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On the System and Phylogeny of the Family Derbidae (Homoptera, Cicadina)*[1]

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Abstract. A new and more detailed system based on external morphological characters of the family Derbidae is presented. Three subfamilies and 18 tribes are recognized: Cedusinae E., 1992, STAT. N.; Ipsnolini TRIB. N.; Phrygiini TRIB. N.; Goneokarellini TRIB. N.; Vinatini Em., 1992; and Cedusini Em., 1992); Derbinae Spin., 1839 (Cedochreini TRIB. N.; Derbini Spin., 1839; Dawnarioidini TRIB. N.; Cenchreini Muir, 1917; Nicertini Em., 1992, STAT. N.); Otiocerinae Muir, 1917 (Rhotanini Muir, 1917; Kamendakini TRIB. N.; Otiocerini Muir, 1917; Neocyclokarini TRIB. N.; Phenicini TRIB. N.; Zoraidini Muir, 1918; and Sikaianini Muir, 1917). Two new subtribes are established in the tribe Zoraidini: Zeugmatina SUBTRIB. N. and Lyddina SUBTRIB. N. Several new genera and species are described: *Melusa* GEN. N., type species *Eocenchrea dardanus* Fenn. (Cedusini); *Cedochrea costaricana* GEN. ET. SP. N. (Cedochreini); *Synavea* GEN. N. (type species *Patara apicemaculata* Syn.); *Anapatara* GEN. N. (type species *Patara nigeriensis* Syn.) (Patarini); *Metaphenice* GEN. N., type species *Derbe stellulata* Boh.; subgenus *Diplophenice* SUBGEN. N., type species *Phenice bicornis* Muir (Phenicini); *Ceropupa trismegista* GEN. & SP. N. (Sikaianini).

The new system is based mainly on the presence and locality of sensorial pits, patterns of transformation of the antennal sensorial complex comprising some parts of the head and prothorax, as well as on the wing shape, venation, and leg armature. A sketch of morphological evolution of the family with a tentative phylogenetic cladogram is presented.

Key words: Homoptera; Derbidae; systematics.

In the process of describing and assembling a catalog of the Derbidae proposed since Muir, a strange tradition to start a list with the most advanced representatives of the subfamily Zoraidinae and end it with the least transformed tribe Cenchreini became established. This is even more surprising because even in 1952 Fennah (1952) made very convincing model of the evolution of the family. There are no reasons to declare that such an accomplished scientist as Muir could present such an obvious direction of evolution in the family in a reverse sequence.

The Derbidae are a compact family with a uniform plan of structure of ♂ genitalia, which permits its atypical representatives to be recognized by ♂'s. Such genera are *Vinarta* Dist., *Phrygia* Stål., *Goneokarella* Fenn., and *Ipsnola* Sign. Formerly the author (Yemel'yanov, 1992) separated the tribe Vinatini, describing the tribe Cedusini and the subtribe Nicertina, which was shown by subse-

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quent analysis to be more correct to consider as a tribe. Also, several more tribes should be distinguished out of the tribe Cenchreini, which would be placed between Cenchreini s. stricto and higher representatives such as Zorasidini and Otiocerini.

Unfortunately in the description of genera and tribes and in the analysis of the systematic position of individual representatives even in contemporary works many essential characters not requiring recording with any tools except the binocular microscope are not taken into account. Such characters are the presence and arrangement of sensory pits on the head and wings; extension of the apex of the clavus, and presence of transverse, small veins in the area of the primary apex of the clavus; stridulatory wing apparatus; type of ovipositor; and some others.

In the family such phenomena of morphologic restoration, involving subantennal crests and paranotal lobes of the pronotum forming either separately or together a peculiar funnel around antennae, are interesting. In almost all tribes, representatives with or without such lobes are present.

HEAD, PRONOTUM, AND ANTENNAL MORPHOFUNCTIONAL COMPLEX

In the family numerous and, in many traits, unique transformations are associated with the enhancement of function of antennae. They involve the entire cranial area and lateral parts of the pronotum (Fig. 1). The immediate meaning of such transformations is not clear, but it is clear that they are somehow associated with the enhancement and specialization of sensory functions of antennae. Basic transformations of antenna took place in its second segment (the pedicel) densely covered with sensilla. The pedicel often is extended barlike, in several genera in Otiocerini and Nicertini it is somewhat doubled, in ♂ at the base it bears a lateral branch (the process), which is as long, wide, and with appearance of the stem itself. In the genus *Phenice* Westw. (*P. bicornis* Muir) the process appears on the scape. In the genus *Kaha* Kirk. placoid or basiconical sensilla of the second segment are transformed into very large barlike structures covering the entire segment like a brush. The segment also may be ball-like swollen (enlarged). Among structures of the head and pronotum, around the antennae a funnellike bordering is formed, which may serve for direction or enhancement of sensitive functions of the antenna, although actual functions of these structures are not known. If bordering structures are developed, then the antenna is not extended. The cranial part of the head often is strongly flattened laterally and converted into a slender plate—a septum bearing eyes and antennae. If barlike antennae are present the metopa and corypha do not extend upward and forward from the eye surface, and in case of short antennae, the metopa and corypha, or more precisely, preoculary and supraoculary areas of the head take part in the formation of bordering of the antennae so that they would be separating areas of functioning of the left and the right antennae (Nicertini and Otiocerini). The role of "reflectors," "directors," and "isolators" is performed by subantennal crests, the upper (the lateral), posterior, and lower crests of paranota. In the tribe Rhotanini subantennal crests are united with foliate crests of lateral margins of the metopa. The foliate process of the first antennal segment of *Phenice bicornis* Muir also possibly plays the role of reflector instead of the subantennal crest.

SENSORY PITS

On the head of many Derbidae, sensory pits are developed on margins of the metopa. This is the second conspicuously developed sensory complex.

The third sensory complex similar to the metopal sensory complex is situated on the wings. The pitted complex of elytra and the head are distinctly correlated; on the wings pits occur more rarely than on the head, and almost always in cases when pits are present on the metopa (except Patarini). Pits on the costal margin, which appeared in the process of evolution only once in *Cedochrea* gen. n. and since became lost, are an exception. It is possible that the imaginal sensory apparatus reached a peak in the middle steps of the evolution of the family.

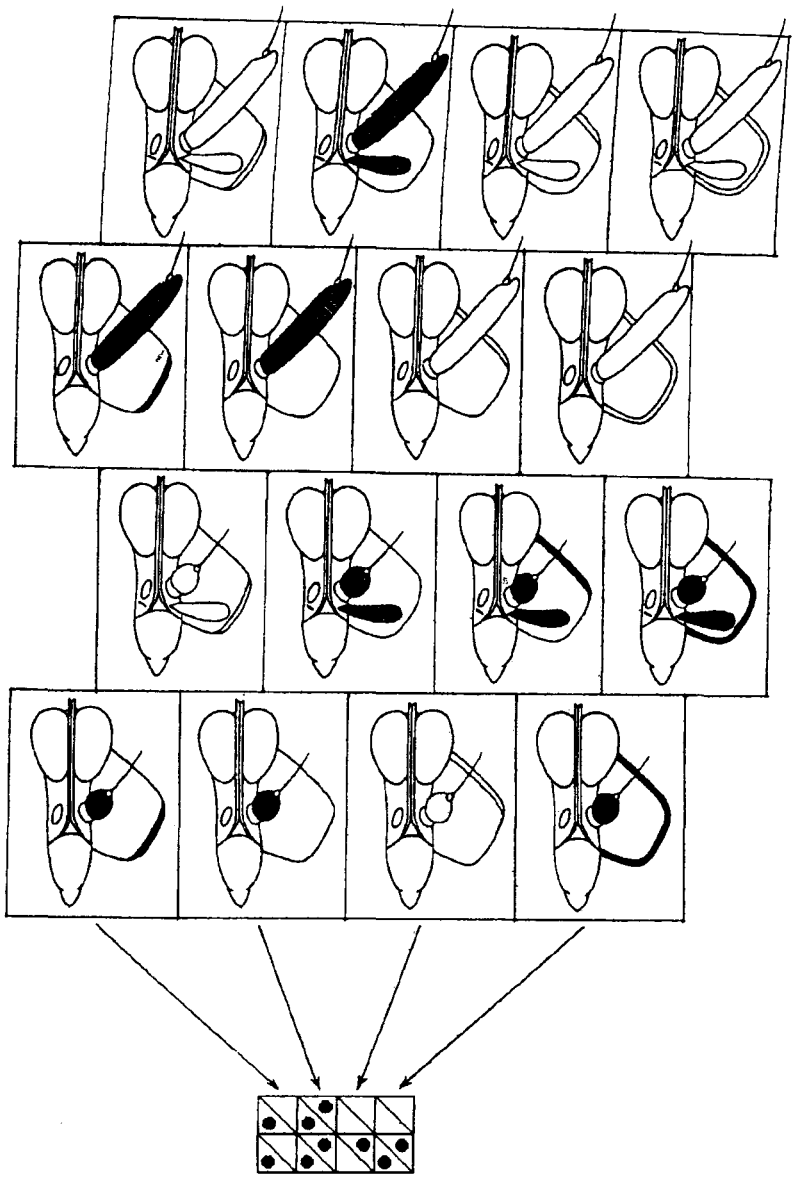

Fig. 1. Variants of structure of antennal cephalothoracic complex (morphocycle) in Derbidae (model drawings). The two upper rows represent variants with long antenna (long pedicel), the first row - variant with subantennal lobe, the second row - without lobe; two lower rows (the 3rd and the 4th) represent variants with short antenna, the 3rd row from above - with subantennal lobe, the 4th row - without subantennal lobe. The first column represents variants with crestlike posterior margin of pronotum, the second column with simple (not transformed) pronotum, the third column with crestlike lateral carina of pronotum, the fourth column with the completely developed pronotal funnel formed of lateral, posterior, and lower carinae. Variants of the complex actually found are filled with black; theoretically possible variants, but not known, are left white. Under the table of model drawings distribution of variants in a simple model is shown. The second part of the table shows the presence of individual variants of the complex by carinae.

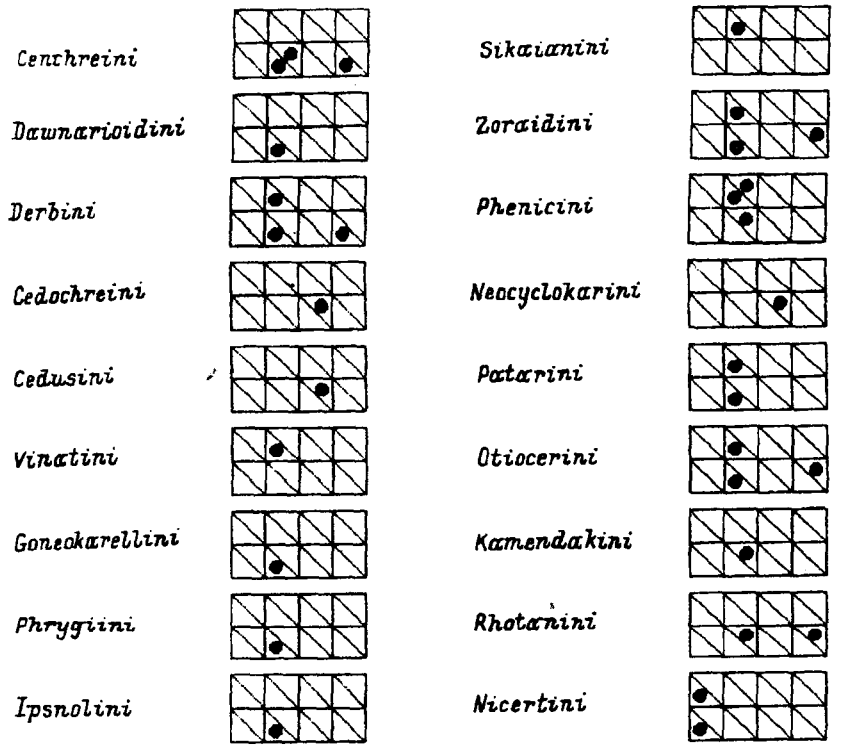

Fig. 1 (continued)

Probably the general sensory complex becomes stronger before the time in the imaginal life when mating flight with extended forewings and reduced hindwings becomes predominant, and also before the possible decline of the role of imaginal feeding

The problem of correlation between the sensoria of antennae and those of the metopa is not quite clear.

Origin and prehistory of crests. Subantennal crests occur in Cixiidae (Oecleini and Bothriocerini). Crests of the pronotum bordering antennae are known only among Derbidae.

Sensory pits. A larval system remaining in adults as a result of fetalization of imago (loss of morphological block of pits during molting into adult). In the imago pits on the metopa occur in Delphacidae, are not known in Cixiidae, and are characteristic of Meenoplidae related to Derbidae; on wings they occur only in Meenoplidae and Derbidae, and also in very remote Flatidae. Pits on the costal margins are known in *Borysthenes* Stål, from Cixiidae. The delay of formation of sensory pits until imago may be understood as parallelism but in such related groups as Derbidae and Meenoplidae this cannot be called a pure parallelism.

Here a general (ancestral synapomorphic) decline of security of the block of pits during molting into imago should be supposed.

A more complex mechanism of origin should be hypothesized concerning subantennal crests; their formation should be assigned to the common ancestor of Cixiidae and all higher Fulgoroidea. In Delphacidae such crests are not known.

