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## SOME NOTES ON HETEROPTERAN TRICHOBOTHRIA\*

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There has been much recent interest in the comparative morphology of the Heteroptera. This work has emphasized the land bugs, or Geocorisae, and has been concerned with working out the relationships and taxonomic placement of the higher categories (categories above the genus), and with the phylogenetic lines and sequences of these higher categories. The geocoristine groups with which I have been most concerned are in the closely related superfamilies Lygaeoidea, Pyrrhocoroidea, and Coreoidea (see Schaefer, 1964, for a discussion of the relationships among these groups). Another superfamily, the Pentatomidea, is less closely related. All four of these superfamilies have arolia and pseudarolia, and all four have trichobothria. Because they possess this last character in common, the four are grouped together under the name Heteroptera Trichophora (Tullgren, 1918), a name of no nomenclatorial standing but nevertheless convenient.

Trichobothria are long hairs arising from often darkened sockets on the relatively bald abdominal venter. They are usually easy to distinguish from other hairs, because they are longer, have a darkened base, and are arranged symmetrically in a distinctive pattern on each segment.

These patterns and the number of trichobothria in them are characteristic of the higher categories of the Trichophora. Since the trichophoran families are closely related, and since this close relationship has been established on evidence from other morphological features than trichobothria, one might look for phylogenetic significance in the variety of patterns. However, very little is known about the function and phylogenetic origin of trichobothria. I shall speculate here on their function and their phylogenetic significance, but more must be learned about trichobothria before speculation becomes knowledge.

The ventral position of trichobothria supports the idea that they are tactile, telling the insect something about the substrate over which it is moving. Another possibility is that they aid in flight, by detecting changes in the force and direction of air currents. However, many of their possessors fly only rarely and clumsily; others do not fly at all, and there is no correlation between presence of trichobothria and brachyptery, as there is, for example, between the absence of ocelli and brachyptery.

\*A shorter version of this paper was read at the annual meeting of the Entomological Society of America, December, 1965.

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Several people, most recently Leston and Pringle (1964), have suggested that trichobothria are sound-receptors. Some objections can be raised to this idea, but they may not be valid. One objection is that *all* members of the Trichophora have trichobothria, although sometimes few in number; yet only in relatively few trichophorans have sound-producing structures been discovered. There are two possible answers to this objection. First, stridulatory devices have been found in many heteropterans heretofore thought to lack them. Second, the sounds may be produced not by special mechanisms but by the impact of some part of the body against the substrate (Haskell, 1961). This latter method might explain why trichobothria are ventral. If they were designed to receive airborne sounds, one would expect them to be dorsal, particularly in these rarely flying insects.

Another objection to the idea that trichobothria are sound-receptors is the presence of stridulatory devices in heteropterans lacking trichobothria (non-trichophorans). This objection too is not wholly valid. Some of the Aradidae and Reduviidae have stridulatory devices and appear to lack trichobothria. However, trichobothria *have* been found by Stys (1964, *in epist.*) in some reduviids, and trichobothria will perhaps be found in others. Moreover, it is possible that various setae, not externally modified to appear as trichobothria, may function as sound-receptors. There is no doubt that a great many land Heteroptera produce sounds, but as far as I am aware no "hearing" mechanism has been discovered, unless it be the trichobothria.

Leston and Pringle (1964) hypothesize that trichobothria receive species-specific sounds and thereby prevent hybridization of closely related species. This seems unlikely as the sole purpose of these sounds and their reception, for trichobothria are found in immature as well as adult trichophorans. Nevertheless, I know of no immature terrestrial trichophoran that produces sound, and indeed many sound-producing structures are associated with adult features (like wings); perhaps, then, trichobothria serve different functions in nymphs and adults. If so, adult sound might well have a courting function and serve also as an isolating device.

