CHARACTERS OF TAXONOMIC IMPORTANCE IN THE PRETARSUS OF AUCHENORHYNCHA (Homoptera)

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Before dealing with the subject indicated in the title the writer wishes to take this opportunity of correcting an error of lettering in figure 4 accompanying his paper on the morphology of the tegmina and wings in Fulgoroidea (Proc. Ent. Soc. Wash., vol. 46, no. 7, plate 14). In this figure of the tegmen of Mnemosyne arenae Fenn. the anterior branch of the media has been incorrectly assigned to the radial sector, and the lettering of the apical veinlets of the radius and media should be as follows: R1, Rs, MP1, MP2, MP3a, MP3b, MP4a, MP4b.

In the present paper an attempt is made to assess the taxonomic significance of differences in the structure of the pretarsus in the four superfamilies of the Auchenorhyncha, principally with reference to the Fulgoroidea; to clarify the meaning of the terms used a brief account is offered below of the morphology of the pretarsus as found in this Series. The auchenorhynchous pretarsus (Figs. 5, 6) comprises (1) a pair of tarsal claws. or ungues (U), which articulate basally with a small condyle (C) projecting from the upper side of the apical margin of the third tarsal joint; (2) a membranous sac, the arolium (A) which is essentially an extension of the membrane at the apex of the tarsus between the tarsal claws, and (3) a strongly sclerotised unguitractor plate (P), which lies ventrally at the base of the arolium, being partly invaginated into the third tarsal joint. Distally the unguitractor plate is expanded into a broad line of fusion with the arolium; basally it is narrowed and connected to a sublinear plate (S) from which a long thread-like tendon passes through the leg to the fe pur, giving attachment to the levator and depressor muscles of the claws and of the tarsus. When the depressors are contracted the tendon pulls the unguitractor plate basad, and this in turn pulls on the lower portion of the base of the ungues, causing them to become deflexed, and also by tensing the plantar surface of the arolium brings its marginal lip into contact with the substratum. This lip is narrow and delicately corrugated at right angles to the margin: it is likely that it adheres under tension to surfaces too smooth to offer purchase to the ungues. The dorsal surface of the arolium is partly sclerotised, either in a single large plate or in a more or less elongated tract inside and basally closely adjoining each of the ungues (Fig. 15, DLP). The latter, together with the dorso-lateral plates and the plantar surface of the arolium may be ornamented with setae. The pretarsus of the fore and middle leg is generally larger than that of the hind leg, but is of similar structure. The pretarsus of the nymphal stages in general resembles that of the adult; in fulgoroid nymphs the dorsolateral aroliar sclerites may be absent or scarcely perceptible and the setae on the sides of the ungues fewer, while the fanlike folds of the upper surface of the arolium may be sclerotised and pigmented.

In his search for morphological characters whereby the Auchenorhyncha might be divided into natural groups Hansen in 1890 (Ent. Tidskr. 11:19-34) briefly considered the structure of the pretarsus, and after recording the principal features of this organ in a number of genera in the Cercopoidea, Fulgoroidea, Jassoidea and Membracoidea concluded that characters which distinguished major groups resided in the shape of the distal margin of the arolium and the apparent extent of the lateral attachment of the arolium to the ungues. With these

two characters he was able to separate the "Cercopidae" (sensu lato), "Fulgoridae" (s. l.) and "Jassidae" (s. l.) the last includ-

ing the Membracidae.

The present study was undertaken partly to test the applicability of Hansen's observations by using different material but chiefly to seek new data which might illuminate major relationships in Auchenorhyncha, and in particular add to our scant knowledge of the affinities of the Tettigometridae. The material examined by the writer included the following: Cicadoidea: Fidicina sp.; Cercopoidea: Tomaspis saccharina Dist.: Membracoidea: Horiola picta Coq.; Jassoidea: Oncometopia sp., Diestostemma sp., Tettigoniella lineata (Sign.), Graphocephala humeralis Osb. Platygonia praestantior (Fowl.) (Tettigoniellidae), Fulgoroidea: Euphyonarthex phyllostoma, Schmidt, Hilda undata (Wlk.) (Tettigometridae), Pintalia decorata (Uhl.) (Cixiidae), Syntames sp., Derbe semifusca Fenn. (Derbidae). Delphacodes teapae (Fowl.), Perkinsiella vitiensis Kirk. (Delphacidae), Nisia atrovenosa (Leth.) (Meenoplidae), Bytrois nemoralis Fenn. (Kinnaridae), Taosa herbida (Wlk.), Toropa ferrifera (Wlk.), Hyalodictyon truncatum (Wlk.) (Dictyopharidae), Laternaria laternaria L., Cathedra serrata (F.) (Fulgoridae), Catonia intricata Uhl. (Achilidae), Remosa cultellator (Wlk.), Cyphoceratops sp. (Tropiduchidae), Bladina fuscana Stal, Nogodina reticulata (F.) (Nogodinidae), Acanalonia sp. (Acanaloniidae), Colpoptera sp., Thionia musca (Uhl.), Ugoa glauca Fenn. (Issidae), Poekilloptera phalaenoides (L.) and Ormenis antoniae Mel. (Flatidae) in the adult stage, and one or more nymphal stages of one Membracid, 3 Jassoids and the Fulgoroids Ormenis sp., Colpoptera sp., Toropa ferrifera, Ugoa glauca and Alcestis sp.