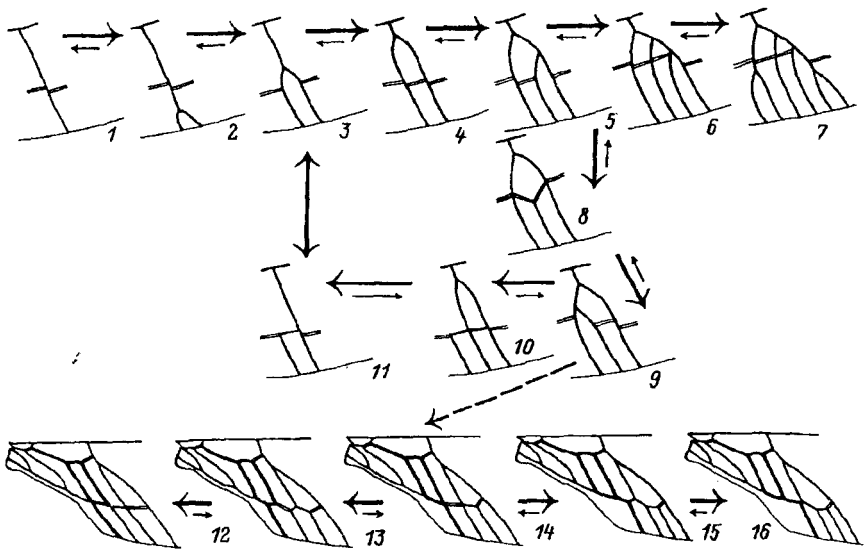

Fig. 2. Some transformations of posteromedial (*MP*) and anterocubital (*CuA*) systems of veins in forewings of Derbidae, Zoraidini (fragments of wing shown). *1-11*) Transformation series of system *MP*, *12-16*) transformation series of system *CuA*. Solid lines show longitudinal veins, doubled narrow line show transverse veins; in Figs. *12-16* system of *CuA* is shown by the widest line; large arrows show predominant direction of changes, and small arrows show a recurrent, least likely direction.

The trend toward narrowing of the metopa and their foliate crests is distinctly traced from Cixiidae, but it reaches complete development only in Derbidae.

HOMOLOGY OF VEINS *CuA* AND *MP* ON FOREWINGS

In the homologization of veins in the forewings in advanced representatives of the family an old controversy of opinions of Muir (1918) and of Synave (1973) exists. I previously supported Muir's viewpoint (Anufriyev and Yemel'yanov, 1988), but now after more careful consideration of the venation in the family I join the understanding of Synave (Fig. 2). Among recent important publications concerning the venation in the tribe Derbini (+Mysidiini), Broomfield (1985) took the side of Muir, and Dworakowska (1988) took the side of Synave. Dworakowska's understanding of *Cu-M* in the tribe Zoraidini is close to Synave's views because she accepts the two-branched *CuA*, but she understands the first cubital area as open (both branches extend to the margin of the wing). In my view the second part is not correct.

In less advanced Derbinae sensu Muir (Cedusini, Cenchreini s. str.) *CuA* certainly has a double apex and is not closed. With permanent transverse vein near the apex of the clavus connecting *CuA*2 with the marginal vein of the membrane this extraordinarily characteristic vein never becomes reduced, but it may change its direction sharply, a wrinkle indicating the place of its origin on *CuA*2 in the area of the apex of the clavus and often contiguous with it. In families close to Derbidae accessory branching of *CuA* is not characteristic, but the closed first cubital cell in form of so-called island cell, as in Kinnaridae, Meenoplidae, and Achilixiidae, is very characteristic. The closing of the fork of the first cubital vein occurs already in some Cenchreini s. str., for example, in some species of the genus *Phaciocephalus* (see in Fennah, 1950: 51)—*P. troas* Fenn. and *P. marpsius* Fenn.

The cell (field or area) closed by branches *CuA* for brevity, I propose to designate procubital cell.

The procubital cell is stably closed at the stage of Patarini trib. n. Closing (anastomosis) of veins *CuA* is very clear in tribes Patarini and Phenicini and less clear in the tribe Otiocerini. In Zoraidini, without taking into account the origin of the tribe, it can be understood differently: according to Synave, Dworakowska, etc. Arrangement of veins in this area among representatives of Phenicini (*Metaphenice* gen. n., *Phenice* Westw.), Photanini (for example, in *Decora* Damm.), and some Zoraidini (*Losbasnosia* Muir and *Neozoraida* Muir) forces us to consider that the procubital cell in these groups is closed. With this point of view the posterior branch of *MP* in most Zoraidini has a broken-line shape and would result in *CuA* mimicking its independent anterior branch; this secondary state reached a special degree of perfection in the genus *Lydda* Westw. The possibility of similar broken-line bend of vein *MP* may be seen in comparing *Paraphenice* Muir and *Metaphenice* gen. n. In *Paraphenice, MP* becomes joined to the system *CuA* through the transverse *mcu*. A similar process took place in Derbini, in which the least modified state is observed in *Pseudomysidia* Metc.

KEY TO TRIBES OF DERBIDAE

1 (20). Jugal margin of hindwings without stridulatory plate. Branches of *CuA* of forewings not anastomosing.

2 (11). Sensory pits on head and on wings absent. (Subfam. Cedusinae Em., 1992).

3 (8). Hindtibia with lateral tooth. Apical segment of proboscis 3 times or more as long as wide.

4 (7). 2nd antennal segment of usual size, its width approximately equaling length. *ScR* and *M* originating from basal cell as single stem.

5 (6). Clavus with series of oblique transverse veins masking apex of vein *Pcu*. Corypha with sharp medial longitudinal crest. Proximal procubital cell separated from apical cell by punctately anastomosing *CuA*1 + *CuA*2. ..... **Ipsnolini** TRIB. N.

6 (5). Clavus lacking accessory veins. Corypha without medial crest. Procubital cells divided by simple transverse vein. ..... **Goneokarellini** TRIB. N.

7 (4). 2nd antennal segment long, barlike. *ScR* and *M* originating from basal cell separately..... ..... **Vinatini** Em., 1992.

8 (3). Hindtibia without lateral teeth. 2nd segment of proboscis no more than twice as long as wide.

9 (10). Subantennal crests well developed. ..... **Cedusini** Em., 1992.

10 (9). Subantennal crests absent. ..... **Phrygiini** TRIB. N.

11 (2). Sensory pits present on head and forewings or only on forewings. (Subfam. Derbinae Spinola, 1839).

12 (19). Procubital cell open. 2nd segment of hindtarsi with 4 teeth.

13 (18). Corypha without sensory pits. Veins of clavus without sensory pits.

14 (15). Subantennal lobes present. ..... **Cedochreini** TRIB. N.

15 (14). Subantennal lobes absent.

16 (17). Sensory pits present only on costal vein. Ocelli absent. Clavus extended at least to half length of forewings. Costal margin of wing slightly obtusely ungulate and emarginate in area of nodule. ..... **Dawnarioidini** TRIB. N.

17 (16). Sensory pits present, except on costal, radial, and medial stems. Lateral ocelli present. Clavus occupying no more than 1/3 total length of wing. Costal margin of wing straight. . ..... **Derbini** Spinola, 1839.

18 (13). Corypha with sensory pits. Postcubitus on clavus (forewings) with sensory pits. .... **Cenchreini** Muir, 1917.

19 (12). Procubital cell closed. 2nd segment of hindtarsi with 2 teeth. .... **Nicertini** Emeljanov, 1992, STAT. N.

20 (1). Jugal margin of hindwings with stridulatory plate. *CuA* of forewings closed. (Subfamily Otiocerinae Muir, 1917).

21 (26). Stridulatory plate with concave external margin.

22 (25). Clavus closed.

23 (24). Stem *CuA* on forewings without sensory pits. ..... **Kamendakini** TRIB. N.

24 (23). Stem *CuA* of forewings with sensory pits. ..... **Rhotanini** Muir, 1917.

25 (22). Clavus open. ..... **Otioerini** Muir, 1917.

26 (21). Stridulatory plate with convex external margin.

27 (32). Second claval area on forewings with numerous sensory pits. ..... **Patarini** TRIB. N.

29 (28). *Clavus lacking sensory pits.*

30 (31). Head without sensory pits. ..... **Neocyclokarini** TRIB. N.

31 (30). Head with sensory pits. ..... **Phenicini** TRIB. N.

32 (37). Clavus open.

33 (34). Margins of eyes not close to epistomal suture. ..... **Zoraidini** Muir, 1918.

34 (33). Margin of eyes extending to epistomal suture anterior to antennae in area of bridle. .... **Sikaianini** Muir, 1917.

DESCRIPTION OF NEW TRIBES AND GENERA

Subfam. **CEDUSINAE** Emeljanov, 1992, STAT. N.

Tribe **IPSNOLINI** Emeljanov, TRIB. N.

Head (Fig. 3, *1, 2*) *without sensory pits.* Face generally diamond-shaped and truncate in dorsal

view. Corypha extended, narrowed anteriorly, with sharp medial crest. Metopa widening to clypeus, with sharp medial crest, clypeometopal border indistinct, entering metopa at obtuse angle; middle ocellus absent; medial crest of postclypeus in lower 2/3 replaced by longitudinal swelling as enlarged effaced crest. Antennae small and with rounded 2nd segment. Cheeks without crests, ocelli distant from eyes almost as far as their diameter. Eyes with emargination above antennae. Proboscis extending to medial corners (margins) of hindcoxae; last segment extended, more than 3 times as long as wide, twice length of segment preceding last segment. Pronotum (Fig. 3, *1*) with sharp crests limiting disc, with medial discal crest, postorbital crests transient into lateral crest and with collateral crests. Paranotal lobes simple, without crests and without margins turned outwardly. Mesonotum with 3 longitudinal crests. Forewings (Figs. 4, *1*; 10, *4*) without sensory pits. In area of membrane veins continue in broken line, *RP* on nodal level closer to *m*, and median with 3-4 apices. Branches of *CuA* punctately anastomose with each other, forming island cell. Clavus with series of oblique transverse veins. Apex of clavus truncate, claval vein touching *CuP*.

Hindwings (Fig. 12, *5*) without stridulatory plate. *CuA* with 3 apices, root of *CuA* toward arch reduced, secondary base of *CuA* is arched. Hindtibia with small lateral tooth in basal 1/3, on apex 7 teeth without gap, inner tooth considerably longer than other teeth. Apex of 1st hindtarsal segment with 7-8 teeth, apex of 2nd segment with 8-9 teeth, with subapical setae on inner teeth.

On abdominal tergites VI and VII of imago, larval wax-crater-like pores, one on each side of both segments, retained (Fig. 3, *4*).

♂ **genitalia** (Fig. 3, *4-10*). Pygophore slightly compressed bilaterally, in dorsal view disconnected at place of contact with anal tube, posteriorly below anal tube with pair of cuneate processes present which touch each other at their apices, upper (primarily posterior) side of process freely touching anal tube, and in ventral view with T-shaped widened upper margin of theca attached. Lateral margins of pygophore in dorsal view protruding in form of rounded lobes, ventrally pygophore with rounded obtuse process. Anterior margin of pygophore in ventral view fused with narrow sternite VIII. Anal tube extended, basally with lateral processes between pygophore and sternite VIII, at apex with rounded emargination, lower wall of tube sclerotized from apex over most length, but closer to described above lobes becoming membranous. Penis almost symmetric, structurally similar to that in Derbini and Nicertini. Upper hanging part of phallobase posteriorly deeply concave. Stem of theca moderately slender, slightly curved with concave part directed downward. Apex of penis with 2 pairs of recurrent biapicate processes. Endoconnective distributed below basal funnel, stem absent, and therefore transverse part connecting styli not connected with penis. Styli with even ventral margin protruding, apices bent inward toward to each other and 3 lobes on upper margin; basal lobe sensory, covered with robust, short-conical setae; middle and preapical lobes almost bare, bent out: middle part bent outwardly and preapical part bent out inwardly.

In the tribe one monotypic genus, *Ipsnola* Signoret, is known.

Material from the British Museum (Fig. 3) determined as *Ipsnola* sp. by I. Dworakowska was examined. She published a drawing of the forewing (Dworakowska, 1988): 2 ♂s and 1 ♀, Chile: Nuble; (72 km SE) Chillan [Chil'yan] Trankas, nr. Termas, 6.XII.84-19.II.85, S & J. Peck, Notofagus for [est], FIT, 1700 m.

Tribe **GONEOKARELLINI** Emeljanov, TRIB. N.

Head without sensory pits. Corypha transverse and without medial crest. Metopa parallel-sided and with medial crest. Antennae small, with oval 2nd segment. Lateral ocelli distant from eye as far as

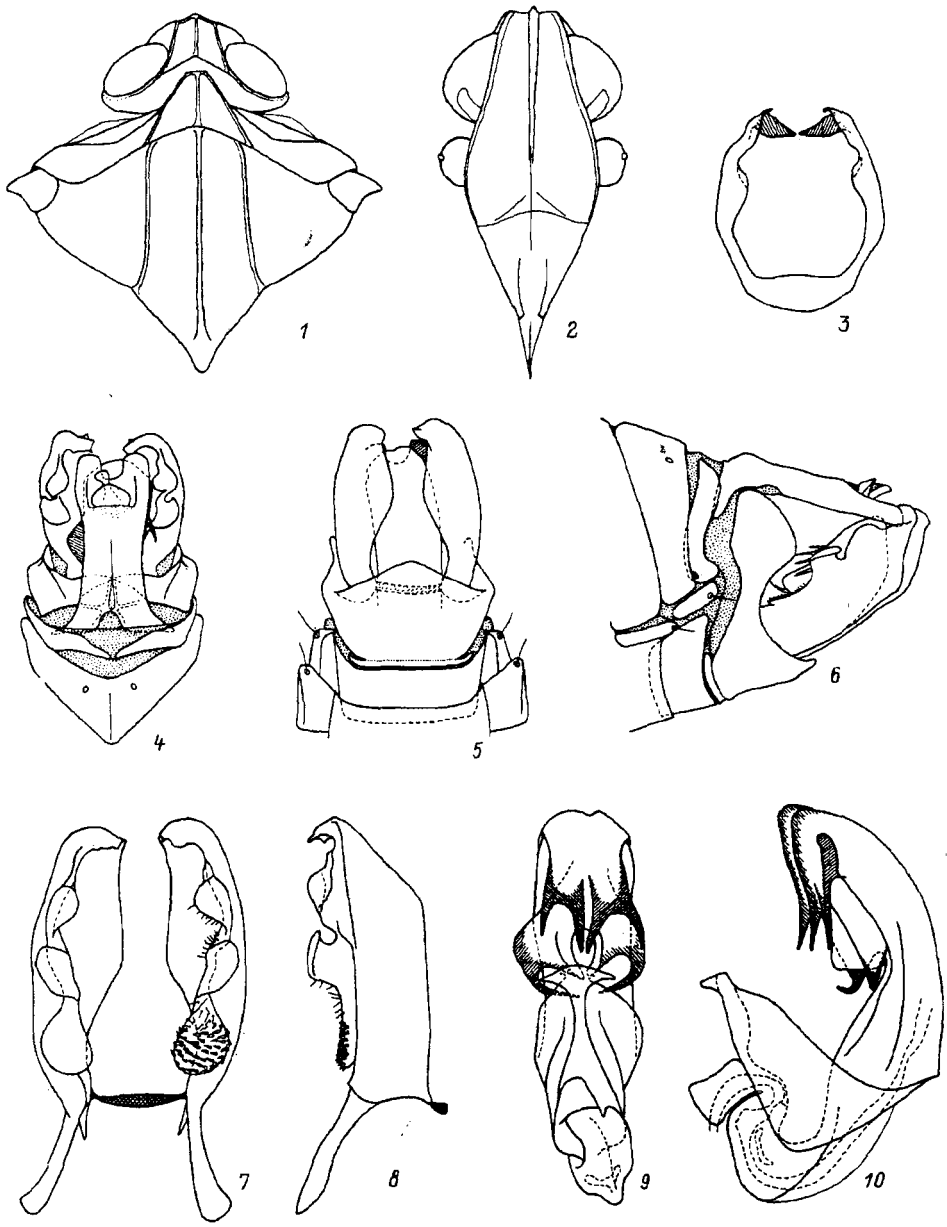

Fig. 3. *Ipsnola sextuberculata* Sign.: *1*) anterior part of body in dorsal view, *2*) head in anteroventral view (face), *3*) pygophore of ♂ in posterior view, *4*) apex of abdomen of ♂ in dorsal view, *5*) same in ventral view, *6*) same in lateral view, *7*) styli and basal plate in dorsal view, *8*) left stylus in sinistral view, *9*) penis in dorsal view, *10*) penis in sinistral view.

