

# Revision of the fossil ricinuleids

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**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* (Petrunkévitch, 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 Petrunkévitch (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 Petrunkévitch'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 Petrunkévitch 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). Petrunkévitch 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 Petrunkévitch 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

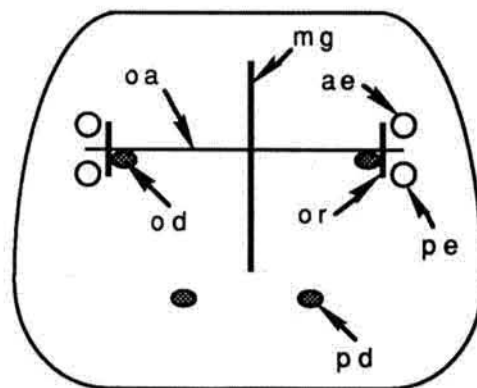
For this study, all fossil ricinuleids in institutional collections, except the doubtful Beijing specimen and *Curculioides adompha* Brauckmann, 1987, were examined. Additional specimens from Mazon Creek are known to be in private collections, and one of these was seen in latex peel form (Pohl specimen). 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.



The computer program MacClade 2.1 (Maddison & Maddison 1987) was used as an aid in the phylogenetic analysis.

**Terminology.** The terminology of Pittard and Mitchell (1972) is followed for the most part. The pedipalp podomeres are interpreted according to van der Hammen (1979, 1989); their coxae are fused to form an infracapitulum.

Terms introduced here for the first time (see Fig. 1) are: ocular axis, an imaginary line running from the left to right pairs of eyes, joining points mid-way between the two eyes of a pair; ocular depression, one of a pair of shallow pits, with small tubercles on its surface, situated median to the ocular ridge on the carapace; ocular ridge, the longitudinal ridge which runs just median to the eyes; posterior depression, one of a pair of shallow pits, with small tubercles on its surface, situated to one side of the midline about two-thirds of the way back from the anterior edge of the carapace. The ocular ratio is the fraction of the total carapace length that the ocular axis lies from the front of the carapace, expressed as a decimal (e.g. 0.33).

Abbreviations used in the text and on figures are as follows: 1, 2, 3, 4, walking legs 1, 2, 3, 4; a e, anterior eye; ab, abdomen; car, carapace; ch, chelicera; cx(1, 2, ...), coxa (of leg 1, 2, etc.); cuc, cucullus; fe, femur; gen, genital apparatus; i m, internal mould; icap, infracapitulum; m g, median groove; m line, median line, m sul, median sulcus; mt, metatarsus; o a, ocular axis; o d, ocular depression; o r, ocular ridge; p d, posterior depression; p e, posterior eye; pa, patella; ped, pedipalp; scap g, subcapitular gutter; t line, transverse line; ta, tarsus; tg, tergite; ti, tibia; tr<sup>(1,2)</sup>, trochanter (first, second, where necessary); tubs, large tubercles on inferoproximal side of tr<sup>1</sup>; v sul, ventral sulcus. Small arrows (»») represent holes in the specimens, podomeres disappearing into the matrix or folds of the abdominal cuticle for example. Enclosed, unornamented areas are tuberculate (coarse and fine tubercles are not distinguished). Fine stipple represents areas devoid of tubercles, which may be internal mould surfaces, arthrodial membranes, fine mineralisation, or pedipalp cuticle, for example. Coarse stipple represents mineralised areas; black areas are pyrite or deep cracks; these special ornaments are referred to in the figure legends where appropriate.

#### 4. Historical background

Prestwich (1834) mentioned some arthropods in W. Anstice's collection of ironstone nodules from the Coal Measures of Coalbrookdale, Shropshire, and later, Buckland (1837) described one of these specimens as a curculionid beetle, naming it *Curculioides ansticii*. One year later, the first living ricinuleid, *Cryptostemma westermanni* from West Africa, was described as a harvestman by Guérin-Méneville (1838). Westwood (1874) described the second living species, *Cryptocellus foedus*, from the Amazon, and established the family Cryptostemmidae for both living species. Scudder (1884) described the second fossil ricinuleid, *Poliochera punctulata*, from Mazon Creek, and placed it in the new family Poliocheridae of the Anthracomarti. Scudder (1884, 1886) also suggested that *Curculioides ansticii* Buckland belonged with the arachnids, and was probably an *Architarbus subovalis* Woodward, 1872, which was also included in Anthracomarti at that time. Scudder (1890) gave a more complete description of *Poliochera* and described the third fossil ricinuleid, *Geratarbus scabrum*, placing it too in Anthracomarti. Two years later, Thorell (1892) described the third living species,

*Cryptostemma afzelii*, from a specimen in Stockholm Museum of Natural History, which had been collected by A. Afzelius in Sierra Leone sometime between 1789 and 1799. He also established the name Ricinulei for the suborder of Opiliones containing the family Cryptostemmidae. Having originally coined the name Ricinulei in 1876, Thorell gave this date, but later authors quote 1892, being the date of the diagnosis of the suborder. So, by 1900, three species of living ricinuleids and three fossil forms had been described; the living ones were assigned to the Opiliones and the fossils to Anthracomarti.

Pocock (1902, p. 439, footnote) recognised the similarity between *Curculioides ansticii* and the Recent *Cryptostemma*. The fourth fossil ricinuleid, *Kustarachne* (= *Amarixys* nov.) *sulcata*, was described by Melander (1903) as an anthracomartid. Hansen and Sørensen (1904) elevated Ricinulei to an order apart from Opiliones in their classic work 'On Two Orders of Arachnida', and described five new living species. Pocock (1911), in a monograph on fossil arachnids, placed all the fossil species mentioned above, together with a new British species, *Poliochera alticeps*, in the new order Ricinulei. Three more specimens of *Curculioides ansticii* were described by Pocock in 1911, though it is probable that he did not study the holotype, and he also placed *Geratarbus scabrum* and *Kustarachne sulcata* in *Curculioides*. Petrunkevitch (1913) described a new species of *Polyochera* (his spelling), *P. glabra* from Mazon Creek, redescribed *P. punctulata*, *Curculioides scaber* (= *Geratarbus scabrum*), and *C. sulcatus* (= *Kustarachne* (*Amarixys* nov.) *sulcata*), and erected the family Holotergidae for *Curculioides*, placing *Poliochera* in Cryptostemmidae. He also gave keys to the fossil ricinuleids.

Cockerell (1916) suggested Holotergidae be replaced by Curculioididae, since the former name was not based on a known genus. McAtee and Malloch (1925) pointed out that *Cryptostemma* had been preoccupied since 1835 by a genus of Hemiptera, so Ewing (1929) replaced it with *Ricinoides* for the African ricinuleids, and replaced Cryptostemmidae (= Cryptostemmidae, Cryptostemmatidae) with Ricinoididae. Ewing (1929) included all living and fossil genera within this family, and also described four new species of *Cryptocellus*. Thus, by 1930, three species of *Poliochera* and three of *Curculioides* were known; the extant genera *Ricinoides* and *Cryptocellus* contained six species each according to Ewing (1929) (although Hansen (1921) had described another, *C. feae*). Of the twelve extant species known to Ewing, two were known by one or two juveniles, five from single adults, and the remainder from only two to seven specimens, including juveniles.

