

Contribution to classification and phylogeny of the family Cixiidae (Hemiptera, Fulgoromorpha)

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Abstract

Taxonomically most valuable supra-generic characters in the family Cixiidae both previously used and new ones are surveyed and discussed. The subfamily Cixiinae is divided into 15 tribes, seven of them (Brixidiini trib. n., Brixiiini trib. n., Andini trib. n., Semonini trib. n., Eucarpiini trib. n., Cajetini trib. n. and Duiliini trib. n.) described herein as new. The tentative cladogram of the family Cixiidae on tribal level is proposed. The tribes Benna-rellini, Gelastocephalini and the subfamily Borystheninae (with one tribe) remain unrooted and missing in the cladogram.

Key words: Cixiidae, phylogeny, Brixidiini trib. n., Brixiiini trib. n., Andini trib. n., Semonini trib. n., Eucarpiini trib. n., Cajetini trib. n. and Duiliini trib. n.

Introduction

Cixiidae, one of the most basal fulgoroid families, is known since the preanthophytan Mesozoic. Cixiids are distributed worldwide and show a high diversity, especially in the tropics. The family Cixiidae currently comprises no less than 146 genera (Holzinger, Emeljanov, Kammerlander in this volume). It is difficult

are also variable. In this report a preliminary attempt is made to distinguish the principal tribes. A number of genera in both the Old and New World still remain placed preliminarily, and I intend to fill up partly this gap in the future.

I consider Delphacidae a sister - group of the Cixiidae plus all the other Fulgoroidea (probably, except Tettigometridae). In addition to the synapomorphies already published (EMELJANOV 1990), there is one more reliable synapomorphy of Cixiidae + all the other Fulgoroidea, namely the fusion of the eighth abdominal laterotergite with tergite. In Delphacidae this laterotergite is free like in preceding segments.

Characters

Comparison with the out-group lower Delphacidae, shows the polarity of two morphoclines: within the Cixiidae first, medially divided or not divided sclerotization of the eighth and the seventh abdominal sternites in male, and second, the position of intercubital veinlet which meets the end of claval suture or shifted distally. The polarity of the third morphocline concerning nymphal wax - pore plates, may be determined through a more complicated logical operation, because the wax - pore plates primarily appeared in Cixiidae and are inherent in all cixiid nymphs studied.

Some examples of partial degradation of wax - pore plates demonstrate that the plates are situated behind and between the sensory pits. Consequently fore position of sensory pits is plesiomorphic.

Now I shall review the phylogenetical weight and stability of the characters used to distinguish the tribes and reconstruct cixiid phylogeny.

Head

1. Loroclypeal keels (Figs 1, 2). Rarely they could disappear if the clypeus is large and inflated (*Duilius*, *Gelastoccephalus*); in *Trigonocranus* also with the inflated clypeus are incompletely developed. All three examples belong to the related tribes Oecleini, Gelastoccephalini and Duiliini. Generally the absence of these keels indicates certain embryonization.

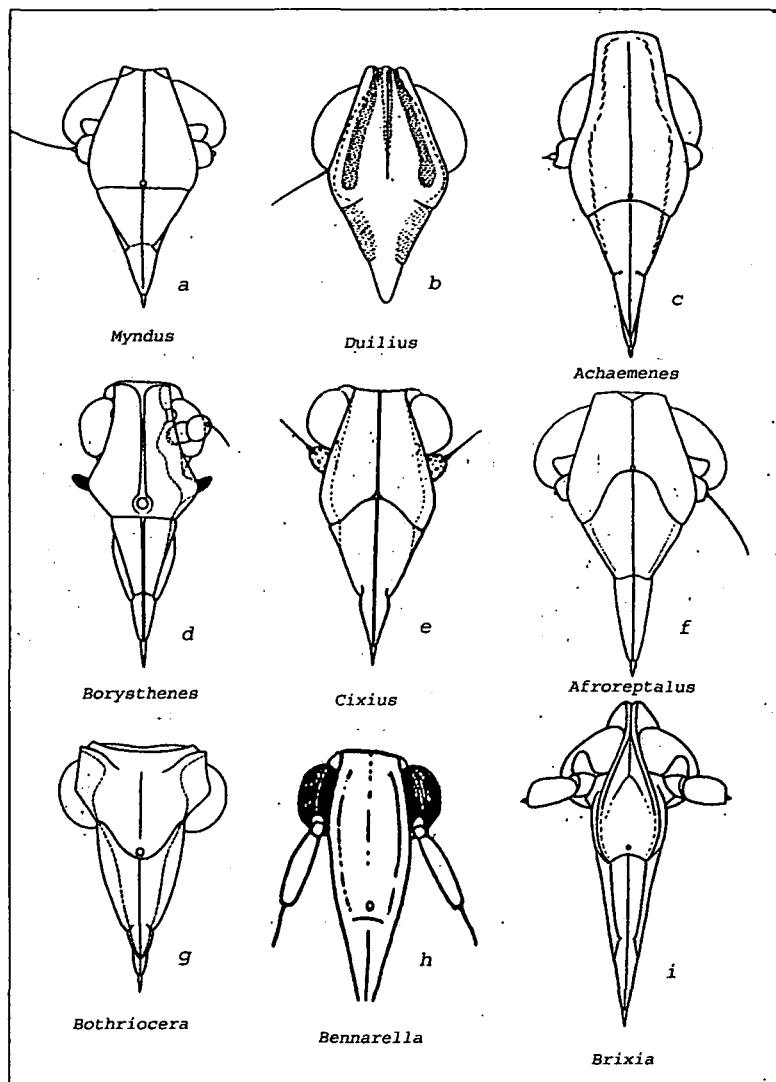


Fig. 1. Head of Cixiidae.
 a - *Myndus (Myndodus) velox* Em.,
 b - *Duilius tenuis* Stål,
 c - *Achaemenes notatinervis* Stål,
 d - *Borysthene fatalis* Em.,
 e - *Cixius nervosus* L.,
 f - *Afroreptalus daemon* Em.,
 g - *Bothriocera* sp.,
 h - *Bennarella bicoloripennis* Muir,
 i - *Brixia natalensis* Stål
 (a, f - by EMELJANOV 1993, d, g - by EMELJANOV 1989, e - by HAUPT 1935, h - by MUIR 1930).

