

PHYLOGENETIC RELATIONSHIPS OF THE TRIGONOTARBIDA, AN EXTINCT ORDER OF ARACHNIDS

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The arachnid Order Trigonotarbida (Middle Devonian, Middle to Late Carboniferous) was established by PETRUNKEVITCH in 1949, by separating from the Order Anthracomartida all those species with each tergite divided into three transverse plates rather than five. Despite this very obvious difference between the two groups, PETRUNKEVITCH chose instead to emphasize the manner of attachment of the abdomen to the cephalothorax. In Anthracomartida he retained those forms in which the attachment appeared to be across the full width of the first abdominal tergite, while in Trigonotarbida he placed what appeared to him to be a potpourri of genera with the attachment "...either by the full width of the carapace or only by a median portion of it, while the width of the first tergite remains that of the carapace (PETRUNKEVITCH, 1949, p. 235)." He also stated that anthracomartids had ten segments in the abdomen, while in trigonotarbid the number appeared to vary from eight to eleven.

More puzzling is the fact that PETRUNKEVITCH considered these characters so important (even though he stated that "...certain characters [of Trigonotarbida] were still in a labile condition when its representatives faced extinction [ibid., p. 234].") that he placed the Order Trigonotarbida alone in its own Subclass Soluta. (His arrangement of the chelicerates into subclasses, based on the manner of transition from prosoma to opisthosoma, the arrangement of the coxae, and the segmentation of the abdomen, has not been accepted by subsequent workers.)

Based on our work on the Devonian forms, we have composed a new diagnosis and description of the order, which follows:

Order TRIGONOTARBIDA Petrunkevitch 1949

DIAGNOSIS

Fossil Order of Chelicerata with abdominal tergites divided into broad median plates and narrower lateral plates; book lungs present; chelicerae of the "clasp-knife" type. Fossil Araneae, Amblypygi, and Uropygi have undivided abdominal tergites; in the related Anthracomartida, the tergites are divided into five transverse plates.

DESCRIPTION

Fossil terrestrial Chelicerata with abdomen and cephalothorax broadly joined. Abdomen with 11 segments, last two (sometimes?) reduced a short pygidium. Carapace entire, eyes various, either entirely absent, or median pair alone present, or median pair and lateral reduced compound eyes with major and minor lenses present. Cephalothoracic sternum entire, labium not seen. Abdominal tergites divided by two sutures slightly converging posteriorly, so that each tergite consists of a broad median plate and two

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narrower lateral plates; arrangement tending to become arcuate posteriorly as lateral plates are displaced posteriorly. First tergite partly concealed beneath carapace. Second and third tergites fused. Ninth tergite and sternite fused, biconvex around posterior end of abdomen, with socket for two-segmented pygidium. Sternites entire. Booklungs present on second and third segments of abdomen. Genitalia (?) medial on abdominal segment two. Anus not operaculate. Chelicerae two-segmented, fang-like distal segment closing on ventral edge of basal segment ("clasp-knife" type), basal segment with strong teeth. Palpal coxae with endites; palpi six-segmented, lacking metatarsus. Legs seven-segmented, trochanter single, patella present, tarsi of some legs may have false articulations. Paired claws set on apotele; apotele tip prolonged into median claw. Devonian (Siegenian) to Carboniferous (Stephanian).

The above diagnosis and description differ in a number of details from that originally given by PETRUNKEVITCH in 1949, and emended by him in 1953 and 1955. At least some of PETRUNKEVITCH's errors were due to the fact that he did not carefully study the Rhynie material with its superb preservation, and paid little attention to HIRST's excellent 1922 descriptions.

Despite the clear depiction by HIRST (1922) of lateral eyes with major and minor lenses for *Palaeocharinus*, PETRUNKEVITCH (1955) referred only to the median eyes, and called the lateral eyes "lateral organs." He missed the significance of the partly concealed first abdominal tergite, and though he correctly described the second and third tergites as fused in Anthracomartida, he failed to extend his analysis to the related Trigonotarbitida. He also provided different interpretations of the ninth tergite and sternite for different genera, which led him to believe that there existed in this order a variable number of abdominal segments. Our interpretation gives a consistent number (11) for all genera, although the presence of a pygidium of two segments requires verification for the Carboniferous forms. We think PETRUNKEVITCH misinterpreted this structure as a two-part (anterior/posterior) anal operculum.

We found no evidence in material from Gilboa (Givetian), in that from Rhynie (Siegenian), or in published photographs of Carboniferous specimens, for the presence of a labium, or for more than two pairs of book lungs.

