very long, nearly reaching posterior edge of VI abdominal segment. Pronotum convex, with five carinae; outer carinae short, developed only in the most convex part of pronotal disc; inner carinae laminate, especially high in the most convex part of pronotum; paranota rather narrow, their lateral margins sinuated. Posterior part of pronotum distinctly prolonged backward, but posterior edge of pronotum straight; scutellum (except a small prominent tubercle at scutellar apex) covered by posterior part of pronotum. Hemelytra very broad, abruptly dilating from bases; areolae small, irregular; costal area bearing 10–12 rows of areolae in its widest part; subcostal area with two transverse veins; discoidal area divided into three smaller areas by two transverse veins.

Species known by macropterous forms. Body length about 6.5 mm.

List of species:

1. *Nectocader gounellei* (Drake)

Cantacader gounellei Drake, 1923: 81.

Nectocader gounellei: Drake 1928: 42, 1950: 165; Drake and Ruhoff 1965: 29.

Type material: Holotype male; [BRAZIL]: Novo Friburgo [= vicinity of Rio de Janeiro (USNM).

Distribution: Brazil.

Material examined: 1 ex., BMNH; 2 ex., ISNB.

Tribe *Cantacaderini* s. str.

Diagnosis. Head either relatively short with apex not surpassing second antennal segment, or with very long clypeus; pronotum with five carinae (exceptionally tri- or unicarinate); posterior edge of pronotum prolonged backward along median carina; scutellum either totally covered by the posterior margin of pronotum, or partially uncovered, but without prominent tubercle in its posterior part; paranota rather wide, sometimes bilobed; hemelytral areolae occasionally diverse in size (sometimes these of sutural or costal area a little bigger than those of the remaining parts); costal area broad (even 15–16 rows of areolae in its middle part).

Key to genera of *Cantacaderini*

1. Head distinctly surpassing the second antennal segment;

costal area very wide (15–16 rows of areolae at apex of clavus) *Teratocader*

- . Head shorter, at best reaching the apex of second antennal segment; costal area narrower (at best 10 rows of areolae at apex of clavus) 2
2. Paranota bilobed (Fig. 52) *Pseudophatnoma*
- . Paranota without lobes (Fig. 50) *Cantacader*

Genus *Cantacader* Amyot and Serville
(Figs 50, 51)

Cantacader Amyot and Serville, 1843: 299. Type species by monotypy: *Piesma quadricornis* Le Peletier and Serville, 1828.

Canthacader [!]: Amyot and Serville 1843: 652 (index); Schouteden 1916: 290, 1923: 83, 1955: 162, 163.

Taphrostethus Fieber, 1844: 40 (syn. by Fieber 1861: 117). Type species by monotypy: *Taphrostethus quinquecostatus* Fieber, 1844.

Diagnosis. Head slightly prolonged in its preocular part, but its apex not surpassing the second antennal segment; dorsal surface with two pairs of spines (short or long, stout or delicate, blunt or sharply ended, adjacent or erect); preocular spines located nearby eyes, the jugo-frontal pair just in a front the former. Bucculae usually very long, surpassing head apex, their apices angularly curved or sometimes rounded, their laminae of may touch each other apically. Rostrum reaching III–IV abdominal segment, sometimes shorter, slightly surpassing posterior margin of metasternum. Posterior margin of pronotum distinctly (angularly or roundly) prolonged backward; scutellum entirely covered by posterior margin of pronotum. Paranota more or less developed, moderately wide, sometimes recurved upward, their anterolateral angles may be porrect, sometimes with small tooth-like outgrowth. Pronotal disc usually with five carinae, but sometimes with three or single carina (including intermediate forms); carinae high and laminate, or low and carinate. Hemelytra moderately wide, sometimes prolonged backward; costal area bearing 1–5 areolae in the middle part; subcostal area sometimes with a transverse vein in the middle; discoidal area usually long and narrow, without transverse veins. Genital segment of males partially telescoped into VIII abdominal segment, VIII paratergites developed as subtriangular lobes laterally to the genital segment. Body length: 3.5–6.3 mm.

The genus is represented by 38 species.

List of species:

1. *Cantacader abdivitus* Drake

Cantacader abdivitus Drake, 1950: 161; Drake and Ruhoff 1965: 23.

Type material: Holotype female; [AUSTRALIA]: Redlynch, Queensland (USNM).

Distribution: Australia (Queensland).

Material examined: HT, USNM.

2. *Cantacader afzelii* Stål

Cantacader afzelii Stål, 1873: 116; Drake 1950: 163; Drake and Ruhoff 1965: 23.

Cantacader tener Bergroth, 1894: 167, syn. by Duarte Rodrigues 1992: 12.

Cantacader Afzelii: Villiers 1952: 125; Schouteden 1965: 168.

Cantacader affzelii [!]: Štusaák 1984: 238, 239.

Type material: Holotype male: [SIERRA LEONE]: Sierra Leone (NHRS).

Distribution: Angola, Congo-Brazzaville, Ethiopia, Ghana, Ivory Coast, Kenya, Liberia, Madagascar, Mauritius, Mozambique, Nigeria, Namibia, Sierra Leone, Somalia, South Africa, Sudan, Tanzania, Togo, Zaire, Zambia.

Material examined: 57 ex., MNHN; 29 ex., BMNH; 1 ex., ISNB; 3 ex., AMNH; 9 ex., MZLU; 3 ex., ZMAS; 26 ex., ZMHB; 2 ex., NMSA; 2 ex., JP; 1 ex., HNHM.

3. *Cantacader agilis* Drake

Cantacader agilis Drake, 1951: 166; Drake and Ruhoff 1965: 24.

Cantacader agilis var. *tricarinata* Drake, 1951: 167.

Cantacader agilis var. *tricarinatus*: Drake and Ruhoff 1965: 24.

Type material: Holotype male: [NEW GUINEA]: Deslacs Island (HNHM); 3 paratypes: [NEW GUINEA]: Island Deslacs (HNHM); 1 paratype: [NEW GUINEA]: Berlinhafen, Tamara (HNHM).

Distribution: Bismarck Archipelago, New Guinea (incl. Deslacs Island).

Material examined: HT, 3 PT, HNHM.

4. *Cantacader allaeri* Schouteden

Cantacader Allaeri Schouteden, 1965: 169.

Cantacader allaeri: Duarte Rodrigues 1978: 300; 1984: 79.

Type material: Syntype(s): [ZAIRE]: De Sandoa, Katanga (MRAC).

Distribution: Nigeria, Zaire.

5. *Cantacader amplicostatus* Duarte Rodrigues

Cantacader amplicostatus Duarte Rodrigues, 1981a: 135; 1984: 79.

Type material: Holotype male: [NIGERIA]: Mokwa, J.A.R., Mile 4, N.W. State, Nigeria (BMNH).

Distribution: Nigeria.

Material examined: HT, BMNH; 2 ex., HNHM; 1 ex., MNHN.

6. *Cantacader amydis* Drake

Cantacader amydis Drake, 1960: 342, 343; Drake and Ruhoff 1965: 24.

Type material: Holotype female: [NEW GUINEA]: Wakaiuna, Normanby I. (AMNH); paratypes: 1 female: [NEW GUINEA]: Wakaiuna, Normanby I. (USNM); 1 female: [NEW GUINEA]: Tamelele, Fergusson I. (USNM); 1 female: [NEW GUINEA]: Deidei, Gompa Bay, Fergusson I. (USNM).

Distribution: New Guinea (D'Entrecasteaux Islands; Fergusson and Normanby).

Material examined: 2 ex., AMNH.

7. *Cantacader angustecostatus* Štusák

Cantacader angustecostatus Štusák, 1979: 142; Duarte Rodrigues 1984: 80.

Type material: Holotype male: [GHANA]: Ghana, Ashanti region, Kumasi (HNHM); 5 paratypes: [GHANA]: Ghana, Ashanti region, Kumasi (HNHM).

Distribution: Congo-Brazzaville, Ghana, Nigeria, Togo.

Material examined: 2 ex., MNHN; 6 ex., HNHM; 2 ex., ZMHB.

8. *Cantacader attenuatus* Distant

Cantacader attenuatus Distant, 1902b: 238; Drake and Ruhoff 1965: 24;

Schouteden 1965: 168; Duarte Rodrigues 1984: 80.

Cantacader attenuatus [!]: Drake 1950: 163.

Type material: Lectotype male (present designation): [REPUBLIC OF SOUTH AFRICA]: South Africa (BMNH).

Distribution: South Africa.

Material examined: LT, 1 ex., BMNH.

9. *Cantacader basilewskyi* Schouteden

Cantacader [!] *Basilewskyi* Schouteden, 1955: 163.

Cantacader basilewskyi: Drake and Ruhoff 1965: 24; Duarte Rodrigues 1984: 80.

Cantacader Basilewskyi: Schouteden 1965: 169.

Cantacader basilewskyi [!]: Drake 1958: 102.

Type material: Holotype: [RWANDA]: Ruanda (MRAC).

Distribution: Angola, Nigeria, Rwanda, Sudan, Zaire.

Material examined: 1 ex., ISNB; 3 ex., AMNH.

10. *Cantacader bomansi* Schouteden

Cantacader Bomansi Schouteden, 1965: 169, 170.

Cantacader bomansi: Duarte Rodrigues 1984: 80.

Type material: Syntype(s): [ZAIRE-RWANDA]: de la Vallée de la Ruzizi, Sanghe (MRAC).

Distribution: The species is known only from one locality, namely the Ruzizi river Valley just on the frontier between Zaire and Rwanda.

11. *Cantacader clairi* Schouteden

Cantacader Clairi Schouteden, 1965: 169, 170.

Cantacader clairi: Linnavuori 1977: 6; Štusák 1979: 145; Duarte Rodrigues 1980: 263, 1982a: 57; 1984: 542.

Type material: syntype(s): [ZAIRE]: Provenance, Lubudi, Katanga (MRAC).

Distribution: Ghana, Congo-Brazzaville, Tanzania, Zaire, Zambia.

Material examined: 2 ex., MRAC; 2 ex., BMNH; 1 ex., ISNB; 4 ex., MNHN; 2 ex., AMNH; 6 ex., ZMHB; 10 ex., ZMPA.

12. *Cantacader claratis* Drake

Cantacader claratis Drake, 1950: 160, 163; Drake and Ruhoff 1965: 25.

Type material: Holotype female: [MALAYSIA]: Perak, Bukit Gautang, Malaya (USNM).

Distribution: Malaysia.

Material examined: HT, USNM.

13. *Cantacader curtulus* Linnavuori

Cantacader curtulus Linnavuori, 1977: 6; Duarte Rodrigues 1984: 80.

Type material: Holotype female: [YEMEN]: Yemen (REL).

Distribution: Yemen.

Material examined: HT, REL.

14. *Cantacader diffidentis* Drake and Poor

Cantacader diffidentis Drake and Poor, 1936: 141; Drake 1950: 163; Drake and Ruhoff 1965: 25; Péricart 1985: 28.

Cantacader diffidentis [!]: Drake 1960: 343.

Type material: Holotype male: [INDIA]: New Forest, Dehra Dun, United Provinces (USNM); paratype female: [INDIA]: India, Dehra Dun (USNM).

Distribution: India, Indonesia (Java).

Material examined: HT, USNM.

15. *Cantacader divisus* Bergroth

Cantacader divisus Bergroth, 1908: 108; Drake and Ruhoff 1965: 25; Schouteden 1965: 169, Linnavuori 1977: 6; Duarte Rodrigues 1980: 262, 1984: 80.

Cantacader dividus [!]: Drake 1950: 163.

Type material: Syntypes (males and females): [ETHIOPIA]: Süd Abissynien (not located).

Distribution: Angola, Ethiopia, Kenya, Tanzania, Zaire, Zambia.

Material examined: 1 ex., BMNH; 1 ex., ISNB; 3 ex., AMNH; 1 ex., MNHN.

16. *Cantacader duffelsi* B. Lis

Cantacader duffelsi B. Lis, 1997a: 603.

Type material: Holotype female: [INDIA]: Madras State, Coimbatore (ZMAN).

Distribution: Indie.

Material examined: HT, ZMAN; 11 ex., HNHM.

17. *Cantacader formosus* Drake

Cantacader formosus Drake, 1950: 164; Drake and Ruhoff 1965: 25.

Type material: Holotype male: [CHINA]: Formosa [=Taiwan] (USNM).

Distribution: China (Taiwan).

Material examined: HT, USNM.

18. *Cantacader gerardi* Schouteden

Canthacader [!] *Gerardi* Schouteden, 1955: 162.

Cantacader gerardi: Drake and Ruhoff 1965: 25; Linnavuori 1977: 6; Duarte Rodrigues 1984: 80.

Cantacader Gerardi: Schouteden 1965: 169.

Type material: syntype(s): [ZAIRE]: Mulungu, Nyunzu, Katanga, Belgian Congo (MRAC).

Distribution: Zaire.

Material examined: 1 ex., AMNH.

19. *Cantacader hirsutus* B. Lis

Cantacader hirsutus B. Lis, 1999b: 23.

Type material: Holotype female: [LAOS]: Laos, Ban Theuong, 18 km NW of Xieng Khouang (BMH).

Distribution: Laos.

Material examined: HT, BMH.

20. *Cantacader hulstaerti* Schouteden

Cantacader Hulstaerti Schouteden, 1965: 169, 171.

Cantacader hulstaerti: Štusák 1979: 145; Duarte Rodrigues 1984: 80.

Type material: syntype(s): [ZAIRE]: Bamanja (Equateur) (MRAC).

Distribution: Congo-Brazzaville, Ghana, Nigeria, Zaire.

Material examined: 3 ex., AMNH; 1 ex., ZSMC; 5 ex., HNHM.

21. *Cantacader ilongaensis* Duarte Rodrigues

Cantacader ilongaensis Duarte Rodrigues, 1982b: 326; 1984: 80.

Type material: Holotype male: [TANZANIA]: Ilonga, Tanzania (AMNH); paratype: [TANZANIA]: Ilonga, Tanzania (AMNH).

Distribution: Tanzania.

Material examined: HT, PT, AMNH.

22. *Cantacader infuscatus* Distant

Cantacader infuscatus Distant, 1903: 124; Drake 1950: 164; Drake and Ruhoff 1965: 25.

Type material: Holotype male: [MYANMAR]: Rangoon, Burma (BMNH).

Distribution: Myanmar.

Material examined: HT, BMNH.

23. *Cantacader insularis* Drake

Cantacader insularis Drake, 1957: 399; Drake and Ruhoff 1965: 25; Duarte Rodrigues 1984: 80.

Type material: Holotype female: [REUNION]: Reunion, Plaine des Cafres (MNHN).

Distribution: Madagascar, Mascarene Islands.

Material examined: HT, MNHN; 2 ex., MNHN.

24. *Cantacader japonicus* Drake

Cantacader japonicus Drake, 1947: 225; Drake and Ruhoff 1965: 26; Tomokuni 1987: 118.

Cantacader japonicus [!]: Takeya 1962: 47.

Type material: Holotype male: [JAPAN]: Shimabara Peninsula, Japan (USNM).

Distribution: Japan, Thailand, Vietnam.

