

THE TAXONOMIC POSITION OF THE RHYSODIDAE (COLEOPTERA)¹

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For many years entomologists have debated the taxonomic position of the Rhysodidae. The earlier workers placed them near the polyphagous families Cucujidae and Colydiidae, to which they have a superficial resemblance. In more recent times, evidence has accumulated that they actually belong in the suborder Adephaga. Forbes (1926) pointed out the adephagous character of the hind wings. Böving and Craighead (1930) showed that the larva has the essential characteristics of an adephagan. Crowson (1955) considers them to be the most primitive of living Adephaga and this arrangement has been followed by Arnett (1960). Apparently no contrary idea of the position of the Rhysodidae within the suborder has yet been expressed. We would like to present an alternative hypothesis, that the Rhysodidae are a modified offshoot of the Carabidae.

Crowson considers the following characters to be evidence of the primitiveness of Rhysodidae: the presence of a labrum in the larva, the large size of the intercoxal piece of the first visible abdominal sternite of the adult, the wide separation of the hind coxae, the extremely simple metendosternite, the bark-dwelling habits.

The structure which Crowson regards as the labrum of the larva is considered to be the epipharynx by Böving and Craighead. It is shown in their illustration as a small, apparently membranous protuberance and does not closely resemble a normal labrum in form. Possibly, therefore, it is an independent development, not homologous to a true labrum.

The large size of the intercoxal piece and the wide separation of the hind coxae appear to be interrelated, since the intercoxal piece serves to fill space between the coxae. The aberrant carabid, *Gehringia olympica* Darlington, also has hind coxae that are widely separated, and has an equally broad intercoxal piece. In *Gehringia*, the coxae, though separated, are relatively large and the abdomen is not elongate. Consequently, the intercoxal piece, though broad, is relatively short. In the Rhysodidae, by contrast, the hind coxae are very small and the abdomen is elongate. The intercoxal piece, in consequence, is broad and long.

If the size of the intercoxal piece is a result of the placement of the hind coxae, it becomes important to decide whether contiguous or widely separated hind coxae are the more primitive. If separated coxae were the more primitive kind, Rhysodidae and *Gehringia* would be the most primitive Adephaga. The Cychrini then would occupy an intermediate position between them and the majority of the suborder. If the reverse were true, the widely separated coxae of *Gehringia* and Rhysodidae would be the result of parallel evolution.

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However, evidence suggests that contiguous hind coxae are more primitive than separated ones. In the neuropteroid orders, all pairs of coxae are nearly or quite contiguous at the midline. In these orders the coxae are not retracted into coxal cavities. Since the Coleoptera probably evolved from a neuropteroid ancestor, it is reasonable to suppose that the coxal cavities developed around coxae which were contiguous at the midline. These cavities were confluent internally, but their external openings were separated by the junction of median processes from preceding and following sternites. In the Nebriini and Carabini, all three pairs of coxal cavities are still in this condition. These two tribes are usually considered to be among the most primitive Carabidae because of their open anterior coxal cavities, the simple form of the antenna cleaner, and the generalized character of the male genitalia. None of the Adephaga which were dissected have all three pairs of coxal cavities separated although most have one pair separated and a few have two pairs separated. The middle coxal cavities seem to be the most conservative. Only in *Metrius contractus* Eschscholtz are the middle coxal cavities truly separated by a relatively thin internal partition. By contrast, the majority of the Adephaga have the anterior coxal cavities slightly separated. As pointed out by Sloane (1923), the left and right coxal cavities are separated by a plate in all those Carabidae having closed anterior cavities, excepting the Omophronini. A similar separation exists in the Rhysodidae. Slightly separated posterior cavities occur in the Cychrini; and widely separated ones in Rhysodidae and *Gehringia*. *Metrius* and the Rhysodidae are the only groups known to us in which two pairs of cavities are separated (in *Metrius* the front and middle pairs, and in Rhysodidae the front and hind pairs). Thus it appears that the wide separation of the hind coxae is a derivative and not a primitive condition.