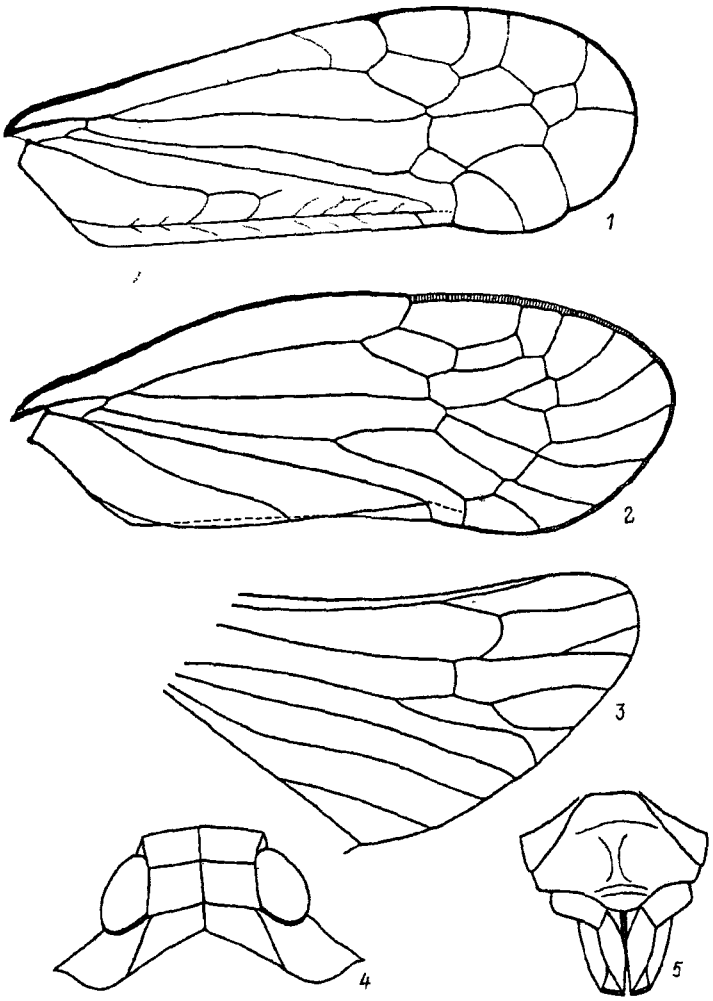

Fig. 4. *Ipsnola* Sign. and *Phrygia* Stål.: *1*) *I. sextuberculata* Sign., forewing, *2-5*) *P. fuscata* Stål., holotype; *2*) forewing, *3*) fragment of hindwing, *4*) head and pronotum in dorsal view, *5*) genital block of ♀ in ventral view.

diameter of ocellus. Eyes emarginate in ventral view above bases of antennae. Cheeks without crests. Proboscis extending to middle of hindcoxae, last segment approximately twice as long as wide. Pronotum with sharp crests restricting disc; medial crest of disc and postorbital crests transient into lateral and collateral crests. Paranotal lobes simple. Mesonotum with 3 longitudinal crests. Forewings without sensory pits. In venation of forewings (Fig. 10, *3*) resembling those of Achilidae (Plectoderini), but in the fork *CuA* anterior branch curving more and posterior branch almost straight. Hindwings (Fig. 12, *8*) without stridulatory plate. *CuA* with 3 apices, root of *CuA* reduced to arch, basal cell compacted. Hindtibia with small lateral tooth slightly proximal of middle, on apex with 6 teeth, inner tooth rather longer and slightly apart from other teeth. On apices of 1st and 2nd hindtarsal segments, 6 teeth on each and subapical setae absent.

♂ genitalia described in Fennah (1965).

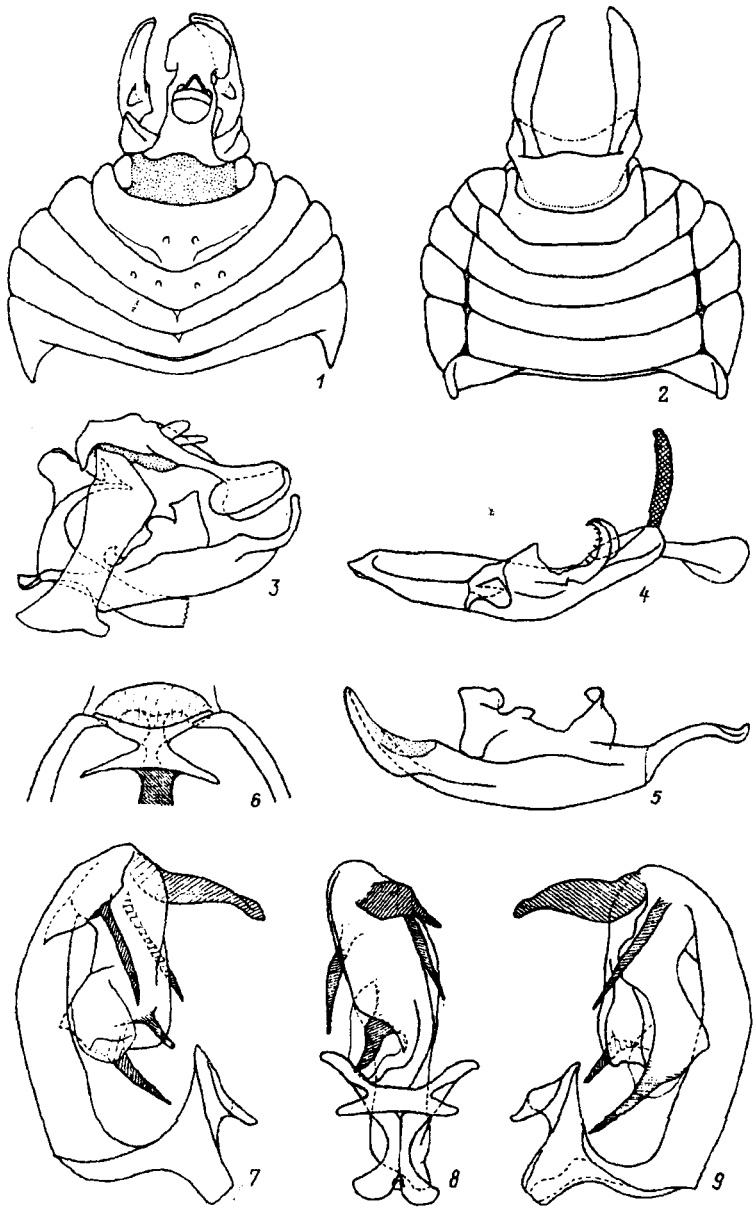

Fig. 5. *Cedochrea costaricana* GEN. ET SP. N., ♂: *1*) abdomen in dorsal view, *2*) abdomen in ventral view, *3*) genital block in lateral view from the left (apex of penis not shown), *4*) right stylus and bridge of endoconnective (basal plate) in dorsal view, *5*) right stylus in lateral view, *6*) area of articulation of pygophore, anal tube, and phallotheca, *7*) penis in dextral lateral view, *8*) penis in dorsal view, *9*) penis in sinistral view.

Tribe consisting of one monotypic genus, *Goneokarella* Fenn.

Tribe **PHRYGIINI** Emeljanov, TRIB. N.

Body robust, well sclerotized, including steeply folded tectate forewings. Anterior part of body weakly transformed and very similar in structure to body of many Achilidae (Fig. 4, *4*). Corypha transverse and contrary to the opinion of Fennah (1950b) anteriorly limited by straight, weak but distinct carina (Fig. 4, *4*). Metopa and corypha form common curved surface. Lateral crests of corypha and metopa straight, subparallel, ventrally toward clypeus distinctly converging, clypeometopal border almost straight, depressed, middle crest of head developed along entire length from occiput to head, effaced near upper margin of postclypeus. Border of cheek and bridle cristate, corresponding surfaces converging like sloped roof. Eyes lacking ommatidia in sinus above antennae; ocelli large, not contiguous with eyes. Antennae simple and small. Postclypeus cuneate, broad and short, with distinct crests. Proboscis relatively small, extending to apices of midcoxae, apical segment short, only slightly longer than wide. Head, like all other parts of body, without sensory pits. Pronotum with distinct medial and lateral crests of disc reaching posterior margin, and lateral crests distinct. Mesonotum with 3 weak, narrowly distant, subparallel crests. Forewings (Figs. 4, *2*; 10, *2*) tough, with convex veins. Costal margin subbasally slightly concave. Subcostoradius cuneate, at branching crest extending to *ScRA* and becoming lost at first branching. Vein *A*1 and its extension *A*1 + *Pcu* cristately elevated, areas bordering it connected steeply tectate, in lateral view vein sloped convexly. Median view originating from basal vein as short common stem with *ScR* (shorter than basal cell). 1st branching of radius slightly distal of 1st branching of anterior cubitus. Pattern of veins in posterior part of membrane differing from that common among Achilidae: transverse vein closer to clavus, cell posterior thereof short, and branches of *CuA* broken at intersections with transverse veins. 1st procubital cell strongly narrowed on distal end. Carinate vein *Pcu* + *A*1 touching truncate apex of clavus, in other words vein *CuP*. Hindwings (Figs. 4, *3*; 12, *9*) without stridulatory plate, with subapical doubled median. *CuA* with 3 apices, root of *CuA* toward arch weakened. Hindtibia with very small lateral tooth slightly before middle. On apex of hindtibia 5 teeth in inner group and 2 teeth in outer group, among them marginal tooth distinctly larger than all others, apex of 1st and 2nd segments with 6 teeth on each. Subapical setae absent.

In the tribe only one genus, *Phrygia* Stål., is known. It has been placed either in Achilidae (Fennah, 1950b) or in Derbidae (Fennah, 1952). Recently O'Brien (1982) again placed *Phrygia* in Achilidae without arguments supporting this. This problem will be solved more securely when genitalia of ♂s of *Phrygia* are examined.

The description was assembled by using the holotype (♀) with labels: "Brasil, Westerman," "art. ultimo rostri breve" and by specimen (♀) from the collection of the Zoological Institute of the Polish Academy of Sciences, Warsaw (ZIW) with label: "S. Catarina/Luderwaldt." The specimen with damaged body, almost entire metanotum and right half of abdomen are absent, and also right foreleg and midlegs, except coxae, are absent.

Tribe **CEDUSINI** Emeljanov

KEY TO GENERA OF TRIBE CEDUSINI

1 (2). Apex of claval vein touching margin of wing, in other words vein *A*2. Branches of stem *MA* forming anterior comb (Fig. 11, *7*). ..... ***Cedusa*** Fowler.

2 (1). Claval vein touching vein *CuP* with its apex near apex of clavus. Branches of stem *MA* forming posterior comb.

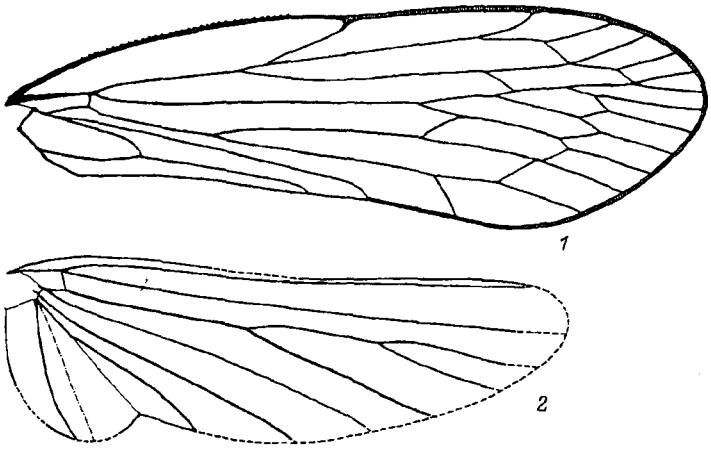

Fig. 6. *Dawnarioides sordidulus* Muir (paratype of *D. musae* Dozier, extremely worn spm.): *1*) forewing, *2*) hindwing.