Material examined: HT, USNM; 3 ex., NSMT; 1 ex., JP.

25. *Cantacader laratanus* Drake

Cantacader laratanus Drake, 1947: 226; Drake and Ruhoff 1965: 26.

Type material: Holotype male: [INDONESIA]: Larat (USNM).

Distribution: Indonesia (Tanimbar Islands).

Material examined: HT, USNM.

26. *Cantacader laticollis* Horváth

Cantacader laticollis Horváth, 1906: 11; Drake 1950: 164; Drake and Ruhoff 1965: 26.

Cantacader quadricornis var. *staudingeri* (non Baerensprung): Puton 1879: 88.

Type material: Lectotype male (designated by Péricart, 1983: 72): [ALGERIA]: Bône (MNHN).

Distribution: Algeria.

Material examined: LT, MNHN; 3 ex., MNHN; 1 ex., JP.

27. *Cantacader letabanus* Duarte Rodrigues

Cantacader letabanus Duarte Rodrigues, 1981b: 202; 1984: 80.

Type material: Holotype female: [REPUBLIC OF SOUTH AFRICA]: Letaba River, Letaba Camp, Krüger Park, Transvaal (PPRI).

Distribution: Republic of South Africa.

Material examined: 1 ex., BMNH; 1 ex., NMSA.

28. *Cantacader lethierryi* Scott

Cantacader lethierryi Scott, 1874: 289; Drake 1950: 164; Takeya 1962: 47; Drake and Ruhoff 1965: 26; Tomokuni 1987: 118.

Type material: Lectotype female (present designation): [JAPAN]: Japan (BMNH).

Distribution: China (incl. Taiwan), Japan, Korea, Thailand, Vietnam.

Material examined: LT, BMNH; 1 ex., MNHN; 8 ex. NSMT; 1 ex., AMNH; 4 ex., NKUM; 2 ex., JP; 4 ex., HNHM.

29. *Cantacader longicornis* Duarte Rodrigues

Cantacader longicornis Duarte Rodrigues, 1980: 3; 1984: 80.

Type material: Holotype female: [MALAWI]: Mpatamango Gorge, Shiré R., S.W. Malawi (NMBZ).

Distribution: Malawi.

30. *Cantacader nocturnis* Hacker

Cantacader nocturnis Hacker, 1929: 324; Drake 1960: 341; Drake and Ruhoff 1965: 26.

Cantacader nocturnis [!]: Drake 1950: 164.

Type material: Holotype: [AUSTRALIA]: Brisbane, Queensland (QMBA).

Distribution: Australia (Queensland), New Guinea.

Material examined: HT, QMBA; 1 ex., BMNH; 4 ex., HNHM.

31. *Cantacader quadricornis* (Le Peletier and Serville)*Piesma quadricornis* Le Peletier and Serville, 1828: 653.*Taphrostethus Staudingeri* Baerensprung, 1858: 205, syn. by Baerensprung 1860: 20.*Cantacader staudingeri* Fieber 1861: 118; Drake 1950: 164.*Cantacader staudingeri* var. *doriae* Ferrari, 1874: 169, syn. by Horváth 1906: 12.*Cantacader quadricornis* var. *nubilus* Horváth, 1906: 12.*Cantacader angulipennis* Horváth, 1906: 12, syn. by Péricart 1983: 70.*Cantacader quadricornis* [!]; Gonzáles 1948: 49.*Cantacader quadricornis* var. *doriae*: Drake 1950: 164.*Cantacader quadricornis* var. *nubilus* [!]: Drake 1950: 164; Stichel 1960: 268.*Cantacader quadricornis quadricornis*: Stichel 1960: 268.*Cantacader quadricornis*: Amyot and Serville 1843: 299; Fieber 1861: 118; Puton 1879: 88; Horváth 1906: 12; Drake 1950: 164; Drake and Davis 1960: 25; Drake and Ruhoff 1965: 27; Péricart 1983: 70.

Type material: Syntype(s) of *Piesma quadricornis*: [SPAIN]: Hispania (MNHN); Syntype(s) of *Taphrostethus staudingeri*: [SPAIN]: Andalusia (ZMHB); Syntype(s) of *Taphrostethus staudingeri* var. *doriae*: [ITALY]: Liguria, La Spezia (MCSN).

Distribution: Algeria, Azerbaidjan, Afghanistan, Armenia, ?Canary Islands, Cyprus, Egypt, Georgia, Greece, France, Iran, Iraq, Israel, Italy, Morocco, Mauretania, Portugal, Russia, Spain, Turkey, Ukraine.

Material examined: 18 ex., 1 ST, MNHN; 32 ex., BMNH; 4 ex., ISNB; 2 ex., RMNH; 1 ex., MZLU; 6 ex., ZMAS; 2 ST, MCSN; 1 ST, ZMHB; 9 ex., NHMW; 5 ex., ZSMC; 1 ex., EH; 2 ex., ZMAN; 1 ex., REL; 4 ex., JP; 4 ex., BL; 28 ex., HHM.

32. *Cantacader quinquecostatus* (Fieber)*Taphrostethus quinquecostatus* Fieber, 1844: 41; Herrich-Schaeffer 1850: 150.*Monanthia subovata* Motschulsky, 1863: 91, syn. by Kirby 1891: 109.*Cantacader subovatus*: Stål 1873: 116; Drake 1950: 164.*Cantacader quinquecostatus*: Drake and Poor 1936: 141.*Cantacader infusca*: Drake 1956: 105.*Cantacader quinquecostatus*: Stål 1873: 117; Distant 1903: 123; 1910: 100; Horváth 1912: 341; 1926: 327; Bergroth 1921: 103; Blöte 1945: 78; Drake 1950: 164, 1956: 103, 106, 1960: 341; Drake and Ruhoff 1965: 28.

Type material: Syntype(s) of *Taphrostethus quinquecostatus* Fieber: "Ostindien" (lost). Syntype(s) of *Monanthia subovata* Motschulsky, 1863: Ceylon (not located).

Distribution: India, Indonesia, Malaysia, Myanmar, Micronesia (Palau), Papua New Guinea, Philippines, Sri Lanka.

Material examined: 24 ex., BMNH; 48 ex., RMNH; 1 ex., AMNH; 35 ex., MZLU; 1 ex., NHMW; 4 ex., JP; 10 ex., HHM.

33. *Cantacader schoutedeni* Štusač*Cantacader schoutedeni* Štusač, 1984: 237.

Type material: Holotype male: [ZAIRE]: Leopoldville (MRAC).

Distribution: Zaire.

34. *Cantacader sejunctus* Duarte Rodrigues*Cantacader sejunctus* Duarte Rodrigues, 1987: 350.

Type material: Holotype female: [REPUBLIC OF SOUTH AFRICA]: Pretoria (TMP); 5 paratypes: [REPUBLIC OF SOUTH AFRICA]: Pretoria (TMP).

Distribution: South Africa.

35. *Cantacader subtilis* B. Lis*Cantacader subtilis* B. Lis, 1999a: 25.

Type material: Holotype male: [PHILIPPINES]: P.J., Misamis Or., Gingoog (BMH).

Distribution: Philippines.

Material examined: HT, BMH.

36. *Cantacader tenuipes* Stål*Cantacader tenuipes* Stål, 1865: 26; 1873: 116; Distant 1902b: 238; Schouteden 1916: 290; 1923: 83; 1965: 169; Drake 1950: 153, 164; Drake and Ruhoff 1965: 28; Linnavuori 1977: 6; Štusač 1979: 146; Duarte Rodrigues 1980: 262; 1984: 80.*Cantacader tenuipes* var. *infusca* Schouteden, 1916: 290; 1923: 83; Drake and Ruhoff 1965: 28.*Cantacader tenuipes* var. *infuscatus*: Drake 1950: 164.*Cantacader tenuipes* var. *furtivus* Drake, 1950: 153 and 164.

Type material: Holotype male: [SIERRA LEONE]: Sierra Leone (NHRS).

Distribution: Angola, Congo-Brazzaville, Ghana, Guinea, Ivory Coast, Kenya, Madagascar, Nigeria, Sierra Leone, Somalia, Sudan, Tanzania, Yemen, Zaire.

Material examined: 21 ex., MNHN; 16 ex., BMNH; 4 ex., ISNB; 6 ex., AMNH; 1 ex., MZLU; 1 ex., ZMAS; 6 ex., HHM; 27 ex., ZMHB; 3 ex., REL; 4 ex., JP.

37. *Cantacader uniformis* Distant*Cantacader uniformis* Distant, 1902a: 353, 1903: 124; Drake 1950: 164; Drake and Ruhoff 1965: 28.

Type material: Lectotype female (present designation): [INDIA]: North India (BMNH).

Distribution: India, Myanmar.

Material examined: LT, BMNH.

38. *Cantacader vandenplasi* Schouteden*Cantacader* [sic!] *Vandenplasi* Schouteden, 1923: 83, 1965: 169.*Cantacader vandenplasi*: Drake 1950: 164; Drake and Ruhoff 1965: 29; Linnavuori 1977: 6; Duarte Rodrigues 1984: 80.

Type material: Syntypes: [ZAIRE]: Belgian Kongo (MRAC).

Distribution: Zaire.

Material examined: 1 ex., AMNH.

Genus *Pseudophatnoma* Blöte

(Fig. 52)

Pseudophatnoma Blöte, 1945: 78. Type species by original designation: *Pseudophatnoma corniculata* Blöte, 1945.*Froeschnerocader* Péricart, 1986: 245 (syn. by Péricart 1991: 49). Type species by original designation: *Froeschnerocader denticollis* Péricart, 1986.

Diagnosis. Head relatively short, its apex not reaching distal ends of the first antennal segment, dorsal surface with two pairs of long, thin spines; jugo-frontal spines located on a level of the base of clypeus, preocular spines located between the eyes. Bucculae very low, narrowing in apical part, hardly surpassing apex of head; their laminae touch each other apically. Rostrum reaching posterior margin of III abdominal segment. Pronotal disc convex, densely punctate, bearing five longitudinal carinae; anterior part of the median carina sometimes developed into a small hood; paranota wide, bilobed, its triangular anterior lobe with tooth-like projection directed forward, the posterior lobe broadly rounded with a small denticle. Posterior margin of pronotum broadly rounded, more or less expanded backward.

Scutellum covered by the posterior pronotal margin, or partially exposed. Hemelytra wide, tiny areolated, broadly expanded at bases; costal area wide, bearing 9–10 rows of areolae in the middle part, its surface with several transverse swells; subcostal area with several, indistinct transverse veins; discoidal area with one or two transverse veins; sutural area with very narrow rudimentary membrane. Genital segment of males partially telescoped into VIII abdominal segment; subtriangular paratergites of VIII segments surpassing the posterior margin of abdomen. Macropterous forms. Body length: 6.5–7.5 mm.

List of species:

1. *Pseudophatnoma corniculata* Blöte

Pseudophatnoma corniculata Blöte, 1945: 78; Drake 1950: 166; Drake and Ruhoff 1965: 40.

Type material: Holotype: [INDONESIA]: Durian, Rhio-Archipelago (RMNH).

Distribution: Indonesia (Riau Archipelago).

2. *Pseudophatnoma denticollis* (Péricart)

Froeschnerocader denticollis Péricart, 1986: 245.

Pseudophatnoma denticollis Péricart 1991: 49.

Type material: Holotype male: [MALAYSIA]: Sabah, North Borneo, Mt. Kinabalu National Park, Poring Hot Springs (MHNG).

Distribution: Malaysia (Borneo-Sabah).

3. *Pseudophatnoma laosana* B. Lis

Pseudophatnoma laosana B. Lis, 1999b: 26.

Type material: Holotype male: [LAOS]: Laos, Khammouane Prov., Phon Tioue (BMH).

Distribution: Laos.

Material examined: HT, BMH.

Genus *Teratocader* Drake (Fig. 53)

Teratocader Drake, 1950: 158. Type species by original designation: *Cantacader magnificus* Drake, 1923.

Diagnosis. Head very long, distinctly surpassing the second antennal segment; cephalic spines rather short and sharply ended; jugo-frontal spines located at the base of clypeus, preocular spines located in the middle of line drawn between the eyes and the jugo-frontal spines. Bucculae long, rather low, slightly surpassing head apex, their narrowly rounded apices separated apically. Rostrum very long, reaching anterior edge of the genital segment of male. Pronotum convex, with five low carinae, outer carinae short, developed only in the posterior part of pronotum, inner lateral carinae disappear near the anterior edge of the collar; paranota moderately wide, somewhat bilobed; anterior subtriangular lobe directed forward, rather narrow, posterior lobe broadly rounded. Posterior margin of pronotum distinctly prolonged backward, totally covering scutellum. Hemelytra very wide, abruptly dilated at bases, tiny areolated; costal area very broad, bearing 15–16 rows of

areolae in the middle part, and about 25 rows of areolae in the posterior part; subcostal area with several transverse veins; discoidal area divided into three smaller areas by two transverse veins; sutural area with very narrow, rudimentary membrane. Mesocoxal and metacoxal cavities placed more laterad than procoxal cavities. Macropterous forms. Length: 8.6 mm.

List of species:

1. *Teratocader magnificus* (Drake)

Cantacader magnifica Drake, 1923: 83.

Teratocader magnificus: Drake 1950: 158, 166; Drake and Ruhoff 1965: 30.

Type material: Holotype male: [MALAYSIA]: Perak, Malacca (USNM).

Distribution: Malaysia.

Material examined: HT, USNM.

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Table 1. Character state matrix for Tingidae and its outgroup used in cladistic analysis.