The pretarsal structure found in these species is shown in the accompanying figures: such examples as have been omitted are virtually identical in pretarsal structure with the species

of the same family that is shown.

The morphological features which the writer considers to be of value in characterising superfamilies of Auchenorhyncha are summarised as follows:

Cicadoidea: Ungues simple. Arolium reduced, bearing one or two plates in the middle line. Unguitractor plate subrectangular with distal margin transverse, with a narrower and distinct lobe basally, both ornamented with transverse rows of minute oval callosities.

Cercopoidea: Ungues with a decurved subapical tooth projecting from ventral margin. Arolium with a broad median plate dorsally, beset with three setae near each latero-apical angle; medially, distad of this plate, a long seta arising from a tubular base; ventrally a pair of oblique narrow sclerotised bands traversing plantar surface from unguitractor plate to margin, each bearing four long setae inserted in a row in its distal half; apical margin of arolium entire and transverse. Unguitrac-

tor plate quadrangular, ornamented with minute oval callosities in oblique series.

Jassoidea and Membracoidea: Ungues simple, ornamented with very distinct imbrication, overlapping arolium dorsally on their inner faces. Arolium exceeding ungues, medially cleft on distal margin, with two or three pairs of setae on plantar surface; dorsally a pair of subquadrate sclerotised plates each bearing a long seta. Unguitractor plate subfusiform, ornamented with minute oval callosities in oblique series. It may prove possible to separate these superfamilies as follows:

Distal portion of unguitractor plate subquadrate, imbricate, not spiculate.

Fulgoroidea: Ungues simple, smooth, or ornamented with faint broad imbrication, not overlapping arolium on inner face, or scarcely so (Remosa), usually beset with setae laterally. Arolium rarely reaching to apex of ungues, distal margin entire, truncate; a pair of setae on plantar surface, a pair of more or less narrowed sclerotised rods or plates dorso-laterally, each loosely articulating basally with a minute projection on inner face of unguis at its basal third. Unguitractor plate elongate-triangular, distally expanded and truncate, ornamented with transverse ridges, somewhal trilobitiform.

The structural differences exhibited by the pretarsus in various families are of much smaller magnitude than those in different superfamilies, but in Fulgoroidea, the only superfamily whose families have been compared in this regard with any degree of completeness, they appear sufficiently distinct to provide corroborative evidence in settling the affinities of puzzling genera. It is likely that pretarsal structures will be found to be of similar value in the Jassoidea. The features at present considered likely to be constant in various families of Fulgoroidea are respectively as follows:

Arolium approximately reaching to apex of ungues, dorso-lateral sclerites broad, prominent: Tettigometridae; one or two spines on each unguis, or none, dorsolateral sclerites slender, straight or curved, arolium sometimes narrowed: Cixiidae, Delphacidae, Derbidae, Meenoplidae, Kinnaridae; dorsolateral sclerites narrow, rather long, tapering distally, distinctly articulated at base with condyle on unguis; unguis with three or four setae: Dictyopharidae; ungues large, arolium and dorsolateral sclerites reduced: Fulgoridae pars; dorsolateral sclerites two-thirds length of ungues forming a deep V: Tropiduchidae; ungues stout, bi- or tri-setose, dorsolateral sclerites relatively small: Acanaloniidae, some Issidae; dorsolateral sclerites broad, curved, placed laterally rather than dorsally: Achilidae; ungues tri- or quadrisetose, dorsolateral sclerites rather broad, placed laterally to a marked extent and only partially seen in dorsal view: Nogodinidae, Flatidae.

The pretarsal structure in all the species examined agrees well with such details as are given by Hansen for his material in corresponding families, and there appears good reason to believe that the structural patterns noted for each superfamily will be found in all included species. The most interesting

single fact which has emerged in the present study is that in the Tettigometridae the pretarsus is of orthodox fulgoroid structure. It would seem on present evidence that a pair of setae on the plantar surface of the arolium, dorsolateral sclerites devoid of setae, and a triangular and transversely ridged unguitractor plate constitute the most fundamental of all fulgoroid characters, transcending in their universality both the presence of tegulae and the non-segmented condition of the antennal flagellum. If it be supposed that the general patterns typical of the other superfamilies are no less fundamental, the fact that the jassoid and membracoid types are almost indistinguishable would indicate that these groups are far more closely allied than is revealed by their present status as separate superfamilies.