In the early 1930s, ricinuleids were considered both primitive (Ewing 1929) and rare. However, Finnegan (1935) pointed out that whereas up until 1932 only 32 specimens of extant ricinuleids were known to exist, in 1933 Sanderson had collected 317 specimens of *Ricinoides sjoestedti* in West Africa, of which 17 were adult, one a larva, and the rest nymphs; 20 or more were kept alive in England for some time (though Hansen (1921) reported that 'many' specimens of *R. feae* were available to him). Ricinuleid primitiveness was later disputed by Millot (1945a, b, c), who was able to make dissections thanks to the more abundant material then available.

In 1945, Petrunkevitch published the first of four important works on fossil arachnids which spanned the following decade. He kept Ewing's (1929) family Ricinoididae only for the Recent genera, preferring Polyocheridae and Curculioididae for the fossils. He described a new species from Mazon Creek, *Curculioides gracilis*, and

produced keys to the families and the species of *Curculioides*. Petrunkevitch (1949) described two new British species, *Curculioides granulatus* and *C. eltringhami*; he also gave new keys to the families and genera. Petrunkevitch (1953) listed the then known fossil species with their synonymies, and in the "Treatise" (Petrunkevitch 1955) he produced comparative outline drawings of them all. Since 1955, two new fossil ricinuleids have been described: '*Poliochera* vel *Curculioides*' *pustulatus* Laurentiaux-Vieira and Laurentiaux, 1963 from China, based on a supposed partial carapace and cucullus, and the well preserved *Curculioides adompha* Brauckmann, 1987 from Germany.

In recent years, many papers on the biology of living ricinuleids have appeared, concerning their mating habits (Cooke 1967; Pollock 1967; Legg 1977c), morphology of all life stages (Pittard & Mitchell 1972; Legg 1976a,b, 1982), ultrastructure (Kennaugh 1968; Alberti & Palacios-Vargas 1984), and comparative morphology (van der Hammen 1979, 1989). Many recent works have dealt with the description of new species, particularly from Central and South American caves (Bolivar 1941, 1946; Coronado 1970; Gertsch 1971; Dumitrescu & Juvara-Bals 1973; Márquez & Conconi 1974; Armas 1976; Platnick 1988), and taxonomic revisions of the species (Beck & Schubart 1968; Cooke & Shadab 1973; Tuxen 1974; Legg 1976a, 1977a,b; Dumitrescu & Juvara-Bals 1977; Platnick & Shadab 1976, 1977, 1981a,b; Platnick & Paz 1979; Platnick 1980; Platnick & Pass 1982). Thus our knowledge of these animals has increased considerably over the last 20 years, and the three currently recognised extant genera, *Cryptocellus*, *Pseudocellus*, and *Ricinoides*, contain 25, 21, and 10 species respectively.

## 5. Comparative morphology of fossil and Recent ricinuleids

The morphology of Recent *Cryptocellus* and *Pseudocellus* was described by Cooke and Shadab (1973), van der Hammen (1979), and Pittard and Mitchell (1972), and *Ricinoides* by Legg (1976a,b, 1977a,b) and Tuxen (1974); a classic work on the group is Hansen and Sørensen (1904). In this section, the morphology of the fossil ricinuleids (Palaeoricinulei subordo. nov.; Fig. 4) is compared to that of the extant forms (Neoricinulei subordo nov.).

### 5.1. Cuticle

The cuticle of ricinuleids was described by Kennaugh (1968). It is extremely thick (around 0.05 mm); on some podomeres the thickness equals the diameter of the lumen. Surprisingly, it is thicker on unsclerotised parts than on the sclerites. The cuticle of the fossil ricinuleids was similar in thickness to that of the extant forms, around 0.05 mm, as evidenced by the kaolin-filled casts separating internal and external moulds. The reason for the tough cuticle in ricinuleids is not known, but whatever its function, there is a disadvantage in the lack of flexibility which is required for distention of the abdomen, after a large meal or when gravid with eggs, for example. In living ricinuleids and in the Poliocheridae this problem is overcome by having flexible areas of cuticle (thickened perhaps to prevent undue water-loss) which can expand at the sides of the abdomen and between the inflexible tergites. In the Curculioididae on the other hand, the flexibility must either have been taken up by the normal abdominal cuticle or the dorsal median line or sulcus had flexible cuticle associated with it in life, so that distention of the abdomen was taken up at the suture.

In living ricinuleids, the sclerotised cuticle bears pits, tubercles, and a variety of other phaneres, but no trichobothria. Apart from some local evidence for setae and spines in certain specimens (see later) the only cuticular structures preserved in the fossil ricinuleids are the abundant tubercles covering nearly all of the body parts. In living ricinuleids, some species (e.g. most *Ricinoides*) are almost entirely covered with tubercles, whilst others (e.g. some *Pseudocellus*) are nearly devoid of them. The tubercles of Neoricinulei exhibit a wide variety of shapes: conical, spheroidal, and button-shaped, for example, and many are corrugated (Legg 1976a; van der Hammen 1979; Pittard & Mitchell 1972). They vary in size from 0.01–0.03 mm in *Pseudocellus pelaezi* (Pittard & Mitchell 1972) and 0.012–0.02 mm in *Ricinoides sjoestedti* (Kennaugh 1968), to 0.04–0.08 mm in *R. afzelii* (Kennaugh 1968; personal observation). In the fossil ricinuleids, the shapes of the tubercles cannot be determined, although they always appear to be symmetrical. The major ones range in size between the species, from 0.05 mm or less in *Curculioides pococki*, *Poliochera glabra* and *P. gibbsi* to approaching 0.1 mm in *Amarixys sulcata*. Minor tubercles are present between the larger ones, especially in *Curculioides gigas*, where a strong bimodal size distribution is evident.

Internal moulds of fossil ricinuleids bear pits which reflect tuberculation of the internal surface of the cuticle, for example on *C. gigas* and the holotype of *C. mcluckiei*; the internal features are noticeably smaller than the external tubercles. Kennaugh (1968) reported that the tubercles in living ricinuleids were connected to the inside of the cuticle by ducts, but Pittard and Mitchell (1972) disputed that the ducts passed completely through the cuticle. Nevertheless, pits and setae are connected to the internal surface of the cuticle by prominent ducts (e.g. Kennaugh 1968, pl. 1b; Pittard & Mitchell 1972, figs 36, 37). It is possible that the tubercles of fossil ricinuleids occupied the thickness of the cuticle; alternatively, during fossilisation the more resistant tubercles may have left an impression on the internal moulding mud after the rest of the cuticle had decayed. The latter possibility is less likely than the former because in *C. gigas* and *C. mcluckiei* (holotype) the thick kaolin present between the internal and external moulds suggests that the cuticle had not decayed prior to the formation of an internal mould.

### 5.2. Cucullus

The cucullus in living ricinuleids is a hood in front of the carapace which can be moved from the horizontal down to the vertical plane, in which position it covers the chelicerae and mouth. Apart from the protection afforded whilst creeping through litter, the cucullus functions in feeding and transportation of the egg (Pollock 1966; Cooke 1967). In general proportions and morphology, the cucullus of the fossil ricinuleids is similar to that in the Neoricinulei. The main difference lies in more pronounced dorsal furrows, and corresponding ventral ridges, in the Palaeoricinulei which extend forwards from the posterolateral articulations, and presumably help to strengthen the cucullus. These features are present, but less obvious, in the Recent genera.