to classify cixiids, except for some specialized groups, and many tribes (for example Cixiini) still remain partly unnatural. It is unclear which cixiids are the most basal ones, this situation exists because the majority of elementary characters are subjected to great homologous variability and, consequently, to reversals; on this reason they can not be interpreted as sound synapomorphies. In this paper in addition to the characters already in use, some new ones are introduced, but they

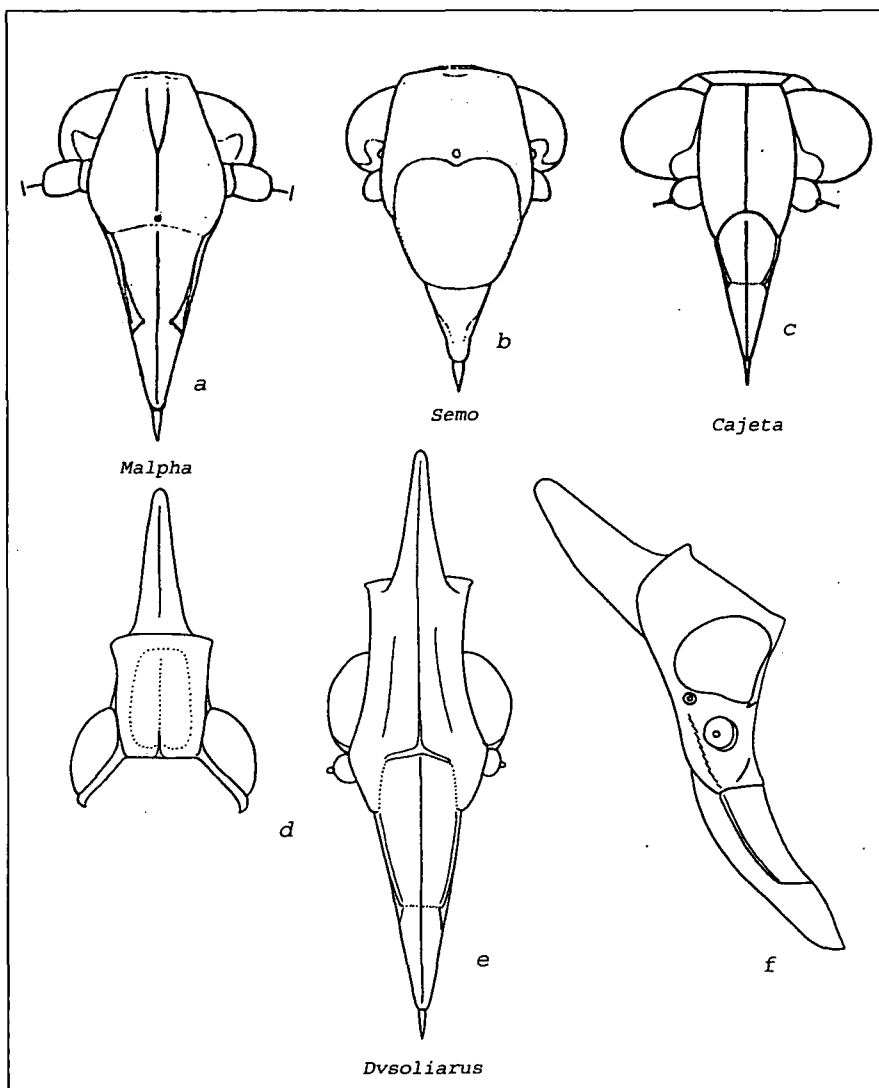
2. Median ocellus (Figs 1, 2). Absent in some tribes (Eucarpiini, Duiliini, Gelastocephalini (Figs 1b, 2c, 2e) and present in the others (Fig. 1a, 1c-1i, 2a, 2b), but constantly absent in subbrachypters. The loss of the median ocellus may be independent and multiple. There are no evidence that having once disappeared, the ocellus may reappear again.

3. Frontoclypeal suture - the upper border of the postclypeus (Figs 1, 2). Approximately straight in some tribes (Oecleini (Fig. 1a), Bennini etc). In other tribes the inflated clypeus is produced into the metope (Figs 1e, 1f). I use the terms first proposed in 1988 (ANUFRIEV & EMELJANOV 1988) for the areas of fulgoroid head: metope for so-called frons, and coryphe for so-called vertex, as more morphologically correct. WEBER (1935) shows, that genuine frons in Cicadina is the little triangular area around middle ocellus. It could form a shallow, obtuseangulate intrusion, or a deep sinusoidal one with clearly developed epiclypeal lobes of the metope (Semonini, Cixiini, Pentastirini, Duiliini). Increase of the clypeus is certainly convergent in many cases; the reversals due to relative decrease of cibarial muscles are also possible. Configuration of frontoclypeal suture in Bothriocerinae (Fig. 1g) is unique and paradoxal. The reversal to initial state may occur due to retardation (retention) of larval condition. However, the inflated clypeus is possibly synapomorphic to the tribes Cixiini, Pentastirini and Semonini.

4. Intermetopal keel, dividing the metope ('frons') into the eumetope and acrometope. Usually present except for Eucarpiini, Bennini, some Oecleini (including Mundopa) and some genera of uncertain position. Absent or poorly developed in some *Duilius* species (Duiliini). An opposite condition, with intermetopal keel present and anterior keel of coryphe absent, could be found for example in some *Myndus* species. When only one transverse keel is developed between the clypeus and coryphe (vertex of usual terminology), it is difficult to recognise its homology. *Gelastocephalus* and *Carolus* have probably an intermetopal keel (EMELJANOV 2000).

Wings

5. Mode of keeping of the fore wings (tegmina) in repose. Probably primary mode is more or less flat or shallowly tectiform and even semicylindric (encircling) position. In some tribes (for example, Oecleini) the character is highly variable. However in these cases more steep wing position does not correlate with common plesiomorphic state of their



possessors, and may be frequently negatively correlated (*Gelastocephalus*). In the tribes with stable steeply tectiform wing position in repose the subbasal concavity of costal margin is usually developed (Figs 5c, 5d). This concavity facilitating hind leg movement when jumping was independently formed in various tribes. An analogous process is observed in the families Achilidae and Derbidae. Reversal from steeply tectiform state to flat or encirc-

Fig. 2.
Head of Cixiidae.
a - *Malpha muiri* MYERS,
b - *Semo clypealis* F.B. WHITE,
c - *Cajeta singularis* STÅL,
d, f - *Dysoliarus* sp.
(d - head, dorsal view,
e - face,
f - left side)
(a, b - by DEITZ & HELMORE 1979).