The extremely simple form of the metendosternite of Rhysodidae could also be a secondary condition. In a typical carabid such as *Nebria* (Fig. 3) the endosternite extends the whole length of the metasternum. At its anterior end it bifurcates, forming the "anterior arms" of Crowson. The latter make contact with the rear wall of the middle coxal cavities. Posteriorly, the metendosternite gives off a pair of lateral branches which parallel the anterior margin of the hind coxae. These antecoxal branches terminate laterally without making contact with the edge of the sternum. The position of the antecoxal branches shows externally as the antecoxal suture. In *Gehringia* (Fig. 4) the metendosternite is much shorter, and the "anterior arms," although well developed, lie far posterior to the middle coxal cavity. The antecoxal branches are well developed but are recurved so that they make contact with the suture between the metasternum and the hind coxae, producing what appears to be a pair of distinct sclerites. The shortening of the metendosternite in *Gehringia* might be the first stage of its reduction. In Rhysodidae the reduction has proceeded much further. The "anterior arms" are entirely absent. The endosternite itself is reduced to a shallow ridge on the inner surface of the metasternum. In *Rhysodes americanus* Laporte (Fig. 5) there are vestiges of the antecoxal branches in the form of a slight widening of the endosternite at the level where antecoxal branches would be expected to arise. In *Clinidium sculptile* Newman, antecoxal branches are entirely absent. Many polyphagous beetles

have a well-developed metendosternite and, as shown in Crowson's figures, it is often similar in form to that of *Nebria*. We believe, therefore, that the simple metendosternite of Rhysodidae is a result of a process of reduction which has begun also in *Gehringia*.

Crowson's theory that the bark-dwelling habits of Rhysodidae are primitive is based on two suppositions—that the Coleoptera first evolved in this habitat and that the distinctive features of the Adephaga were originally adaptations to life under bark. His evidence for the first point is based largely on the structure and habits of the Cupedidae, which are generally conceded to be the most primitive living beetles. He presents a convincing argument that the evolution of elytra would be likely to occur in a bark-inhabiting insect. However, even if the earliest beetles lived under bark, it does not necessarily follow that all those beetles living today have been bark dwellers throughout their evolutionary history. Bark-dwelling is certainly secondary in the carabids *Morion*, *Helluomorpha*, and *Ardistomis*, which are derived, respectively, from Pterostichini, Lebiini, and Scaritini.

There are a number of features of Rhysodidae which are highly specialized and which could not have been present in the ancestors of other adephagous beetles. The most prominent of these are the features of the mouthparts. The maxillae are extremely reduced and are retracted into pockets in the dorsal face of the mentum. The ligula and labial palpi are likewise very small and are similarly concealed. The well-developed maxillae and ligula of a typical carabid approximate much more closely what one might expect of an ancestral Adephagan. Even if the bark-dwelling habits of Rhysodidae were primitive, their feeding mechanism certainly is not.