The shape of the cucullus in *Curculioides* is best seen in the holotype of *C. mcluckiei* because in this specimen the cucullus is outstretched in the horizontal plane. In *C. ansticii* there is a shallow median depression on the dorsal surface of the cucullus. The cucullus in Poliocheridae is not greatly different from that of *Curculioides*, and is seen well in *Poliochera glabra* (UMMP 7223) and *Terpsicroton alticeps*. In the latter, the cucullus is preserved as an internal mould



on the dorsal part, and shows a small, median longitudinal depression close to the posterior border, as in the modern *Cryptocellus* (Pittard & Mitchell 1972).

### 5.3. Carapace

The carapace is broader than long in most *Ricinoides* and *Cryptocellus* species but is slightly longer than broad in a few (e.g. *C. narino* Platnick & Paz, 1979; *R. olounoua* Legg, 1977a) and in most species of the Central American genus *Pseudocellus* (e.g. *P. spinotibialis* (Goodnight & Goodnight, 1952), *P. dissimulans* (Cooke & Shadab, 1973), and *P. paradoxus* (Cooke, 1972)). The carapace in the living forms has a straight anterior border, which may be rather narrow in some species (e.g. *R. hansenii* Legg, 1976a), and the other sides appear curved in dorsal view; in adults, the carapace is widest behind the midline (Pittard & Mitchell 1972). In addition to the tubercles mentioned above, the carapace bears a median longitudinal depression, generally deepest behind the mid-point (thus resembling the fovea of spiders); it may be rather deep or barely present. In the *Cryptocellus magnus* group of species (Platnick & Paz 1979), the median depression contains a row of pits with tubercles inside; other rows of tubercle-bearing pits occur on the carapace of this group. Most living ricinuleids bear a pair of translucent patches of cuticle, lacking tubercles, one on each lateral edge of the carapace just above the coxae of leg 2 in *Cryptocellus* and extending to a more posterior position in

*Pseudocellus* (Platnick 1980). These were called ocelli by Cooke and Shadab (1973), and have been interpreted as the vestiges of eyes, possibly two pairs (van der Hammen 1979, 1989). Carapace tuberculation varies from near absence (e.g. *C. lampeli* Cooke, 1967 and *C. albosquamatus* Cooke, 1967, in which numerous hairs are present) to a dense covering (e.g. *C. foedus* and *C. peckorum* Platnick & Shadab, 1977). Pittard and Mitchell (1972) noted that the apparent reduction in the number of tubercles on the carapace (tubercle density) with increasing maturity reported by Cooke (1967) is actually due to the similar number of tubercles in each instar migrating towards the edges of the carapace.

Table 1 lists a number of measurements of the carapace of fossil ricinuleids. The carapace is broader than long in all of the fossil genera. The width of the carapace has frequently been underestimated in earlier works on fossil ricinuleids, particularly those of Petrunkevitch (e.g. 1913, 1949), who used the carapace length:width ratio as a key character. The greatest width lies in the posterior half of the carapace, and is commonly near the posterior border; the anterior border is straight and wide in all the fossils. The median groove varies from a distinct furrow (e.g. *Curculioides mcluckiei* and *C. scaber*) to extreme reduction and near effacement (e.g. *C. gigas* and *Poliochera punctulata*). Depressions corresponding to those described here in the fossils as ocular and posterior are present in the living ricinuleids, for

**Table 1** Carapace measurements in fossil Ricinulei. Linear measurements are in mm, density is in mm<sup>-2</sup>.

| Specimen                         | Carapace length | Carapace width | Carapace l:w ratio | Tubercle density | Tubercle diameter | Ocular ratio |
|----------------------------------|-----------------|----------------|--------------------|------------------|-------------------|--------------|
| <i>Curculioididae</i>            |                 |                |                    |                  |                   |              |
| <i>Curculioides ansticii</i>     |                 |                |                    |                  |                   |              |
| In 49323                         | 5.1             | 6.6            | 0.77               | 54               | 0.071             | 0.33         |
| USNM 37973                       | 4.6             | 6.1            | 0.75               | 66               | 0.071             | 0.39         |
| <i>Curculioides mcluckiei</i>    |                 |                |                    |                  |                   |              |
| USNM 440519                      | 5.3             | 6.1            | 0.87               | 79               | 0.078             | 0.36         |
| PE 780                           | 5.2             | 6.0            | 0.87               | 72               | 0.080             | 0.33         |
| In 31246/31256                   | 3.6             | 4.7            | 0.77               | 74               | 0.077             | 0.35         |
| <i>Curculioides eltringhami</i>  |                 |                |                    |                  |                   |              |
| In 39771                         | 5.3             | 6.7            | 0.79               | 49               | 0.072             | 0.40         |
| <i>Curculioides granulosus</i>   |                 |                |                    |                  |                   |              |
| In 18592                         | 4.3             | 5.0            | 0.86               | 79               | 0.058             | 0.37         |
| <i>Curculioides scaber</i>       |                 |                |                    |                  |                   |              |
| USNM 37965                       | 4.6             | 6.6            | 0.70               | 90               | 0.075             | 0.35         |
| <i>Curculioides adompha</i>      | 4.6             | 6.0            | 0.77               | 90               | ?                 | 0.33         |
| <i>Curculioides gigas</i>        |                 |                |                    |                  |                   |              |
| PE 784                           | 5.8             | 7.5            | 0.77               | 87               | 0.073             | 0.35         |
| <i>Curculioides pococki</i>      |                 |                |                    |                  |                   |              |
| In 7885                          | 3.3             | 5.0            | 0.66               | 101              | 0.050             | 0.30         |
| <i>Amarixys sulcata</i>          |                 |                |                    |                  |                   |              |
| UC 9235                          | 3.8             | 5.2            | 0.73               | 40               | 0.097             | 0.37         |
| <i>Amarixys gracilis</i>         |                 |                |                    |                  |                   |              |
| ISM 14862                        | 3.9             | 5.2            | 0.75               | 68               | 0.064             | 0.41         |
| MCP 548                          | —               | —              | —                  | 68               | 0.052             | —            |
| <i>Amarixys stellaris</i>        |                 |                |                    |                  |                   |              |
| PE 32184                         | 4.6             | 6.1            | 0.75               | 50               | 0.079             | 0.33         |
| <i>Poliocheridae</i>             |                 |                |                    |                  |                   |              |
| <i>Poliochera punctulata</i>     |                 |                |                    |                  |                   |              |
| USNM 37971                       | 4.4             | 5.8            | 0.76               | 103              | 0.062             | 0.29         |
| PE 32206                         | 5.5             | 7.4            | 0.74               | 92               | 0.060             | 0.31         |
| <i>Poliochera glabra</i>         |                 |                |                    |                  |                   |              |
| USNM 37981                       | 4.2             | 5.2            | 0.81               | 103              | 0.046             | 0.38         |
| UMMP 7223                        | 4.6             | 5.2            | 0.88               | 97               | 0.052             | 0.37         |
| <i>Poliochera gibbsi</i>         |                 |                |                    |                  |                   |              |
| PE 29176                         | 3.0             | 4.4            | 0.68               | 190              | 0.041             | 0.26         |
| <i>Poliochera incertae sedis</i> |                 |                |                    |                  |                   |              |
| <i>Terpsicron alticeps</i>       |                 |                |                    |                  |                   |              |
| In 31238                         | 1.8             | 2.35           | 0.77               | no               | no                | 0.39         |

example in *Cryptocellus foedus* (Platnick & Shadab 1977, fig 9); the ocular depression, in particular, is present in most extant species, though, like the median groove, these features are barely defined in some. A pair of eyes is present in all fossil genera (reported by Selden 1986a,b), situated close to the lateral edges of the carapace, above the coxae of leg 2. Each eye-pair consists of two torus-shaped eyes separated by a ridge which meets a longitudinal ridge medially running alongside the eyes and terminates laterally in a longitudinal groove bordering the lateral side of the eyes. These pericocular features may be more or less well-developed and preserved, and are seen well in *Curculioides granulatus*. The carapace tubercle density in the fossils varies from  $40\text{ mm}^{-2}$  in *Amarixys sulcata* to  $190\text{ mm}^{-2}$  in *Poliochera gibbsi*. There is a general suggestion, among the *Curculioides* species, of a decrease in tubercle density with increase in carapace size, but there are insufficient specimens belonging to a single species to investigate this further.