The minor structures which serve to distinguish families or groups of families show a certain degree of plasticity for which due allowance must be made in assessing the value of resemblances in pretarsal structure between families. If the varying degrees of curvature of the dorsolateral sclerites, and in two families the narrowing of the arolium are ignored, the Cixiidae. Delphacidae, Derbidae, Meenoplidae and Kinnaridae share a common type of pretarsus, from which that found in the Dictyopharidae is not greatly different. In the most generally accepted classification of the Fulgoroidea, that of Muir, the first three of these families fall into a group which is separated from that which contains the last three by the great fission (considered as having arisen only once) between the simple tubular aedeagus and the invaginated aedeagus; if this be accepted, then the similarity of the pretarsus in the families listed above may indicate a natural relationship between the first three families, and also between the last three, but between these two sets the resemblance must be explained as being the result of parallel evolution.

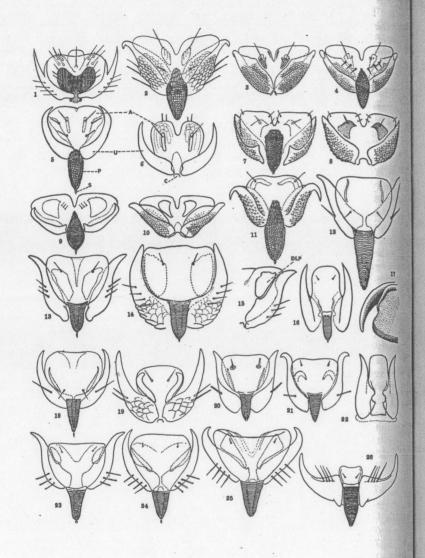
In trying to trace evolutionary trends in a structure it is necessary to characterise a primitive or ancestral type. The writer is inclined to the view that such a type is reproduced in the nymphal stages of unspecialised Fulgoriodea, and includes merely the following elements: Ungues simple, unisetose or unornamented; arolium well developed with two setae on plantar surface, dorsolateral sclerites absent or indicated merely as slight thickenings of the aroliar wall, without definite boundaries; unguitractor plate triangular, transversely ridged but ventrally convex in section rather than trilobed-convex. On this view it is possible to regard the tri- or quadrisetose condition of the ungues and the condylar development on their inner faces as specialisations, while the presence of dorsolateral sclerites in close association with this condyle is a parallel specialisation. It is not possible to decide whether the broad form of dorsolateral sclerite or the linear form is more primitive, and the two forms occur respectively in the most generalised groups—the Tettigometridae and the Pintaliine Cixiidae.

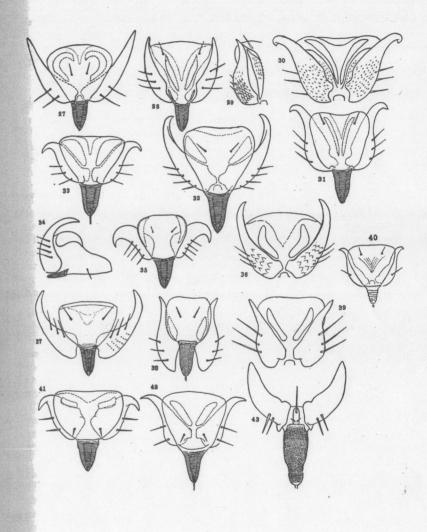
The claim may be advanced that the simplified structure of the pretarsus in the family Fulgoridae (Fig. 26), which is not far removed from the generalised nymphal pattern, represents the most primitive of all pretarsi in adult Fulgoroidea. On halance, the writer considers that the fulgorid pretarsus has attained its present form as a result of specialisation in the direction of adaptation to environment, for the following reasons: (1) the arolium is greatly reduced, whereas in nymphal Fulgoroidea it is well developed; it is well developed in such generalised insects as Orthoptera, as well as in other orders. (2) the ungues are quadrisetose, while the ungues of nymphal forms, and of such generalised families as Tettigometridae, Cixiidae and Delphacidae are not more than bisetose, so that it may be presumed that those of Fulgoridae are specialised in this respect; (3) the dorsolateral sclerites of other adult Fulgoroidea appear in this family, on the basis of the forms examined, to be represented by an immobile, stiffened, but not pigmented, ridge at each lateral margin of the reduced arolium where it lies against the basal portion of the strongly divergent ungues: no such development is seen in nymphal forms, where the arolium is quite pliable and thin-walled in this region; (4) the nearest approach to the pretarsal proportions of the large Fulgoridae is found in the pretarsus of the equally large Cicadidae. This family has the arolium reduced, but on its narrow lower surface between the base of the ungues are one or two adventitious sclerites apparently not represented elsewhere in Auchenorhyncha. Both Fulgoridae and Cicadidae in the adult stage spend their time on the bark of trees, usually on surfaces that, microscopically considered, are roughened and uneven. It is suggested that the similar form of the pretarsi found in these two families has been reached independently by adaptation to the type of surface on which they are used, with relation to the stress to which they are subjected by the weight of the insect.