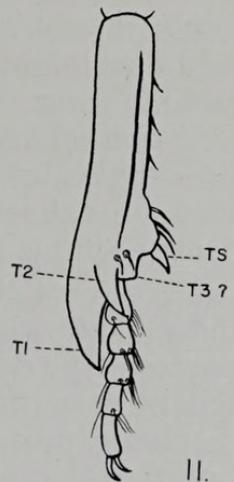
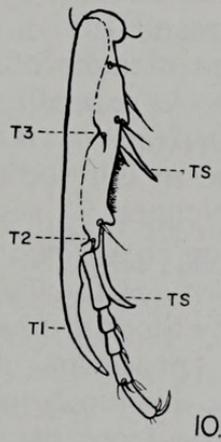
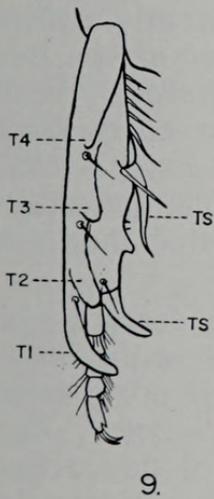
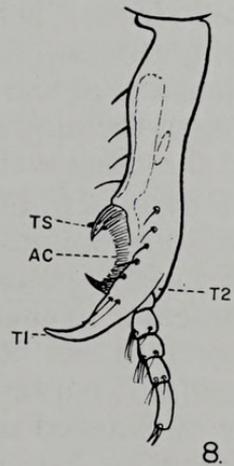
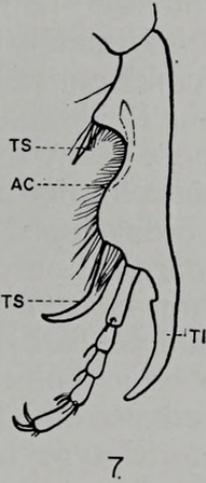
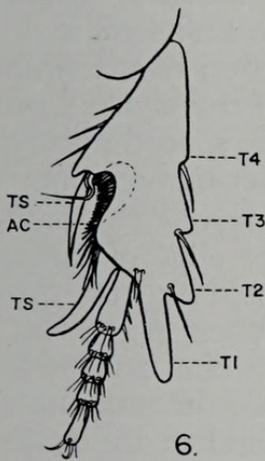
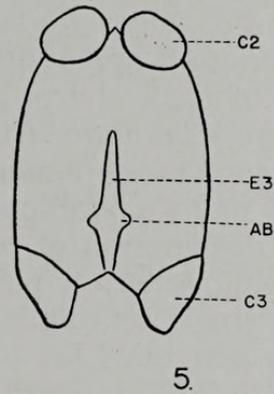
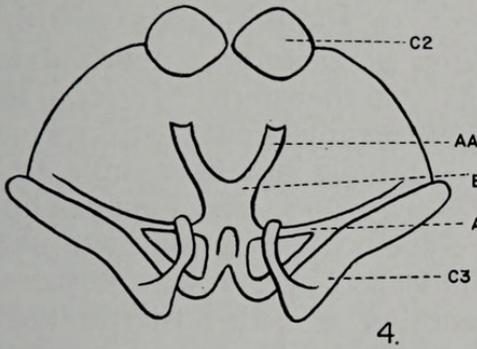
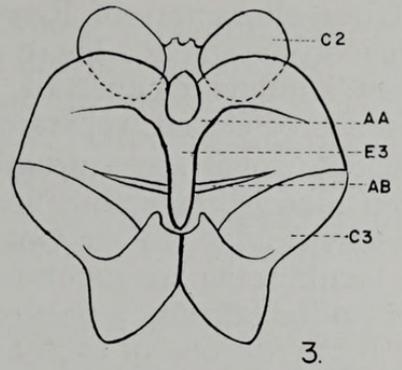
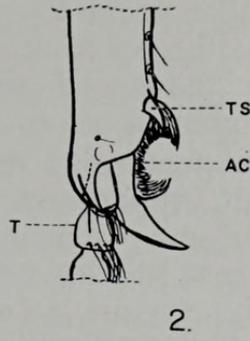
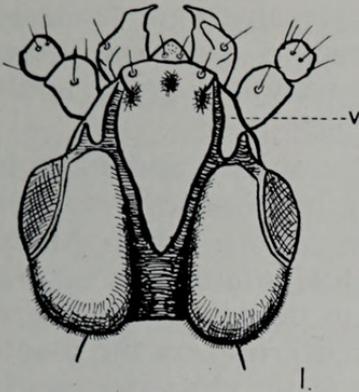
The most distinctive structural characteristic of the suborder Adephaga is the immobilization of the hind coxae which are functionally part of the body wall rather than of the legs. The hind coxae of Rhysodidae differ from those of other Adephaga only in their small size and in their lateral displacement. Crowson feels that the immobilization of the hind coxae can not be explained as an adaptation for running. He concluded that the ancestral Adephagan was unable to move the hind coxa while in confined spaces and subsequently lost the ability to do so.