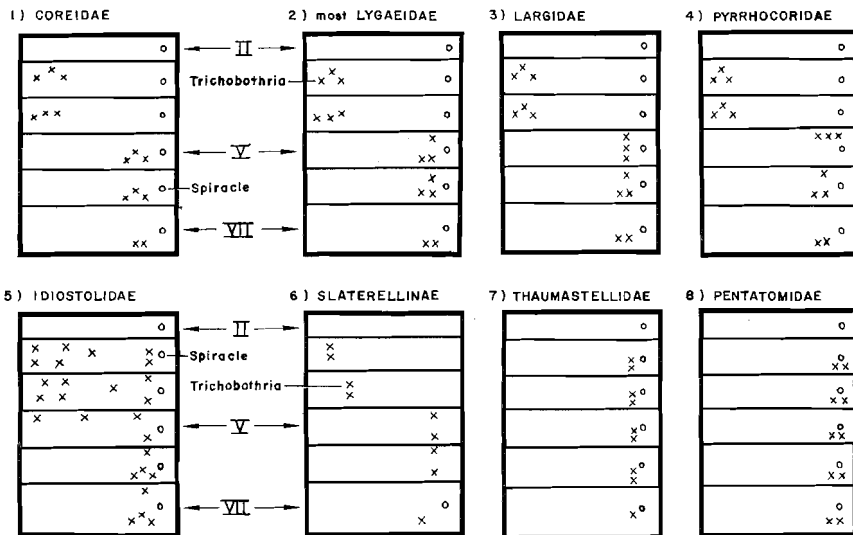
Whatever their function--and sound-reception seems the most likely one--the symmetrical arrangement of trichobothria is certainly of functional significance. The symmetry implies directionality. It implies, that is, an ability of the insect to tell the direction from which the stimulus is arriving. This of course would be highly useful in sound reception; it would be necessary for detecting air currents; and the symmetry would even be useful if trichobothria are devices for the exploration of the substrate, since it would allow better judging of gradients of humidity, chemicals, etc. This attribute of directionality does not distinguish between possible functions.

Closely controlled behavioral and electrophysiological experiments are needed before one can do more than speculate on the function(s) of trichobothria.

The patterns of trichobothria on the abdominal venter are quite constant at the higher taxonomic levels. The Pentatomoidea (Figs. 7-8) have two trichobothria laterally on sterna three through seven. In members of the lygaeoid-pyrrhocoroid-coreoid complex (Figs. 1-4), there are usually three trichobothria on segments three through six, and two on the seventh. In addition, the clusters on segments three and four are medial, while the remainder are lateral, near the spiracle. The important differences in members of this complex are in the arrangement of trichobothria, and the arrangement of the clusters relative to the spiracle. (Spiracles are usually ventral in the Trichophora. Occasionally some are dorsal, as in the Slaterellinae, but the phylogenetic significance of this is not clear.)

Figure 5 shows the trichobothrial pattern of *Idiostolus*. This and the genus *Trisecus* were placed in a separate subfamily (Idiostolinae) of the Lygaeidae by Scudder in 1962; in 1964 Stys raised them to a superfamily, primarily on the basis of their trichobothrial numbers and patterns. In a recently completed morphological study, I have taken a middle view and have placed the two genera in a family, Idiostolidae, in the superfamily Lygaeoidea (Schaefer, 1966). *Idiostolus* shows some very advanced morphological features and some very generalized (or primitive) ones, among which is the trichobothrial number.

All trichophorans with fewer than the usual number of trichobothria are advanced with respect to many other morphological characters. It is reasonable, then, if far from conclusive, that the large number of



Figures 1-8. Trichobothrial patterns of representative Heteroptera Trichophora. The diagrams (adopted from Scudder, 1963) represent the left side of abdominal sterna II through VII. The left-hand border of each diagram represents the ventral midline of the abdomen. The diagrams are not to scale. Symbols: x = trichobothrium; o = spiracle

*Idiostolus* trichobothria is primitive. Another indication that this large number is primitive is the plasticity of position of several of the trichobothria. In the large clusters of segments three and four the arrangement was extremely variable in my specimens, and occasionally a trichobothrium was even missing. I emphasize the absence of *direct* proof that this large number is a primitive characteristic, but there is no evidence, direct or indirect, that it is not.