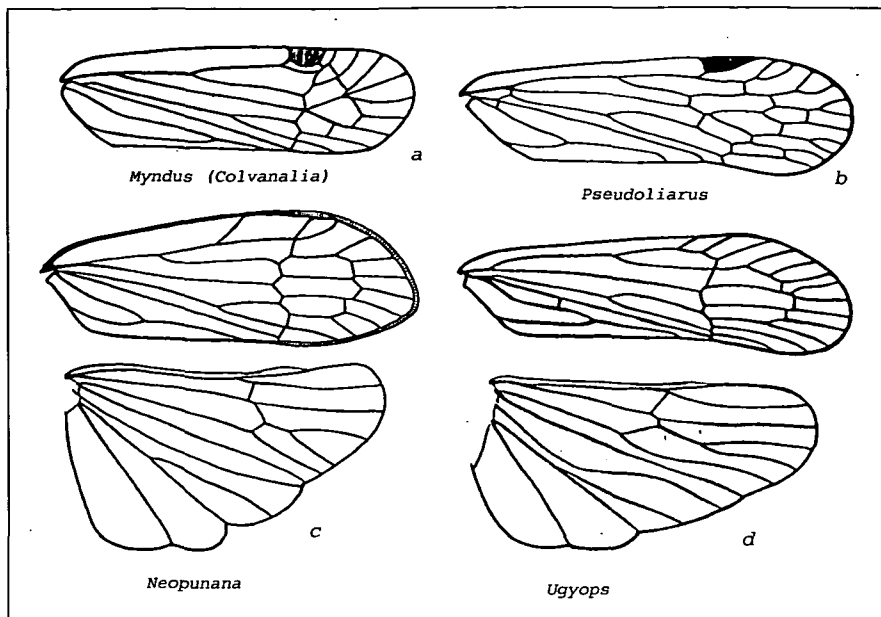


Fig. 3. Wings of Cixiidae (a, b) and Delphacidae (c, d). a - *Myndus (Colvanalia) rumina* FENN., fore wing, b - *Pseudoliarus* sp., fore wing, c - *Neopunana saba* ASCHE, fore and hind wings, d - *Ugyops kinbergi* STÅL, same (a - by FENNAH 1969, c, d - by ASCHE 1985).

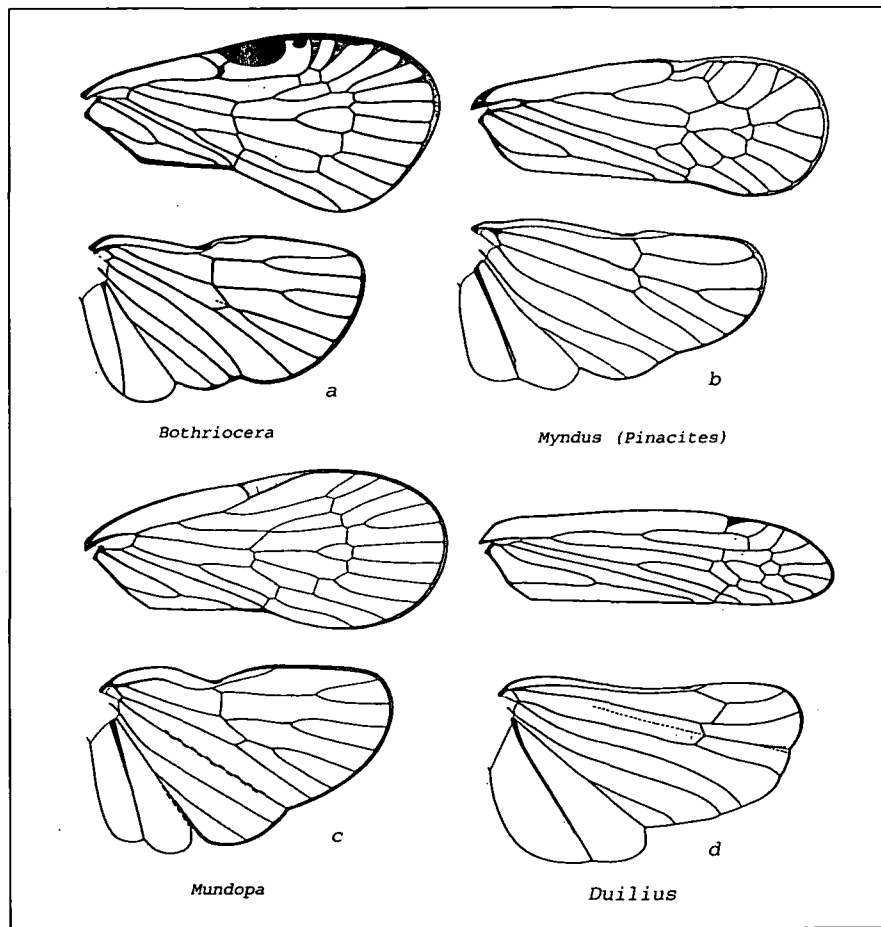


Fig. 4. Wings of Cixiidae. a - *Bothriocera* sp., fore and hind wings, b - *Myndus (Pinacites) calvipennis* EM., same, c - *Mundopa* sp., same, d - *Duilius tamaricis* PUT., same (a, b - by EMELIANOV 1989).

ling seems to be hardly probable. However, the subfamily Flatoidinae of family Flatidae have secondarily acquired a flat position of fore wings in repose, and at least the advanced ricaniids use one of two positions, steeply tectiform or flat, on their choice, the drawingpin-like tegulae provide the fixation of two positions (my observation on *Ricania japonica* MATS.).

6. Association of ScR and M stems in the fore wing (Figs 4-7). These stems initially diverged just beyond the basal cell. Formation of common stem beyond the basal cell took place at least twice - in the ancestor of Oecleini (Fig. 4b) and in the ancestor of Brixini (Fig. 5d). The third case probably occurred in Duiliini (Fig. 4d). Formation and dissociation of the common ScRM stem is labile enough, this character is variable in the species of *Myndus* s. lato, and the common stem is absent in some *Colvanalia* species.