We believe that the structure of the hind coxae of the adephagous beetles can be explained as adaptations to cursorial locomotion. It is instructive to compare the adaptations of adephagous beetles to those of an unrelated groups of running animals, the ungulate mammals. As summarized by Frechkop (1955), two basic features characterize the legs of cursorial ungulates: firstly, a specialization of the front legs for carrying the body weight and of the hind legs for supplying the thrust, and, secondly, a reduction in possible leg movements. The differences in function are reflected in strong anatomical differences of front and hind legs. The bones and muscles of the legs are modified so as to restrict the possible movements to those of direct use in running. The loss of the ability to rotate the feet makes the ungulate limbs of little use in climbing or feeding, but confers an advantage in running since muscular power is not needed to hold the legs in the proper position.

We believe that the adaptations of the Carabidae parallel those of the ungulates, and that the legs of all other adepagous beetles were derived from modifications of legs of the carabid type. The hind leg of a carabid is strongly differentiated from the other legs in its function. The hind coxa is fixed in such a position that the femur moves in an anteroposterior direction with the tibia directed largely rearward, and only slightly downward. Thus the hind leg is of very little use in supporting the animal's weight. It is, however, exceedingly effective in running because the rearward movement of the leg is almost entirely translated into the forward thrust of the body. Unlike those of other beetles, the hind leg of Adepaga has very little ability to rotate forward, an ability not needed in running but possibly of considerable importance in climbing. A slight degree of rotation is possible because of the oblique joint between femur and trochanter. The immobilization of the hind coxa thus may be regarded as analogous to the fusion of the tibia and fibula in the ungulate hind leg. It results in an increase in the efficiency of propulsion with a sacrifice of versatility. In contrast, the highly mobile coxae of the front and middle legs are capable of rapid rotation around a vertical axis. They are thus well adapted for the complex movements necessary for the support and balance of the body during rapid locomotion, often over irregular surfaces. It is true, of course, that not all cursorial beetles show these adaptations, but the Adepaga contain a very high proportion of those beetles which are able to run fast. Rapid locomotion apparently has been achieved by other means in the few cursorial Polyphaga, such as Staphylinidae.

The special features of the rhyssodid hind coxa can be explained as adaptations of the carabid coxa to a relatively sedentary life in narrow tunnels. The few observations which we have made on living rhyssodids indicate that they are incapable of rapid motion. Judging from the small size of the hind coxae, the musculature of the hind legs must be much reduced. The lateral migration of the hind coxae has the effect of shifting the legs to a more vertical position. This makes it possible for the hind legs to play a greater role in supporting the body. Since the femora project less laterally, the leg is less restricted in its movements within narrow confined places. *Gehringia* also seems to be adapted for slow locomotion in confined spaces, in this case in gravel beds rather than under bark. The few collectors who have taken it have commented on its sluggish movements (Lindroth, 1961).

FIG. 1—*Clinidium sculptile* Newman, dorsal view of head; V—possible vestige of frontal plate. FIG. 2—*Clinidium sculptile*, posterior view of left anterior tibia; TS—tibial spur, AC—antenna cleaner, T—base of tarsus. FIG. 3—*Nebria pallipes* Say, dorsal view of metasternum; AB—antecoxal branch, AA—"anterior arm," C2—mesocoxal cavity, C3—metacoxal cavity, E3—metendosternite. FIG. 4—*Gehringia olympica* Darlington, dorsal view of metasternum; abbreviations as in Fig. 3. FIG. 5—*Rhyssodes americanus* Laporte, dorsal view of metasternum; abbreviations as in Fig. 3. FIG. 6—*Clivina bipustulata* (Fab.), anterior view of tibia and tarsus of left front leg; AC—antenna cleaner, TS—tibial spur, T1—apical tooth, T2,3,4—lateral teeth. FIG. 7—*Dyschirius sphaericollis* Say, view and abbreviations as in Fig. 6. FIG. 8—*Clinidium sculptile*, view and abbreviations as in Fig. 6. FIG. 9—*Clivina bipustulata*, posterolateral view of tibia and tarsus of left front leg; abbreviations as in Fig. 6. FIG. 10—*Dyschirius sphaericollis*, posterolateral view of tibia and tarsus of left front leg; abbreviations as in Fig. 6. FIG. 11—*Clinidium sculptile*, posterolateral view of tibia and tarsus of left front leg; abbreviations as in Fig. 6.