EXPLANATION OF PLATES

- 1. Tomaspis saccharina Dist., pretarsus of hind leg of adult, dorsal view.
- 2. Horiola picta Coq., pretarsus of hind leg of adult, ventral view.
- 3. Oncometopia sp., pretarsus of hind leg of adult, dorsal view.
- 4. Oncometopia sp., do., ventral view.
- 5. Tettigoniella lineata (Sign.), pretarsus of hind leg of adult, ventral view.
- 6. Tettigoniella lineata (Sign.), pretarsus of hind leg of adult, dorsal view.
- 7. Platygonia praestantior (Fowler), pretarsus of hind leg of adult, ventral view.
- 8. Platygonia praestantior (Fowler), do., dorsal view.
- 9. Diestostemma sp., pretarsus of hind leg of adult, ventral view.

PLATE 14





10. Diestostemma sp., do., dorsal view.

- 11. Graphocephala humeralis Osb., pretarsus of hind leg of adult, ventral view.
- 12. Pintalia decorata (Uhl.), pretarsus of hind leg of adult, ventral view.
- Euphyonarthex phyllostoma Schmidt, pretarsus of hind leg of adult, ventral view.
- 14. Hilda undata (Wlk.), pretarsus of hind leg of adult, ventral view.
- Euphyonarthex phyllostoma Schmidt, one side of hind pretarsus of adult, dorsal view.
- 16. Delphacodes teapae (Fowl.), pretarsus of hind leg of adult, ventral view.
- Syntames sp., pretarsus of hind leg of adult, one half sho

 n, viewed semilaterally.
- 18. Syntames sp., pretarsus of hind leg of adult, ventral view.
- 19. Derbe semifusca Fenn., pretarsus of hind leg of adult, dorsal view.
- 20. Nisia atrovenosa (Leth.), pretarsus of hind leg of adult, ventral view.
- 21. Bytrois nemoralis Fenn., pretarsus of hind leg of adult, ventral view.
- 22. Delphacodes teapae (Fowl.), pretarsus of hind leg of adult, dorsal view.
- 23. Hyalodictyon truncatum (Wlk.), pretarsus of hind leg of adult, ventral view.
- 24. Toropa ferrifera (Wlk.), pretarsus of hind leg of adult, ventral view.
- 25. Taosa herbida (Wlk.), pretarsus of hind leg of adult, ventral view.
- 26. Cathedra serrata (F.), pretarsus of hind leg of adult, ventral view.
- 27. Catonia intricata Uhl., pretarsus of hind leg of adult, ventral view.
- 28. Cyphoceratops sp., pretarsus of hind leg of adult, ventral view.
- 29. Cyphoceratops sp., do., dorsal view.
- 30. Remosa cultellator (Wlk.), pretarsus of hind leg of adult, dorsal view.
- 31. Remosa cultellator (Wlk.), pretarsus of hind leg of adult, ventral view.
- 32. Nogodina reticulata (F.), pretarsus of hind leg of adult, ventral view.
- 33. Bladina fuscana Stal, pretarsus of hind leg of adult, ventral view.
- 34. Poekilloptera phalaenoides (L.), pretarsus of hind leg of adult, side view.
- 35. Poekilloptera phalaenoides (L.), pretarsus of hind leg of adult, ventral view.
- 36. Ormenis antoniae Mel., pretarsus of hind leg of adult, dorsal view.
- 37. Ormenis antoniae Mel., do., ventral view.
- 38. Acanalonia theobromae Fenn., pretarsus of hind leg of adult, ventral view.
- 39. Acanalonia theobromae Fenn., do., dorsal view.
- 40. Colpoptera sp., pretarsus of hind leg of fifth instar, ventral view.
- 41. Ugoa glauca Fenn., pretarsus of hind leg of adult, ventral view.
- 42. Thionia musca (Uhl.), pretarsus of hind leg of adult, ventral view.
- 43. Fidicina sp., pretarsus of hind leg of adult, ventral view.