7. Two branching pattern of media in the fore wing with standard five ending occur in cixiids: the primary one with trifid MA, and the secondary one with trifid MP. The second variant is present in Brixini (Fig. 5d) and in the unrelated *Mnemosyne* from Pentastirini (Fig. 5e).

8. Anastomosis MP+CuA in the hind wing. There are all transitional stages between the punctuated anastomosis in Andini and Pentastirini (Figs 5b, 7b) and the complete distal fusion in Oecleini, Duiliini, part of Eucarpiini, etc. (Figs 4b, 4d, 5c). In genus *Borysthenes* (Borystheninae) MP and CuA are separated and connected only with a transverse veinlet (Fig. 6b). In Delphacidae the anastomosis MP+CuA is petiolate, bifurcating at the end (Figs 3c, 3d). Probably in Cixiidae as well the primary state is petiolate anastomosis of variable length. A complete terminal fusion of MP and CuA takes place easier than complete separation.

9. Transformation of intercubital veinlet. One may recognize three states of this transverse veinlet which primarily is connected to the apex of claval suture (Fig. 3a), as shown by comparison with cixiid sister-group, Delphacidae (Figs 3c, 3d). In the second state the veinlet is shifted distad losing connection with the clavus (Fig. 3b). In the third state the veinlet elongates and is directed obliquely longitudinally.

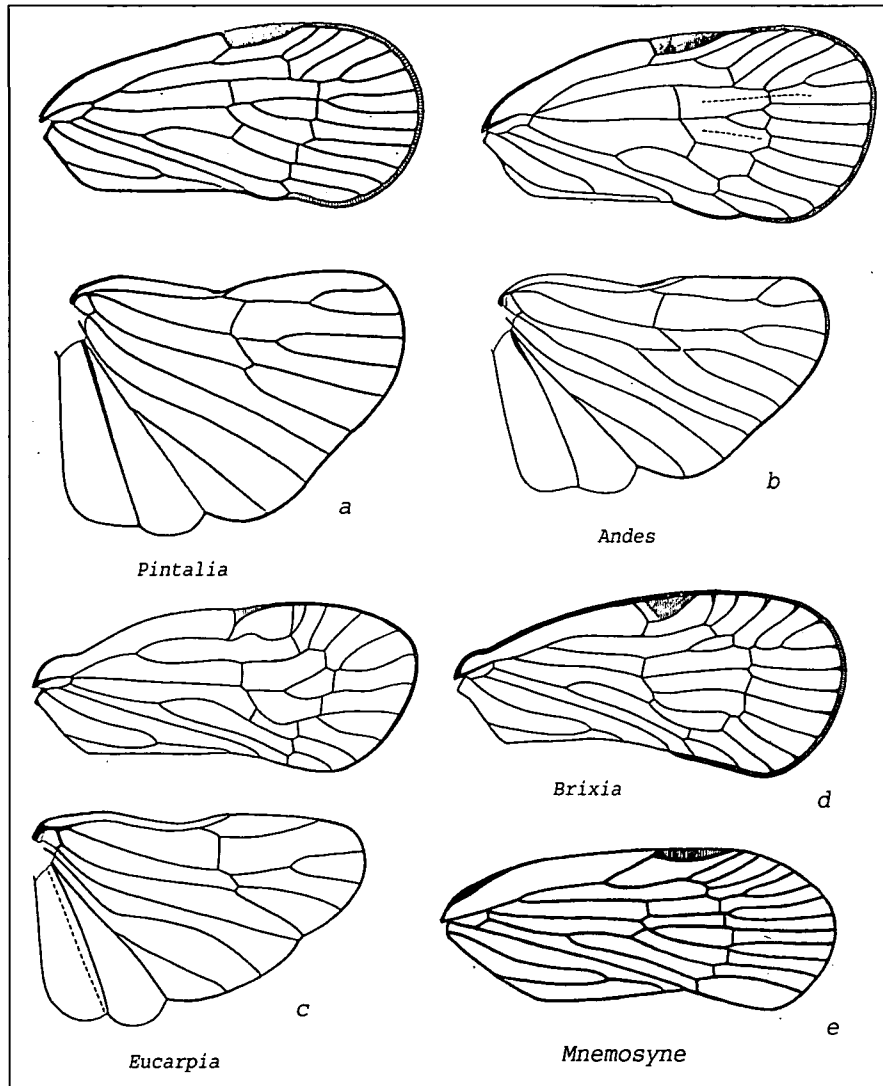
nally, acquiring the shape of the third branch of CuA. The third state is common for two, not very similar tribes Brixidiini and Bennini, and subfamily Borystheninae (Figs 6a, 6b), and could be synapomorphic for them. If so, then the flat folding of the forewings in repose is secondary in Borystheninae, derived from the steeply tectiform one of the other two taxa. In Borystheninae fore wings have flat position and in this case one has to admit a transition from steeply tectiform wing position to flat position, if the long oblique veinlet *icu* is their synapomorphy.

Legs

10. Lateral spines of hind tibiae (Fig. 8). One could consider that the ancestor of Cixiidae should have these spines because they are present in Delphacidae and higher Fulgoroidea. Probably such an ancestor did not belong to Cixiidae but rather to some unknown, intermediate family. Lateral spines of Cixiidae are unique and probably represent a reversal autapomorphic of the family (Fig. 8). In cixiids the spines, if present at all, are formed by a socle crowned with a short thick seta, this construction is probably a result of reversal to the ancestral state of pre-Fulgoroidea which preceded the usual spines (EMELJANOV 2001). It is interesting and significant, that the more primitive representatives of Cixiidae are devoid of any lateral spines, the majority of groups with such socle-seta spines are more advanced, for example Semonini - Cixiini - Pentastirini. Then, the last common ancestor of Cixiidae probably had spinose hind tibiae devoid of spines. [Therefore, it is possible that both conditions, with lateral spines and without them, existed in the group ancestral to cixiids.]