Neither PETRUNKEVITCH nor HIRST detected the small median claw, present in our specimens from Gilboa and in *Palaeocharinus* from Rhynie.

We are not sure that Trigonotarbitida can be maintained as a separate order from Anthracomartida, from which it was carved by PETRUNKEVITCH in 1949. The most obvious difference (as we have stated) seems to be the division in the Anthracomartida of the tergites into five rather than three separate plates. PETRUNKEVITCH's claim that the chelicerae of the Anthracomartida are three-segmented and chelate could not be verified from the literature, or from a cursory examination of some moderately well-preserved specimens. In 1913, PETRUNKEVITCH had no information on the chelicerae of the Anthracomartida. In 1949 he described them as three-segmented and chelate, but provided no photographic evidence, and his drawings permit several interpretations—in no case are all three segments shown together, and each seems more consistently interpreted as showing typical "clasp-knife" chelicerae. By 1955, he had retreated from his position somewhat by asserting that at best only the basal two segments were present and the existence of a third was to be inferred from "articular surfaces" on the second. The second segments illustrated by PETRUNKEVITCH are shaped exactly like strong cheliceral fangs; the "articular surfaces" are not shown. The supposed differences in abdominal segmentation between the two groups and within the trigonotarbitids seem to be entirely due to PETRUNKEVITCH's misinterpretations.

The remaining differences between the two orders are no greater than those that separate suborders (or even families) of spiders. They lie primarily in body shape, the number of divisions of the tergites, and the numbers of eyes. A careful review of the

Carboniferous material of both nominal orders should provide an answer to this dilemma. In view of this uncertainty, we do not think it prudent at this time to discuss the various families of trigonotarbid that have been named. At least some of the generally accepted names are not valid (SELDEN and ROMANO, 1985).

Most recent thinking on arachnid phylogeny recognizes a monophyletic unit including Araneae, Amblypygi, Uropygi, and Schizomida. FIRSTMAN (1973) included this group in his "Pulmonata", which taxon, as it also included Scorpionida, is not monophyletic. Further, it is opposed to "Apulmonata," including all the other arachnid orders, likewise probably not a monophyletic group at that level. FIRSTMAN's conclusions were based primarily on the relationship of the arterial system, nervous system, and endosternite—information not available for fossil forms. However, because of the clear indications of the presence of lungs in some fossil orders, FIRSTMAN placed Trigonotarbida, Anthracomartida, Haptopoda, and Kustarachnida with his pulmonates; we agree with this inference.

VAN der HAMMEN (1977) considered a wider range of characters, giving weight to cheliceral form, leg structure (especially the patterns of articulation), and respiratory organs. He recognized a Class Arachnidea including the Orders Araneae, Amblypygi, Uropygi, Schizomida and Trigonotarbida, while declining to place Haptopoda and Anthracomartida because of a lack of information about the characters he used. VAN der HAMMEN's Arachnidea seems to us to be a monophyletic unit characterized by the "clasp-knife" chelicerae and the specialized rocking joints between patellae and tibiae. Both these characters are present in the Devonian trigonotarbids from Gilboa and Rhynie (SHEAR, BONAMO, GRIERSON, ROLFE, SMITH, and NORTON, 1984; SHEAR, SELDEN, ROLFE, BONAMO and GRIERSON, in prep.). VAN der HAMMEN defers extensive discussion of the relationships of his new classes of Chelicerata pending the completion of his meticulous studies of each group.

WEYGOLDT and PAULUS (1979) made an exhaustive survey of the characters of chelicerates and treated them cladistically. As did VAN der HAMMEN, they associated Araneae, Amblypygi, and Uropygi (including Schizomida) in a (Subclass?) Megoperculata, using as key synapomorphies the cheliceral form and the presence of a 9+3 arrangement of microtubules in the sperm flagellum. They also found no reason not to consider the apulmonate terrestrial chelicerates monophyletic. They discussed the extinct orders only briefly and did not attempt to place them in their cladogram.

In an idiosyncratic (but in many ways penetrating) analysis, GRASSHOFF (1978) reached similar conclusions: his unit 26 includes the same orders as those placed by VAN der HAMMEN in his own Arachnidea, and the living orders grouped by WEYGOLDT and PAULUS in their Megoperculata. No attempt was made to place Anthracomartida or Haptopoda.

Thus the consensus view, with which we concur, is that Araneae + Amblypygi + Uropygi + Schizomida + Trigonotarbida form a monophyletic unit. While Haptopoda, Kustarachnida, and Anthracomartida cannot at this time be confidently included, we hypothesize that detailed study of these extinct groups will verify FIRSTMAN's (1973) intuitive inclusion of them in Arachnidea *sensu* VAN der HAMMEN.