3 (4). Membranes of forewings not extending posteriorly beyond line of suture (nor overlapping in resting position). Apices of terminal veins on membrane slightly bent out anteriorly (Fig. 10, *6*). ..... ***Melusa*** GEN. N. (Type species *Eocenchrea dardanus* Fennah).

4 (3). Membranes of forewings extending posteriorly beyond line of suture (overlapping with each other in resting position). Apices of terminal veins on membrane straight (Fig. 11, *14*). ..... ***Eocenchres*** Muir.

The genus *Melusa* gen. n. is monotypic: *Melusa dardanus* (Fennah), COMB. N. (=*Eocenchrea dardanus* Fennah, 1958).

Subfam. **DERBINAE** Spinola, 1839

Tribe **CEDOCHREINI** Emeljanov, TRIB. N.

Tribe including one genus, *Cedochrea* gen., with characters of tribe.

Genus ***CEDOCHREA*** Emeljanov, GEN. N.

Type species *Cedochrea costaricana* SP. N. (Figs. 5; 10, *5*; 12, *7*).

General structure of anterior part of body as in *Eocenchrea* Muir and *Cedusa* Fowler. Corypha sloped, transverse-trapezoid, anterior margin bordered from metopa by straight transverse crest. Metopa narrow, approximately 3.5-4 times as long as wide, dorsally before corypha longitudinally convex, making transition rounded, slightly widening downward, almost flat in dorsal view, ventrally with slightly concave lateral areas and sloped, broad medial crest. Postclypeus narrow, cuneate, depressed dorsally, without medial crest and ventrally with crest. Subantennal lobe approximately equidistant from eye and bridle, crest extending forward to metopa, almost horizontal, with only slightly bent downward anterior end. Antennae small, apices of 2nd antennal segments distant distinctly less than eyes, 2nd segment reverse conically truncate (with narrow base). Proboscis with short apical segment, approximately 1.5 times as long as wide, apex rounded, penultimate segment long, approximately 3 times as long as apical segment. Apex of proboscis extending approximately to posterior

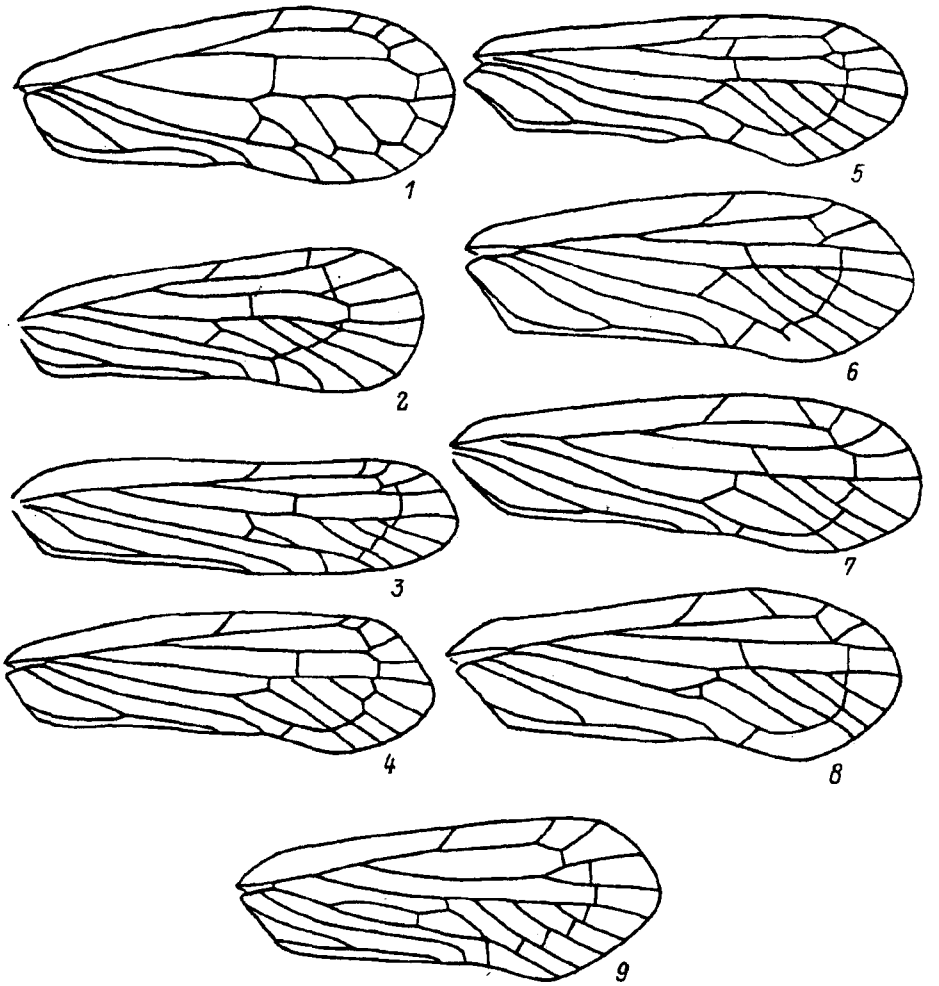

Fig. 7. *Synavea* gen. n. and *Aquelicium* Dist., forewings. *1*) *S. pusilla* V. St., *2*) *S. recurvata* V. St., *3*) *S. rusticola* V. St., *4*) *S. apicemaculata* Syn., *5*) *S. pattersoni* Muir., *6*) *S. hargreavesi* Muir, *7*) *S. hyalina* Syn., *8*) *S. radiata* Syn., *9*) *A. typicum* Dist. (*1-3* - from Van Stalle, 1983; *4* - from Synave, 1971; *5, 6* - from Synave, 1979; *9* - from Distant, 1917).

margin of hindcoxae. Pronotum short, with effaced crests, except high lateral crests, separate cell formed by paranota and subantennal lobe. Mesonotum large, convex, with poorly developed crests. Legs slender, hindtibia extended, without lateral teeth, apices with 6 teeth (1 + 5), apices of 1st and 2nd segments of hindtarsi with 5 teeth on each, subapical setae absent. Forewings (Fig. 10, *5*) extended, closely folded, with long and broad membrane, occupying almost 3/5 total length of wing. Membrane extending as far as 3/4 its length beyond apex of abdomen (in ♂). Costal vein with sensory pits approximately in basal 2/5, then anterior crest bending down and lost. *RA*, besides nodal vein *ScRA*1, with only 1 free branch *RA*2. *RP* subapical doubled, originating from common stem slightly distally of transition of anterior crest of costa into lower position. Basal cell extended, arch not distinct, but situation well determined by converging veins. Median originating from basal cell as stem common with *R* of length comparable to that of basal cell. 1st branching of *M* slightly distal of apex of clavus,

MA with 3 ends in posterior comb, *MP* doubled only subapically. *CuA* doubled at level of *R* and farther does not branch. Vein *ir* shifted to apex of stigmal cell. At nodal level transverse vein *rm* present, 2nd *rm* submarginal, extending, as well as *im*, into adjacent medial area; besides *im* present between *MA*2 and *MP* in apical 1/3 membrane at level of vein *ir*, vein *mcu* and *icua* present in middle part of membrane, extended almost like extension of one another, and marginal vein *icu* situated in basal 1/3 of membrane. Clavus of achilid type as in *Eocenchera* Muir. Venation of hindwings almost same as in *Cedusa*, but median doubled subapically (Fig. 12, *7*). Abdominal tergites VI and VII (in imago) with larval waxy craterlike pores retained. 2 pores on each side on VI and 1 pore on each side on VII (Fig. 5, *1*).

According to most characters the genus is close to *Eocenchrea*, differing primarily in presence of sensory pits on costal margin of wing and in sharply enlarged membrane.

Cedochrea costaricana Emeljanov, sp. n. (Fig. 5).

♀ not known.

♂. Head brown, more distinct depressed parts between crests darkening to dark brown: 2 spots on corypha, 2 stripes in lower part of metopa, upper part of clypeus entirely and lower part on sides of medial crest and sides of head darkened. Subantennal lobes and antennae pale. Pronotum pale, middle parts of paranota and dorsoposterior part of eyes dark brown. Mesonotum dark brown, with paler posterolateral margins. Forewings whitish, with brown spots, dark brown bases of 1st and 2nd claval cells and adjacent part of corium from apex of basal cell to first branching of radius in costal and medial areas. Brown, diffused oblique band marked from apex of clavus to nodule (vein *ScRA*1) and diffused brown spots in middle part of membrane: simple spot in area from stigmal cell to posterior branch of *M*, and oval diffused spots in both cubital areas in area of near-marginal transverse vein. Lower body and legs brown, with paler crests and margins of sclerites.

♂ **genitalia** (Fig. 5, *1-9*). Tergite VIII sclerotized only on sides, middle broad part membranous (Fig. 5, *1*). Sternite VIII narrow, fused with pygophore (Fig. 5, *2*). Pygophore in posterior view with sharp processes dorsolaterally and ventrally in middle. Anal tube with extended apical part posterior of segment XI and anal column bearing round lateral lobes bent out downward similar to those in *Cedusa quixoa* Kramer (this possibly is also a representative of the genus *Cedochrea* gen. n.). Styli approximately similar, with 3 complex processes, basal of which uncate and with steep, short setae. Penis of same type as in *Cedusa*, at base of distal segment bearing 3 processes and near apex with 2 more processes.

Length of ♂ 4.7; without wings, length 3.9 mm.

Material. Holotype: ♂, Costa Rica, H. Schmidt S. (ZIW).

Tribe **DAWNARIOIDINI** Emeljanov, TRIB. N.

Insects long winged with short body. Head small and without sensory pits. Corypha triangular, between lateral crests deeply depressed. Metopa from clypeus approximately to level of antennae narrowing to contact with lateral crests diverging only at border with corypha. Ocelli absent. Antennae small and tilted upward. Subantennal lobes small, anteriorly transient into distinct subantennal crest. Head shifted to anteroventral side and slightly extending beyond margin of thorax. Proboscis long, extending to genital block, apical segment slightly longer than wide. Pronotum wide, rather wider than head, steep, appearing displaced by mesonotum. Single postorbitolateral crest of pronotum sharp, disc with distinct medial crest, but not sharply separated from parapsidal areas. Large flat paranotal lobes

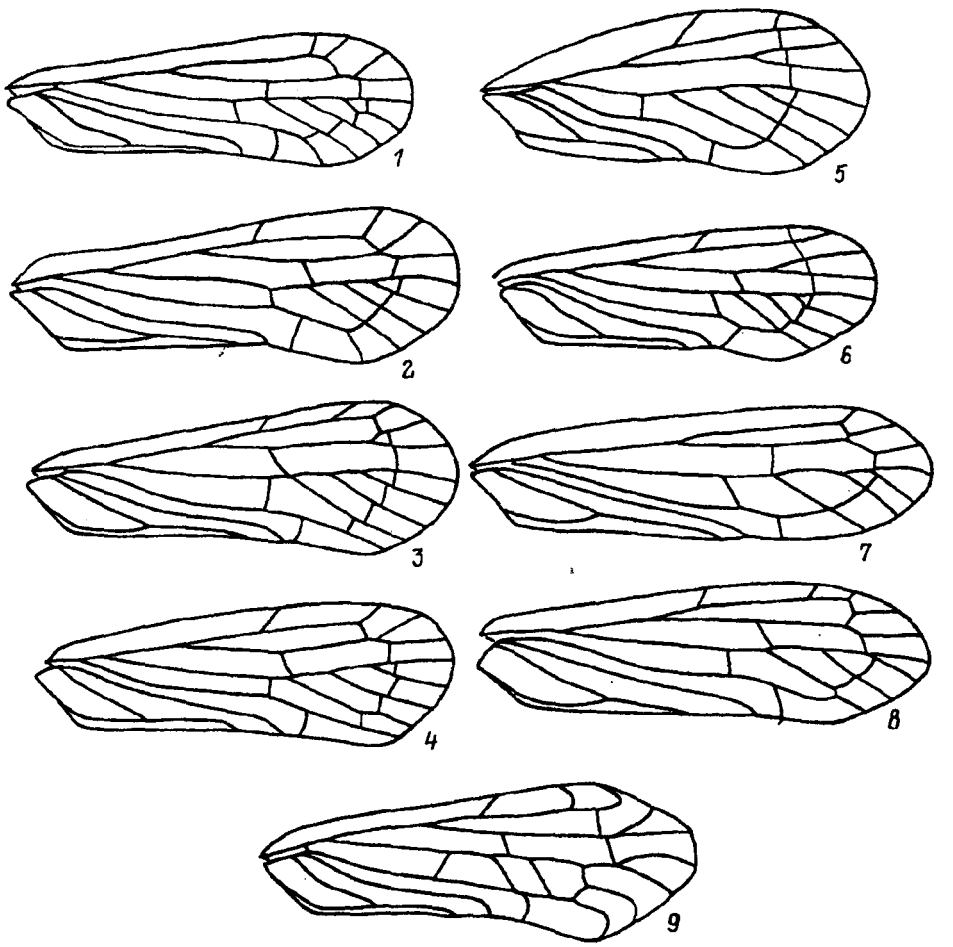

Fig. 8. *Anapatara* gen. n. and *Patara* Westw., forewings: *1*) *A. nigeriensis* Syn., *2*) *A. costalis* Syn., *3*) *A. lootensi* Syn., *4*) *A. kivuensis* Syn., *5*) *A. trispinosa* Syn., *6*) *A. monstruosa* Syn., *7*) *A. quadrispinosa* Syn., *8*) *A. eloides* Muir, *9*) *P. guttata* Westw. (*1* - from Synave, 1971; *2, 5-7* - from Synave, 1979; *3, 4, 8* - from Synave, 1973; *9* - from Fennah, 1952).

directed forward and downward, in lateral view only lateral margin visible (in other words, margin originally posterior). Mesonotum large, strongly convex, with depression of parapsidal grooves.

