

Revision of the fossil ricinuleids

Paul A. Selden

ABSTRACT: The fossil ricinuleids are described, and their systematic relationships revised, based on a study of all British and American specimens. Phylogenetic analysis, utilising a new character set, indicates a probable basal dichotomy between the fossil and extant forms. The order is divided into two new suborders: Neoricinulei subordo, nov., for the extant genera, and Palaeoricinulei subordo, nov., for the fossil forms. Two new genera are erected: *Amarixys* gen. nov. for *Curculioides gracilis* (Petrunkevitch, 1945) and *A. stellaris* sp. nov., and *Terpsicroton* gen. nov. for *Poliochera alticeps* Pocock, 1911. Three new species are erected in the genus *Curculioides*: *C. mcluckiei* sp. nov., *C. pococki* sp. nov., and *C. gigas* sp. nov., and one in the genus *Poliochera*: *P. gibbsi*, sp. nov.

KEY WORDS: Arachnida, arthropod, Carboniferous, Chelicerata, morphology, Namurian, palaeobiogeography, Pennsylvanian, phylogeny, systematics, taxonomy, Westphalian.



In recent years, much new information on living ricinuleids has become available, necessitating a review of the functional morphology and phylogeny of the fossils. Furthermore, the holotype of *Curculioides ansticii* Buckland, 1837, the first described ricinuleid, has been rediscovered (Torrens 1981, 1982), and new fossil material has come to light, so that the total number of fossil ricinuleids now known is 25 specimens.

The systematic work of Petrunkevitch (1913, 1945, 1949, 1955) has proved to be erroneous in many respects, so that new descriptions and taxonomic revision are necessary. For example, he asserted that the fossil ricinuleids lacked eyes, presumably based on the fact that living ricinuleids lack eyes (although they have an area of thin cuticle on the lateral edge of the carapace which is thought to be light-sensitive), yet a pair of eyes is present on each side of the carapace in nearly every fossil studied. These organs are visible in Petrunkevitch's photographs (e.g. 1913, pl. VII, fig. 38), but he made no mention of them in the text. Nearly all of the criteria used by Petrunkevitch to separate the species of fossil ricinuleids is based on characters which are subject to taphonomic distortion: the width of the carapace for example (see below). Petrunkevitch commonly confused ridges and furrows between descriptions of the same specimen (a good example of this was described for the trigonotarbid *Aphantomartus* in Selden & Romano 1983), because of the effects of internal and external moulds.

Therefore, new descriptions are given here. Discussion of the differences between the new descriptions and the older excludes minor corrections to measurements: the width of the carapace for example. In the present work, the characters used are different from those on which Petrunkevitch based his taxonomy, and whereas the current taxonomic system of fossil ricinuleids presented here is far from satisfactory, it is hoped the new taxobases will be more useful in the future. Resulting from the fossil study, a phylogenetic analysis of all ricinuleids is presented, including a cladogram (Fig. 2) illustrating the hypothesis of relationships among fossil species and modern genera based on the new work.

1. Age and provenance of the fossils

All known fossil ricinuleids are Carboniferous in age; the oldest is *Curculioides adompha* Brauckmann, 1987, from rocks of upper Namurian B age of the Ruhr area, Germany. All other fossil ricinuleids are Westphalian in age. One doubtful specimen, called '*Poliochera vel Curculioides pustulatus*' by Laurentiaux-Vieira and Laurentiaux (1963), comes from near Beijing, China; all other Westphalian ricinuleids are from the U.S.A. and England. *C. ansticii* is from Coalbrookdale, Shropshire, and Sedgley, Worcestershire, single *Curculioides* specimens are known from Ilkeston, Derbyshire, and Ryton-on-Tyne, Tyne and Wear, and the other four British specimens are from Coseley, West Midlands; all are Westphalian B in age. All American fossil ricinuleids are from Mazon Creek, Illinois (Westphalian D, Pfefferkorn 1979), except one, which is from near Morris, Oklahoma.

2. Sedimentary environment and preservation

The sedimentary environment in which the fossil ricinuleids occur, in both the European and American situations, is one of a delta. The fossils occur in concretions within shales, and in all localities well studied (e.g. Mazon Creek, Richardson & Johnson 1971) these shales include upright trees or other evidence of rapid deposition in an otherwise low energy situation, such as a flood basin fed by crevasse splays or storm surges.

All specimens studied are preserved in ironstone nodules composed of clays and siderite, weathered to a greater or lesser extent to haematite and limonite (see Woodland & Stenstrom 1979; Woodland 1985). The majority are preserved as external moulds, but in some cases internal moulds of part of the specimen are present. Kaolinite, and in some cases, calcite and pyrite, forms a natural cast of the cuticle of most specimens, and this material has been scraped out in order to reveal the morphological details preserved on the mould surfaces. Where both internal and

external mould are present, as on PE 784, features of the internal surface of the cuticle can be seen, which give evidence for the nature of the cuticle (see Section 5.1). Though preserved in three dimensions, the fossils are distorted in a number of ways. The prosoma is commonly slightly separated from, and rotated relative to, the opisthosoma (abdomen), though the two body parts were probably still attached by the pedicel in death. The cuticle of both carapace and abdomen is commonly crumpled, that of the abdomen of *Curculioides*, in particular, bears longitudinal folds which suggest a rather flexible, perhaps leathery, cuticle in life or at the time of death. The carapace outline appears, at first sight, to be readily discernible, but careful probing at the lateral edges on most specimens reveals that the carapace has actually been compressed between the leg trochanters, so that the apparent lateral edges of the carapace are really artefacts of this compression; the true lateral borders lie further beyond. The walking legs are normally outstretched so that their ends reach the periphery of the nodule, where preservation is poor. The pedipalp, when found, is flexed beneath the body, and is thus rarely preserved complete.