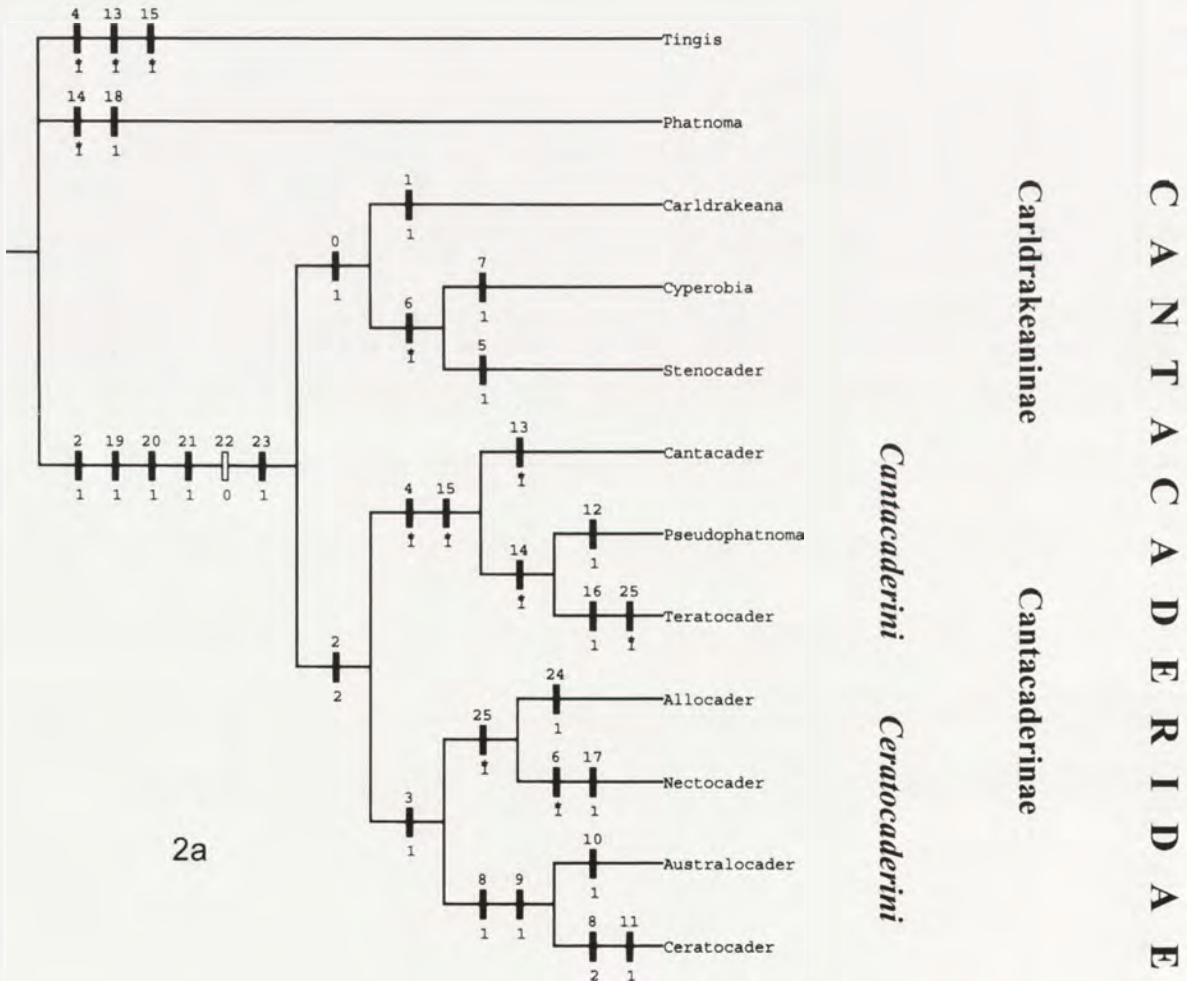
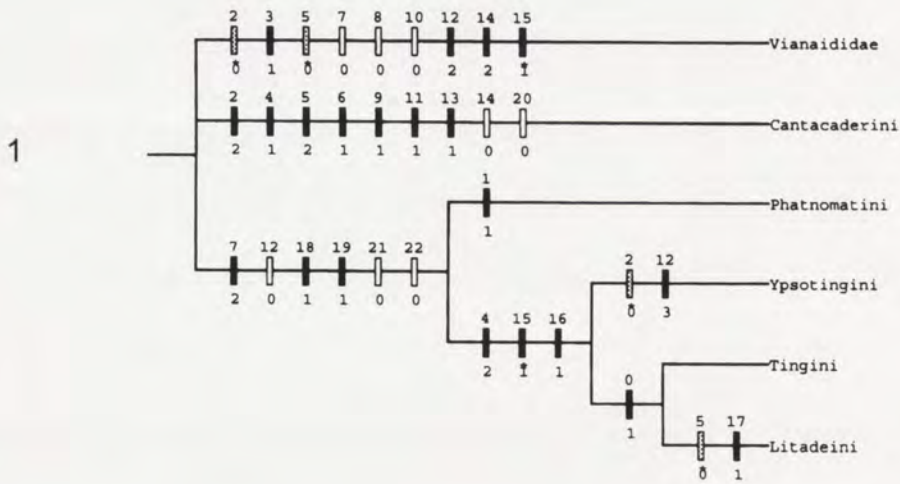
Taxa	Characters																						
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Vianauididae</i>	0	0	0	1	0	0	0	0	0	0	0	0	2	?	2	1	0	0	0	?	1	1	1
<i>Cantacaderini</i>	0	0	2	0	1	2	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1
<i>Ypsotingini</i>	0	0	0	0	2	1	0	2	1	0	1	0	3	0	1	1	1	0	1	1	1	0	0
<i>Tingini</i>	1	0	1	0	2	1	0	2	1	0	1	0	0	0	1	1	1	0	1	1	1	0	0
<i>Litadeini</i>	1	0	1	0	2	0	0	2	1	0	1	0	0	0	1	1	1	1	1	1	1	0	0
<i>Phatnomatini</i>	0	1	1	0	0	1	0	2	1	0	1	0	0	0	1	0	0	0	1	1	1	0	0

Table 2. Character state matrix for Cantacaderini and its outgroup used in cladistic analysis.

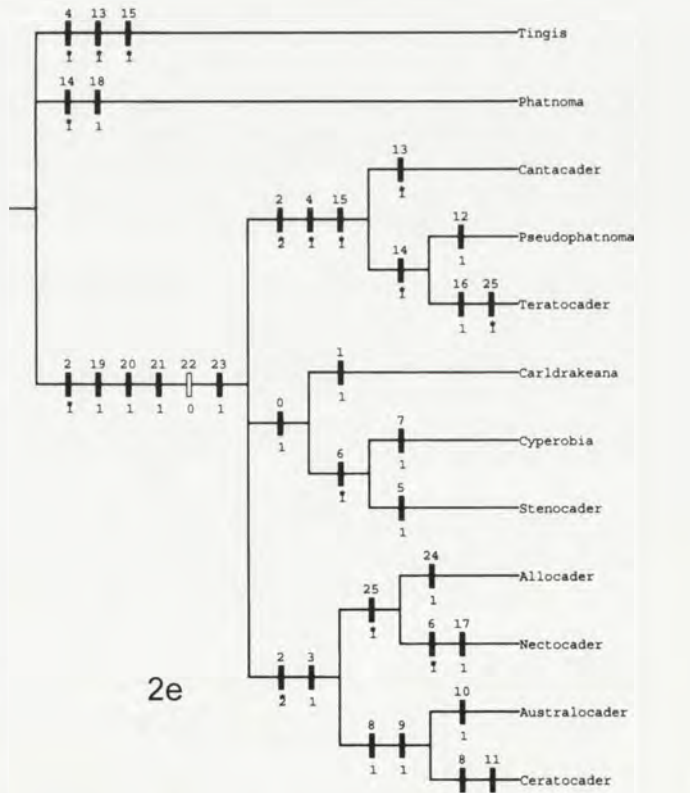
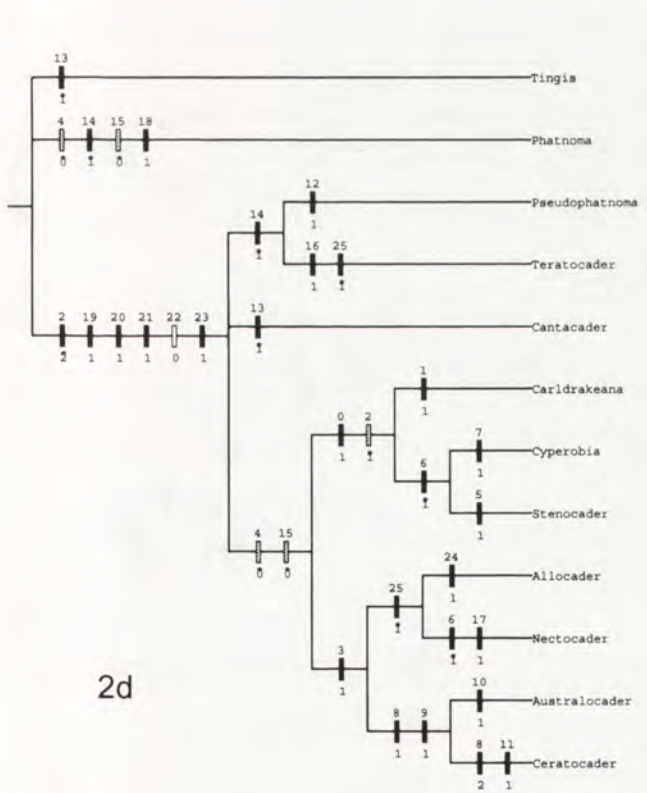
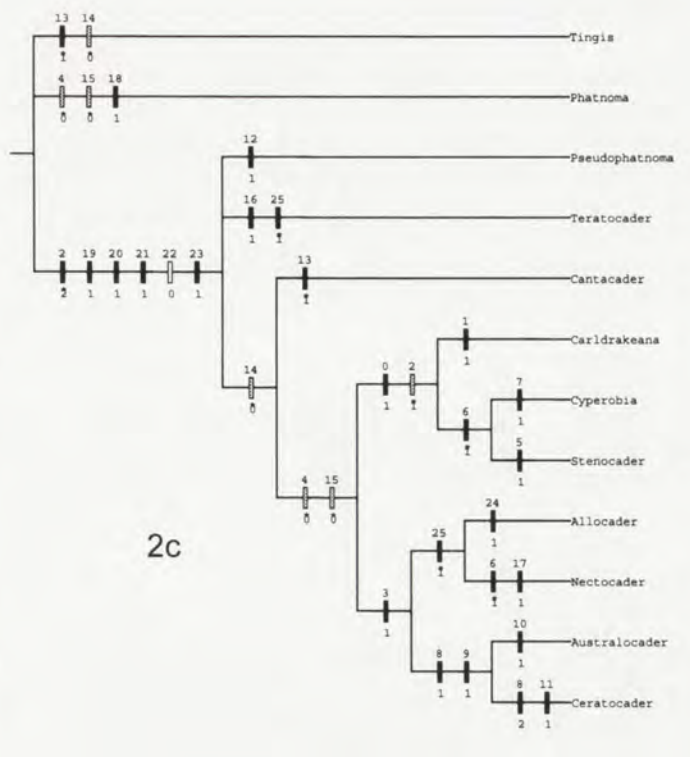
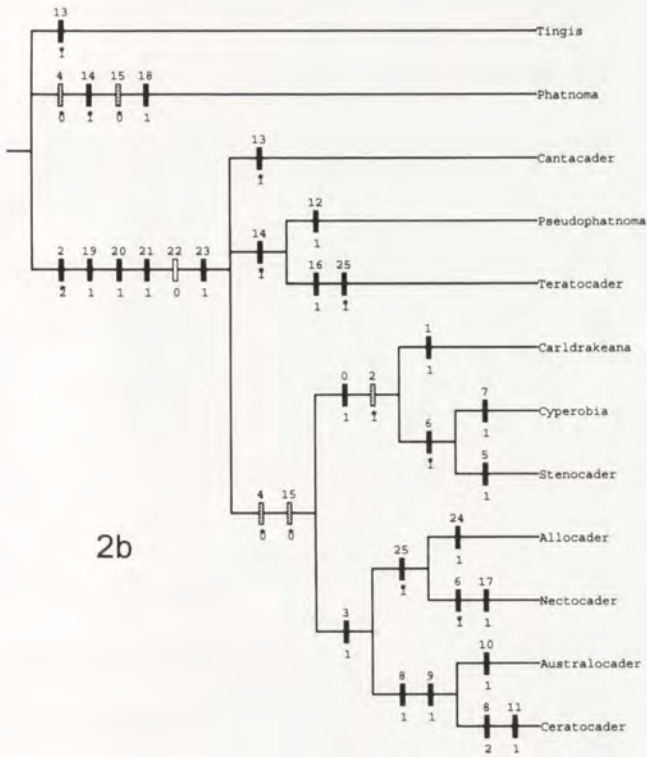
Taxa	Characters																									
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>Tingis</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
<i>Phatnoma</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
<i>Allocader</i>	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1
<i>Australocader</i>	0	0	2	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0
<i>Cantacader</i>	0	0	2	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	1	0	1	0	0
<i>Carldrakeana</i>	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0
<i>Ceratocader</i>	0	0	2	1	0	0	0	0	2	1	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0	0
<i>Cyperobia</i>	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0
<i>Nectocader</i>	0	0	2	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	1
<i>Pseudophatnoma</i>	0	0	2	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	1	0	0	0
<i>Stenocader</i>	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0
<i>Teratocader</i>	0	0	2	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	0	1	0	1

Table 3. Bremer estimation of ancestral area for Cantacaderidae based on the area cladogram in Fig. 3. G = number of gains, L = number of losses, AA = G/L quotients rescaled to a maximum value of 1 by dividing with the largest G/L value.

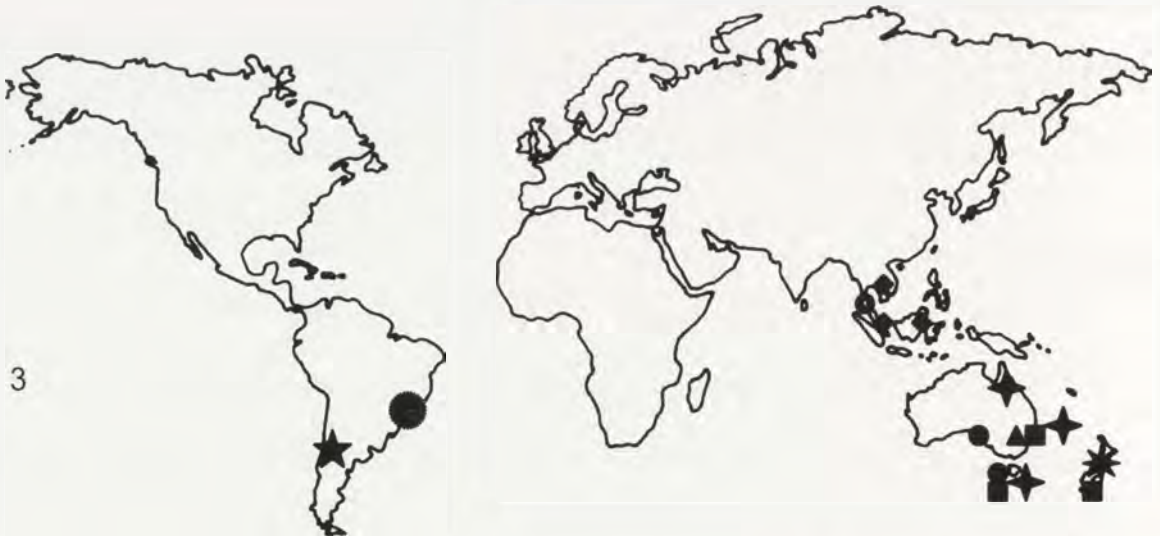
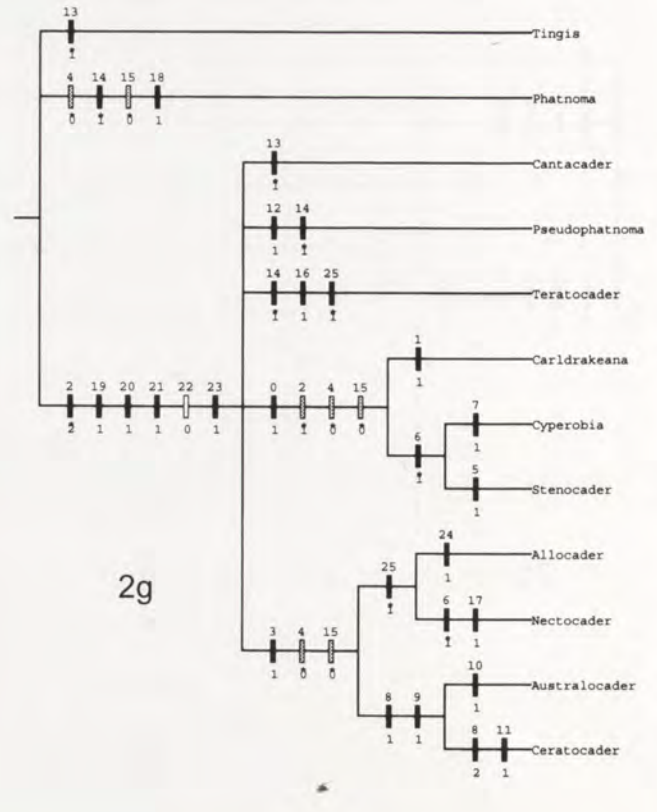
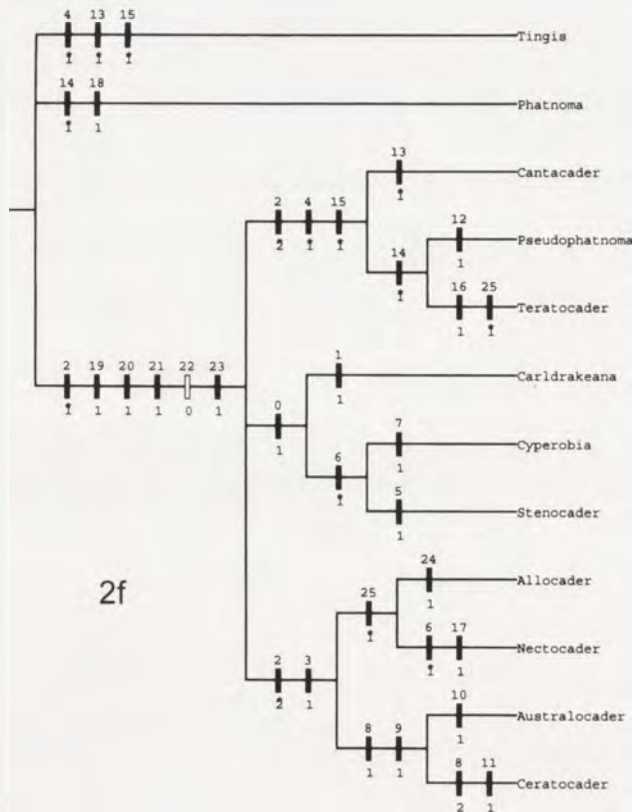
Area	G	L	G/L	AA
PAL	1	3	0.33	0.25
AFR	1	3	0.33	0.25
IND	1	3	0.33	0.25
MAL	1	2	0.50	0.38
NG	1	3	0.33	0.25
AUS	4	3	1.33	1.00
NZ	2	2	1.00	0.75
NEO	2	5	0.40	0.30