#### 5.4. Opisthosoma (abdomen)

The abdomen of living ricinuleids bears dorsal tergites, ventral sternites, and lateral pleurites. The pleurites are very narrow and hidden in folds of the pleural membrane (Pittard & Mitchell 1972). The dorsal surface bears a narrow, anterior, ridge-like tergite which engages with the posterior edge of the carapace during locking of the prosoma and opisthosoma. The four tergites posterior to the first are partitioned into a broad median part and two lateral parts; these are separated by expanses of membrane in nymphs but cover most of the dorsal surface, and may touch, in adults. Pittard and Mitchell (1972) interpreted these four tergites as representing four somites (segments 10–13), but because the three posterior tergites are twice as long as the next anterior tergite, and supernumerary phaneres are present, van der Hammen (1979, 1989) interpreted these longer tergites as representing two somites each (segments 11–12, 13–14, and 15–16). Four sternites are present; the anteriormost bearing a pair of deep depressions which receive the posterior coxae (of leg 4) during locking of the prosoma and opisthosoma. The boundaries of the more posterior sternites are ill-defined in the adult but clearly separated by membrane in nymphs. The sternites, too, possibly represent two somites each. The abdomen is attached to the prosoma by a narrow pedicel. The pedicel represents somites 7 and 8 (van der Hammen 1979, 1989) or 7, 8 and 9 (Pittard & Mitchell 1972). The pedicel bears the genital organs: an opening in the female, and a sclerotised projection in the male (Pittard & Mitchell 1972, figs 41, 42). The pedicel and genital organs are only exposed when the prosoma and opisthosoma are uncoupled.

In fossil ricinuleids, only members of the family Poliocheridae bear opisthosomal tergites and clearly defined sternites. The general morphology of poliocherid tergites and sternites follows the same pattern as that of the living forms. Each tergite of *Terpsicroton* bears two pairs of deep pits, which is evidence of their formation from the fusion of the tergites of two somites. Sternites can be seen in some Curculioididae, but not transverse tergites (but see *C. gigas*, below). In curculioidids, the dorsal abdomen bears a median longitudinal line (in *Curculioides*) or sulcus (in *Amarixys*). This feature is real, and not an artefact; Petrunkevitch misinterpreted it in *C. scaber* as a ridge (it is a furrow preserved as an external mould), and as a fold produced during compression in *Amarixys sulcatus* (Petrunkevitch 1913). Brignoli (1973) suggested that the median line could be produced by crowding of tubercles into a line, but since

tubercles occur over the whole abdomen, and are commonly lacking along the median line or sulcus, this suggestion can be dismissed. There can be little doubt that the longitudinal median line is an advanced feature. In all chelicerates, the expression of segmentation by transverse lines and tergites is always considered plesiomorphic with respect to the loss of the expression of segmentation. Examples include the loss of the expression of segmentation in mites, in the carapace of many arachnids, and in the fusion of segments which can be traced in great detail in the fossil history of the Xiphosura (Selden & Siveter 1987). Moreover, in living ricinuleids there is the tendency towards reduction in the flexibility of the abdomen during ontogeny, resulting in closely conjoined tergal plates dorsally and the nearly complete fusion of sternites in adults (Pittard & Mitchell 1972). In the fossil *Curculioides gigas*, two transverse lines on the dorsal abdomen, occurring on both the internal and external moulds, are interpreted as real features and not artefacts; they most probably represent the vestiges of original tergite boundaries.

Locking was achieved in the palaeoricinuleids in the same manner as in the neoricinuleids: by the interlocking of the posterior edge of the carapace with a dorsal anterior ridge on the abdomen, and with the coxae of leg 4 fitting into pouches on the first abdominal sternite. Traces of genital organs are present in some of the fossils, in *Curculioides gigas* for example.

**Pygidium.** The ricinuleid pygidium consists of three segments, each composed of a ring of sclerotised cuticle representing fused tergite, sternite and pleurite of opisthosomal somites, and is situated at the posterior extremity of the abdomen. The anus is terminal on the last (anal) segment of the pygidium, and the posterior two segments can be telescoped inside the first segment. Pittard and Mitchell's (1972) enumeration of somites in the ricinuleid abdomen results in the anal segment of the pygidium representing somite 16, whereas according to van der Hammen's (1979, 1989) scheme this is somite 19.

The pygidium of the fossils resembles that of the Neoricinulei very closely. It is three-segmented, and features such as the mid-dorsal notch (e.g. in *Ricinoides hansenii* Legg 1976a, fig. 37) and the large prenal setae (e.g. in *Pseudocellus pelaezi*, Pittard & Mitchell 1972, fig. 38) reported in some living forms, can be seen in some of the fossils (e.g. *Curculioides mcluckiei*).

#### 5.5. Appendages

**Chelicera.** Ricinuleid chelicerae are chelate, and both the fixed and movable fingers bear blunt teeth. In life, both fingers are obscured by brushes of long setae. A large, blunt tooth at the base of the fixed finger in *Ricinoides* serves to distinguish this genus from the New World genera. The chelicerae are covered by the cucullus when it is in the closed position. Parts of the chelicerae can be seen in a number of fossil specimens, as external moulds of the fingers between the cucullus and the infracapitulum (see below), in *Curculioides mcluckiei* (In 31256), *C. scaber*, *Amarixys sulcatus*, and *Poliochera punctulata*, for example. These specimens show that the chelicera in the Palaeoricinulei was chelate and toothed as in the modern forms.

**Pedipalp.** The pedipalp consists of coxae fused into an infracapitulum (van der Hammen 1979), four free podomeres, and a chelate claw. The free podomeres are usually referred to as: trochanter 1, trochanter 2, femur, and tibia, with the claw interpreted as a tarsus opposing a fixed finger formed by a tibial extension (Hansen & Sørensen 1904; Pittard & Mitchell 1972). Using evidence of



musculature, van der Hammen (1979, 1989) reinterpreted the podomeres as trochanter, short femur, patella, tibiotarsus, and apotele (claw). The infracapitulum is somewhat pentagonal in shape, with a straight anterior margin, parallel lateral sides, and a posterior border which is V-shaped apart from a posterior notch accommodating a small, kite-shaped tritosternum situated immediately behind the infracapitulum. The tritosternum is commonly obscured by the edges of the surrounding coxae. The infracapitulum bears large excavations laterally to accommodate the trochanters. In the median line is a groove, the subcapitular gutter (van der Hammen 1979), in which may lie two or three long, forwardly directed setae originating from the tritosternum (Pittard & Mitchell 1972). The cuticle of the pedipalps bears the usual tubercles and setae, and a number of unusual pits and setae.