WEYGOLDT and PAULUS (1979) consider Uropygi (which in their view includes Schizomida; we prefer to keep this order separate) the sister group of Amblypygi + Araneae. For the former, synapomorphies include the presence of a prenympal and 4 nymphal stages, use of an abdominal embrace in mating, and the presence of a camero-stome, the ventral wall of which is formed by the pedipalpal coxae (this latter character was evidently also present in the extinct kustarachnids). For the latter, the pedicel and a well developed posterior sucking stomach serve as synapomorphies.

As has so often been noted, each of the arachnid orders has abundant autapomorphies, and Trigonotarbida is no exception. The most obvious specializations are the three-fold division of the tergites, fusion of tergites 2 and 3 (SELDEN and ROMANO, 1985), and

a special locking mechanism between cephalothorax and abdomen, which we will describe fully in a later report. Trigonotarbid, however, seem to be much more generalized arachnids than any of the others in the group. For example, they retain vestiges of the compound lateral eye from which the indirect lateral eyes of the other orders are evidently derived (PAULUS, 1979), and their coxae are more or less unmodified (except for a poorly developed endite on the palpal coxa).

The exact position of the trigonotarbid in this group is difficult to settle. Behavioral characteristics are not available for fossils unless they leave some sort of permanent record (or are suggested by anatomy), internal structures are rarely preserved, and developmental sequences are difficult to work out from scanty fossil material in which several species are likely to be mixed. Despite our detailed studies of the external structure of the extraordinarily well-preserved Devonian *Gilboa* and Rhynie trigonotarbid, we are unable to find any synapomorphic characters that would relate them more closely to one or the other of the pulmonate orders (those in VAN der HAMMEN's Arachnidea, WEYGOLDT and PAULUS's Megoperculata). More information therefore may be required before trigonotarbid can be placed in their proper position with regard to the related orders. Intensive restudy is needed of the Carboniferous forms (which in many respects seem quite different from the Devonian ones) and of the related groups Anthracomartida and Haptopoda, in the light of the new interpretations provided here.

For the present, our cladogram (fig. 1) places the Trigonotarbid as the sister group of all other Arachnidea taken together

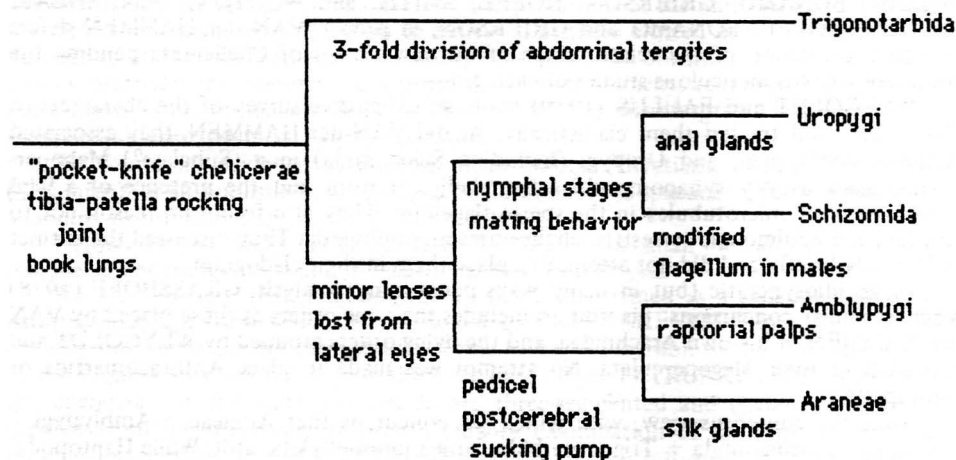


Fig. 1. Cladogram of Arachnidea *sensu* VAN der HAMMEN. Other autapomorphies of living orders can be found in VAN der HAMMEN (1977) and in WEYGOLDT and PAULUS (1979).

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SUMMARY

A new diagnosis of the Order Trigonotarbitida is supplied, though doubt is expressed concerning its distinctness from the Order Anthracomartida (older name). Errors in the descriptions of trigonotarbitids by PETRUNKEVITCH are pointed out. The order is clearly a member of the Class Arachnidea, as established by VAN der HAMMEN (1977); this class probably also includes the extinct Orders Anthracomartida, Haptopoda, and Kustarachnida, but these must be restudied to confirm this placement.