Figures 1–2a. (1) Cladogram for five tribes of Tingidae and its outgroup generated by Hennig86 analysis of the character state matrix (Table 1). (2a) Cladogram, as received using “ie*” option in Hennig86, selected to present the relationships among the studied taxa of Cantacaderidae (L=34, CI=82, RI=77). Apomorphies – black rectangles, plesiomorphies – empty rectangles, homoplasious characters – dotted rectangles (Fig. 1); marked with asterisks (Fig. 2a)

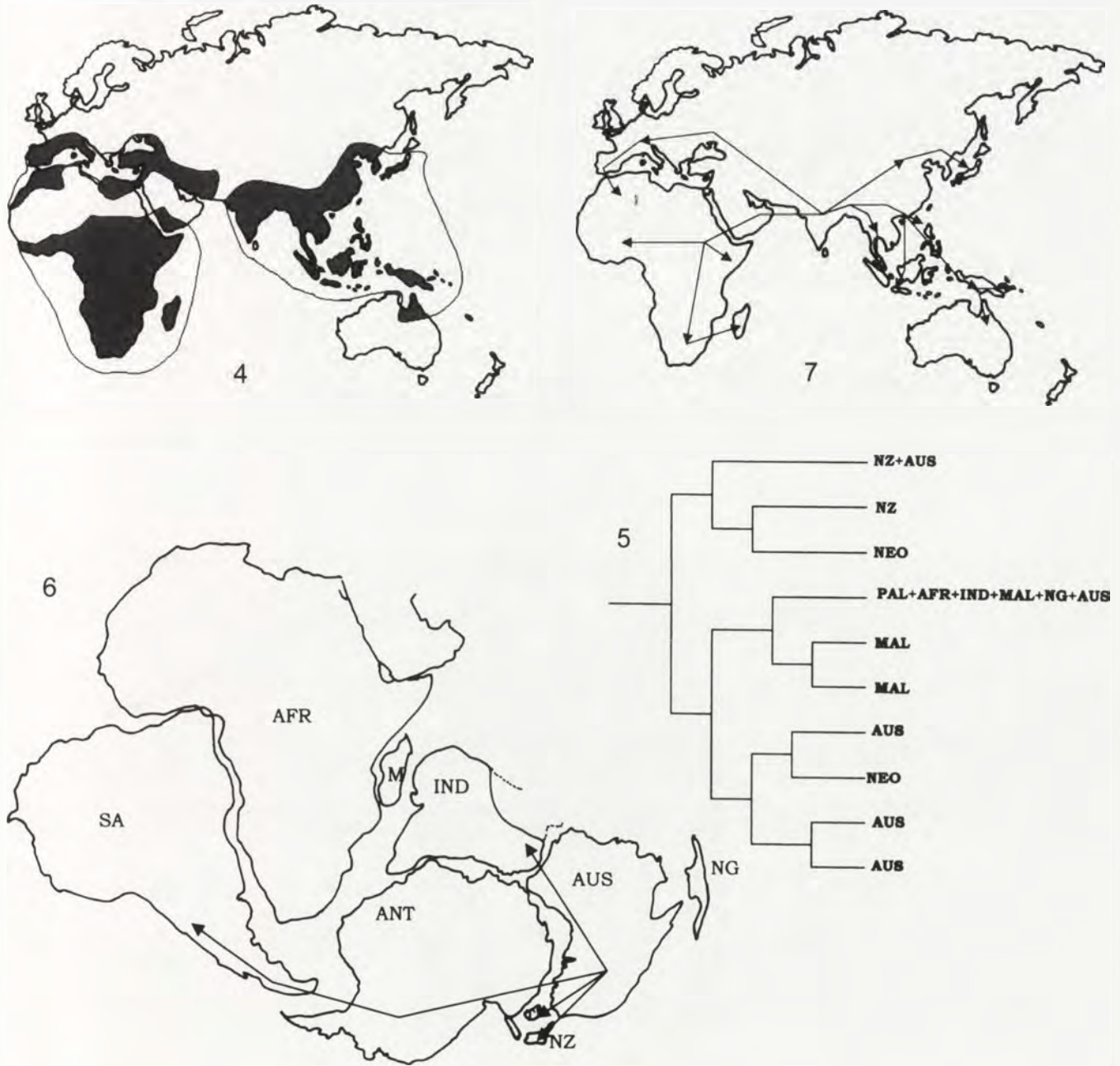


Figures 2b–e. Cladogram of Cantacaderidae and related taxa, as received using “ie*” option in Hennig86. 2b (L=34, CI=82, RI=77), 2c (L=34, CI=82, RI=77), 2d (L=34, CI=82, RI=77), 2e (L=34, CI=82, RI=77). Apomorphies – black rectangles, plesiomorphies – empty rectangles, homoplasious characters – dotted rectangles, additionally marked with asterisks.



- ★ Stenocader
- ▲ Australocader
- ◆ Pseudophatnoma
- Nectocader
- Ceratocader
- Carldrakeana
- ✦ Allocader
- ✱ Cyperobia
- Teratocader

Figures 2f-3. (2f) Cladogram of Cantacaderidae and related taxa, as received using "ie*" option in Hennig86 (L=34, CI=82, RI=77). (2g) Consensus tree for Cantacaderidae and related taxa. Apomorphies - black rectangles, plesiomorphies - empty rectangles, homoplasious characters - dotted rectangles, additionally marked with asterisks. (3) Present distribution of genera of Cantacaderidae (without *Cantacader*)



Figures 4–7. (4) Present distribution area of the genus *Cantacader*; (5) Area cladogram for Cantacaderidae generated from Figure 2a by substituting genera with distribution areas (for explanation see text); (6) Hypothetical ancestral area and main migrational paths of Cantacaderidae in Gondwanaland (AFR – Africa, ANT – Antarctica, SA – South America, AUS – Australia, M – Madagascar, NG – New Guinea, NZ – New Zealand, T – Tasmania); (7) Main migrational paths of the genus *Cantacader*

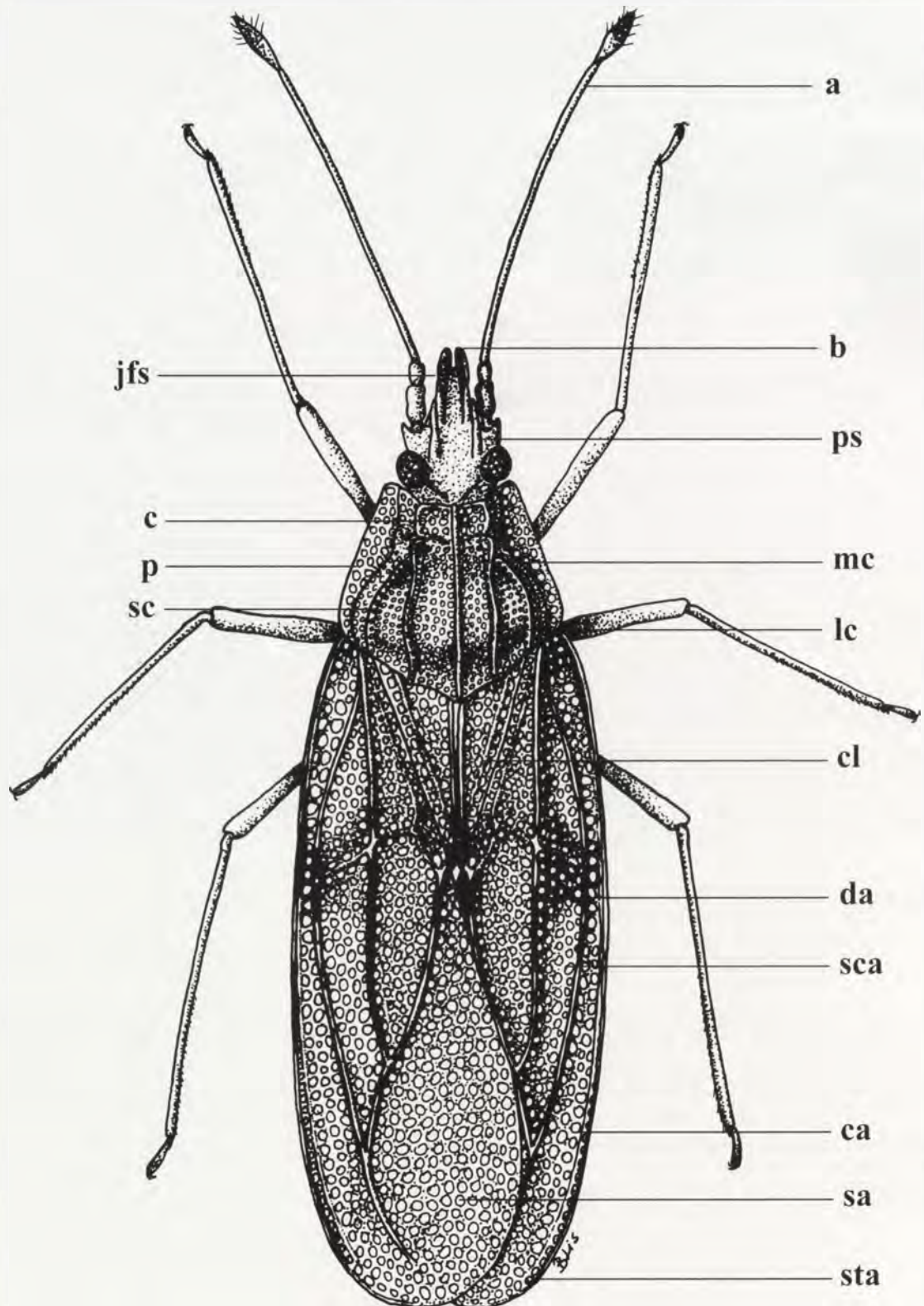


Figure 8. *Cantacader* sp. – dorsal view; a – antennae, b – buccula, c – collar, ca – costal area, cl – clavus, da – discoidal area, jfs – jugo-frontal spine, lc – lateral carina, mc – median carina, ps – preocular spine, p – paranotum, sa – sutural area, sca – subcostal area, sta – stenocostal area