Forewings (Fig. 6, *1*) with sensory pits only on costal margin, anterior margin slightly obtuse, ungulately concave in area of nodus. Longitudinal veins straight, transverse veins oblique, mainly slanted-longitudinal. In resting position rolled along longitudinal axis (O'Brien, 1982). *RA* with 2 postnodal branches, and *RP* also with 2 postnodal branches. Median originating from basal cell at one point with *R* or as common short stem, *MA* with 4 ends in posterior comb, and *MP* with 2 ends. *CuA* with 2 ends, precubital cell open, postclaval transverse vein oblique, slanted toward apex of wing or recurrent to apex of clavus. Clavus closed, and claval vein meeting margin of wing (*A*2).

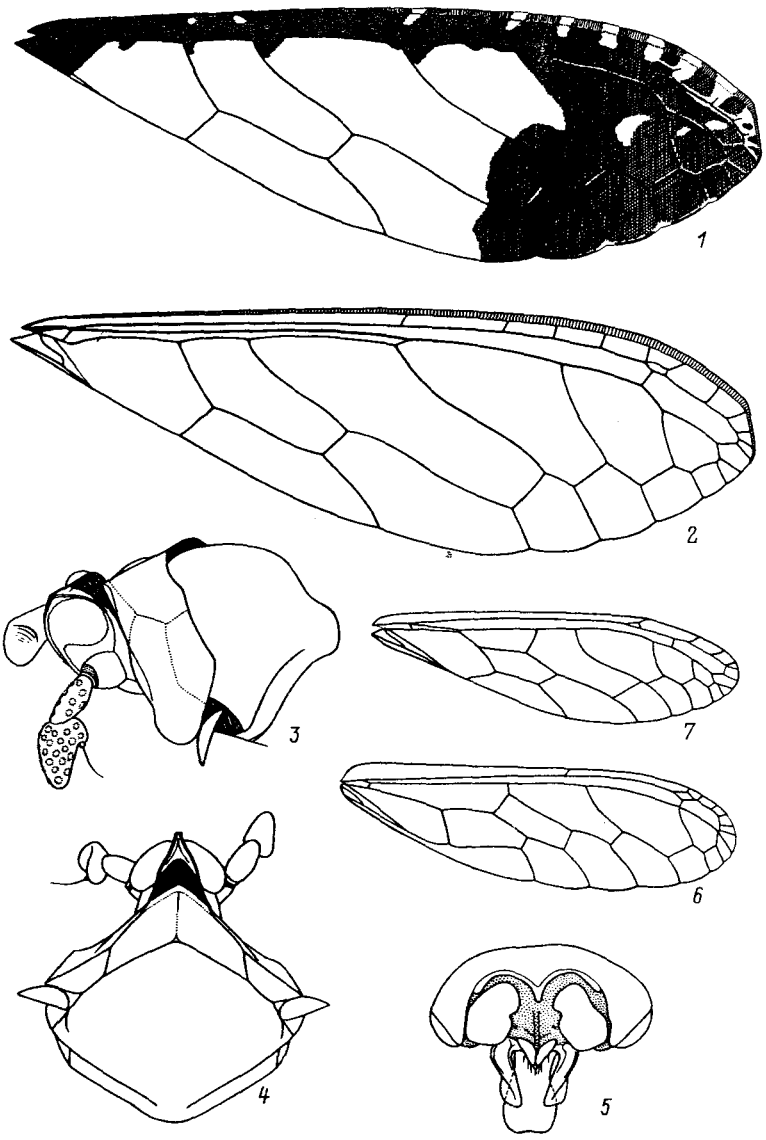

Fig. 9. Representatives of tribe Sikainanini: *1-5*) *Ceropupa trismegista* gen. & sp. n.: *1, 2*) wing (*1* - pattern, *2* - venation); *3, 4*) anterior part of body (*3* - in laterodorsal view, *4* - anterodorsal view); *5* - ovipositor; *Muiria stridula* Kirk. (after Kirkaldy, 1907, with different reconstruction of clavus venation); *7*) *Distantinia nigrococuminis* Muir (from Muir, 1917 with modifications, veins in base of wing reconstructed).

Hindwings (Fig. 6, *2*) narrow, extended, without transverse veins (*rm* and *mcu* absent), and *R* and *M* not branching. *CuA* with 3 apices, *A*2 extending posterior to 2nd anal fold, arcuate, reaching margin of wing. Stridulatory plate absent. (1 poorly preserved spm. with strongly worn wings was examined, paratype of *Dawnarioides musae* Dozier.) Hindtibia without lateral teeth, on apex with 6 teeth, large apical tooth strongly distant, marginal inner tooth smaller than preceding tooth and above it. 1st and 2nd tarsal segments with 5 teeth each, teeth with no apical setae.

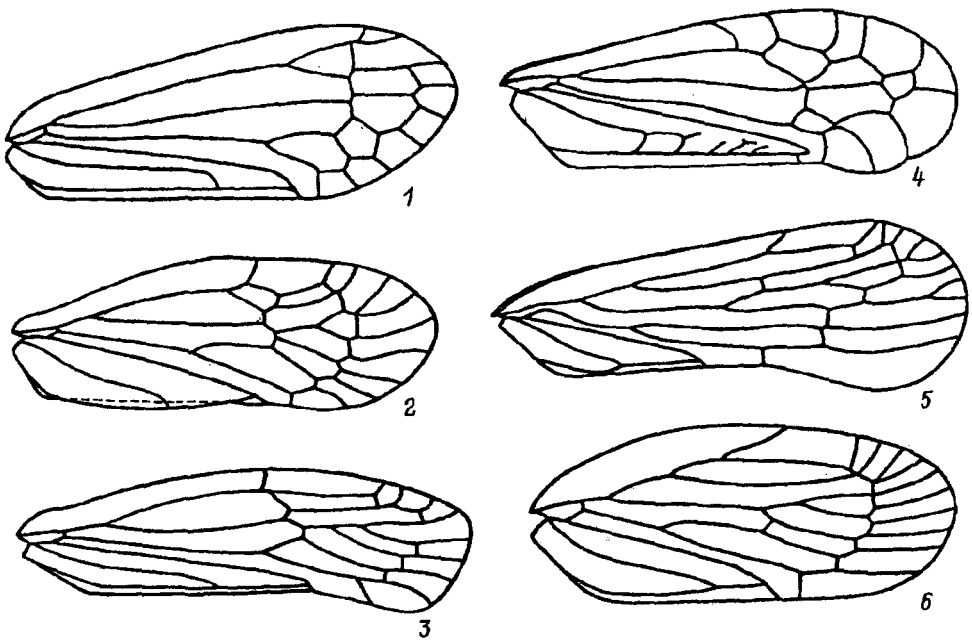

Fig. 10. Representatives of Cedusinae (*1-4, 6*) and Derbinae (*5, 7*), forewings. *1*) *Vinata operosa* Walker (from Walker, 1857), *2*) *Phrygia fuscata* Stål (spm. from ZIW), *3*) *Goneokarella maculivensis* Fenn. (from: Fennah, 1952); *4*) *Ipsnola sextuberculata* Sign. (example from British Museum), *5*) *Cedochrea costaricana* Em., holotype, *6*) *Melusa dardanus* Fenn. (from Synave, 1973).

The tribe includes 2 Neotropical genera, *Dawnarioides* Dozier and *Neodawnaria* O'Brien.

Subfam. **OTIOCERINAE** Muir, 1917

Tribe **KAMENDAKINI** Emeljanov, TRIB. N.

Metopa from clypeus to lower margins of eyes narrowing and deeply depressed. Lateral crests shifted almost adjacent to each other, separated only by shallow groove. Corypha broad, lateral and anterior margins forming somewhat common arch, margins of corypha in anterolateral view extending above eyes. Lateral crests of metopa and corypha with chain of sensory pits. In lateral view metopa convex, forming sharp angle (straight, obtuse, or acute) with straight horizontal corypha; latter deeply depressed, anteriorly and laterally limited by high crest with sensory pits, posteriorly open in direction of pronotum. Lateral crests of metopa connected by ends at angle connected with sharp subantennal crests. Lateral crests of postclypeus continuing crests of metopa, in upper half high, and surface of clypeus depressed, in lower half crests and becoming medium. Eyes and antennae relatively small, eyes with facetless area under antennae. Ocelli absent. Pronotum simple, with developed lateral and sharp medial crests, disc not developed. Mesonotum convex, with 3 blunt longitudinal crests. Forewings (Fig. 11, *9*) extended, parallel-sided or widened to apex. Clavus closed. Costal margin in basal half with sensory pits, distally cristate, bent out and upward, radial vein cristate, at 1st branching both branches less convex and not differing in this respect. Generally venation as in tribe Otiocerini, but clavus closed and claval vein meeting apex, immediately beyond apex of clavus with short postclaval transverse vein. Hindwings (Fig. 13, *4*) with stridulatory plate, *CuA* with 3 apices. Hindtibia without lateral teeth, on apex largest external tooth separated by gap from 4 teeth of external row. On apex of 1st hindtarsal segment 6 teeth and on apex of 2nd segment 5 teeth.

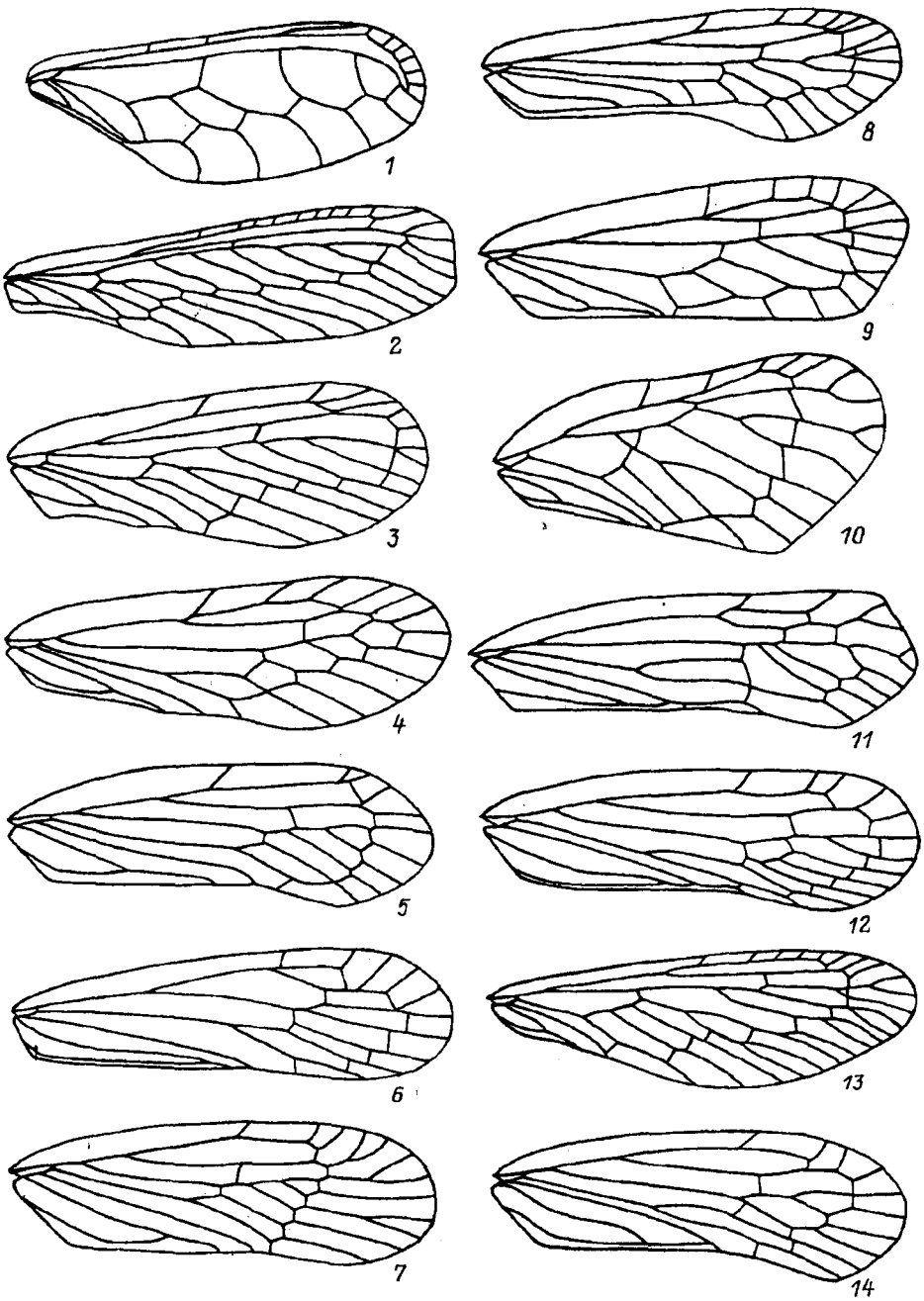

Fig. 11. Forewings, examples of wings from different tribes: *1*) *Sikaiana lycotas* Fenn. (Sikaianini), *2*) *Zoraida angolensis* Syn. (Zoraidini), *3*) *Phenice fasciolata* Boh. (Phenicini), *4*) *Neocyclokara* sp. (Neocyclokarini), *5*) *Synavea apicemaculata* Syn. (Patarini), *6*) *Cenchrea dorsalis* Westw. (Cenochreini), *7*) *Cedusa medleri* Syn. (Cedusini), *8*) *Oticerus regalis* Fenn. (Oticerini), *9*) *Kamendaka izzardi* Syn. (Kamendakini), *10*) *Rhotana lalage* Venn. (Rhotanini), *11*) *Epotioceras flexuosus* Uhl. (Nicertini), *12*) *Herpis* sp. (Cenchereini), *13*) *Pseudomysidia fuscovaria* Netc. (Derbini), *14*) *Eocenchrea maorica* Kirk. (Cedusini). (*1, 10* - from Fennah, 1969; *2, 3, 5, 7, 9, 14* - from Synave, 1973; *6* - from Westwood, 1842; *8* - from Fennah, 1952; *13* - from Broomfield, 1985; *4, 11, 12* - original drawings).

Tribe consisting of one genus, *Kamendaka* Distant, with subgenera *Eosaccharissa* Kirkaldy and *Nicertoides* Matsumura; descriptions by Kirkaldy and Matsumura of inner structure of genus have never been revised. The names *Chaprina* and *Tapoosa* Distant are considered as synonyms of the genus *Eosaccharissa*.