11. Apical spines of hind tibiae (Fig. 9). Usually there are six spines of different length in uninterrupted row. Often the elongate outer spine of the external group stands out and the two next spines of the same group are shorter; these three spines form a medial group, and three external spines form an opposed group. In the tribes Brixini, Brixidiini and Bennini three spines of medial group decrease in length outwards, so that the longest spine is

the middle one, which is usually even longer than the outer external spine. The third variant of spinulation is characteristic of the tribes Stenophlepsiini and Cajetini, probably it is their synapomorphy. In these tribes the spines are polymerized up to 8 to 12, and form an uniform regular row without the division into the external and medial groups. In the tribe Oecleini and Gelastocephalini the spines of



external and medial groups are separated with an interspace - the row is interrupted by diastema. This state with diastema corresponds to the intermediate ontogenetic stage of all Fulgoroidea, transforming into an uninterrupted spine row of adult. The same spinulation with diastema is present also in some myrmecophilous species of the subgenus Podaplus in Pentastiridius (Pentastirini), which also have no lateral tibial spines.

Fig. 5. Wings of Cixiidae.
a - *Pintalia* sp. (Puerto-Rico), fore and hind wings;
b - *Andes undulatus* Stål, fore and hind wings;
c - *Eucarpia* sp., fore and hind wings,
d - *Brixia natalensis* Stål, fore wing,
e - *Mnemosyne* sp., fore wing (e - by SYNAVE 1978).

Nymphal wax-pore plates

12. Abdominal wax-pore plates in cixiid nymphs are of five types, two of which were recently described by YANG & YEH (1994) (Fig. 10). The wax-pore plates are absent in the outgroup (Delphacidae), but nevertheless the instances of partial degradation of wax-pore plates (for example in Flatidae) indicate

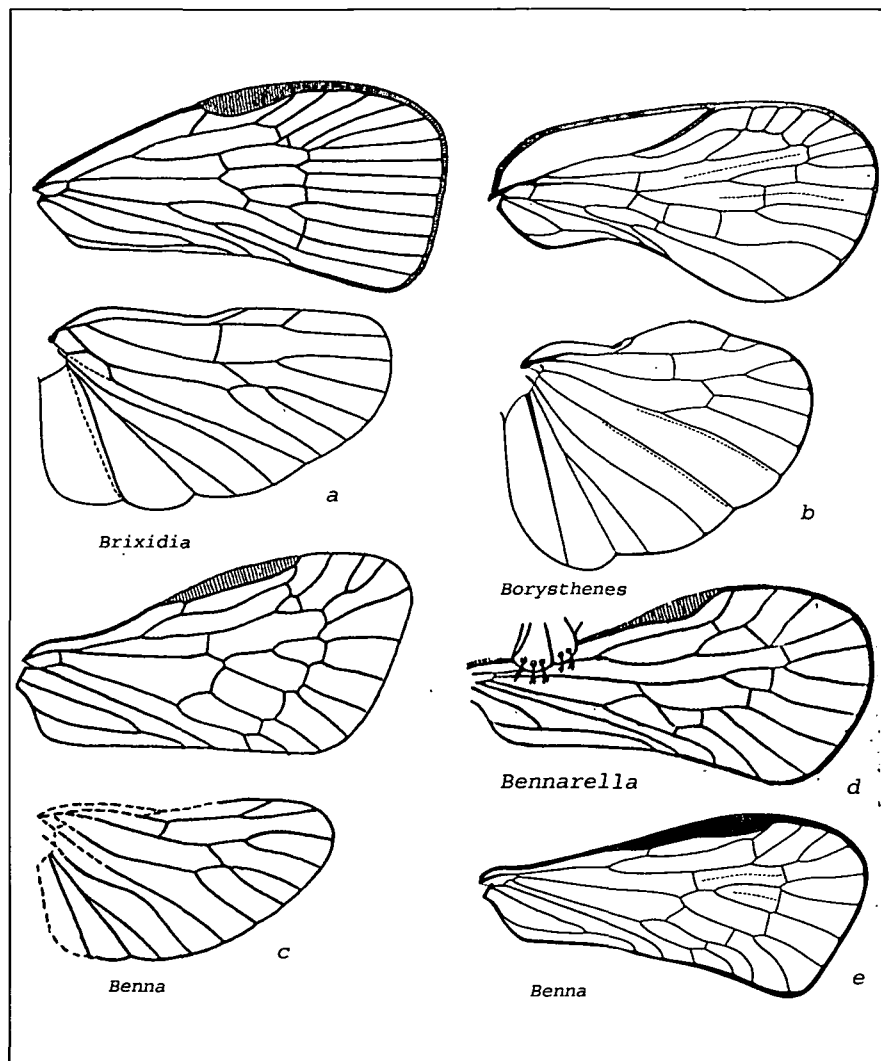


Fig. 6. Wings of Cixiidae.
 a - *Brixidia* sp., fore and hind wings,
 b - *Borysthenes fatalis* EM., same,
 c - *Benna capitulata* WALK., same,
 d - *Bennarella* sp., fore wings and sensory outgrowth of abdomen,
 e - *Benna nasti* EM., fore wings
 (a - fore wing by SYNAVE 1980,
 b, e - by EMEJANOV 1989,
 c - by WALKER 1857, modified with reconstruction, d - by MUIR 1930).

that initially the plates were situated behind and between sensory pits. Plesiomorphic type of the plates with the sensory pits at anterior margin, is known in Oecleini (WILSON & TSAI 1982; WILSON et al. 1984), Brixini (SYNAVE 1953) and Bothriocerinae (MYERS 1929), whereas the other types are characteristic of Semonini - Cixiini - Pentastirini branch. The absence of knowledge on the nymphs of most tribes is distressing.

Abdomen

13. Sclerotization of the eighth and the seventh abdominal sternites in the male (Fig. 11). The primary state of sternite was evidently a single uninterrupted sclerotized plate, but already in the primitive fulgoroids - in Delphacidae (in Tettigometridae also) considered the sister-group of cixiids, the seventh to fourth sternites are divided along the midline. Such a construction evidently permits to increase considerably the extensibility of the abdomen. Nevertheless the majority of higher fulgoroids have sternites entirely sclerotized. Therefore the divided eighth and seventh sternites are considered plesiomorphic in Cixiidae. In certain advanced cixiids the eighth sternite becomes entirely sclerotized. In the tribe Pentastirini the seventh sternite also may be single, or divided into three parts (Figs 11a, 11b). Transformation of the eighth sternite into a single sclerite undoubtedly took place more than once, for example an entire eighth sternite of Bothriocerinae certainly developed independently of most higher Cixiinae.