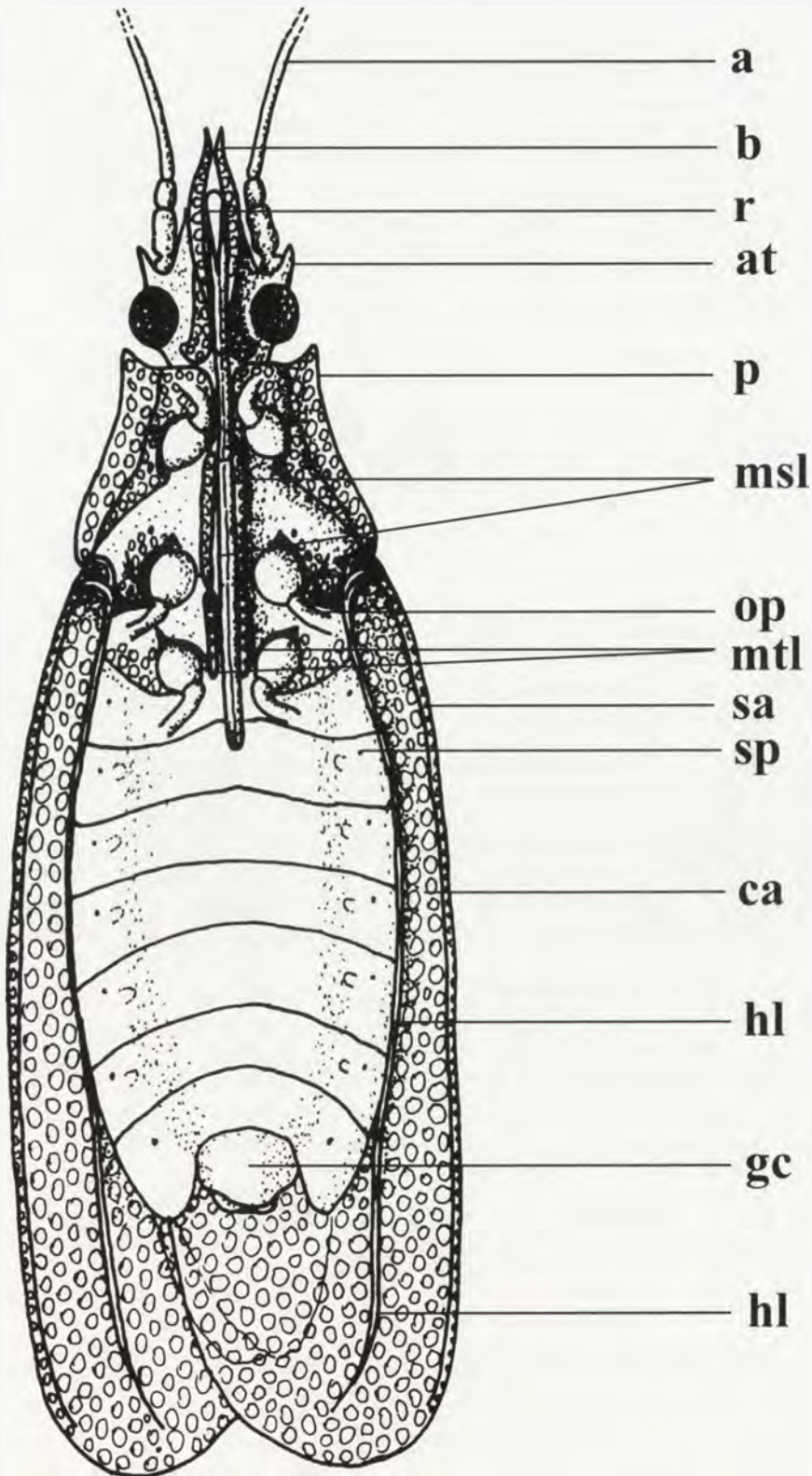
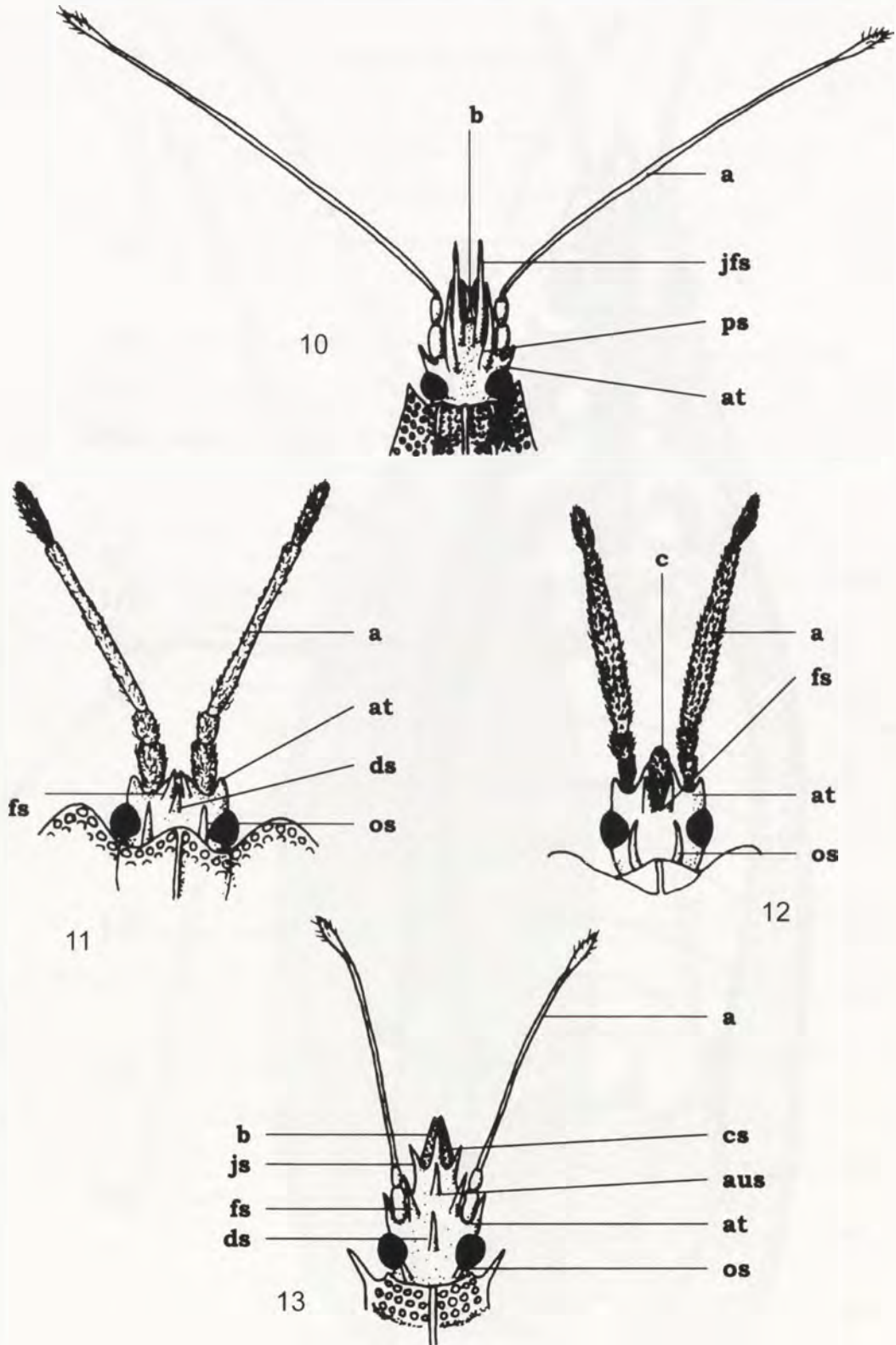
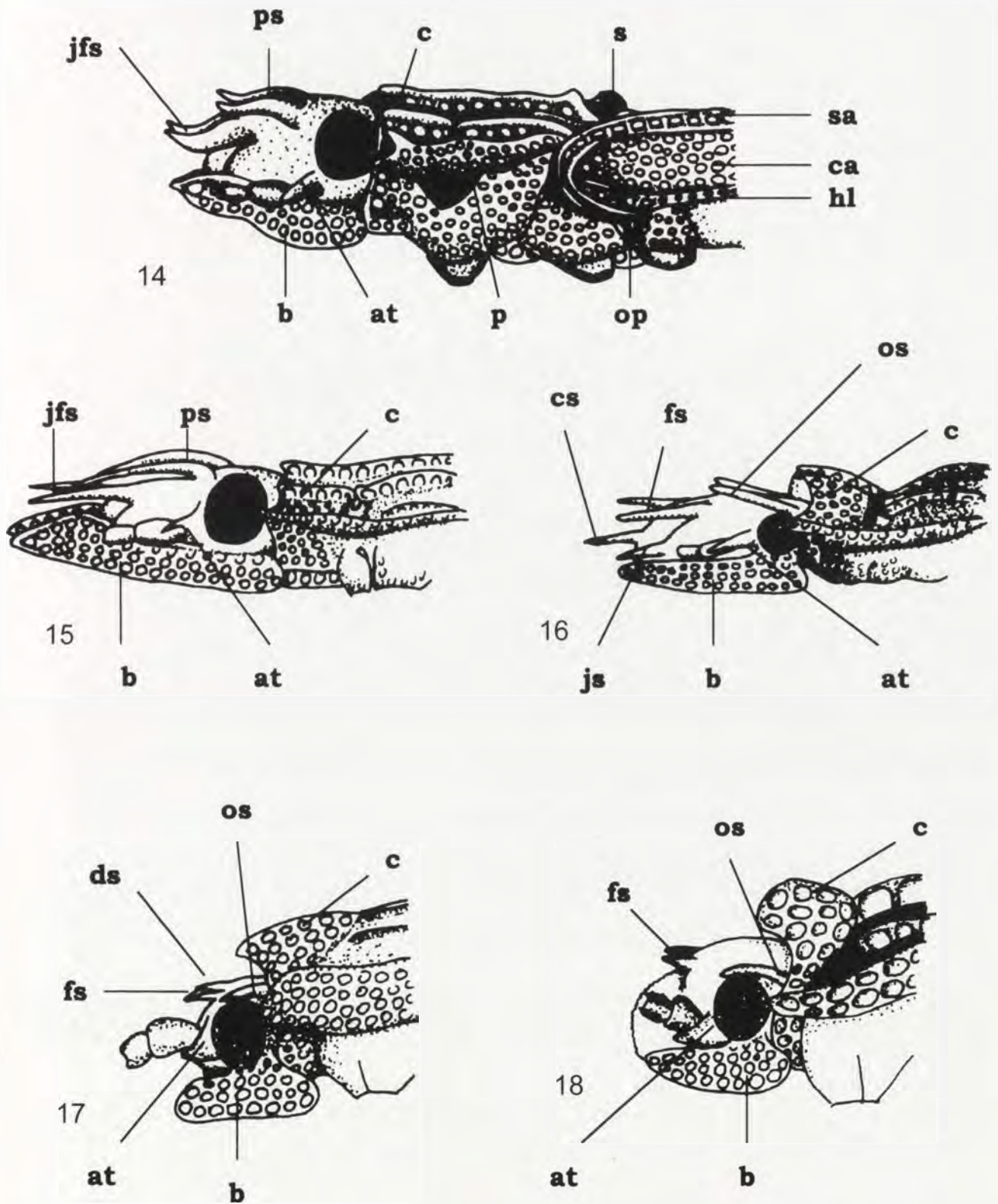


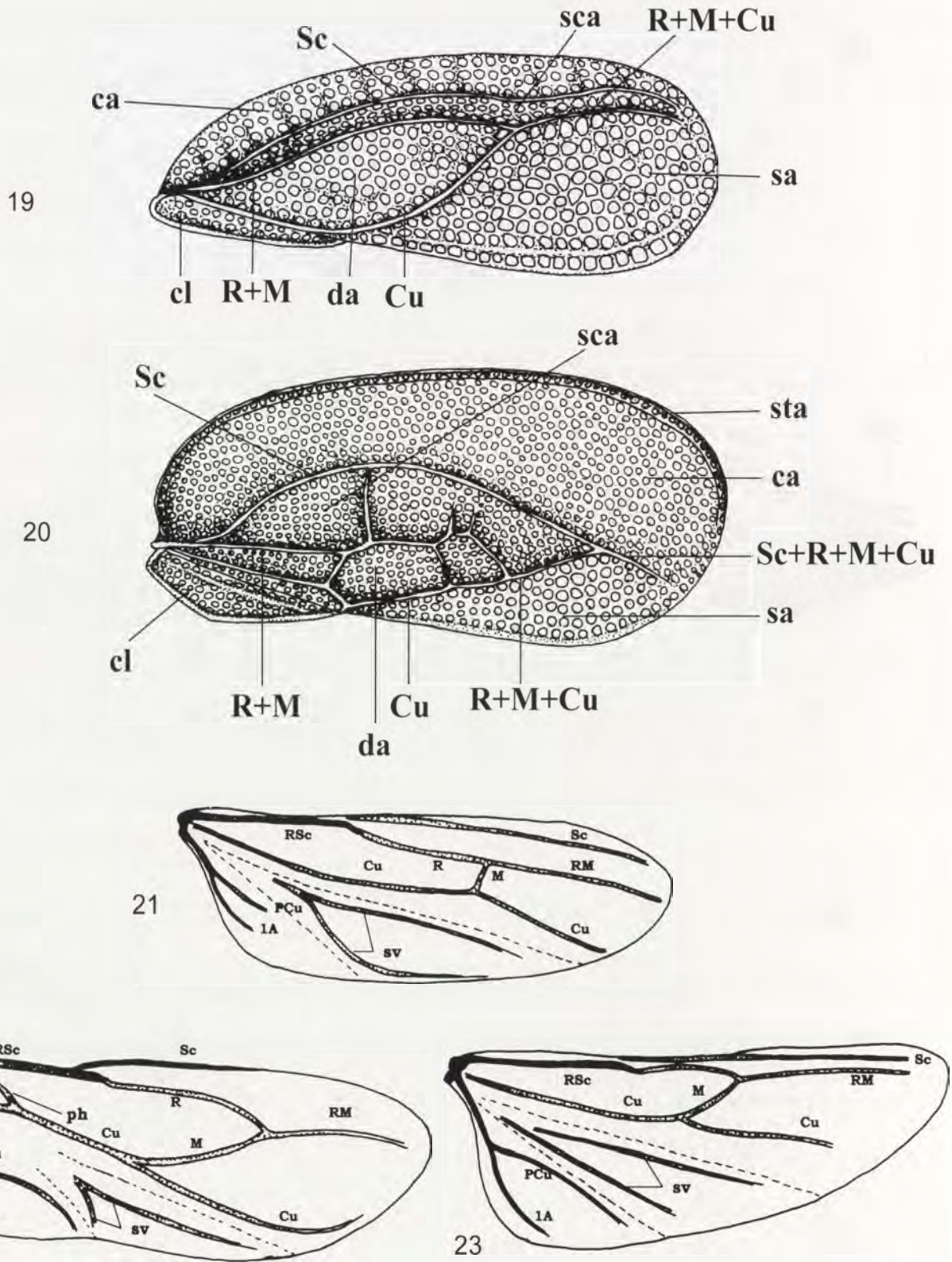
Figure 9. *Cantacader* sp. - ventral view; a - antennae, at - antennal tubercle, b - buccula, ca - costal area, gc - genital capsule, hl - hypocostal lamina, msl - mesosternal lamina, mtl - metasternal lamina, op - ostiolar pore, p - paranotum, r - rostrum, sa - stenocostal area, sp - spiracle



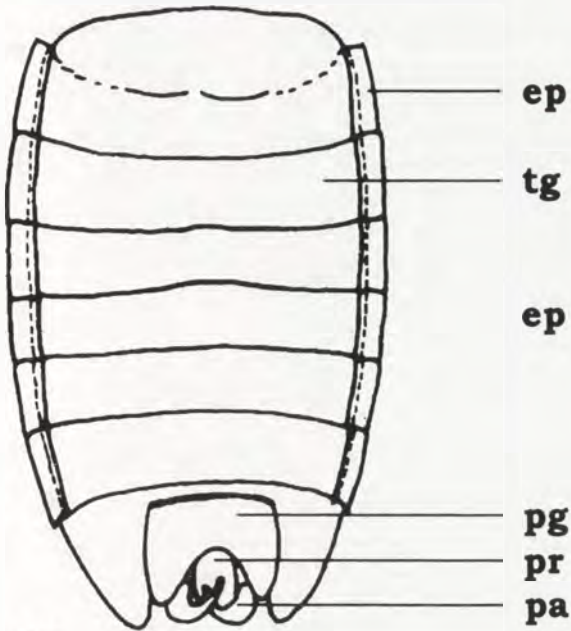
Figures 10–13. Head in dorsal view. (10) *Cantacader subtilis*, Cantacaderini; (11) *Tingis ampliata*, Tingini; (12) *Dictyonota strichnocera*, Ypsotingini; (13) *Ulmus eteosa*, Phatnomatini; a – antennae, at – antennal tuberele, aus – additional unpaired spine, b – buccula, c – clypeus, cs – clypeal spine, ds – dorsomedial spine, fs – frontal spine, jfs – jugo-frontal spine, js – jugal spine, os – occipital spine, ps – preocular spine