Tribe **PATARINI** Emeljanov, TRIB. N.

Metopa strongly compressed bilaterally, its lateral crests shifted together and divided only by groove. Sensory pits absent. Corypha triangular, without sensory pits. Antennae with enlarged 2nd segment, often robust and strongly extended, larger in ♂s. Eyes with concave anterior margin against bases of antennae. Postclypeus convex, with weak lateral crests. Pronotum short, without differentiated disc, with distinct middle and humeral crests, but without any specific structures. Mesonotum large, convex, without distinct crests. Forewings (Figs. 7; 8; 11, *5*) with closed clavus and closed procubital cell. On clavus with vein *Pcu* completely densely covered with sensory pits, on stem of *ScR* sensory pits also present, sometimes few. Hindwings (Fig. 13, *2*) with stridulatory plate having convex outer margin, nodal vein not developed. Hindtibia without lateral teeth, apex with even row of 6 teeth, on apices of 1st and 2nd segments of hindtarsi 5-6 teeth each.

KEY TO GENERA OF TRIBE PATARINI TRIB. N.

1 (4). Anterior cubitus of forewings doubled, closing anterior cubital area of one of 2 cells.

2 (3). Anterior cubitus doubled basad of claval fork. Anterior cubital area formed of 2 cells..... ..... ***Aquaelicium*** Distant.

3 (2). Anterior cubitus doubled near apex of clavus rather more distally than claval fork. Anterior cubital area formed of 1 cell..... ..... ***Synavea*** gen. n. (Type species *Patara apicemaculata* Synave, 1971).

4 (1). Anterior cubitus not branching and therefore without anterior cubital area (cell).

5 (6). Anterior vein *MA* beginning more distally than adjacent submarginal transverse veins. Usually transverse vein *mcu* connecting both stems to their branching is present..... ..... ***Patara*** Westwood.

6 (5). Anterior vein *MA* beginning more proximally than adjacent submarginal veins, almost always after this fork being also crossed by its own submarginal transverse vein..... ..... ***Anapatara*** GEN. N. (Type species *Patara nigeriensis* Synave, 1971).

The genus *Synavea* gen. n. includes the following species (all originally described in the genus *Patara*): *S. apicemaculata* Syn., 1971, COMB. N.; *S. pattersoni* Muir, 1918, COMB. N.; *S. hargreavesi* Muir, 1930, COMB. N.; *S. hyalina* Syn., 1979, COMB. N.; *S. radiata* Syn., 1979, COMB. N.; *S. pusilla* V. St., 1983, COMB. N.; *S. recurvata* V. St., 1983, COMB. N.; *S. rusticola* V. St., 1983, COMB. N.; *S. minazi* M. Wils., 1987, COMB. N.; *S. chambeziensis* M. Wils., 1987, COMB. N.; and also probably *S. albibaltea* V. St., 1986, COMB. N.; *S. compaginata* V. St., 1986, COMB. N. The genus *Anapatara* GEN. N. includes species, described in the genus *Patara*, as follows: *A. nigeriensis* Syn. 1971, COMB. N.; *A. costalis* Syn., 1979, COMB. N.; *A. lootensi* Syn. 1973, COMB. N.; *A. kivuensis* Syn., 1973, COMB. N.; *A. trispinosa* Syn., 1979, COMB. N.; *A. monstruosa* Syn., 1979, COMB. N.; *A. acantha* V. St., 1985, COMB. N.

Tribe **NEOCYCLOKARINI** Emeljanov, TRIB. N.

Metopa extended, higher of subantennal lobes narrowed and troughlike. Corypha trapezoid,

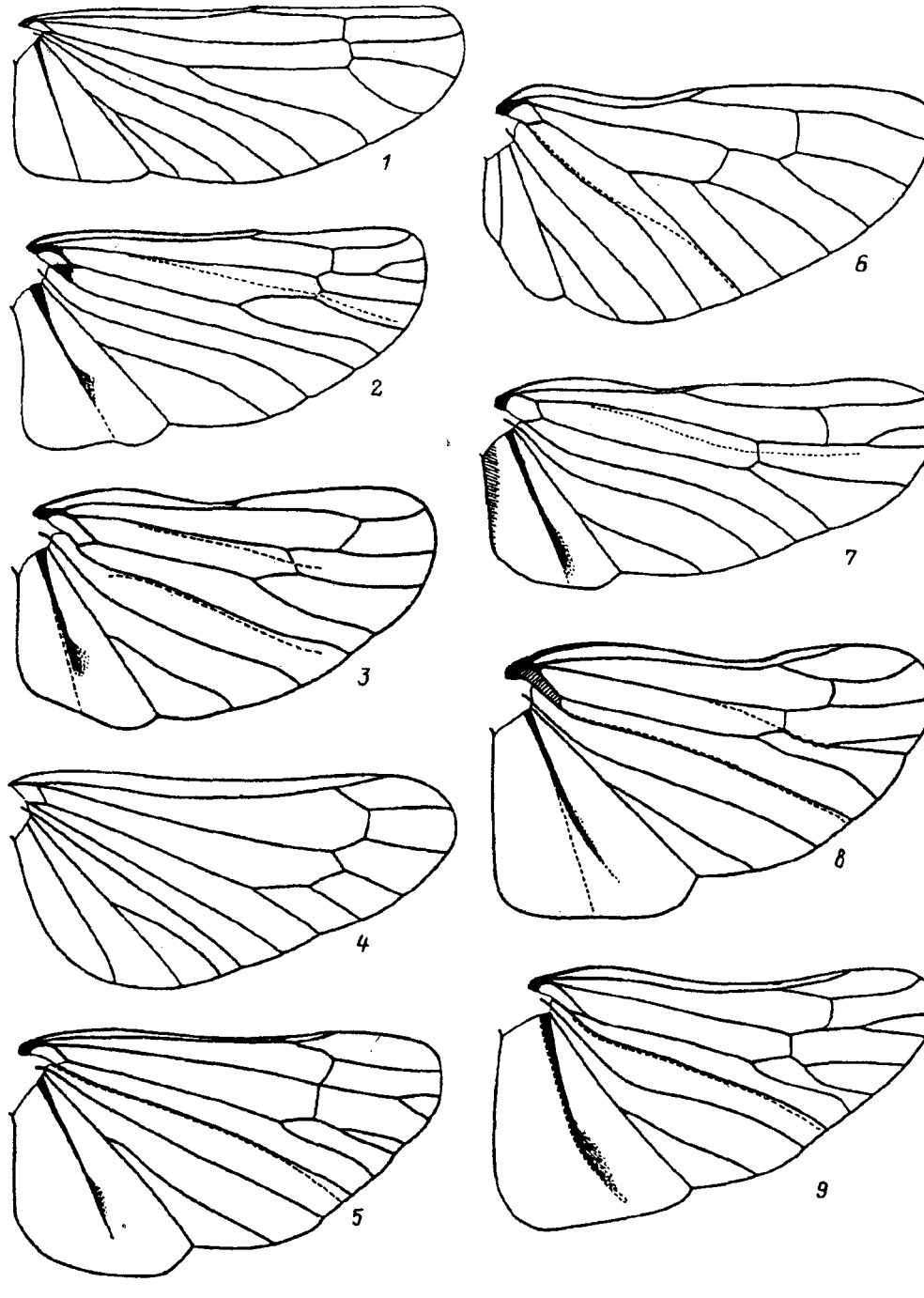

Fig. 12. Hindwings of Cedusinae and Derbinae: *1*) *Epotiocerus flexuosus* Uhl., *2*) *Vekunta malloti* Mats., *3*) *Cedusa ussuriensis* Anufr., *4*) *Vinata operosa* Walk., *5*) *Ipsnola sextuberculata* Sign., *6*) *Mysidia* sp., *7*) *Cedochrea costaricana* Em., *8*) *Goneokarella maculivenis* Fenn., *9*) *Phrygia fuscata* Stål (spm. from ZIW). (*4* - from Walker, 1857).

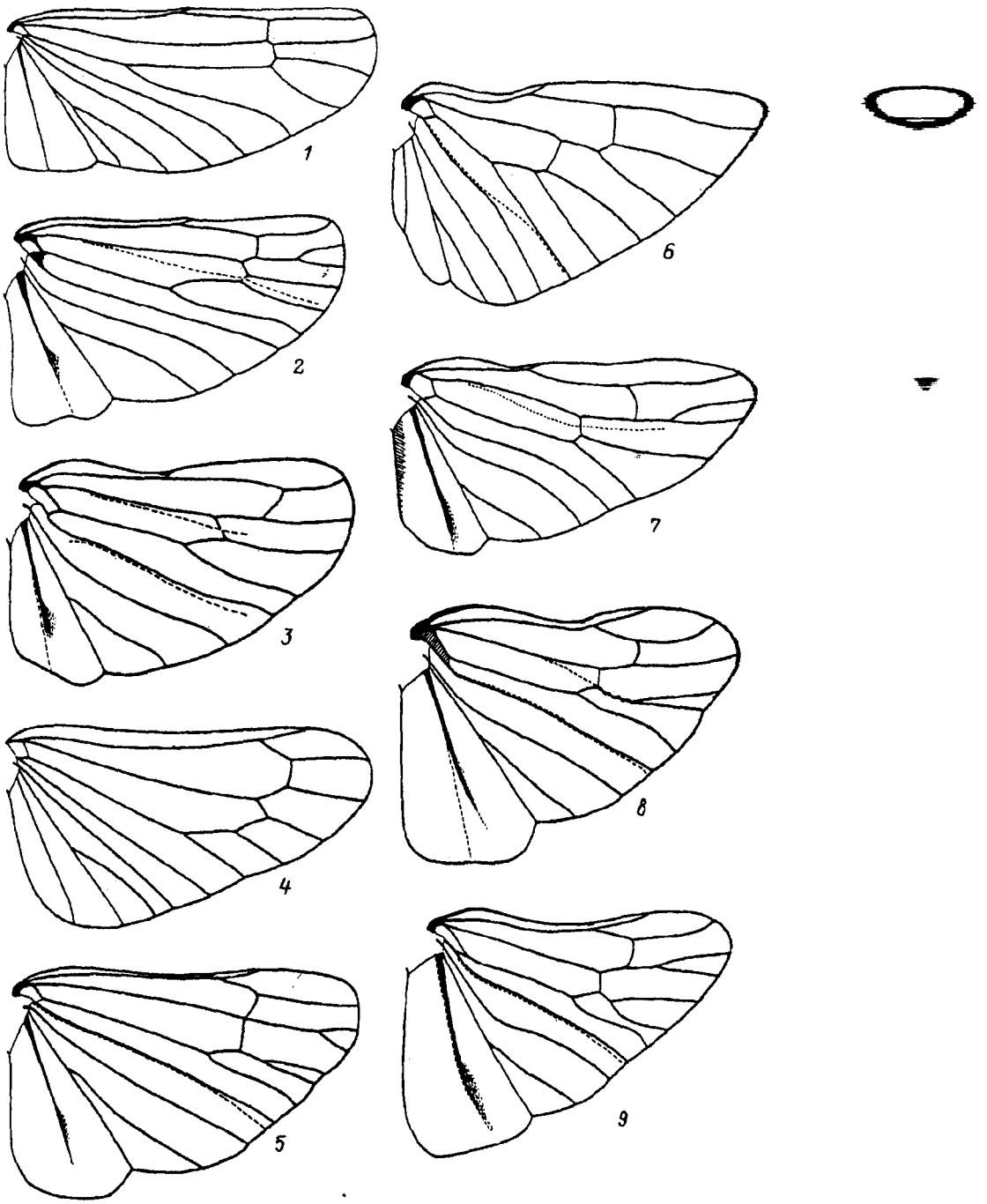

Fig. 12. Hindwings of Cedusinae and Derbinae: *1*) *Epotiocerus flexuosus* Uhl., *2*) *Vekunta malloti* Mats., *3*) *Cedusa ussuriensis* Anufr., *4*) *Vinata operosa* Walk., *5*) *Ipsnola sextuberculata* Sign., *6*) *Mysidia* sp., *7*) *Cedochrea costaricana* Em., *8*) *Goneokarella maculivenis* Fenn., *9*) *Phrygia fuscata* Stål (spm. from ZIW). (*4* - from Walker, 1857).