Three characters of Rhysodidae seem to indicate an origin from some group of Carabidae. These are: the presence of tactile setae, the presence of an antenna cleaner of the "advanced anisochaetous" type, and the presence of closed, separated anterior coxal cavities.

Tactile setae are a prominent feature of the Carabidae and have been much used in their classification. Apparently they have gone unnoticed in the Rhysodidae. In the two rhysodids occurring in eastern North America, the tactile setae are much reduced. In *Clinidium sculptile* they consist of a pair on the labrum, a pair on the clypeus, a pair on the last visible sternite, one on the scrobe of each mandible, and a scattered group on the mentum. In some specimens, at least, there is also a seta at the posterior angle of the pronotum. *Rhysodes americanus* has the same setae except that those on the pronotum apparently are absent. In addition, there are three setae at the tip of each elytron. In *Clinidium mexicanum* Chevrolat and in an unidentified *Clinidium* from Chiapas, southeastern Mexico, the tactile setae are much more numerous, and their arrangement is strongly suggestive of that of many Carabidae. As yet, we have not been able to study in detail the distribution of setae in *C. mexicanum*. The Chiapas species has the following setae: a pair on the clypeus, apparently two pair on the labrum, a single seta above and behind each eye, a seta at the middle of the lateral margin of the pronotum, another at each posterior angle, a pair on the last visible sternite, and a very well-developed series on the elytra. The elytral setae, like those of many carabids, are situated in the odd-numbered striae. There are approximately four in the first stria, five in the third stria, at least one in the confluent posterior portion of the fourth and fifth striae, and at least five along the lateral margin of the elytron, probably belonging to the ninth stria. Those of the third stria are placed evenly, while those of the other striae are concentrated in the posterior portion.

The Rhysodidae have a well-developed antenna cleaner consisting of a comb of hairs bounding an emargination on the inner edge of the anterior tibia (Fig. 2). On the posterior face of the tibia near the proximal end of the antenna cleaner is a small peglike structure. When cleared in KOH, this projection can be seen to be a separate sclerite. This and its location indicate that it is probably a reduced tibial spur. If so, the antenna cleaner is of the "advanced anisochaetous" type which is found in the majority of the Carabidae. The apical tibial spur has completely disappeared. The "advanced anisochaetous" antenna cleaner has apparently evolved independently in several different lines of Carabidae, so that its evolution in Rhysodidae might be the result of convergence. However, practically all Carabidae have an antenna cleaner of one type or another, and the "advanced anisochaetous" type is generally thought to have been derived from the simple type found in *Nebria* and *Carabus*. The presence of an "advanced anisochaetous" type in Rhysodidae implies that their ancestors had at least a simple antenna cleaner.

The structure of the anterior coxal cavity is another feature which the Rhysodidae share with a majority of the Carabidae. It is of the fully closed and separated type described by Sloane. The left and right coxal cavities are separated by a vertical plate (prosternal declivity of Sloane). The coxal cavity is closed posteriorly by the junction of the tip of the proepimeron with a postcoxal process arising from the top of the prosternal declivity.

Together they form a postcoxal bar. In Bembidiini, Elaphrini, Patrobini, and certain other tribes the tip of the proepimeron merely fits into a shallow concavity in the postcoxal process of the prosternum. In the Rhysodidae, as well as in the Scaritini, Cicindelini, Harpalini, Pterostichini, and many other tribes, a firm suture has developed. The tip of the proepimeron is dilated to form a ball or disc. It is exactly fitted into a deep concavity in the postcoxal process. The orifice of the cavity is more or less narrowed to fit the neck of the proepimeron.