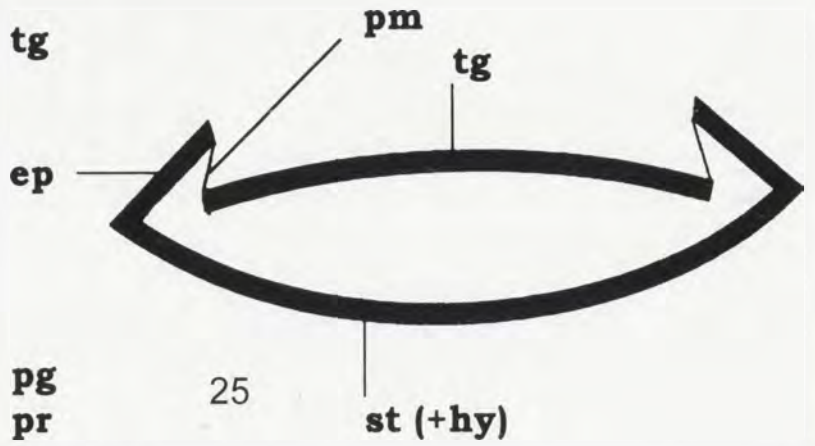
Figures 14–18. Head in lateral view. (14) *Australocader kerzhneri*, Cantacaderini; (15) *Cantacader temuipes*, Cantacaderini; (16) *Phatnoma veridica*, Phatnomatini; (17) *Tingis ampliata*, Tingini; (18) *Dictyonota strichnocera*, Ypsotingini; at – antennal tubercle, b – buccula, c – collar, ca – costal area, cs – clypeal spine, ds – dorsomedial spine, fs – frontal spine, hl – hypocostal lamina, jfs – jugo-frontal spine, js – jugal spine, op – ostiolar pore, os – occipital spine, p – paranotum, ps – preocular spine, s – scutellum, sa – stenocostal area



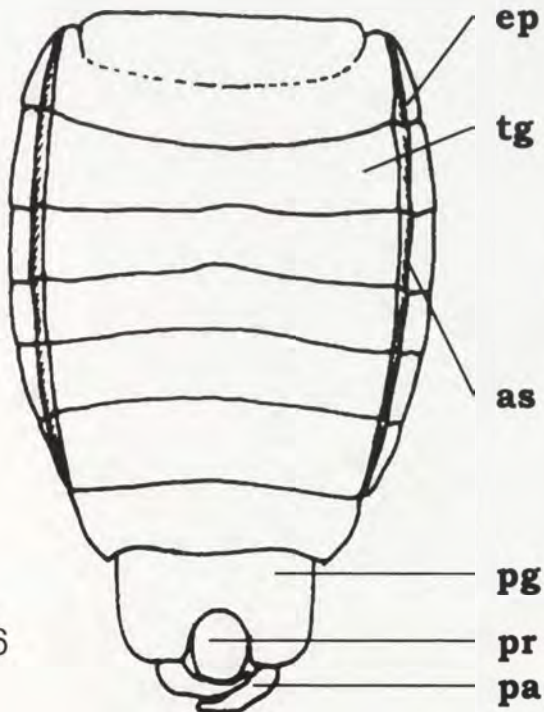
Figures 19–23. (19–20). Hemelytron. (19) *Tingis cardui*, Tinginae; (20) *Nectocader gounellei*, Cantacaderini; ca – costal area, cl – clavus, da – discoidal area, sa – sutural area, sca – subcostal area, sta – stenocostal area. (21–23). Venation of metathoracic wings. (21) *Cantacader quinquecostatus*, Cantacaderini; (22) *Phatnoma* sp., Phatnomatini; (23) *Tingis cardui*, Tingini; ph – pseudohamus, sv – secondary veins sutural area, sca – subcostal area, sta – stenocostal area



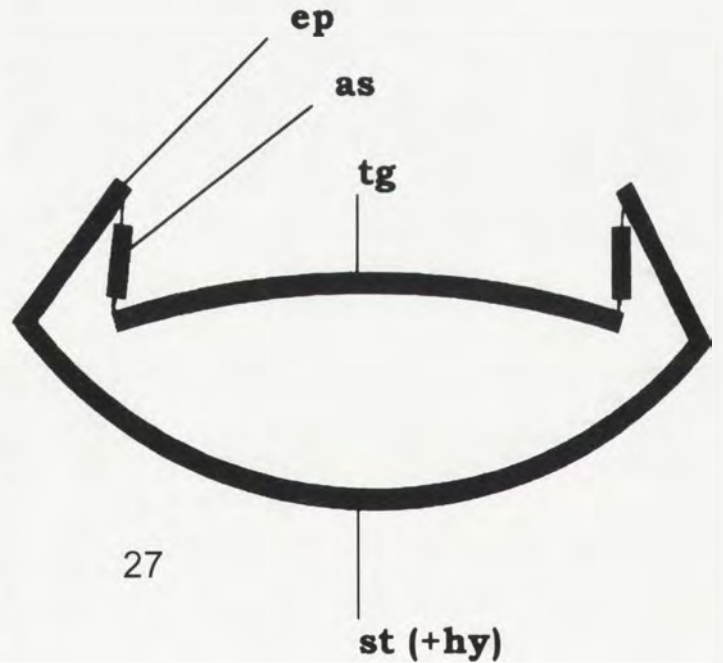
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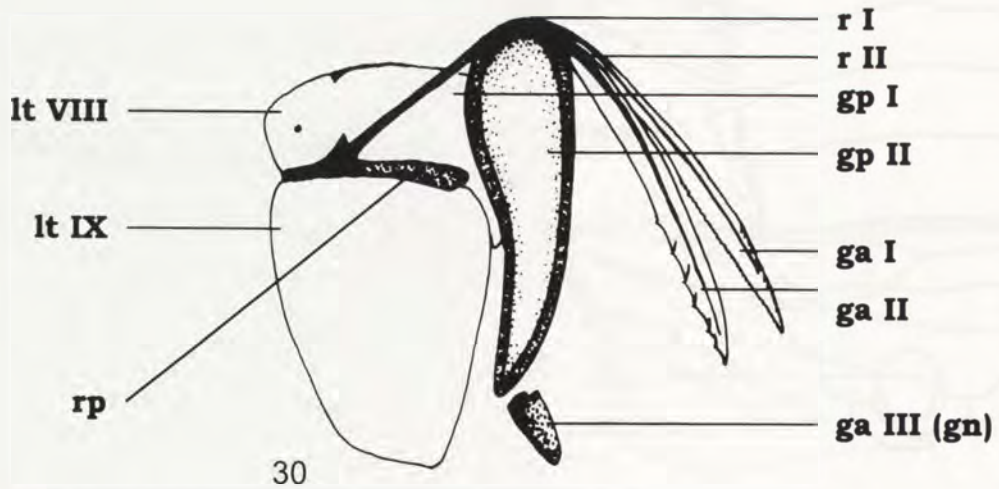
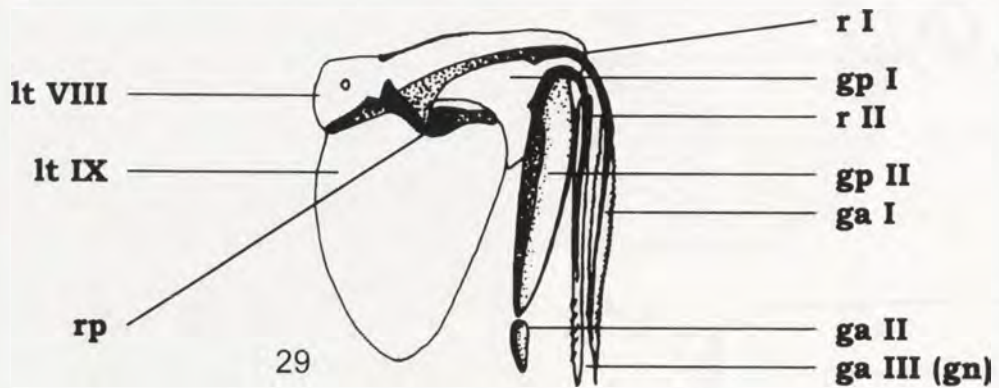
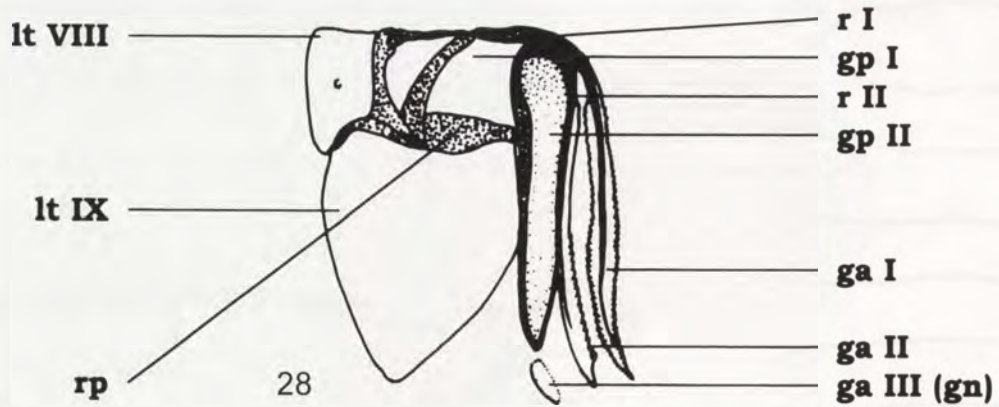


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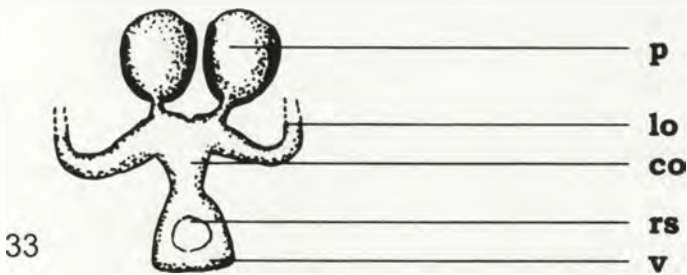
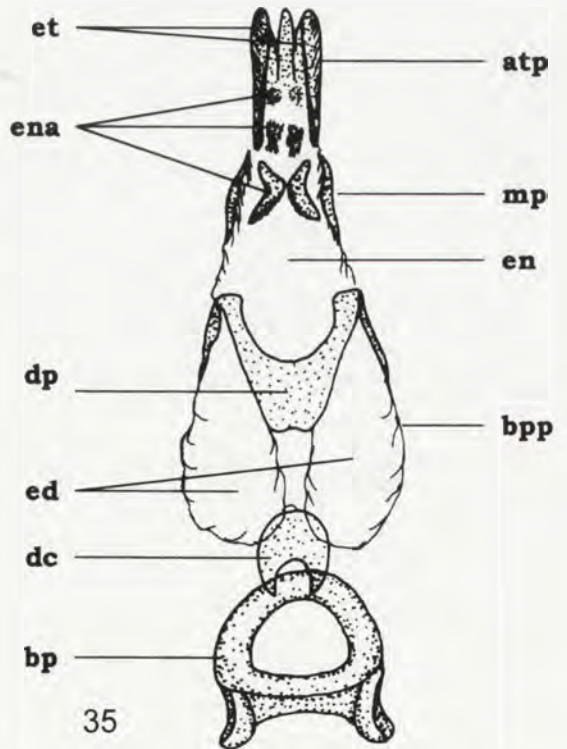
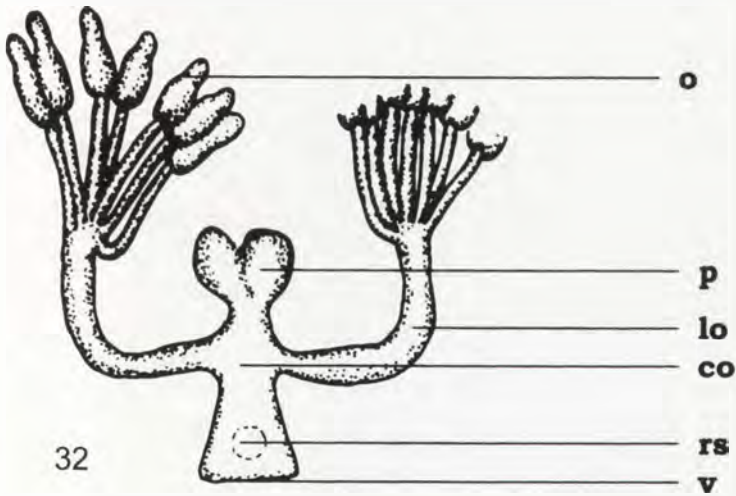
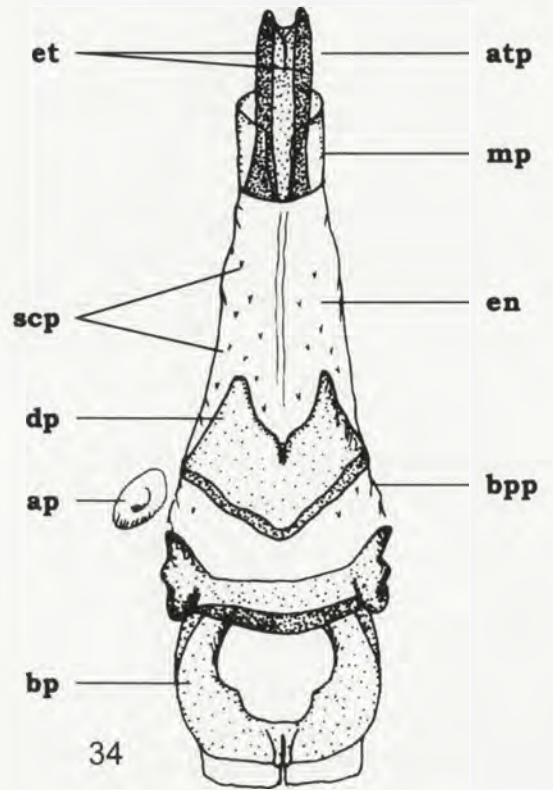
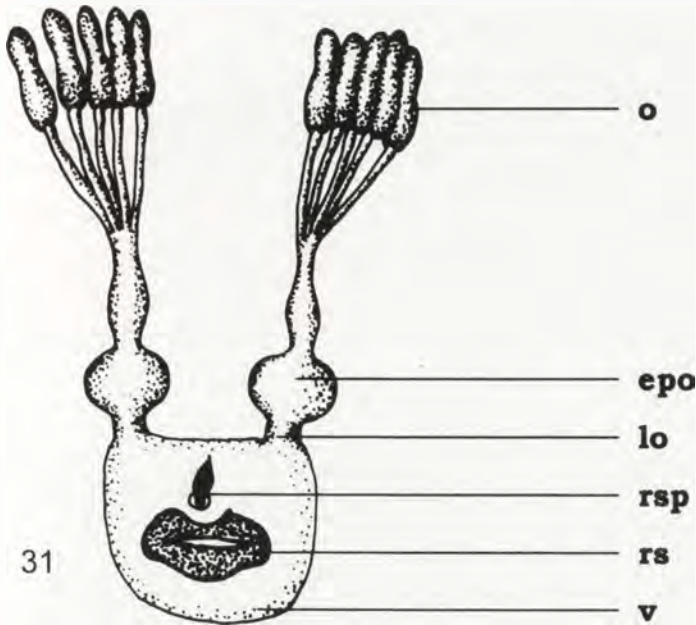