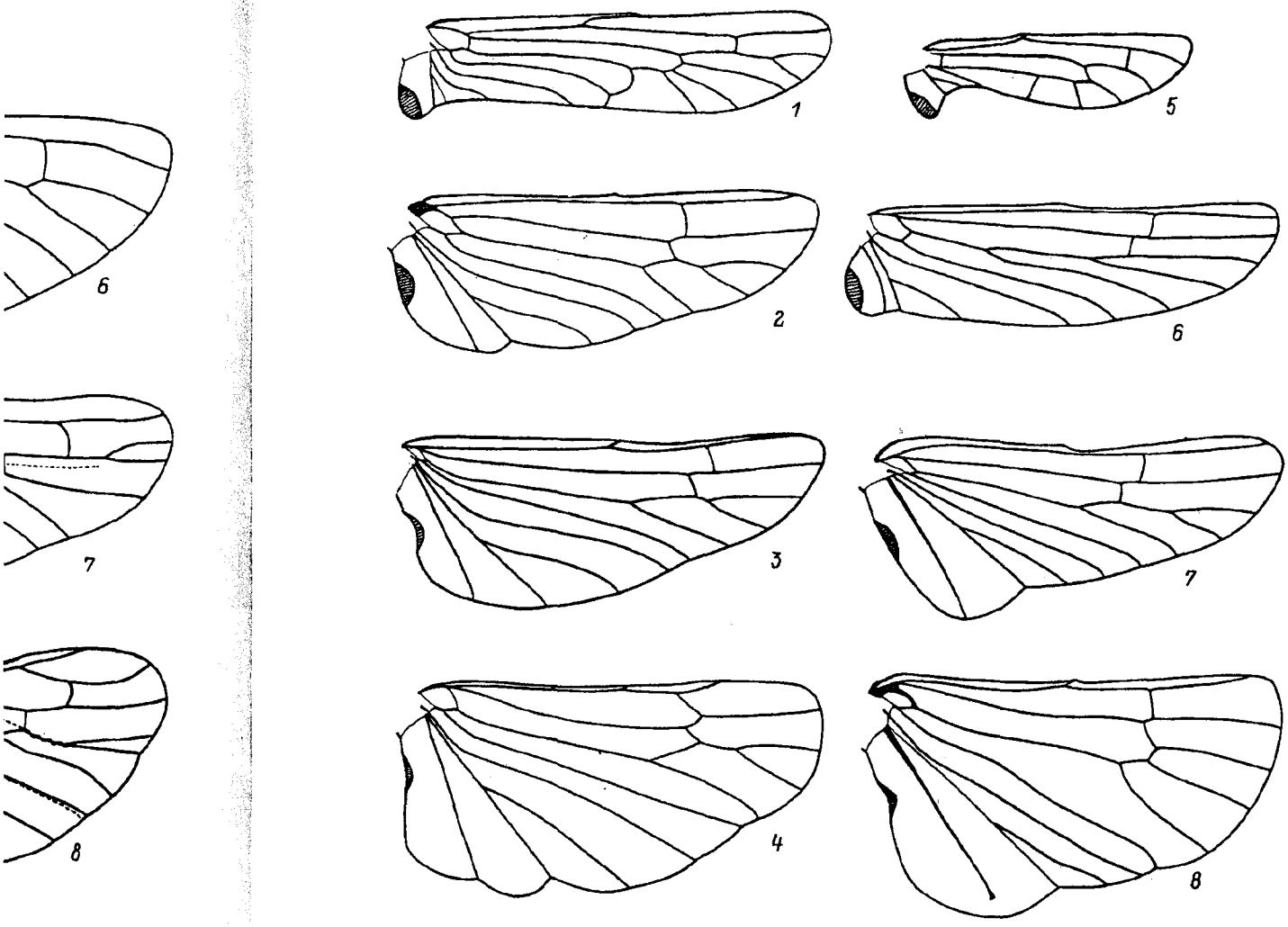

Fig. 13. Hindwings of Otiocerinae: *1*) *Zoraida horishana* Mats.; *2*) *Patara* sp.; *3*) *Pyrrhoneura citharista* Kirk., 1907; *4*) *Kamendaka ugandensis* Syn., 1973; *5*) *Muiria pulchra* Muir, 1928; *6*) *Paraphenice squamifer* Hees, 1925; *7*) *Neocyclokara* sp.; *8*) *Rhotana* sp. (*3* - from Kirkaldy, 1907; *4-6* - from Synave, 1973).

separated from metopa by sharp crest. Lateral crests of corypha and metopa without sensory pits and sharp. Antennae with small rounded 2nd segment. Cheeks with subantennal crest. Eyes round, with area lacking ommatidia under antenna. Ocelli absent. Postclypeus large, extended, with sharp lateral crests. Pronotum short, with well developed disc and obtuse angularly extended posterior margin, middle and lateral crests of disc distinct, humeral crests sharp. Head considerably narrower than pronotum. Mesonotum convex, with 3 blunt, straight, subparallel close crests. Forewings (Fig. 11, *4*) extended, widened to membrane, clavus closed, procubital cell closed. Sensory pits present only on costal margin. Hindwings (Fig. 13, *7*) with stridulatory plate, nodal vein not developed and *CuA* with 3 apices. Hindtibia without lateral teeth, apex with very large outer tooth separated by deep emargination, from remaining row of 3 teeth; on apex of 1st segment of hindtarsi 5 teeth, and on apex of second segment 4 teeth.

The tribe includes one genus, *Neocyclokara* Muir.

Tribe **PHENICINI** Emeljanov, TRIB. N.

Metopa narrow, extended, lateral crests bearing sensory pits. Corypha trapezoid, narrowed anteriorly, lateral margins also bearing sensory pits, separated from metopa by distinct, weak crest. Antennae with slightly enlarged, ovate or cylindrical 2nd segment. Cheeks with subantennal crest or rudiment thereof. Eyes reniform and with emargination above antennae. Postclypeus extended, with sharp lateral and middle crests. Pronotum short, without separate disc, tectate in dorsal view, with distinct middle and humeral crests, without specific structures. Mesonotum large, convex, without distinct crests. Forewings with closed clavus and closed procubital cell, sensory pits present only on costal margin. Hindwings with stridulatory plate, nodal vein not developed, *CuA* with 3 apices. Hindtibia without lateral teeth, apex with large outer tooth developed, separated by deep gap from basal row of 4 teeth, apex of 1st tarsal segment with 6 teeth, apex of 2nd segment with 4-5 teeth.

KEY TO GENERA OF TRIBE PHENICINI TRIB. N.

1 (4). Subantennal lobe absent. Transverse vein *mcu* attached to stem of *MP* before its branching.

2 (3). Apex of forewing broadly rounded, terminal margin convex. Base of clavus obliquely truncate. ..... ***Phenice*** Westwood.

a(b). 1st antennal flat. Base of *MP* and last branch of *MA* subbasally not connected with transverse vein. ..... ***Phenice*** s. str.

b(a). 1st antennal segment with long process. Base of *MP* and last branch of *MA* subbasally connected by transverse vein. .... ***Diplophenice*** subgen. n. (Type species *Phenice bicornis* Muir, 1930).

3 (2). Apex of forewing narrowly rounded, terminal margin straight and concave. Base of clavus truncate, approximately straight. ..... ***Metaphenice*** gen. n.

4 (1). Subantennal lobe well developed. Transverse vein *mcu* attached to posterior branch of *MP* after division into 2 branches. ..... ***Paraphenice*** Muir.

The genus *Metaphenice* includes the following species: *M. stellulata* (Boh.), COMB. N., *M. medleri* (Syn. 1979), COMB. N. (*Phenice medleri* Syn.), *M. pongwei* M. Wils., 1987, COMB. N. (*Phenice pongwei* M. Wils.), *M. brocha* V. St., 1986, COMB. N. (*Phenice brocha* V. St.). The subgenus *Diplophenice* SUBGEN. N. of the genus *Phenice* is monotypic. The tribe possibly includes also the genus *Equirria* Distant. described from the Seychelles and *Fescennia* Stål from Madagasar Island.

Tribe **ZORAIDINI** Muir, 1918

The tribe may be divided into 3 subtribes, differences among which are shown in the following key.

1 (2). *MA* of forewings bearing 8 simple branches in posterior comb. Subantennal lobes present. Hindwings relatively large and not narrowed. ..... **Zeugmatina** SUBTR. N.

2 (1). *MA* of forewings bearing 4-5 branches in posterior comb, branches simple or only first

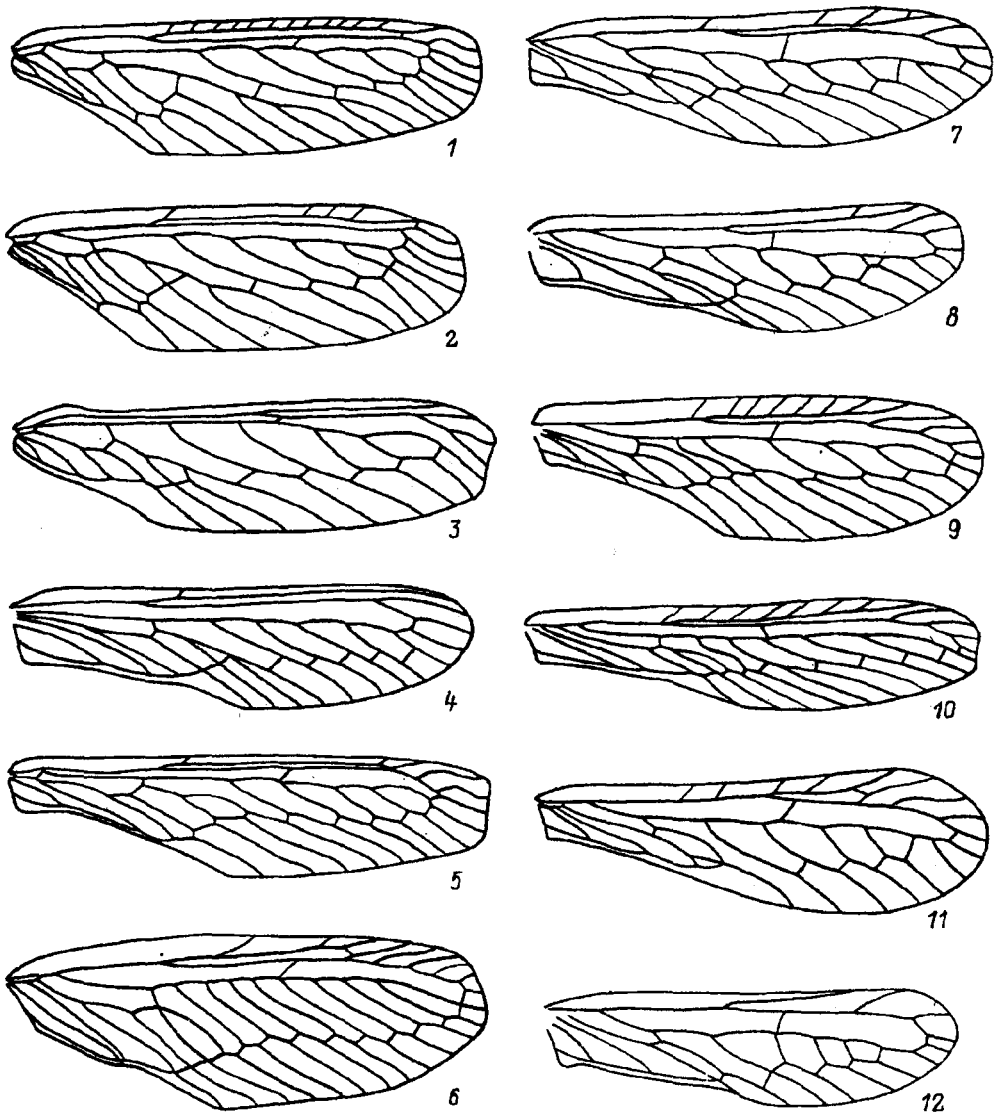

Fig. 14. Forewings of Zoraidini: *1*) *Neozoraida maculicostata* Muir, *2*) *N. ugandensis* Dist., *3*) *Peggia nitida* Stål, *4*) *Shirakiana infumata* Mats., *5*) *Zoraida horishana* Mats., *6*) *Zeugma* sp., *7*) *Lyddastrombus mayumbensis* Syn., *8*) *Zorabana maculata* V. St., *9*) *Pamendanga neavei* Sist., *10*) *P. neolei* Dist., *11*) *Proutista fritillaris* Boh., *12*) *Shizuka formosana* Mats. *1, 2, 7, 9-11*) From Synave, 1973; *3*) from Muir, 1917; *4, 12*) from Matsumura, 1914; *8*) from Van Stalle, 1983.

branch present (*Neozoraida* Muir and *Neocamma* Mel.), or one second branch forked. Hindwings smaller and narrower or reduced to stridulatory appendage.

3 (4). Ovipositor developed normally. ..... **Zoraidina** Muir.

4 (3). Ovipositor reduced. ..... **Lyddina** SUBTR. N.

The tribe Zeugmatina includes one genus, *Zeugma* Westw. The subtribe *Lyddina* includes genera *Lydda* West., *Helcita* Stål, *Proutista* Kirk., *Pamendanga* Distr., *Diostrombus* Uhl., *Shizuca* Mats., *Neoproutista* Yang & Wu, *Formodanga* Yan & Wu, and *Lyddastrombus* V. St., possibly also *Acanthocerana* Muir and some other genera with similar venation and structure of ovipositor not described.

Tribe **SIKAIANINI** Muir, 1917

Genus ***Ceropupa*** Emeljanov, GEN. N.

Type species *Ceropupa trismegista* sp. n. (Fig. 9, *1-5*).

Genus similar to *Leomelicharia* Muir. Vertex relatively short, triangular, posteriorly rectangularly rounded and emarginate. Metopa narrow-linear, lateral crests divided by narrow groove, preocular and supraocular areas narrow. Antennae extraordinarily peculiar: 1st segment small, annulate, large 2nd segment divided by oblique constriction into 2 segments (Fig. 9, *3*), proximal segment (IIa) fusiform and distal segment (IIb) reniform, most of body consisting of large subapical process of upper margin, 3rd segment with seta resting on side on lower concave side of segment IIb, not far from base. Medial surface of segment IIb concave. Proboscis very short and broad. Pronotum rather large, with weak carinae restricting disc and lateral lobes of upper side, middle crest of disc distinguished only in middle half. Mesonotum large, swollen, without distal crests. Forewings most specialized in tribe (Fig. 9, *2*), in shape most similar to wings of genus *Distantinia* Muir (Fig. 9, *7*) and *Leomelicharia* Muir. Unlike in the first species vein *R* (*ScR*) not branching, and vein *CuA* adjacent to vein *mcu*, which also situated adjacent to median, therefore subbasal cell becoming completely lost. This cell is still retained in *Distantinia*. Another peculiarity of the new genus common with *Distantinia* is complete fusion of part of vein extending apex of clavus to margin of wing. Claval veins barely developed. Hindwing well diminished, as in *Muiria*. Ovipositor of ♀ underdeveloped (Fig. 9, *5*).

Ceropupa trismegista Emeljanov, SP. N. (Fig. 9, *1-5*).

Head, including antennae, dark brown to black and proboscis white. Pronotum dark brown, crests slightly paler. Mesonotum mainly brown, middle part before scutellum darker and scutellum white. Metanotum brown. Thorax in ventral view brown and red-brown. Legs pale.