Although it appears that many other trichophoran patterns could be derived from the idiostolid pattern by eliminating selected trichobothria, the *Idiostolus* trichobothrial arrangement on the fifth sternum cannot be directly ancestral to any other. There are only two trichobothria on the fifth sternum of *Idiostolus* and three in most other members of the lygaeoid-pyrrhocoroid-coreoid complex.

*Idiostolus* may be advanced with respect to this character on the fifth sternum, and primitive elsewhere. This seems unlikely. If the *Idiostolus* pattern does resemble that of the presumed common ancestor of the complex, a third lateral trichobothrium may have been developed in either of two ways. An existing seta may have been modified to a trichobothrium, or a medial trichobothrium may have been shifted laterally. Such a medial trichobothrium would have been homologous to one of the two found in *Idiostolus* but now absent elsewhere in the complex. The variability of trichobothrial position in *Idiostolus* indicates that such a shift might have occurred before these positions became "fixed." Also, other migrations of a trichobothrium and part of the fifth sternum occur normally in the Lethaeini (Lygaeidae) and at least once anomalously in the coreid *Anasa tristis* De Geer (Schaefer, in press).

In one small group of the lygaeoid-pyrrhocoroid-coreoid complex the fifth-sternal pattern resembles the idiostolid pattern. Members of the lygaeid subfamily Slaterellinae have two lateral trichobothria and no median ones on the fifth sternum (Fig. 6). However, the number of trichobothria on the other segments is also much reduced. If this reduction of trichobothria on the fifth sternum in the Slaterellinae is advanced (as I have suggested above it is), and if the reduction in the Idiostolidae is primitive (as I believe it is), the similarity between the two patterns on the fifth sternum is not phylogenetically significant.

It seems clear, then, that the idiostolid trichobothrial pattern, although certainly primitive, is *not* directly ancestral to any existing pattern. At least one intermediate form must be postulated to provide evidence for a lateral migration of one of the two median trichobothria on sternum five. But the idiostolid pattern very probably comes the closest to representing that of the trichophoran ancestor. Much other evidence suggests strongly that that ancestor was lygaeid-like (Schaefer, 1964); and it is significant that the general morphology of the Idiostolidae is very similar to that of the Lygaeidae (Schaefer, 1966).

The other group of the Heteroptera Trichophora is the Pentatomoidea. The origins, relationships, and phylogeny of the major groups in this superfamily are very poorly known. The pentatomoid trichobothrial

patterns are more advanced than most of those in the lygaeoid-pyrrhocoroid-coreoid complexes, as there are no more than two trichobothria per segment. This is true even of the most primitive groups, the Thaumastellidae (Stys, 1964) and (probably) the Garsauriinae (Cydnidae). These two trichobothria are arranged in various ways--transverse, oblique, longitudinal--and they may bear varying relationships to the spiracle. The thaumastellid pattern (Fig. 7) may well be the primitive one, and that of the Pentatomidae (Fig. 8) the more advanced. Ruckes (1962) has described these patterns, and, from his descriptions, it may be possible to work out some general evolutionary trends. I shall do this soon as part of a general study of the morphology and relationships of the Pentatomoidea.

Further studies of the relationships between the major trichophoran groups will contribute much to a better understanding of the origin and evolution of trichobothria. But a knowledge of structure is not enough, and, as I have said, final understanding awaits experimental evidence for trichobothrial function.

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Finally, I am grateful to my wife, Stephani Schaefer, for the diagrams.

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ANOTHER RECORD OF WILLIAMSONIA FLETCHERI IN MICHIGAN  
(ODONATA: CORDULIIDAE)

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*Williamsonia fletcheri* Williamson was first taken in the United States in the upper peninsula of Michigan near Manistique, Schoolcraft County (Gloyd, 1932). On June 4, 1966, I collected two males of this rare species at Island Lake, a small lake heavily overgrown with jack pine and poplar in southeastern Grand Traverse County. The specimens were identified by Mrs. Leonora Gloyd of the University of Michigan.

This is the first report of this species from the lower peninsula of Michigan, and the second for the United States.

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