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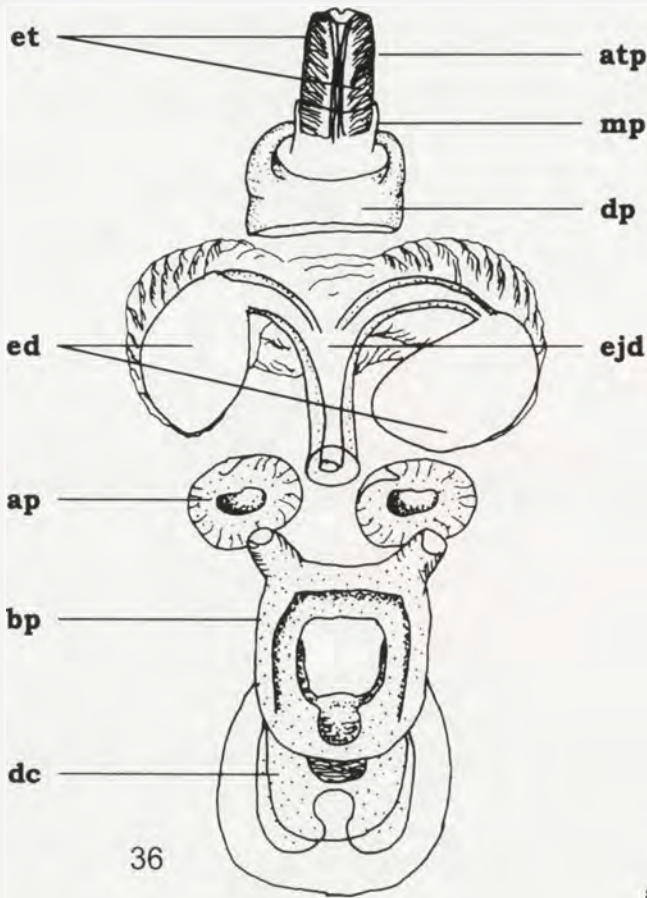
Figures 24–27. Abdomen in dorsal view (left) and transverse view (right). (24–25) Cantacaderini; (26–27) Tinginae and Phatnomatini; as – additional sclerite in pleural membrane, ep – epipleurite, hy – hypopleurite, pa – paramere, pm – pleural membrane, pr – proctiger, pg – pygophore, st – sternite, tg – tergite



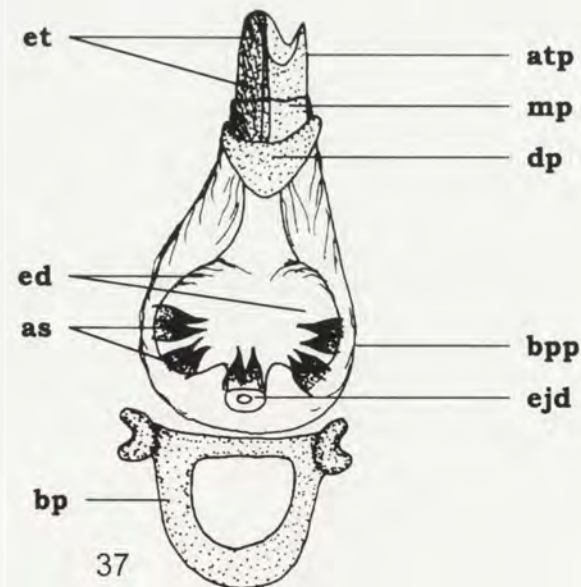
Figures 28–30. Female genital plates. (28) *Cantacader duffelsi*, Cantacaderini; (29) *Cnemiandrus typicus*, Phatnomatini; (30) *Tingis auriculata*, Tinginae; ga – gonaphophysis, gn – gonoplac, gp – gonocoxopodite, lt – laterotergite, pt – paratergite, r – ramus, rp – ramal plate



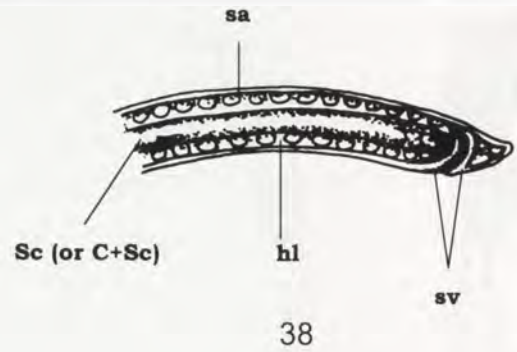
Figures 31–35. 31–33. Female internal genitalia; co – common oviduct, epo – expanded part of oviduct, lo – lateral oviduct, o – ovariole, p – pseudospermatheca, rsp – rudimentary spermatheca, rs – ring sclerite, v – vagina. 34–35. Phallus; ap – apodeme, atp – apical tubular portion of phallotheca, bp – basal plate, bpp – bulbous portion of phallotheca, dc – ductifer, dp – dorsal plate, ed – endosomal diverticula, en – endosoma, ena – endosomal sclerites and appendages, et – endosomal thickening, mp – medial portion of phallotheca, scp – sclerotized conical protuberances. (31) *Allocader cordatus*, Cantacaderini; (32) *Phatnoma costalis*, Phatnomatini; (33) *Tingis auriculata*, Tinginae; (34) *Cantacader afzelii*, Cantacaderini; (35) *Stephanitis oberti*, Tingini



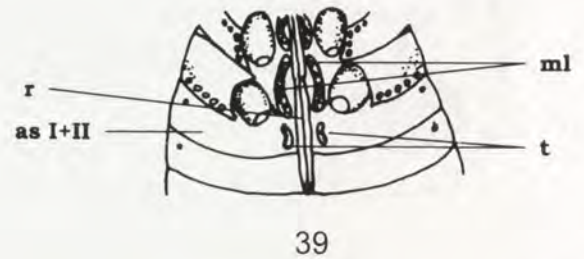
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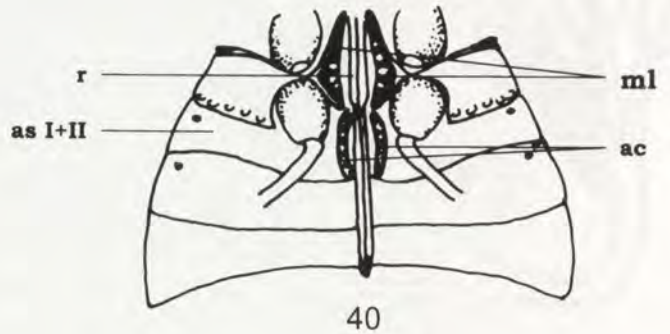
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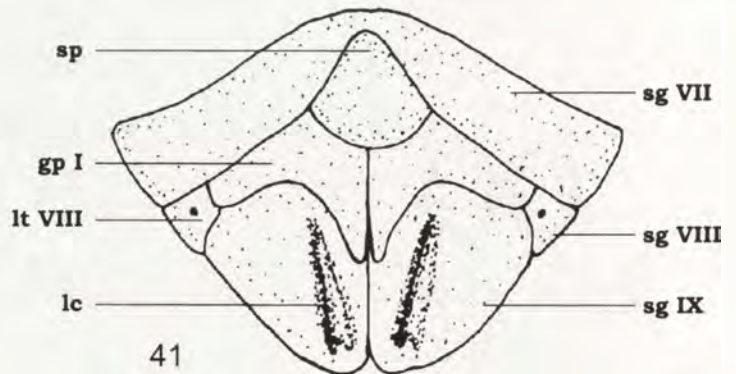
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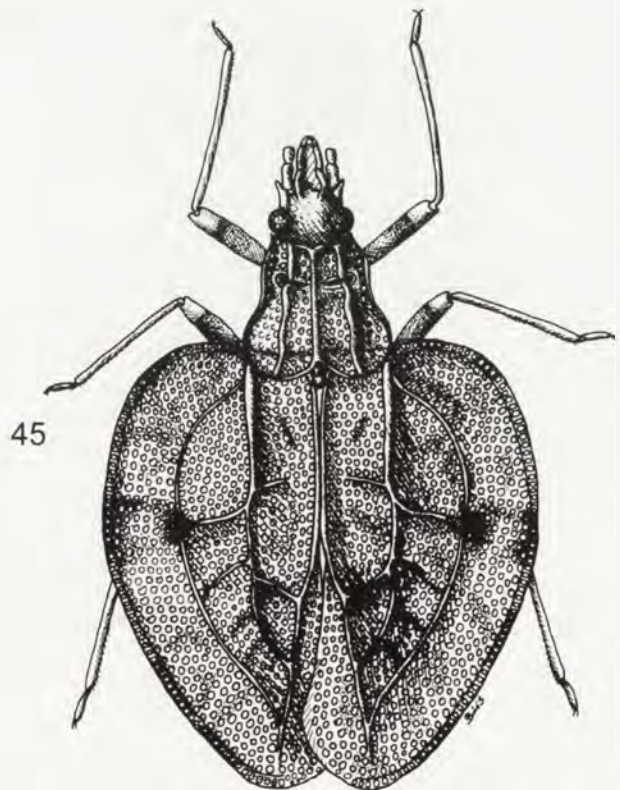
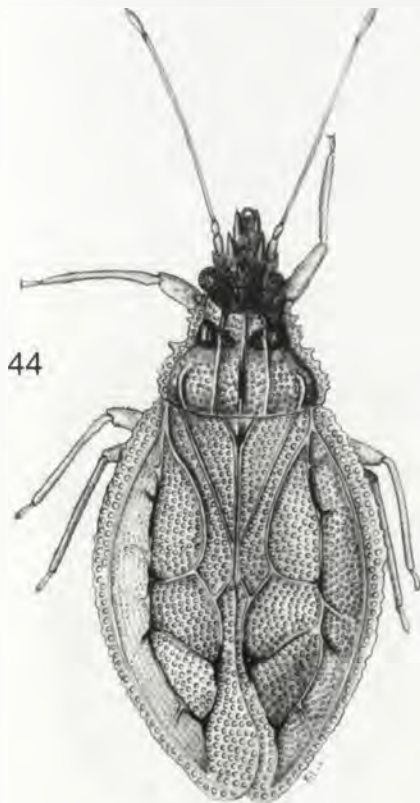
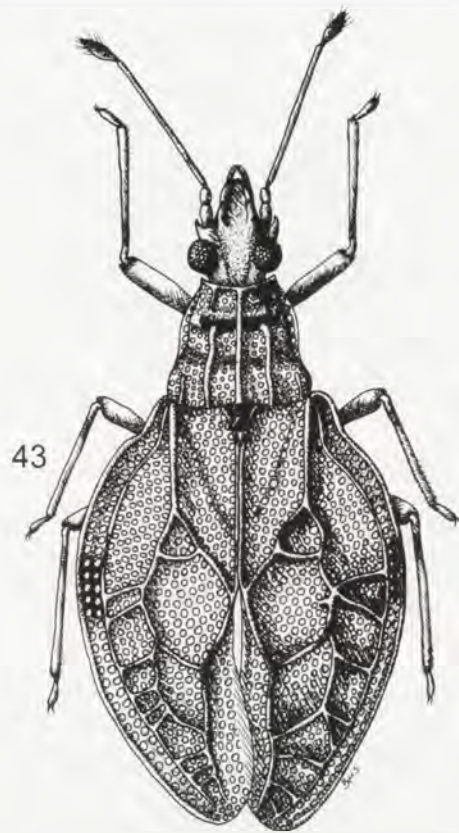
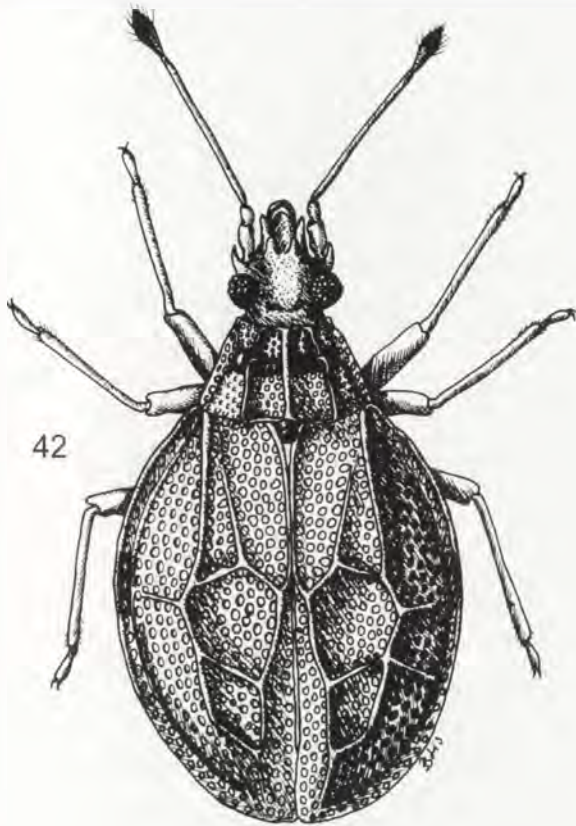


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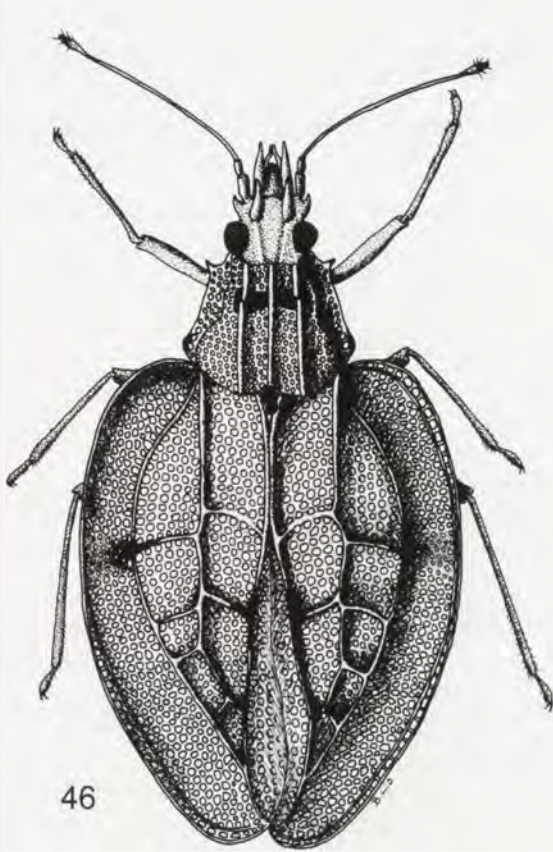