The infracapitulum in the fossil ricinuleids is similar in shape to that of the living forms. The subcapitular gutter is distinct in all specimens in which the infracapitulum can be seen, and either side of this, at the posterior of the plate, there is commonly a low mound bearing fine tubercles. The remainder of the infracapitulum lacks tubercles. The proportions of the podomeres: short trochanter and femur, long patella and tibiotarsus, are similar in the fossils and in the Recent ricinuleids. The pedipalps in the fossils are readily identified by their lack of tubercles, except for a few at the base of the patella in *Curculioides mcluckiei* (In 31256). The tritosternum is not distinct in any of the fossils, but may be present in a small quadrangular area behind the infracapitulum.

**Walking legs.** The coxae of leg 1 are the smallest of the walking leg coxae; they appear triangular in ventral view, with their apices separated by the tritosternum. Coxae 2 are the largest; they are rectangular in ventral view, and their median edges meet in the midline. Coxae 3 are smaller than those of leg 2, and their median edges also meet in the midline. Coxae 4 are nearly as small as those of leg 1; these coxae also meet in the midline. During locking of the prosoma and opisthosoma, coxae 4 (which, unlike the coxae of other legs, are movable) fit into pouches excavated into the most anterior abdominal sternite.

The relative sizes and arrangement of the coxae of the Palaeoricinulei are different from those of the Neoricinulei. In the fossils, coxae 1 and 2 are both small and triangular, and neither of them meet their opposite in the midline. Coxa 3, however, is large (generally the largest in ventral area) and rectangular in ventral view, and these coxae meet in the midline. Coxa 4 is also large, nearly as large as coxa 3, they meet in the midline, and just as in the living forms, are accommodated in sternal pouches during locking.

In the adult, walking leg 1 consists of: trochanter, femur, patella, tibia, metatarsus, and tarsus. Leg 2 is similarly constituted except that the tarsus consists of 5 tarsomeres. Leg 3 consists of 2 trochanters, femur, patella, tibia, metatarsus, and tarsus consisting of 4 tarsomeres; in this leg in the male, the metatarsus and tarsus are modified for sperm transfer. Leg 4 has a similar constitution as leg 3 (female), except that 5 tarsomeres are present instead of 4. The larva is hexapodous, lacking the fourth leg, and differences in tarsomere number during ontogeny are given in Pittard and Mitchell (1972) for *Pseudocellus* and Legg (1976a, 1982) for *Ricinoides*. In all living ricinuleids leg 2 is the longest, the femur, in particular, and the metatarsus contributing most of the difference in length between this leg and the others, and in the male of some species (*Pseudocellus pelaezi*, for example, Pittard & Mitchell 1972) femur 2 is thickened.

Leg joints in ricinuleids are remarkable because of the compromise between the selection pressure for a thick cuticle and the necessity for movement at the joint. As a result, nearly all joints are bicondylar and the articulations are enclosed within extensions of the proximal podomere. The distal podomere is restricted to a single plane of movement, which nevertheless may be great. Cuticle surfaces which come into contact lack tubercles, and there is much invagination of the proximal podomere to accommodate a fully flexed distal podomere. By these means, the amount of soft arthrodial membrane exposed at the joint is kept to a minimum. Details of leg joints in ricinuleids are given in van der Hammen (1979). Curved, paired claws are present on the tarsus, with associated specialised setae and other structures. (Pittard & Mitchell 1972, figs 80–87).

The walking legs of fossil ricinuleids are similar in nearly every detail to those of the living forms. In spite of the differences in the sizes of the coxae, leg 2 is the largest in the Palaeoricinulei as it is in the Neoricinulei. Femur 2 is the longest, and appears thicker in some specimens, suggesting the male sex, but with small sample sizes of each species the speculation must remain. The joints in the fossils are similar to those in the Recent forms, and the opposable surfaces at the joints can be determined by their lack of tubercles. Features which could give information about the sex or ontogenetic stage of a fossil specimen, the tarsomeres and the tarsal region of leg 3, are missing in all fossil ricinuleid specimens studied. Only *Curculioides adompha* Brauckman, 1987 preserves the tarsal region, but provides ambiguous information (see below).

## 6. Phylogeny of the Ricinulei

The living Ricinulei consist of three genera, the New World *Cryptocellus* and *Pseudocellus*, and the West African *Ricinoides*, included in a single family, Ricinoididae. All fossil ricinuleids are Carboniferous in age and belong to four genera: *Curculioides*, *Amarixys*, *Poliochera*, and *Terpsicron*. All seven ricinuleid genera, living and fossil, are included in the phylogenetic analysis.

Problems were encountered when attempting to run a formal cladistic analysis using a character matrix; too few characters are sufficiently widespread for a useful matrix to be generated. Numerous characters are autapomorphic for a single species, and thus supply no helpful information. Also, aspects of tuberculation, widely used herein as an aid in species identification, are not well understood, and when included in the analysis produced neither comprehensible patterns nor useful information. However, a few characters do provide the basis for separation of the ricinuleids at the higher level, and these have been used to define the suborders and families (Table 2). A cladogram (Fig. 2) is presented which gives the hypothesis of relationships based on the current work. Note that below the family level, there are too few characters for a reliable analysis, and the relationships presented are somewhat arbitrary. Similarly, the relationships between the three extant genera are poorly known because of too few characters (Platnick 1980).

The Palaeoricinulei and Neoricinulei are separated in time, so it is possible that the Neoricinulei are derived from the Palaeoricinulei rather than the two groups sharing a common ancestor. Such a relationship cannot be shown on a cladogram. If this were the case, then the Poliocheridae is the group most likely to be the ancestor of Neoricinulei. It is rational to envisage the relative sizes of the coxae changing and the eyes atrophying over time to produce the neoricinuleids from the Poliocheridae.

**Table 2** Characters and character states used in the phylogenetic analysis

| Characters       |            |             | Character states |             |        |        |
|------------------|------------|-------------|------------------|-------------|--------|--------|
| 1. Tergites      | present    | absent      | median sulcus    |             |        |        |
| 2. Abdomen       | (tergites) | median line |                  |             |        |        |
| 3. Ventral sulci | absent     | present     |                  |             |        |        |
| 4. Eyes          | present    | vestigial   |                  |             |        |        |
| 5. Coxae         | 2 < 3      | 2 > 3       |                  |             |        |        |
| 6. Deep pits     | absent     | present     |                  |             |        |        |
| 7. Tuberculation | random     | pattern     | absent           |             |        |        |
| 8. Tubercles     | unimodal   | bimodal     | absent           |             |        |        |
| 9. Tub. size     | <0.040     | 0.040–0.055 | 0.055–0.065      | 0.065–0.085 | >0.085 | absent |
| 10. Tub. density | <45        | 45–65       | 65–85            | 85–120      | >120   | absent |
| 11. Ocular ratio | <0.33      | ≥0.33       | absent           |             |        |        |

The classification scheme suggested for the Ricinulei is given below.

#### Order RICINULEI Thorell, 1892

##### Suborder NEORICINULEI nov.

##### Family Ricinoididae Ewing, 1929

Included genera: *Ricinoides* Ewing, 1929;

*Cryptocellus* Westwood, 1874;

*Pseudocellus* Platnick, 1980

##### Suborder PALAEORICINULEI nov.

##### Family Curculioididae Cockerell, 1916

Included genera: *Curculioides* Buckland, 1837;

*Amarixys* nov.