Forewings (Fig. 9, *1, 2*). Weakened costal vein red, posterior of it anterior margin as far as medial vein brown, darkened, toothlike darkening extending posteriorly along veins obliquely from anterior tuft (2 branches of *CuA* and *MP*). Transverse veins of costal area white, in basal part of costal area against cubital vein 2 white spots present. Base of wing to half length of clavus entirely darkened. Apical part of wing slightly before fork *MA* darkened to posterior margin, in cells after 1st and 2nd branching of *MA* one pale spot in each, 3rd pale spot distally between veins *RP* and *M*. In darkened apical part transverse veins and following branches of *M* red.

Abdomen in dorsal view with longitudinal rows of diffused dark brown spots occupying entire length of segments and separated by narrow pale brown intervals. Ventral side of abdomen on sides and posteriorly reddish brown to dark brown, middle part pale.

♂ not known.

Length of body of ♀ 2.55 and forewing 6.2 mm.

Material. Holotype; ♀, Vietnam, Ha Shon Bing, Hoa Bing, and Cao Phong Provs., 27.X.1990 (Belokobyl'skiy).

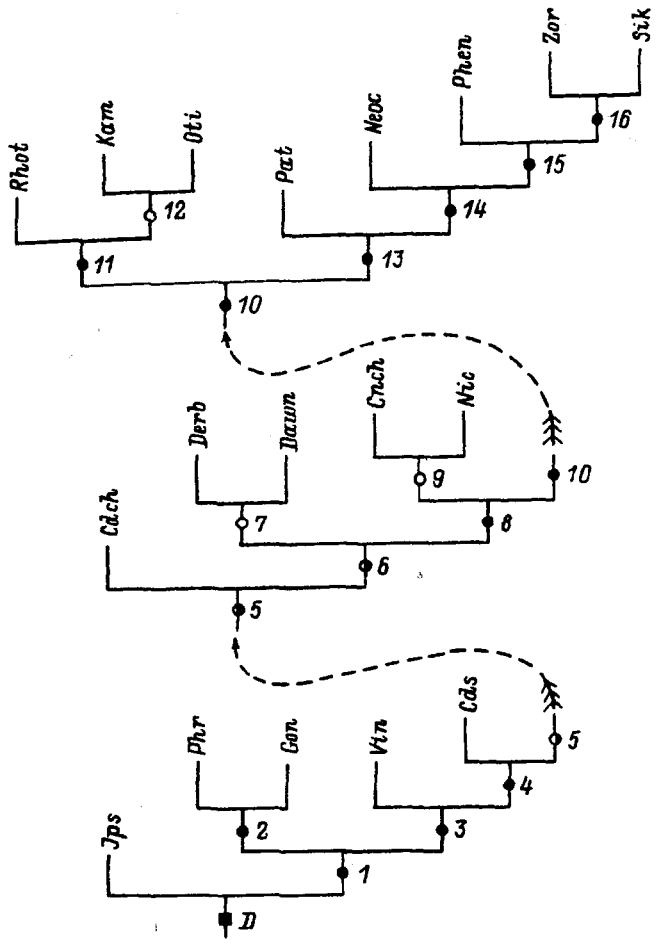

Fig. 15. Cladogram of suggested phylogenetic relationships of tribes of Derbidae. Nodes are numbered, the letter *D* designates the original node of the family. Synapomorphies are cited in the text, pp. 95-98. Filled circles show notes at which relatively reliable synapomorphies are known; half-filled circles mark only conditional synapomorphies not known in all tribes above the node because of supposed reversions or losses; white circles show hypothetic nodes not having necessary substantiation. Names of tribes are abbreviated to 3-4 first letters (see checklist of tribes on pp. 75-76) except: *Cds* - Cedusini, *Cdch* - Cedochreini, *Cnch* - Cenchreini.

PHYLOGENETIC REMARKS

The evolution of the family was probably chiefly unidirectional and almost all tribes an be arranged in a single phylogenetic series. In the family wings evolve most clearly, from normal cixioid wings to very extended and narrow wings suitable only for mating swarming (Figs. 9-13). Probably the use of wings predominately for swarming is typical of the family from its first representatives and determined unidirectional evolution of wings in several parallel lines of Derbini s. 1. and Zoraidini (Fig. 11, *2, 13*). For rigorous substantiation of the phylogeny there are not yet enough data and distribution of some characters is controversial. Considerations offered here do not contradict anything in the views of Fennah (1952).

A single reliable apomorphy of the family in general consists of the fusion of sternite IX with the anal tube in ♂s (Fig. 15, *D*). Another rather likely synapomorphy is peculiar wax pores on the abdomen (Yang and Yeh, 1994).

Two peculiarities often occurring in lower Derbidae, the achilid clavus with blunt apex, in which *Pcu* + *A*1 enters the vein *CuP* (Fig. 9, *1-6*; 10; 11, *6*; 14). Presence of the subantennal lobe cannot be accepted as synapomorphies of all or a majority of subdivisions of the family because a clavus of such a type is characteristic of Achilidae, and a similar subantennal crest occurs in Cixiidae (*Euryphlepsia*) and Kinnardidae. The third peculiar character occurring in Derbidae is the large, extended second antennal segment, which is more specific, but a remote similarity may be found in Delphacidae. Besides, all three characters cited above are developed only in some representatives of most tribes.

These characters are only a certain state (display) of morphocycle of transformations of corresponding structures of the family. The transformation of the humeral crest of the pronotum and its lower margin into a foliate emargination of the antennae is more specific of the family, but such a construction is characteristic only of some representatives of the most advanced tribes (Fig. 1).

The achilid type clavus possibly indicates an ancestor common with Achilidae that already had such a clavus, or it indicates morphoevolutionary flexibility in the common ancestor of these families with positions of the veins *Pcu* + *A*1, in other words the presence in the ancestor of the morphocycle: cixiid apex of clavus—achilid apex of clavus. The achilid clavus is characteristic of *Goneokarella, Phrygia, Vinata, Eocenchrea*, most Derbini, and sometimes it occurs in Cenchreini s. str. A pair of close genera, *Cedusa* and *Eocenchrea*, differing essentially only in the structure of the clavus, is most remarkable.

It is possible that the three lowest stages of evolution of the family are represented by genera *Goneokarella, Phrygia*, and *Ipsnola*, in which antennae are not hypertrophic and subantennal lobes are absent.

All remaining tribes of the family are opposed to Ipsnolini by the absence of subapical setae on the first and second hindtarsal segments (Fig. 15, *1*). Tribes Phrygiini and Goneokarellini are synapomorphic in the X-wise converged branches of *CuA*1 in hindwings (Fig. 15, *2*). Following tribes are characterized by reduction of the branching of *CuA*1 in the hindwing (Fig. 15, *3*).

O'Brien, without citing reasons, transferred *Phrygia* back to Achilidae, which contradicts at this point the view of Fennah, who previously did the opposite. Strictly speaking the ♂ genitalia are not yet described, and *Phrygia* and *Tropiphlepisa* may equally well be placed in Achilidae and Derbidae.

The fourth stage, *Vinata*, is characterized by the first appearance of the large and long second antennal segment and the absence (phenotypical blocking?) of the subantennal lobe—the antagonist of the hypertrophic antenna.

The fifth stage, Cedusini, is characterized by the appearance (deblocking in genotype?) of the subantennal lobe with the absence (blocking in genotype?) of the hypertrophic antenna. In this tribe the achilid clavus occurs together with the cixiid clavus. Converging of the nodal vein *ScRA*1 with the hook on the hindwings is also characteristic (Fig. 15, *4*). Further evolution is associated with the appearance of sensory pits in the imago, first on the costal vein of forewings only (Fig. 15, *5*) in Cedochreini.

The sixth stage of evolution is associated with the tribe Derbini (including Mysidiina), It is characterized by the appearance of larval sensory pits on the head (only on the metopa) and on veins of forewings (Fig. 15, *6*) in imago. Besides in this tribe for the first time the distinct tendency to

narrowing of the metopa to a foliate state (morphocycle: normal metopa, narrow metopa, extremely narrow metopa - linear metopa) is displayed. The morphocycle of the antennae is displayed entirely. The subantennal lobe is absent (blocking in genotype?). In this tribe for the first time dipterization is displayed, the contraction of hindwings and extension of forewings. Fennah (1952: 122, Fig. 6, *D*), using the hindwing of *Mysidia costata* F., showed the stridulatory plate, but nowhere discussed it; specimens from *Mysidia* and *Derbe* in my possession do not have such a plate. The plate on the drawing is situated distally of the apex of vein *A*2; even if such a plate occurs in *Mysidia* it is not homologous to the plate of higher Derbidae, in which it is situated distally of the apex of *A*2. In the shape of wings Derbini "run further forwards." It is possible that in them, as well as in Zoraidini, the wings are used mainly for swarming. Insufficiently investigated Dawnarioidini probably should be understood as a side branch of Derbini.

The seventh stage of evolution is the tribe Cenchreini s. str. characterized by the fusion of *tg* VII and *st* VIII in ♀ s, the appearance of sensory pits on the clavus (as in Meenopidae) and on the corypha. Proportions of wings retain standard ratio. The foliate lateral crests and lower margin of the pronotum appear for the first time, and a subantennal crest is often developed. The hypertrophy of antennae is not typical. Integuments are tough. At the specific level, cases of closed precubital cell appear (Fig. 15, *8*).

Further evolution of Derbidae is associated with the loss of pits in the clavus and on veins of the corium except the costal vein. In the tribe Nicertini a preparation stage for complete opening of the clavus, the apex of the clavus becomes strongly narrowed and extended (Figs. 10, 11). Cases of hypertrophy of antennae are common. One conditional autapomorphy of the tribe is a two-toothed second hindtarsal segment. Within the family it also occurs in some Sikaianini (Fennah, 1956: 132).

The eighth stage of evolution of the family (Fig. 15, *10*) was marked by the appearance of the stridulatory plate on the jugal margin of the hindwings proximally of the apex of vein *A*2 (Fig. 12). The structural basis of the appearance of the plate could be a more sclerotized jugal margin of the wing often occurring in many tribes of Derbidae, and in some tribes the stridulatory plate is absent. The clavus typically is open, vein *CuP* is gradually transient into submarginal transverse veins of the membrane.

The 9th stage, in which Rhotanini, Kamendakini, and Otiocerini may be placed, is characterized by the primary structure of stridulatory plate with concave outer margin (Fig. 15, *10*), whereas at a later time the outer margin of the plate became convex (Fig. 15, *13*); these tribes are synapomorphic in the shift of the apex of the vein *RP* of hindwings to the anterior margin of the wing (Fig. 15, *11*).

The 10th stage is represented by the tribe Patarini. It is characterized primarily by the closing of the procubital cell and slenderizing: structures of the integument become thinner, the sculpturation weaker, wings weaker, warped, wrinkled, and reticulate. Sensory pits on the head are lost. Conditional autapomorphies of the tribe are as follows: the linear metopa, and large secondary antennal segments. Examples of the subantennal crest and foliate crests of the pronotum are antagonistic to hypertrophy of antennae and are absent.

It is possible that Nicertini and Otiocerini are sister groups, a common ancestor of which first became separated from the common stem leading to Sikaianini. In this case it should be admitted that in Nicertini the stridulatory plate became lost secondarily, and the open clavus of Otiocerini formed convergently. This is a very likely variant. In any case tribes Phenicini and Neocyclokarini with closed clavus and developed stridulatory plate are most likely ancestors of Zoraidini and together of Sikaianini.

During formation of Neocyclokarini vein *mcu* of forewings became shifted distally of the first

branching of the median (Fig. 15, *14*), and in Phenicini a more secure fixation of the base of the clavus with the scutellar groove formed (Fig. 15, *15*).

The tribe Rhotanini also displays maximal similarity to Phenicini in the complex of most reliable evolving characters, including the closed clavus. However, in this tribe, unlike in all other groups of the family, evolution of wings went in the direction of widening and shortening. Antennae are small, subantennal crests are well developed and united with foliate margins of the metopa; On the stem of the anterior cubitus, unlike in all other Derbidae, there are sensory pits and this is the only area where they are present.

The highest degree of specialization is found in tribes Zoraidini and Sikaianini, sensu strictu; at this specialization wings completely lost their flight function and remain only locked with the forewing by the stridulatory appendage.

The subfam. Zoraidinae (Zoraidini and Sikaianini) in Muir's understanding (Fig. 15, *16*) is characterized by a series of synapomorphies: the appearance of vein *icu* and fusion of bases of anal veins in hindwings, and also by the appearance of lateral teeth on hindtibia and opening of the clavus.

In the tribe Zoraidini antennae are usually hypertrophic, and foliate structures of cheeks and pronotum are not developed, but in the genus *Zeugma* bordering structures are present, and antennae are small. In the tribe Sikaianini in the genus *Ceropupa* gen. n. the second antennal segment is extended and divided into two (Fig. 9, *3*). At some middle stage of evolution of the tribe Zoraidini reduction of the ovipositor took place (*Lydda, Helcita, Pamendanga, Proutista*, etc.), possibly inherited by the ancestor of the tribe Sikaianini. If so, then Zoraidini is a paraphyletic group in Henning's sense. A preliminary stage toward transition to the state of Sikaianini is probably demonstrated by *Zoraidoides* Dist., *Stenopeggia* Fenn., and *Parapeggia* Yang et Wu, but their ovipositor is developed normally.

As is shown in the preceding discussion, in the family evolution went through many stages without sharp steps to a higher level and therefore it is easy to understand Fennah, who did not distinguish subfamilies and justly criticized Muir for distinguishing Zoraidinae (Fennah, 1952). Yet another essential evolutionary step was made during formation of the tribe Rhotanini and following tribes, and therefore I propose to distinguish together with Derbinae also the subfamily Otiocerinae Muir, 1917, with tribes Patarini, Otiocerini, Phenicini, Rhotanini, Zorasidini, and Sikaianini. It is also necessary to distinguish the subfamily Cedusinae, uniting tribes without sensory pits in imagines.

As is shown in the catalog of Metcalf (1945) the name Zoraidini (Zoraidinae) was published by Muir a year later than the name Otiocerini or Sikaianini. Therefore I offer to name the second subfamily Otiocerinae; if the subfamily Zoraidinae is accepted according to Muir, then its name should be formed of the name of the tribe Sikaianini.

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