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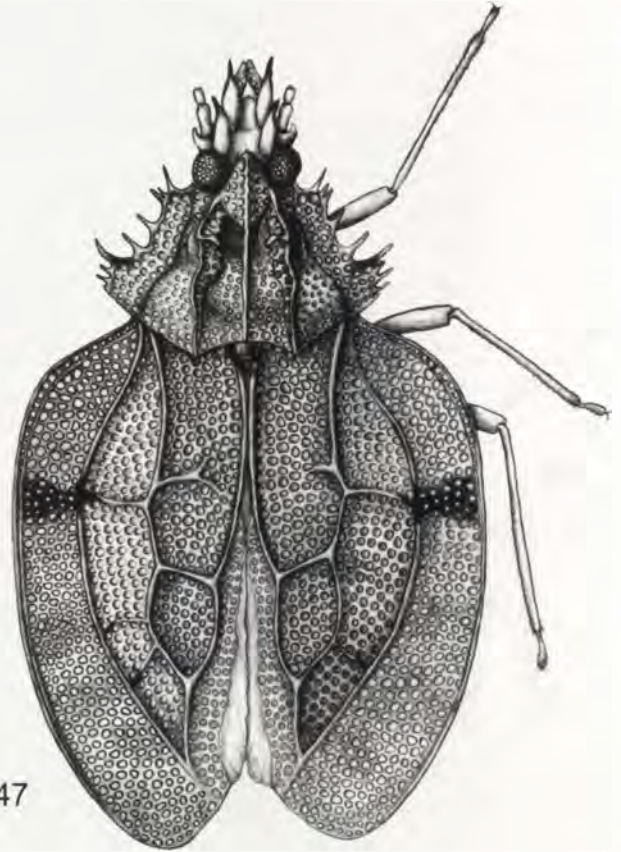
Figures 36–41. 36–37. Phallus; ap – apodeme, atp – apical tubular portion of phallotheca, as – additional sclerites, bp – basal plate, bpp – bulbous portion of phallotheca, dc – ductifer, dp – dorsal plate, ed – endosomal diverticula, ejd – ejaculatory duct, et – endosomal thickening, mp – medial portion of phallotheca. 38. Basal part of hemelytron in ventral view; hl – hypocoel lamina, sa – stenocostal area, sv – subbasal veins forming trough across hypocoel lamina. 39–40. Basal part of abdomen in ventral view; ac – additional carinae, as – abdominal sternite, ml – metasternal laminae, r – rostrum, t – tubercles. 41. Female genital plates; gp – gonocoxopodite, lc – longitudinal cavity, lt – laterotergite, sg – segment, sp – subgenital plate. (36) *Derephysia cristata*, Ypsotingini; (37) *Cnemidandrus typicus*, Phatnomatini; (38) *Carldrakeana engista*; (39) *Carldrakeana engista*; (40) *Australocader kerzhneri*; (41) *Australocader kerzhneri*



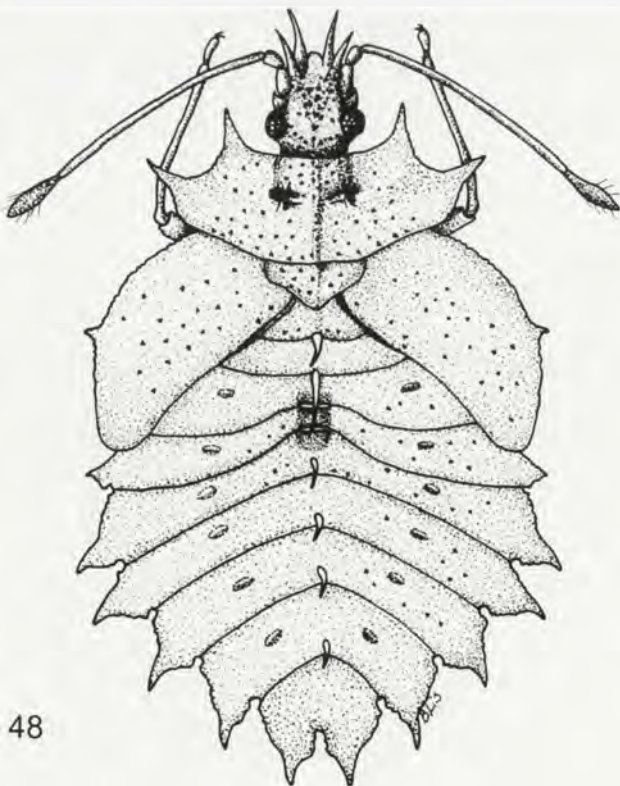
Figures 42–45. Adult habitus. (42) *Carldrakeana socia* (Drake and Ruhoff); (43) *Cyperobia carectorum* Bergroth. (44) *Stenocader tingidoides* (Spinola); (45) *Allocader cordatus* (Hacker)



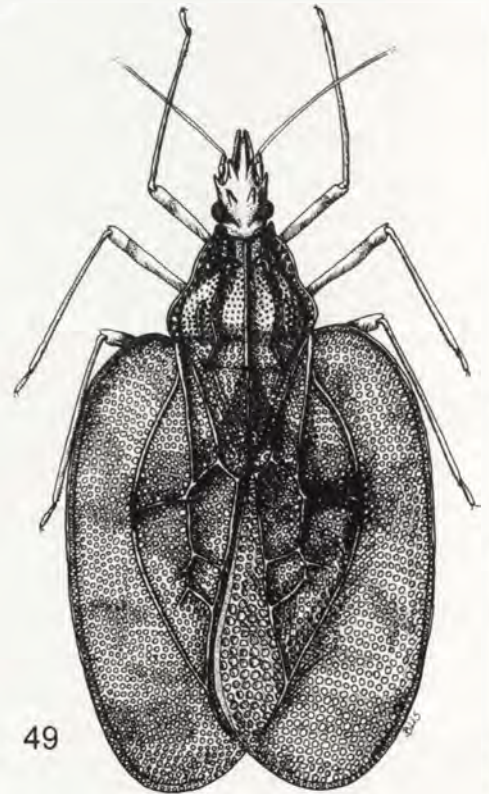
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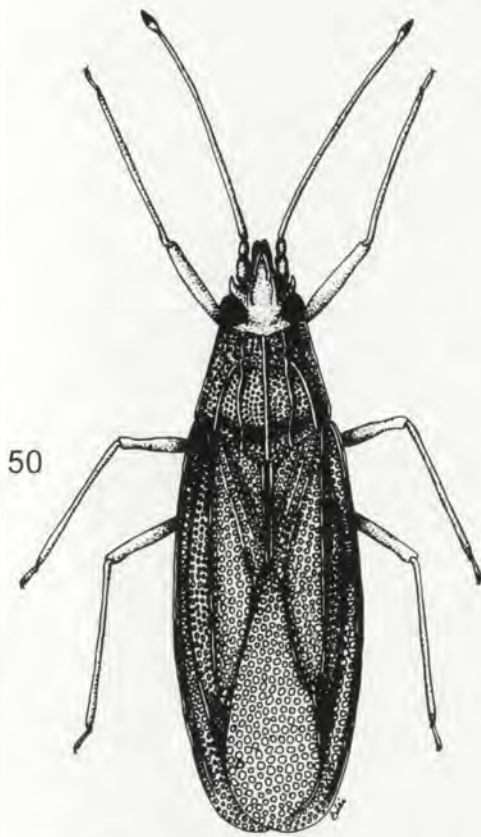


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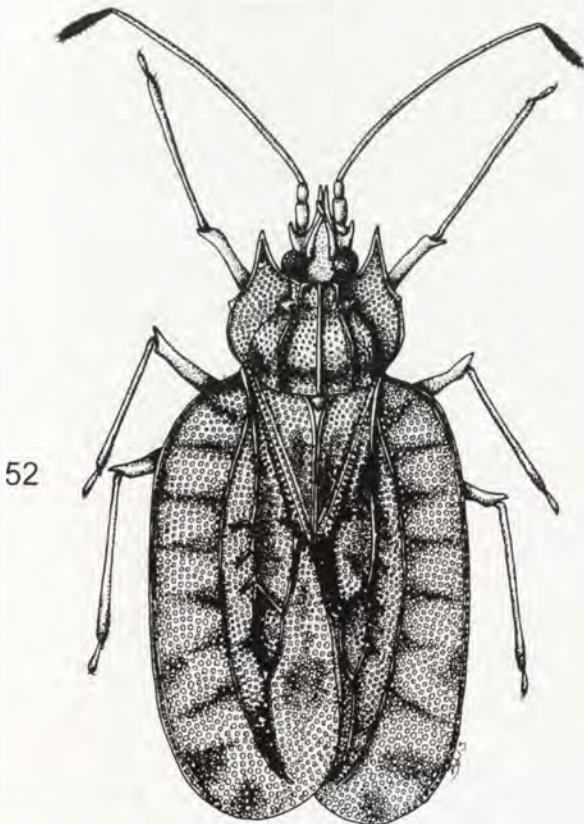
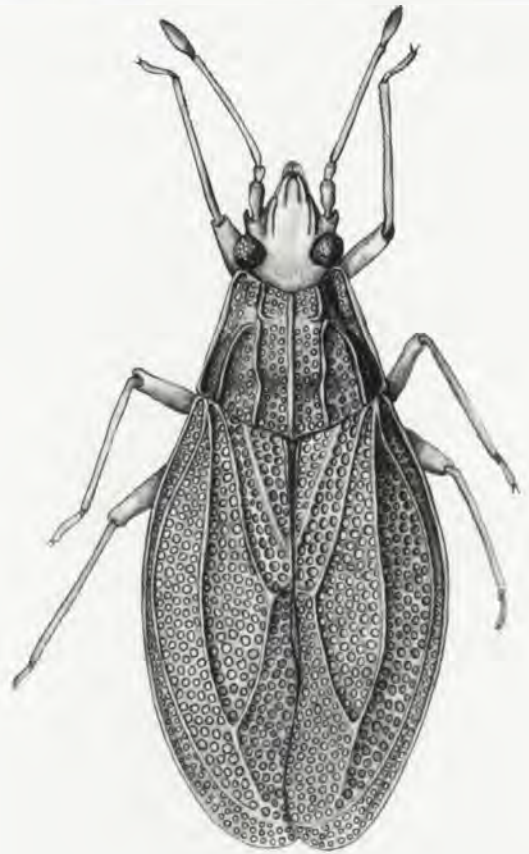


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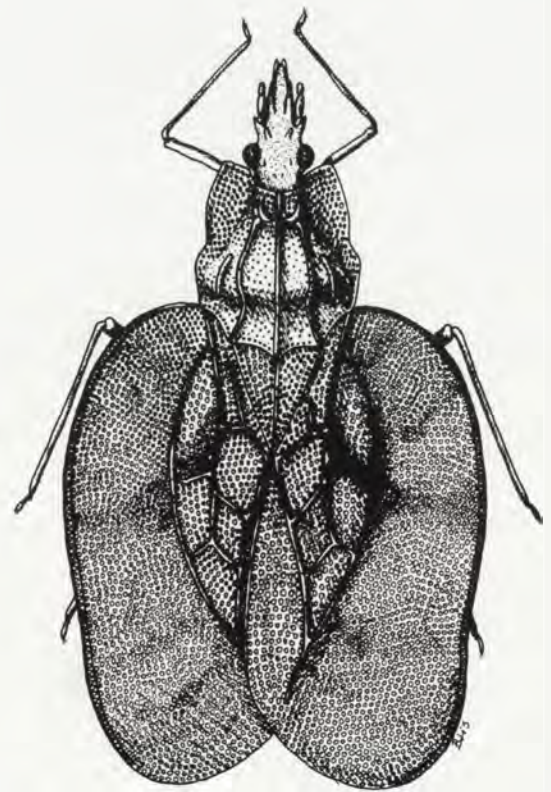
Figures 46–49. 46, 47, 49. Adult habitus: (46) *Australocader kerzhneri* B. Lis; (47) *Ceratocader armatus* (Hacker); (49) *Nectocader gounellei* (Drake).
48. *Ceratocader armatus* (Hacker), larva



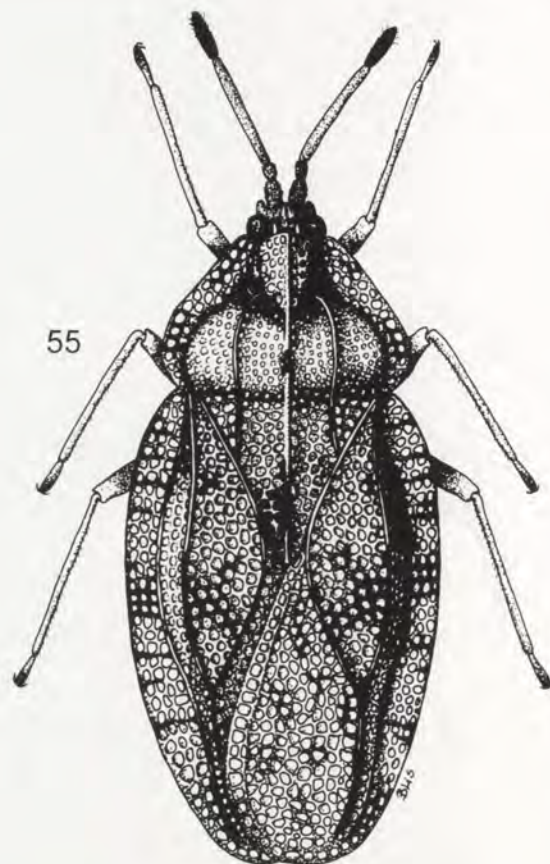
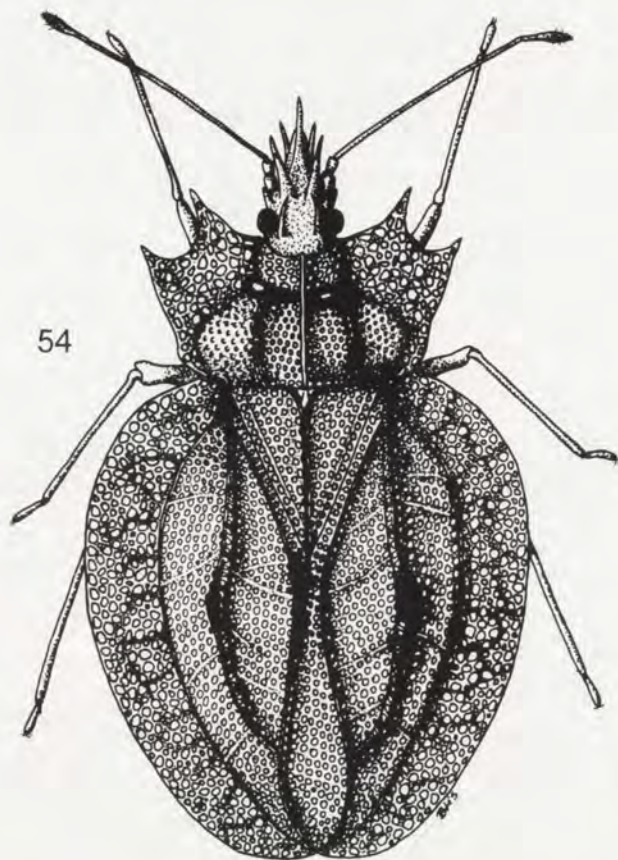
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Figures 50–53. Adult habitus. (50) *Cantacader afzelii* (Stål); (51) *Cantacader insularis* Drake; (52) *Pseudophatnoma laosana* B. Lis (53) *Teratocader magnificus* (Drake)



Figures 54–55. Adult habitus. (54) *Phatnoma costalis* Distant; (55) *Tingis cardui* (Linnaeus)