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## A STUDY OF THE PHYLOGENY OF THE ANTEONINAE<sup>1</sup>

F. A. FENTON

A study of the biology of insect parasites and their relationships with that of their hosts offers a most attractive and productive field for research, and as yet, comparatively speaking, but little has been done in this field. This is particularly true with the *Hymenoptera*, and the writer has been interested in working out the biology of the Anteoninae, one of the parasitic groups of this order. These insects are parasitic on three families of the *Homoptera*, namely, the Cicadellidae, and Fulgoridae, commonly known as leafhoppers, and the Membracidae or treehoppers.

With the possible exception of members of the most primitive genus, the larvæ of the Anteoninae in their later stages are all attached externally to the host, protected and encased in the larval exuviæ, which instead of being cast off as is the case with other insect larvæ, are retained as a sort of sac for protection. Furthermore, with the exception of the genus *Aphelopus*, all the females have the front pair of legs greatly lengthened and otherwise adapted for grasping purposes. The coxa is excessively elongated, being often more than half as long as the femur; the trochanter is long and often somewhat curved; the femur is strongly club-shaped; and the tibia is thicker and shorter than the others. The greatest and most striking change has taken place in the fore tarsi, however, these being modified to form a chela or grasping organ fitted for holding the active prey, a character not found in any other insect group (Fig. 56. 7). The chela is composed of two arms or "pincers," one being the fifth tarsal joint which is proximally more or less lengthened, and the other one of the tarsal claws which has become greatly elongated. The remaining claw is much reduced or normal and is enveloped by the lobes of the empodium. These chelae show a great range of variation and complexity within the group, being variously provided with spines and lamellae (Fig. 56). In addition to this structure, which is peculiar only to the females, this sex has

<sup>1</sup> This group has been variously given the rank of family (Dryinidae) and sub-family (Anteoninae) by different writers. It is also included by some in the super-family Proctoturpoidea, and by others in the Vespoidea.

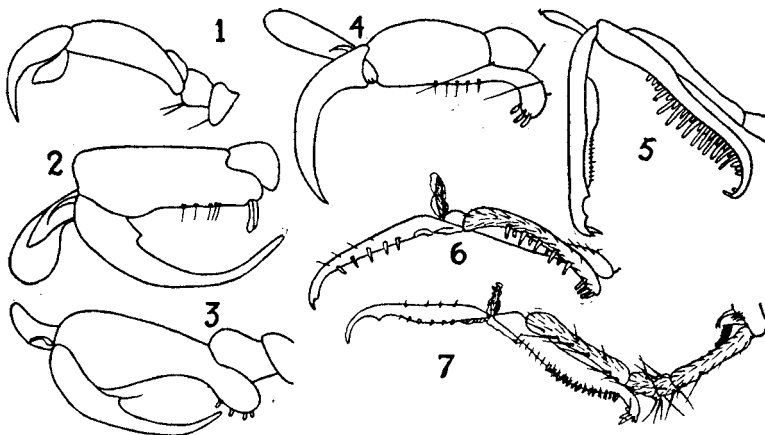


Fig. 56. Chelae of Anteoninae. 1. *Paranteon myrmecophilus*. 2. *Anteon vicinus*. 3. *Anteon arcuatus*. 4. *Anteon brevicollis*. 5. *Thaumatodryinus koebeleii*. 6. *Haplogonatopus americanus*. 7. *Gonatopus erythrodes*. (Fig. 1 from Perkins, Figs. 2-5 from Kieffer.)

also lost the wings in a great many cases and the body has become ant-like. On the other hand, the males throughout the whole group are more primitive in structure and do not show the specialization that has taken place in the females.

Recent writers have placed the Anteoninae in Ashmead's superfamily Vespoidea because of the habit the females have of stinging and paralyzing the host before ovipositing. Since this is not true, at least in certain species of *Aphelopus* which is now considered the most generalized genus of the group, this fact should be reconsidered. If we assume that the paralyzing habit was developed later on in the phylogeny of the group, as the above fact seems to indicate, it appears that this subfamily and therefore the Bethyloidea, should be removed from the Vespoidea. Probably the theory advanced by Perkins<sup>2</sup> that "they constitute a natural group, synthetic between the old Fossoreal series of the Aculeata and the true Serphoidea (Proctotrupeoidea)" is more correct and that for the present they should be included in the latter superfamily.

Fortunately, owing to the rather large number of host records on hand and the smallness of the entire group, we are able to get a series of adults which illustrates nicely the evolution of the extreme specialized types from the most primitive species. Even here, however, there is some divergence of opinion as to the exact relationship of the different genera to each other.

<sup>2</sup> Perkins, R. C. L., Report of work of the Experiment Station of the Hawaiian Sugar Planters' Association: Bull. 1, part 1, 1905, page 27.