Living ricinuleids are terrestrial, and the fossil animals are presumed to have been also, so the preservation of fossil animals in a deltaic situation implies they are allochthonous. It is uncertain whether the fossils represent dead animals or exuviae; if the latter, then it is likely that only juveniles have been preserved since adult moulting is unknown in ricinuleids. There is no evidence that any specimen is a moult; the manner of moulting of living ricinuleids (knowledge of which would give signs of moulting to search for in fossils) has not been reported in the literature, and there are no obvious signs of moulting (e.g. displaced carapace) on any of the specimens. However, in many of the specimens the locking device between prosoma and opisthosoma is undone, the pygidium is extended, and the legs are always outstretched. Cooke (1967) observed that one cause of death in ricinuleids was desiccation, in which case the legs become closely infolded beneath the body; more frequently, he noted, failure to excrete excess water resulted in distention of the body, protrusion of the pygidium, and outstretching of the legs. If the fossils are indeed complete animals, and there are no obvious signs of them being exuviae, then it is likely that the cause of death was not desiccation, and may have been due to surplus water. Possibly they were not dead before being submerged in the river, but were killed by drowning in its flood.

3. Material and methods

For this study, all fossil ricinuleids in institutional collections, except the doubtful Beijing specimen and *Curculioides adompha* Brauckmann, 1987, were examined. Additional specimens from Mazon Creek are known to be in private collections, and one of these was seen in latex peel form (Pohl specimen). All British specimens are housed in the British Museum (Natural History), London (BM(NH)); American specimens are held in the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM). The Field Museum of Natural History, Chicago (FMNH), The Illinois State Museum, Springfield, Illinois (ISM), the Mazon Creek Project collection, Northeastern Illinois University, Chicago (MCP), and Museum of Paleontology, University of Michigan, Ann Arbor, Michigan (UMMP). Comparative extant material examined

included: *Cryptocellus lampeli* Cooke, 1967, Amatuk, Guyana, *Ricinoides afzelli* Thorell, 1892, Bo, Sierra Leone, (J. H. Kennaugh collection), *Cryptocellus* sp., Barro Colorado, Panama (author's collection), *Pseudocellus* sp., Gruta de Zapaluta, Trinitaria, Chiapas, Mexico (W. A. Shear collection).

Specimens were studied, drawn, and photographed using Wild M7S and Olympus SZH stereomicroscopes. Latex peels were useful for visualising the morphology of specimens preserved as external moulds, but not for detailed study. Indeed, fine rock-moulded structures can be lost by peeling with latex, and specimens should be carefully studied and photographed before any such potentially destructive technique is applied.

Carapace tubercle density was measured by making a camera lucida drawing of the tubercles at $\times 40$ magnification onto a 40 mm square drawn on the paper; the number of tubercles was then counted. A number of drawings were made from each specimen, from slightly differing areas of the carapace, to establish a mean figure. The drawings were made from the flattest area in the anterior part of the carapace, left and right of the median groove, and avoiding any distortion. Tubercle size was measured by making camera lucida drawings of tubercles from the same carapace areas as those used in the density measurements, at $\times 80$ magnification. Ten tubercles from each specimen were drawn, and each tubercle drawing was then measured across two axes, totalling 20 measurements for each specimen, and the mean figure was calculated for each specimen. In specimens in which major and minor tubercle sizes were discernible (e.g. *Curculioides gigas*), only the larger tubercles were used for comparative purposes.

Carapace length is, for most specimens, a fairly reliable measurement, since few specimens have suffered anteroposterior distortion. Carapace width is calculated by restoration: taking the width of the half of the carapace which is most fully preserved, and restoring the other half by production of a mirror image, taking into account any distortion as necessary. Abdomen lengths given in the descriptions were measured on the dorsal side (the ventral side is produced anteriorly between the coxae of leg 4). The measurement given for each podomere is the maximum length of the segment. Since the distal end of a podomere commonly overlaps the proximal end of the succeeding one, the length of the complete leg cannot be calculated by totalling the lengths of each podomere; however, an entire leg is not preserved on any ricinuleid specimen examined for this study.

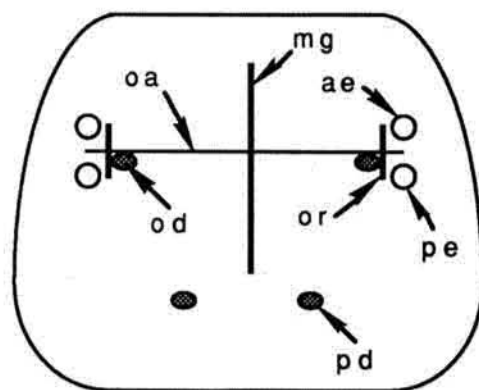


Figure 1 Diagram showing terminology of carapace features of fossil ricinuleids: (ae) anterior eye; (mg) median groove; (oa) ocular axis; (od) ocular depression; (or) ocular ridge; (pd) posterior depression; (pe) posterior eye.