Using these characters, the cladogram was constructed.

The explanation of the cladogram (see Fig. 12).

1. Some plesiomorphies of the family.

1.1. Sclerotization of male VIII and VII abdominal sternites is divided medially (as in Delphacidae) (Figs 11d, 11e).

1.2. Hind end of intercubital transverse veinlet on fore wings touches claval suture near claval apex (Figs 3a, 4a, 4b, 4c, 4d).

1.3. Sensory pits of abdominal wax - pore plates lie on their fore margins (Fig. 10a).

2. Apomorphies of the family.

2.1. Nymphal abdominal wax - pore plate with five linear crosspieces (Fig. 10a).

2.2. Lateral spines of hind femora formed to socle crowned with short thick seta (Fig. 8).

3. or 4. Thick and dentate fossorial fore legs in nymphs.

Described in Bothriocerinae (MYERS 1929) and Oecleini (WILSON & TSAI 1982; WILSON et al. 1984), very probably also in Cajetini because thick imaginal fore legs.

5. Diastema between lateral and medial groups of spines in hind tibiae (Fig. 9c).

6.1. Lateral carinae of postclypeus disappeared (Fig. 1b).

6.2. Hind wings margin incised in MP+CuA1 (Duilini) (Fig. 4d).

7. Thickened fore legs: coxae, femora, tibiae (Cajetini).

8. Displacement of intercubital transverse vein distal of clavus apex (joining wing margin) (Fig. 3b and many other).

9. Fore wings (tegmina) tectiform.

10. Only one transverse carina between clypeus and coryphe (Eucarpiini).

11. Hind margin of the fore wing with convexity situated between the clavus apex and icu (Pintaliini) (Fig. 5a).

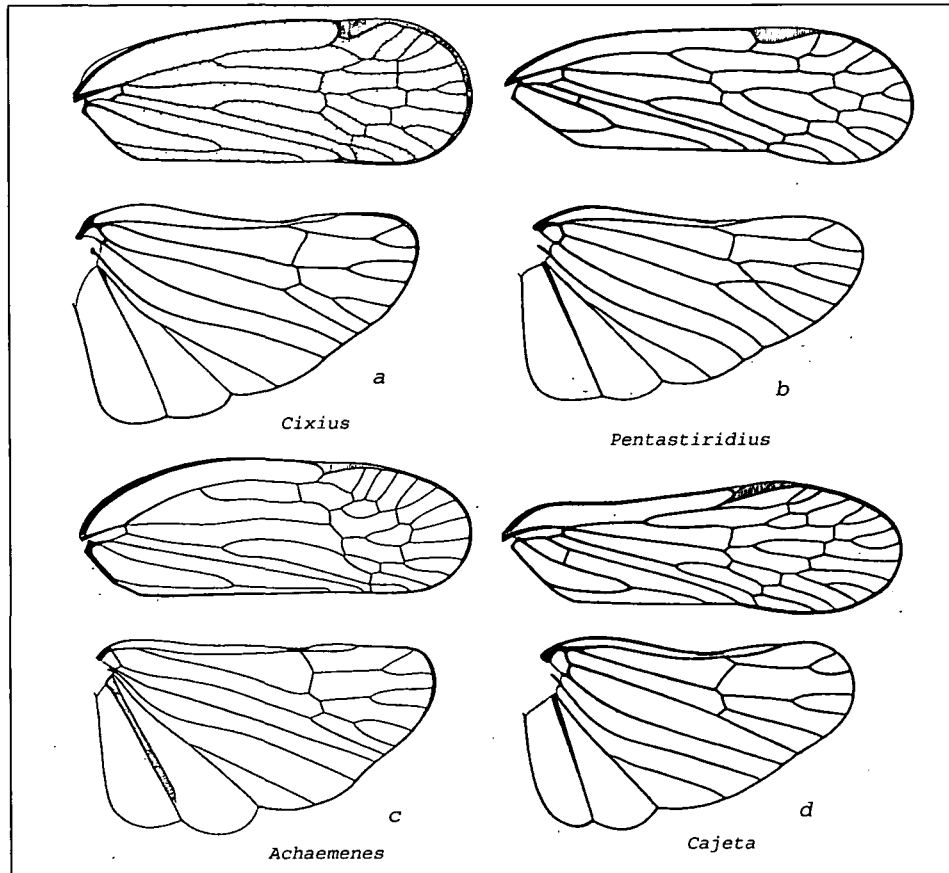


Fig. 7. Wings of Cixiidae. a - *Cixius nervosus* L., fore and hind wings, b - *Pentastiridius leporinus* L., same, c - *Achaemenes notatinervis* STÅL, same, d - *Cajeta singularis* STÅL, same (a - by EMEJANOV 1989, b - by EMEJANOV 1983).

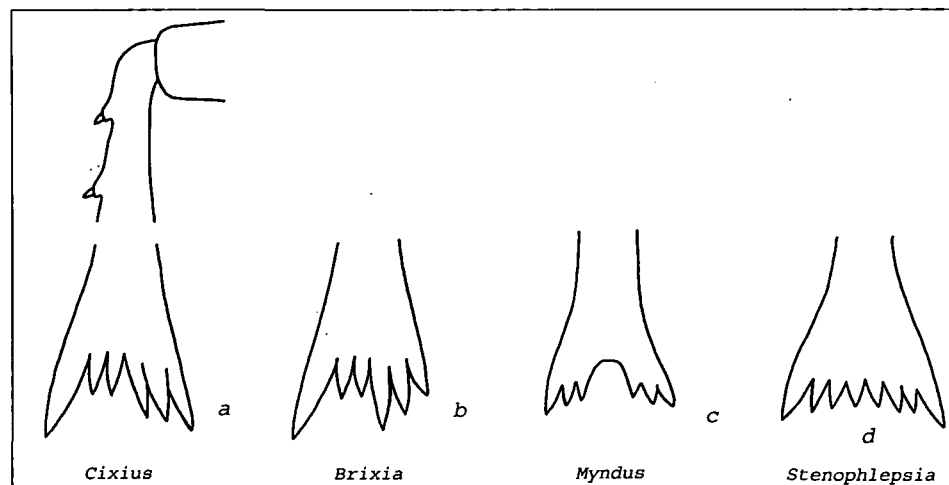


Fig. 9. Types of spinulation of apex of hind tibia in Cixiidae (ventral view of right tibia). a - *Cixius* type, b - *Brixia* type, c - *Myndus* type, d - *Stenophlepsia* type.