It is next proper to ask whether the Rhysodidae can be shown to be related to any particular tribe of Carabidae. In general appearance the Rhysodidae resemble most closely some members of the Scaritini. If they were included in the Carabidae, the rhysoids would trace to Scaritini in Sloane's key. A number of features suggest that this resemblance is not simply a result of convergence. In both groups the anterior tibia is denticulate and has a large apical tooth extending well distad to the insertion of the tarsus. Additional common features are an "advanced anisochaetous" antenna cleaner, disjunct middle coxal cavities, closed and separate anterior coxal cavities with a ball-and-socket suture, and the concealment of the dorsal condyle of the mandible beneath the lateral margin of the clypeus.

In most Scaritini the teeth of the anterior tibia form a row along the lateral margin, and the apical one is curved outward (Figs. 6, 9). In the Rhysodidae the anterior tibia is superficially different (Figs. 8, 11). There are two teeth at the apex, the anterior one being the larger. Both arise at the lateral margin and curve inward, with the tarsus appearing to arise between them. On the posterior surface of the tibia there is a small projection which may represent a rudimentary third tooth. Some species of *Dyschirius* (Figs. 7, 10) show how the rhysoid tibia could have originated from the scaritine type. In *Dyschirius sphaericollis* Say the apical tooth is curved inward rather than outward as in other scaritines. The other teeth of the tibia have migrated to the posterior face and are invisible in anterior view. If the most distal of these teeth were elongated parallel to the apical tooth, the result would be a tibia very similar to that of the rhysoid.

There are several features in which scaritines and rhysoids do not agree. In the Scaritini there is a well-developed frontal plate above the base of the antenna. In the Rhysodidae such a plate is absent, although there is a small swelling above the base of the antenna which might represent a vestige of the frontal plate (Fig. 1). The metepimeron is totally absent from the Rhysodidae, while it is visible as a distinct sclerite in a vast majority of the Scaritini. The mesothorax is strongly constricted and the body pedunculate in Scaritini while the waist is broad in the Rhysodidae. Finally, the scrobal seta, which is present in the Rhysodidae, is absent in the Scaritini.

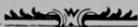
Possibly the Rhysodidae are a highly modified offshoot of the Scaritini. If so, the broad waist and the loss of the frontal plate are secondary modifications. The retention of the mandibular seta is less compatible with an origin from the Scaritini. It is possible that the seta was lost independently by all the surviving genera of Scaritini at some time after the Rhysodidae originated. The more likely explanation is that the Scaritini and Rhysodidae arose from a common ancestor which was basically like a scaritine but

had mandibular setae and possibly lacked the narrowed waist and the frontal plate.

In our view, the Rhysodidae represent a specialized offshoot of the Carabidae. Those coleopterists who prefer to regard the Cicindelidae, Omophronidae, and other highly modified carabids as separate families will probably wish to retain the family rank of the Rhysodidae, also. Those who wish to follow the more natural classification and who reduce the aforementioned to the rank of subfamily or tribe should follow the same course with the Rhysodidae. There is some evidence of a relationship between the Rhysodidae and the Scaritini but it is not sufficiently strong to justify uniting the two. We suggest instead that the Rhysodidae be regarded as a tribe, Rhysodini, of the Carabidae, to be placed next to the Scaritini.

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BOOK NOTICE

THE GROUND-BEETLES (CARABIDAE, EXCL. CICINDELINAE) OF CANADA AND ALASKA, part 2, by Carl H. Lindroth, Opuscula Entomologica, supplementum 20, 200 pp., 1961—The readers of the *Bulletin* are well aware already of the outstanding work of Carl Lindroth. It is sufficient that he is the author to know the value of the work. The present volume represents the first of a projected treatment of this large beetle family, especially well represented in the northern half of North America. (Part I will be published as a final volume of the five proposed, with keys to genera, introduction, and other information.) The present volume, complete with specific keys and descriptions, locality data, and 101 figures covers the subfamily Trachypachinae through tribe Trechini. Future parts will be announced as received.



Bell, Ross T. and Bell, Joyce R. 1962. "The Taxonomic Position of the Rhysodidae (Coleoptera)." *The Coleopterists' Bulletin* 16(4), 99–106.

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