##### Family Poliocheridae Scudder, 1884

Included genera: *Poliochera* Scudder, 1884;

*Terpsicron* nov.

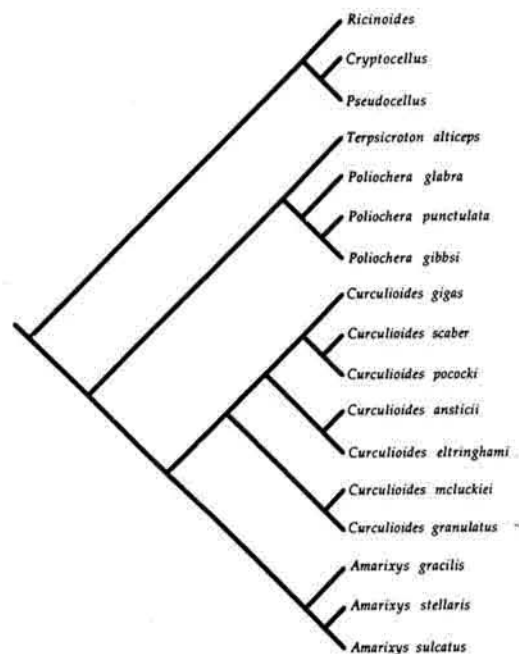
### 6.1. The characters

The validity of ricinuleid characters for taxonomic purposes has been discussed by various authors (e.g. Ewing 1929; Beck & Schubart 1968; Cooke & Shadab 1973; Tuxen 1974). Potentially the most useful character, the form of the

copulatory apparatus on the extremity of leg 3 in the males, is not preserved in the fossils, and important small-scale features such as cheliceral teeth and integumental structures are only rarely present. In the past, use was made of features of size and shape, chiefly length:width ratios of carapace and coxae (e.g. Petrunkevitch 1913, 1945). However, these characters are subject to considerable distortion during compaction of the sediment (which occurs to some extent, possibly in conjunction with distortion due to dewatering, even inside a nodule). In the present paper, particular use is made of tubercle size and density on the carapace, carapace sculpture, and abdominal sclerotisation, though even these may be subject to some distortion during diagenesis.

No sexual organs are preserved in the fossils, so it is uncertain how many represent mature individuals. Therefore, there is the danger that nymphs and adults of the same species could be described as different species; such a possibility is highlighted by the fact that some collections of living ricinuleids consist largely of juveniles (95% in one case: Finnegan 1935). Another problem is that, lacking good diagnostic characters, species which differ only or mainly on their genitalia, but little, if at all, in other features, could be described as the same species. Living ricinuleids are quite restricted in their distributions, such that a new locality frequently reveals a new species, and the same may have been true for the extinct forms.

Using characters of abdominal morphology, it is a straightforward matter to differentiate the genera. In contrast, far less confidence can be assigned to the characters which have been used to differentiate the species. In the Poliocheridae, which have fairly flat carapaces, the ocular ratio is useful, in conjunction with the size and density of carapace tubercles. The ocular ratio is not so useful in curculioidids because of their more domed carapaces and the consequent distortion on compaction. Tubercle sizes and densities are important, but they too show a wide variation in animals otherwise closely related on other criteria. *Curculioides ansticii* is recognisable on ventral abdominal morphology, and two characters separate both *C. gigas* and *C. pococki* from other *Curculioides*, but differentiation of the other species is less secure. The dilemma is whether to split the genus even further than it is already, or to lump the species together. Using the criteria of tubercle density and size, and taking into account overall size, age, and provenance, it could be argued that nearly every specimen represents a different species. This would be compatible with the present-day distribution of ricinuleid species. However, it is possible that two specimens from the same locality, differing mainly in size and tubercle size and density could represent different instars of the same species.



**Figure 2** Cladogram of relationships among living genera and fossil species of Ricinulei; data given in Table 2. The cladogram has a length of 30 and a consistency index of 0.77; it is only one of a number of cladograms which share these characteristics.



Similarly, greater differences could be accounted for by sexual dimorphism. However, with so few specimens from any one locality, and without additional evidence, these theories cannot be investigated further. Consequently, the species of *Curculioides* are differentiated as far as possible on reliable criteria.

Characters used in the phylogenetic analysis are discussed in more detail below.

**The abdomen.** As discussed above, in arthropods the expression of segmentation is generally considered more primitive than its effacement. In addition, on the ventral surface of the abdomen in some Curculioididae, and on the dorsal surface in *Curculioides gigas*, there are faint transverse lines which represent vestiges of original segmentation. Therefore, this character state is plesiomorphic when tergites are present and apomorphic when they are absent. In this respect, the Neoricinulei are less advanced than the Palaeoricinulei. Where tergites are absent, in the Curculioididae, there is no clear polarity between the presence of a median line *versus* a sulcus on the dorsal abdomen.

The tergites present in Neoricinulei and Poliocheridae may be derived from two segments and could be considered as diplotergites, since each bears a double set of phaneres, pits, etc. (van der Hammen 1979). It could be argued, therefore, that these diplotergites are derived relative to the single-tergite state of a hypothetical ancestor. Thus, it is possible that there are two lines in ricinuleid evolution: one leading to diplotergites and another to the complete loss of expression of segmentation in the dorsal abdomen. Each line ran in parallel and was derived from a hypothetical common ancestor with single-somite tergites. Evidence against this hypothesis comes from *Curculioides gigas* in which the vestiges of tergite boundaries on the dorsal abdomen are in similar positions to those in Poliocheridae and Neoricinulei. Therefore, the loss of expression of segmentation in the dorsal abdomen must have occurred after any development of diplotergites so, again, the latter condition would be plesiomorphic within the known Ricinulei.

It is tempting to speculate that the retention of (?diplo-) tergites in Neoricinulei is pedomorphic, and the small size of Neoricinulei compared with curculioidids suggests progenesis (*sensu* Gould 1975) as the mechanism.

**Eyes.** A general trend in the evolution of the chelicerates is the reduction of eyes. This trend can be followed in the fossil record, in the scorpions for example (Selden & Jeram 1989). Whilst further evidence (perhaps from physiology) is necessary to establish that the clear patches on the carapace of recent Ricinulei are really vestigial eyes, a number of authors have suggested this (see above). The presence of well-developed three-dimensional structures in a similar position in the fossils, here interpreted as functional eyes, is evidence for the reduction of two pairs of eyes to vestiges in the ricinuleids from the Carboniferous to the Recent. Presence of eyes is therefore plesiomorphic, and their reduction is apomorphic; further reduction to diffuse areas more posterior on the carapace, or complete absence, in *Pseudocellus* was noted by Platnick (1980).

The ocular ratio is useful in distinguishing the poliocherids at the specific level.