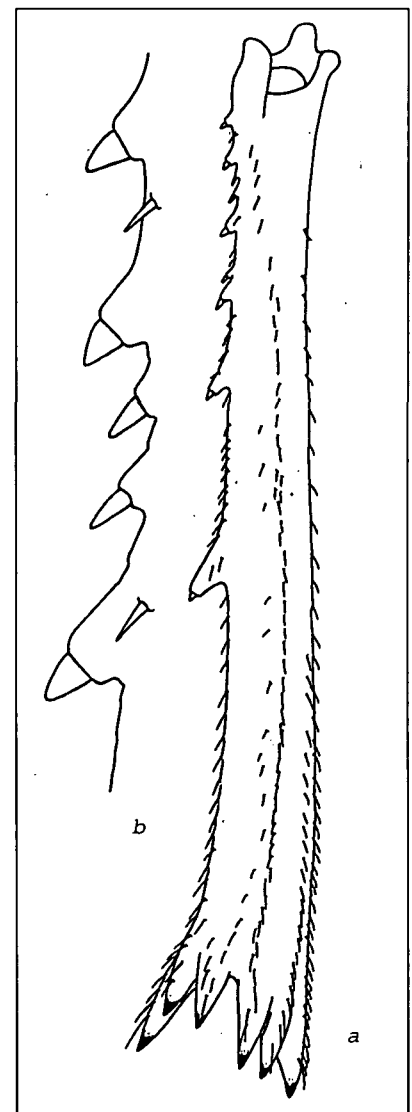
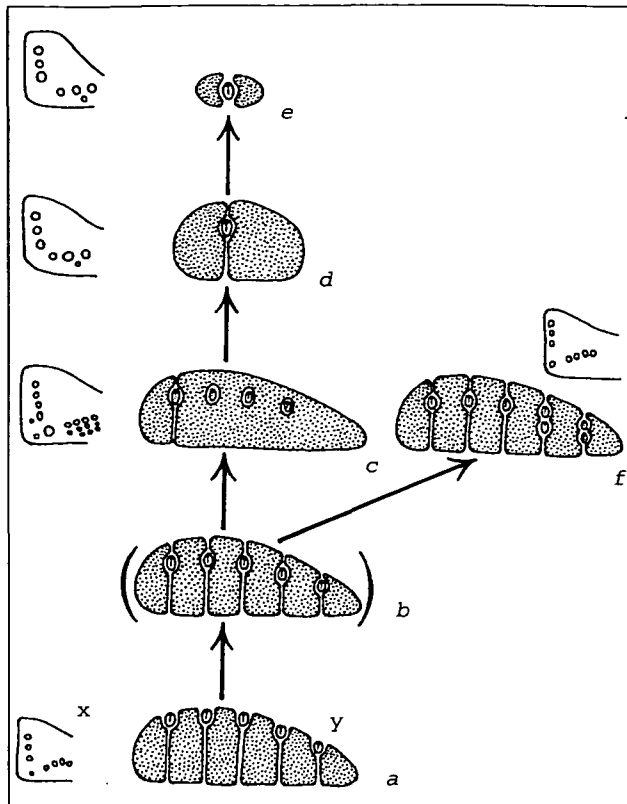


Fig. 8. Legs of Cixiidae. a - hind femur of *Oecleopsis artemisiae* MATS., b - part of spines, magnified (by EMEJANOV 1987).

Fig. 10.
Transformation of wax-pore plates (y) and arrangement of sensory pits on medial part of pronotum (x) in nymphs in some Cixiinae (by EMEJANOV 2001).
a - initial type (tribes Oecleini, Brixini, Bothriocerini),
b - hypothetic intermediate type,
c - first Cixiini type,
d - second Cixiini type,
e - third Cixiini type,
f - Pentastirini type.