Perkins<sup>3</sup> divided the Anteoninae which he considered a family (Dryinidae) into two subfamilies, namely the Aphelopinae, containing the one genus *Aphelopus* and the Dryininae in which he placed all the other genera. This latter subfamily he further divided into three tribes which were separated by the character of the stigma of the fore wing and by the number of joints in the labial palpi.

Kieffer,<sup>4</sup> in his monograph of the Bethyridae, divided the Anteoninae into four tribes; the Aphelopini, Anteonini, Lestodryinini and Gonatopodini. His first two tribes correspond with the Aphelopinae and Anteonini of Perkins. However, he placed the apterous forms in one tribe, the Gonatopodini and the more specialized winged chelate forms in the Lestodryinini.

There is no question about the first two tribes, *i.e.*, the Aphelopini and Anteonini; but the evidence seems to point out that both Perkins' and Kieffer's classification of the genera falling into the other two groups should be modified. There is little doubt, for instance, that the apterous forms have been derived from two different sources, both of which have been classified by Kieffer in his Lestodryinini. It has been noted many times that the males of certain genera of both the apterous *Gonatopus* group and the winged *Lestodryinus* group are very similar, and that at the same time in each of these tribes there is yet another division based on the character of the chela. In other words, in the higher, more specialized chelate genera there are two natural divisions based upon the character of the chelæ, whether the species are apterous or winged. Perkins<sup>5</sup> observed that in those dryinids parasitizing Cicadellidae the claw was not lamellate, while in those attacking Fulgoridae it was lamellate or serrate.

Further proof that the apterous forms are distinct was obtained also by Perkins when he split up the old genus *Gonatopus* into a number of genera, and this number has since been enlarged. The fact that other bethyrid wingless forms superficially resemble the *Gonatopus* group emphasizes these conclusions, and indicates that the apterous ant-like form is the result of a certain condition of habitat.

Figure 57 illustrates what seems to the writer to be the real phylogeny of this subfamily. Group I contains the single genus *Aphelopus*, admittedly the most primitive and generalized

<sup>3</sup> *Ibid.*, Bull. 11, 1912, page 10.

<sup>4</sup> Kieffer, J. J., *Das Tierreich*, 41 Lieferung, 1914, page 11.

<sup>5</sup> Perkins, *loc. cit.*

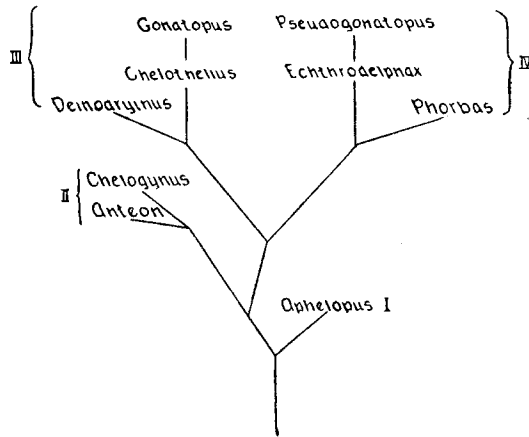


Fig. 57. Diagram illustrating phylogeny of the anteoninae.

of all the other genera. Both sexes are winged, the fore tarsi in the female are not modified to form chelæ, and there is thus no sex dimorphism. The wings show a reduced venation and have a broadly oval stigma. In our one record of oviposition<sup>6</sup> the host is not paralyzed and there is also more range in the kind of insect attacked, the Membracidae and Cicadellidae being subject to parasitism by species of this genus. There is great diversity in the larval habit, polymembrony having been found, the larvae in this case being internal and not being inclosed in sacs. When present the larval sac shows a more generalized structure.

Group II, comprising the genus *Anteon* and other related genera, shows a greater degree of specilization. While both sexes are winged there is some sex dimorphism, the females having the fore tarsi modified into chelæ. The latter are often either non-extensile or only partly so (Fig. 56, 1-4). The stigma is broadly oval as in the case with the first group but the wing venation is different, there being two basal cells present. Species in this group parasitize Cicadellidae only.

Group III comprises *Gonatopus* and related apterous genera as well as *Deinodryinus* and related winged genera. In the winged species the venation is similar to that found in group II, but the stigma is lanceolate. The type of chela is identical in both apterous and winged forms, the claw being non-lamellate (Fig. 56, 5 and 7). Species in this group parasitize Cicadellidae only.

<sup>6</sup> Kornhauser, S. I., Journal of Morphology, vol. 32, no. 3, 1919, pages 547-554.

Group IV comprises *Pseudogonatopus* and related apterous genera as well as *Echthrodolphax* and related winged genera. This group is very similar to the preceding but is differentiated at once by the character of the chela, the claw of which is lamellate or serrate (Fig. 56, 6). Fulgoridae only are parasitized.

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