**Coxae.** Ewing (1929) used the relative sizes of coxae 2 and 3 to distinguish extant ricinuleids from the fossils, and this character has also been used here. Coxae 2 are rhomboidal and larger than coxae 3 or 4 in the Neoricinulei, but subtriangular to kite-shaped and much smaller than coxae 3 or 4 in the Palaeoricinulei. No polarity can be

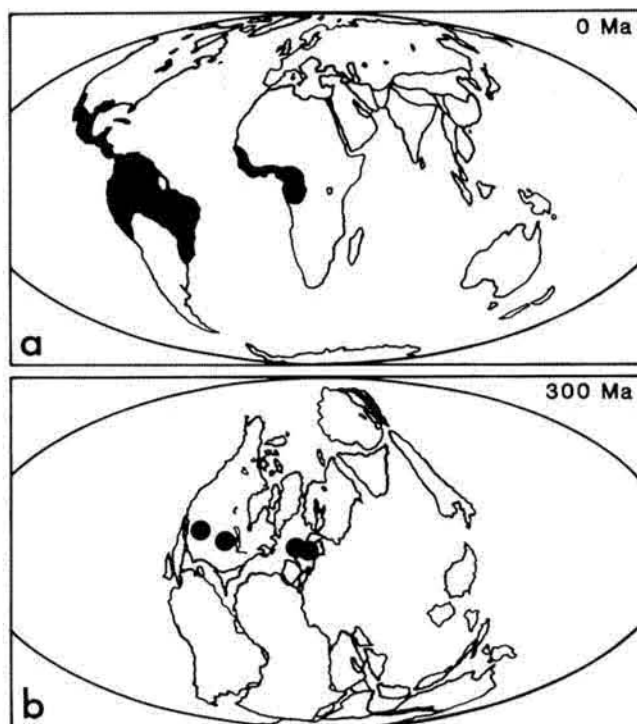
deduced for these character states, although it could be argued that because the  $2 < 3$  state only occurs in the fossils and  $2 > 3$  only occurs in the Recent forms, that the  $2 > 3$  state is derived on the criterion of geological precedence (Wiley 1981).

**Tuberculation.** Characters related to tuberculation: the size of the tubercles and their density on the carapace, are useful only at the species level.

**Large pits.** Deep pits occur on the carapace and abdominal tergites of *Terpsicrpton*. Numerous pits on the carapace and abdomen of *Cryptocellus magnus* were mentioned by Ewing (1929), Platnick and Paz (1979), Platnick and Shadab (1976) and van der Hammen (1979). These are more numerous, bear tubercles within, and are in different positions to those of *Terpsicrpton*. The cuticular pits of *Terpsicrpton* lie in positions where shallow depressions occur in other Poliocheridae and Neoricinulei, so it is likely that they are really a stronger development of these features. To conclude, the pits of *Terpsicrpton* are autapomorphic for that genus and bear no relation to the pits observed in *Cryptocellus magnus*.

## 7. Ecology and biogeography

At present, ricinuleids are known to occur only in tropical forests and caves. *Cryptocellus* and *Pseudocellus* occur in the New World, *Ricinoides* is found in tropical West Africa (Fig. 3). Their distribution lies entirely within the tropics with the exception of a few species found in caves in the north of Mexico and southernmost Texas. It is likely that the troglitic habit, with its constant temperature and humidity, has enabled some species to live in these more arid areas. It would appear that no cavernicole species has been recorded from Africa. Possibly, some cavernicole species occur within or outside the tropics in Africa, but remain to be discovered. Troglitic species of both



**Figure 3** Distribution maps of the Ricinulei: a, present-day distribution; b, Carboniferous distribution. Approximate distribution shown in black.

*Cryptocellus* and *Pseudocellus* are known, from South and Central America respectively.

Cave-dwelling Palaeozoic ricinuleids are unlikely to be preserved as fossils, and all the fossils described here almost certainly tropical forest dwellers. It is most likely that, like living ricinuleids, the fossil forms skulked beneath rotting logs on the forest floor, where a constant temperature and humidity could be assured. The distribution of the Carboniferous ricinuleids, in American and European coalfields (Fig. 3), was also tropical; during the Namurian and Westphalian these areas were within 10° of the equator (Scotese *et al.* 1979, fig. 32). It seems reasonable to assume that the ricinuleids have always been tied to the tropical forest (and possibly cave) habitat, migrating with the forests as the continents drifted beneath them. This hypothesis predicts that ricinuleid fossils should be found in Mesozoic sediments associated with humid tropical forests in those parts of the world which had maintained a land link with the Carboniferous coalfield areas. Nenilin (1988) proposed that the Ricinulei had a more widespread distribution during the Mesozoic, but presented little evidence for this theory. He did suggest that the troglobitic mode of life of many modern species, accompanied as it is by no special adaptations, may have developed along with arid conditions.

Modern Ricinulei are speciose: each new locality commonly yielding a new species, sometimes more than one (Pollock 1967), and the same may have been true of Carboniferous forms too. This suggests that ricinuleids speciate readily, and that, in spite of the apparent evolutionary conservatism in their gross body form, they are able to take advantage of new habitats as they arise. It might be expected then, that ricinuleids are opportunistic, *r*-selected, in their life history strategies, and the suggestion of progenesis (above) in the modern forms might be allied to this. However, the few studies done on ricinuleid life histories have indicated the opposite: ricinuleids produce a single egg at a time (Pollock 1966), and the populations, at least in caves, are rich in adults (Mitchell 1970). Possibly ricinuleids are indeed conservative in their evolution, the species have been separated for a long time, and the Mexican cave systems are long-lived.

Mountains separated the American from the European populations of Carboniferous ricinuleids but there is no fossil evidence that this barrier had any effect on their evolution. One species, *Curculioides mcluckiei*, occurs in both Mazon Creek, Illinois, and Coseley, England. The opening of the Atlantic ocean in the Cretaceous separated the American from the African ricinuleids and may have produced the barrier which caused speciation which eventually gave rise to the modern genera. Platnick (1980) suggested that *Cryptocellus* may be more closely related to *Ricinoides* than it is to *Pseudocellus*. This implies that the New World genera had become differentiated prior to the severance of the tropical land connection of the Americas and Africa in the late Cretaceous. He recommended that additional characters be used to determine the relationships of these three genera. In the light of this discussion, the discovery of fossil ricinuleids in post-Carboniferous strata would be an event of great importance and interest.

## 8. Systematic palaeontology

Order RICINULEI Thorell, 1892

Suborder NEORICINULEI, subordo. nov.

**Diagnosis.** Ricinulei without eyes (but with patches of clear cuticle representing degenerate eyes) on the carapace; coxa 2 rhomboidal and larger than coxa 3 or 4.

**Included families.** This suborder includes only the extant family Ricinoididae.

Suborder PALAEORICINULEI, subordo. nov.

**Diagnosis.** Ricinulei with eyes on carapace; coxa 2 subtriangular to kite-shaped and much smaller than coxa 3 or 4.

**Included families.** This suborder includes the extinct families Curculioididae and Poliocheridae.

Family Curculioididae Cockerell, 1916

1913 Holotergidae: Petrunkevitch, p. 81

**Emended diagnosis.** Palaeoricinulei with dorsal abdomen divided by median line or sulcus; no transverse tergites (but fine transverse lines may be present) on dorsal abdomen.