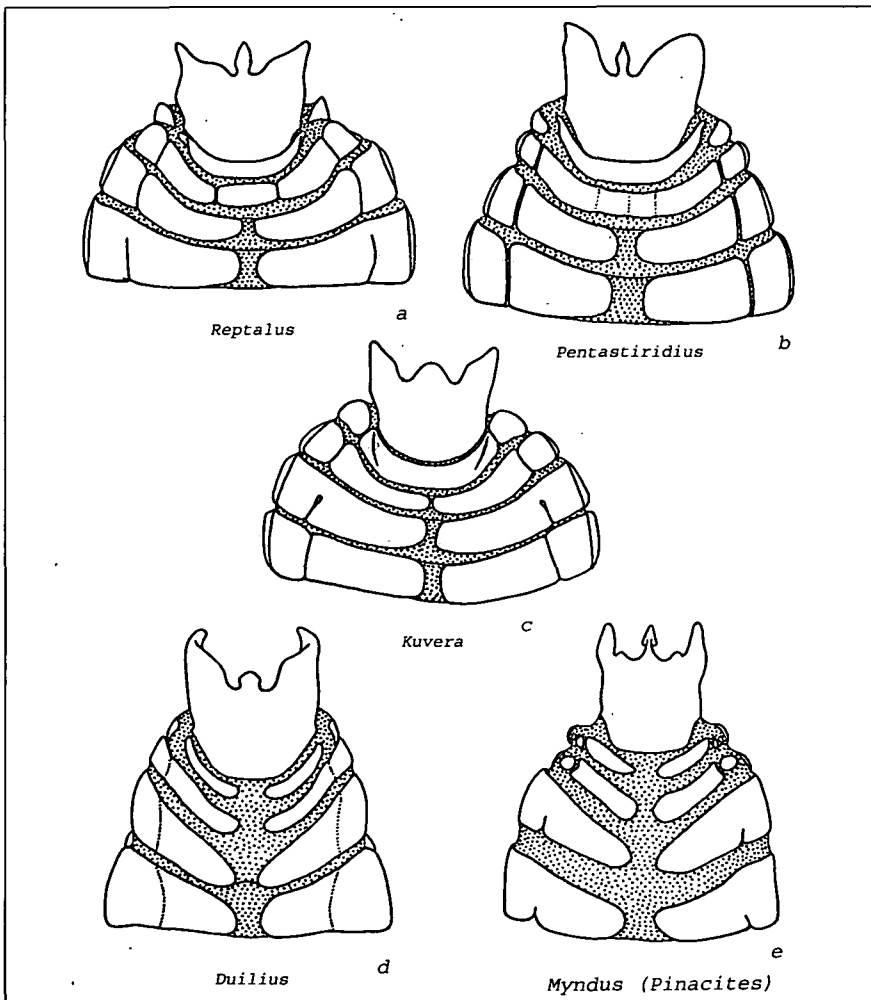


12. Uninterrupted sclerotization of male VIII abdominal sternite (Figs 11a-11c).
13. Forewing in repose steeply tectiform.
14. Middle spine on the apex of hind leg longer than the adjoining spines (Fig. 9b).
15. Intercubital transverse vein of forewing elongated and directed obliquely longitudinally (Fig. 6a).
16. M and CuA of hind wing with basal anastomosis (Brixidiini) (Fig. 6a).
17. RA and RP on fore wing forking near basal cell (Andini) (Fig 5b).
18. Common stem ScRM on fore wing prolonged distad of basal cell (Brixiiini) (Fig. 5d).
19. Sensory pits of abdominal wax-pore plates distant from fore margin of the plate (Figs 10c-10f).
20. Disappearance of 4 of the 5 crosspieces on abdominal wax-pore plate (Figs 10c-10e).
21. Postclypeus swollen, its clypeometopal margin convex, metopo-coryphal boundary obscure (Semonini) (Fig. 2b).
22. Appearance of the middle sternal sclerite on male VII abdominal segment (Pentastirini) (Fig. 11a).

Zusammenfassung

Die wichtigsten bereits bekannten sowie neue Merkmale zur supragenerischen Gliederung der Familie Cixiidae werden überblicksartig dargestellt und diskutiert. Die Unterfamilie Cixiinae wird in 15 Triben unterteilt, sieben von ihnen (Brixidiini trib. n., Brixiiini trib. n., Andini trib. n., Semonini trib. n., Eucarpini trib. n., Cajetini trib. n. and Duiliini trib. n.) werden hier erstmals beschrieben. Ein vorläufiges Kladogramm der Triben der Familie Cixiidae wird präsentiert. Eine Einordnung der Triben Bennarellini und Gelastocephalini und der Unterfamilie Borystheninae (mit einem Tribus) ist gegenwärtig nicht möglich; sie fehlen daher im Kladogramm.

Fig. 11.
Sternal sclerotization of male abdomen in Cixiidae (hind part, ventral view).
a - *Reptalus arcbogdulus* DLAB.,
b - *Pentastiridius leporinus* L.,
c - *Kuvera* sp.,
d - *Duilius fasciatus* HORV.,
e - *Myndus calvipennis* EM.



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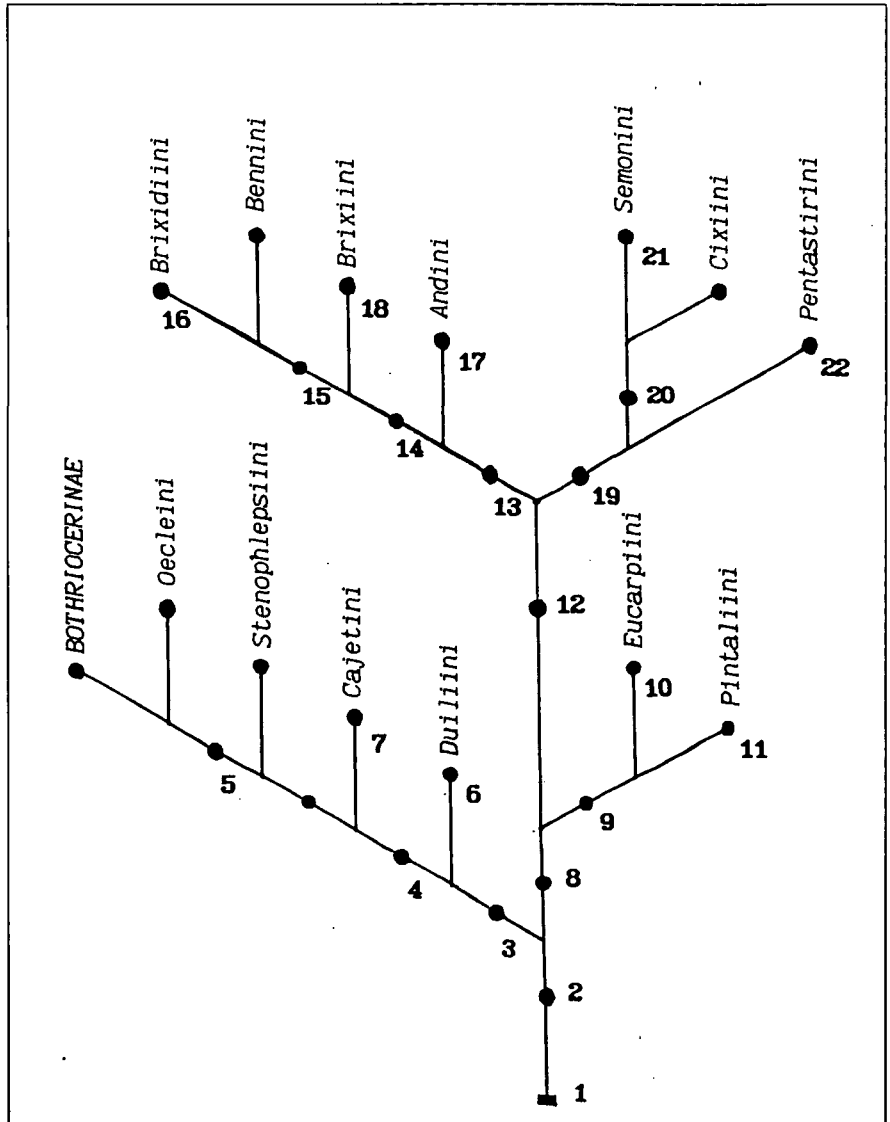
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Fig. 12. Preliminary phylogram of Cixiidae (explanation in the text). Subfamily Borystheninae and tribes Bennarellini and Gelastocephalini not shown – unplaced.



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