Genus *Curculioides* Buckland, 1837

**Diagnosis.** Curculioidids with dorsal median line, not sulcus, on abdomen.

*Curculioides ansticii* Buckland, 1837

(Figures 5; 6a, b, d, e; 7)

1873 *Curculioides ansticii* Buckland, p. 76; pl. 76, fig. 1

1884 *Curculioides ansticii* Buckland: Scudder, p. 17

1886 *Curculioides ansticii* Buckland: Scudder p. 24

not 1911 Pocock, pp. 39, 40; text-figs 12–13; pl. II, figs 7, 7a

1913 *Curculioides ansticii* Buckland: Petrunkevitch, p. 81, ref. to Buckland only

not 1913 *Curculioides ansticii* Buckland: Petrunkevitch, p. 81, ref. to Pocock

1929 *Curculioides ansticii* Buckland: Ewing, p. 586–588

1949 *Curculioides ansticii* Buckland: Petrunkevitch, p. 287, ref. to Buckland

not 1949 *Curculioides ansticii* Buckland: Petrunkevitch, p. 287, refs. to Pocock

1953 *Curculioides ansticii* Buckland: Petrunkevitch, p. 113, ref. to Buckland only

not 1953 *Curculioides ansticii* Buckland: Petrunkevitch, p. 113, Coseley specimens

1955 *Curculioides ansticii* Buckland: Petrunkevitch, p. P159; fig. 115, 4a, b

1962 *Curculioides ansticii* Buckland: Dubinin, p. 444, fig. 1285

1980 *Curculioides ansticii* Buckland: Morris, p. 34, Coalbrookdale specimen only

not 1980 *Curculioides ansticii* Buckland: Morris, p. 34, Coseley specimens

1987 *Curculioides ansticii* Buckland: Brauckmann, p. 99; fig. 4

1991 *Curculioides ansticii* Buckland: Brauckmann, p. 47; fig. 18

not 1991 *Curculioides ansticii* Buckland: Brauckmann, p. 47; fig. 18, ref. to 3 additional specimens

**Emended diagnosis.** *Curculioides* with a pair of smooth, broad-floored, longitudinal sulci, not narrow depressions, on the ventral side of the abdomen.

**Material.** Holotype, In 49323, in the collections of the British Museum (Natural History), London, from ironstone nodules of Westphalian age of Coalbrookdale, Shropshire. The exact locality is not recorded, but the horizon of the holotype of the crustacean *Pygocephalus dubius*, also in the Anstice Collection, was given by Schram (1979) as the White Flat Ironstone Measures, Modiolaris Zone, Westphalian B; this horizon agrees with the description in Prestwich (1840) of the 'Pennystone Measures' of Coalbrookdale.

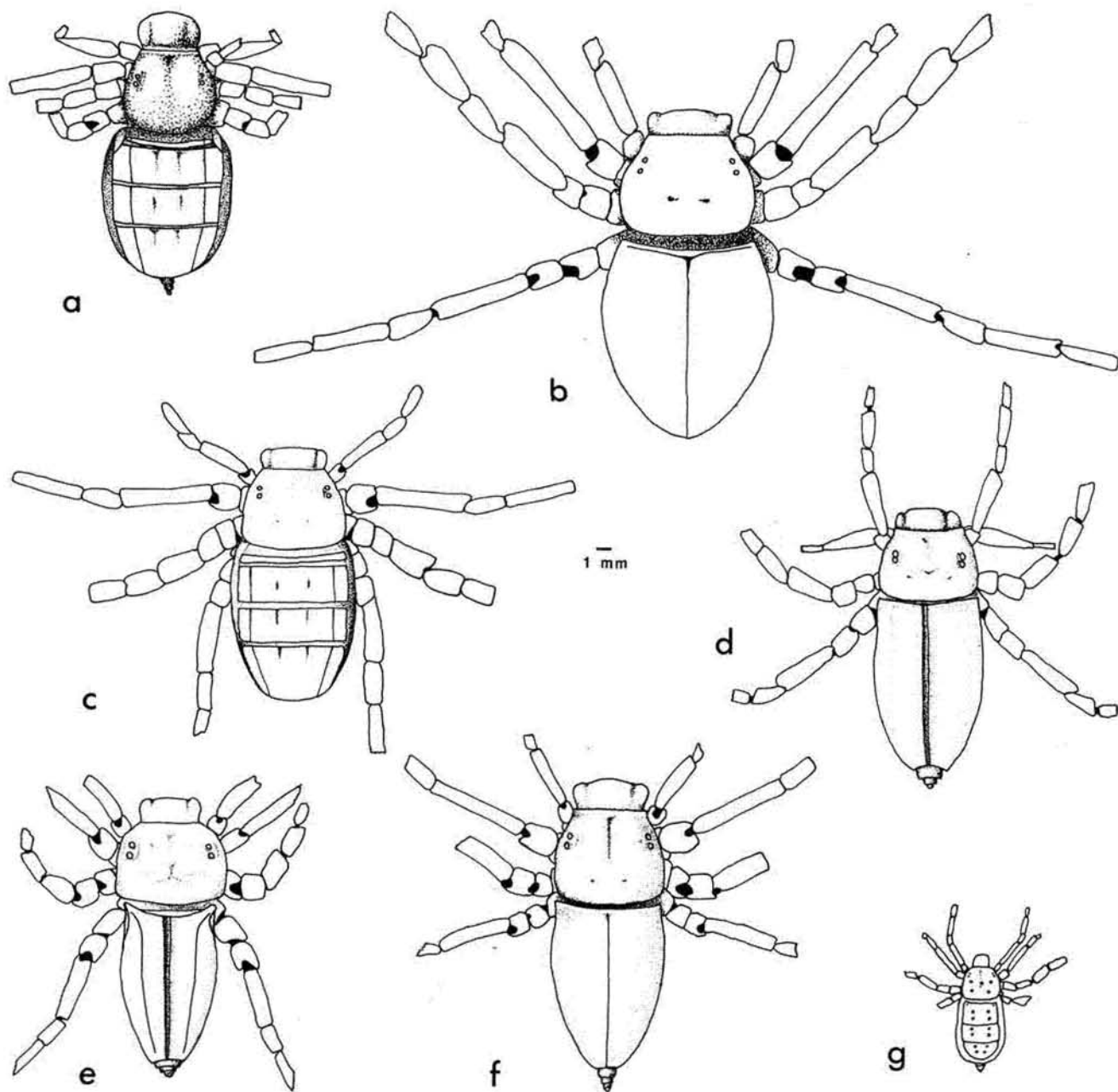


Other material: USNM 37973, in the collections of the National Museum of Natural History, Washington DC, and originally No. 22 in the Beale Collection, from Sedgley, Worcestershire, England. The horizon and locality are not known, though it is likely to have come from the locality at Claycroft Openworks, normally referred to as "Coseley". This specimen has not been previously mentioned or figured in the literature.

**Description of the holotype.** The carapace is preserved as an external mould on the dorsal part, and an internal mould on the ventral counterpart. The cucullus is preserved as a scrap of external mould on the part, and the internal mould of most of the cucullus is preserved on the counterpart. The preserved internal mould of the cucullus is 1.9 mm long, and 2.9 mm between the lateral grooves. The carapace is 5.1 mm long, and 6.6 mm wide. The width is deceptive because a broad lateral area is preserved on the left side of the part,

which cannot be seen on the other sides. Without this information, it would appear that the carapace is narrower and squarer in outline. The eyes are 4.2 mm apart, and the ocular axis lies 1.7 mm from the anterior border of the carapace (=ocular ratio of 0.33). The tubercles are 0.071 mm in diameter, and have a density on the carapace of  $54 \text{ mm}^{-2}$ . A median groove and ocular and posterior depressions are present, the latter being 1.9 mm apart. A depression is apparent at the posterior end of the median groove.

The abdomen is 11.0 mm long and 7.5 mm wide. A median line is present on the part, but somewhat obscured by the presence of iron salts along the line. At first sight, these give the appearance of a median sulcus, or an invaginated sulcus, but the mineralisation appears along all the lines on the dorsal surface. The median line appears as such on the internal mould of the counterpart (Fig. 5a), and

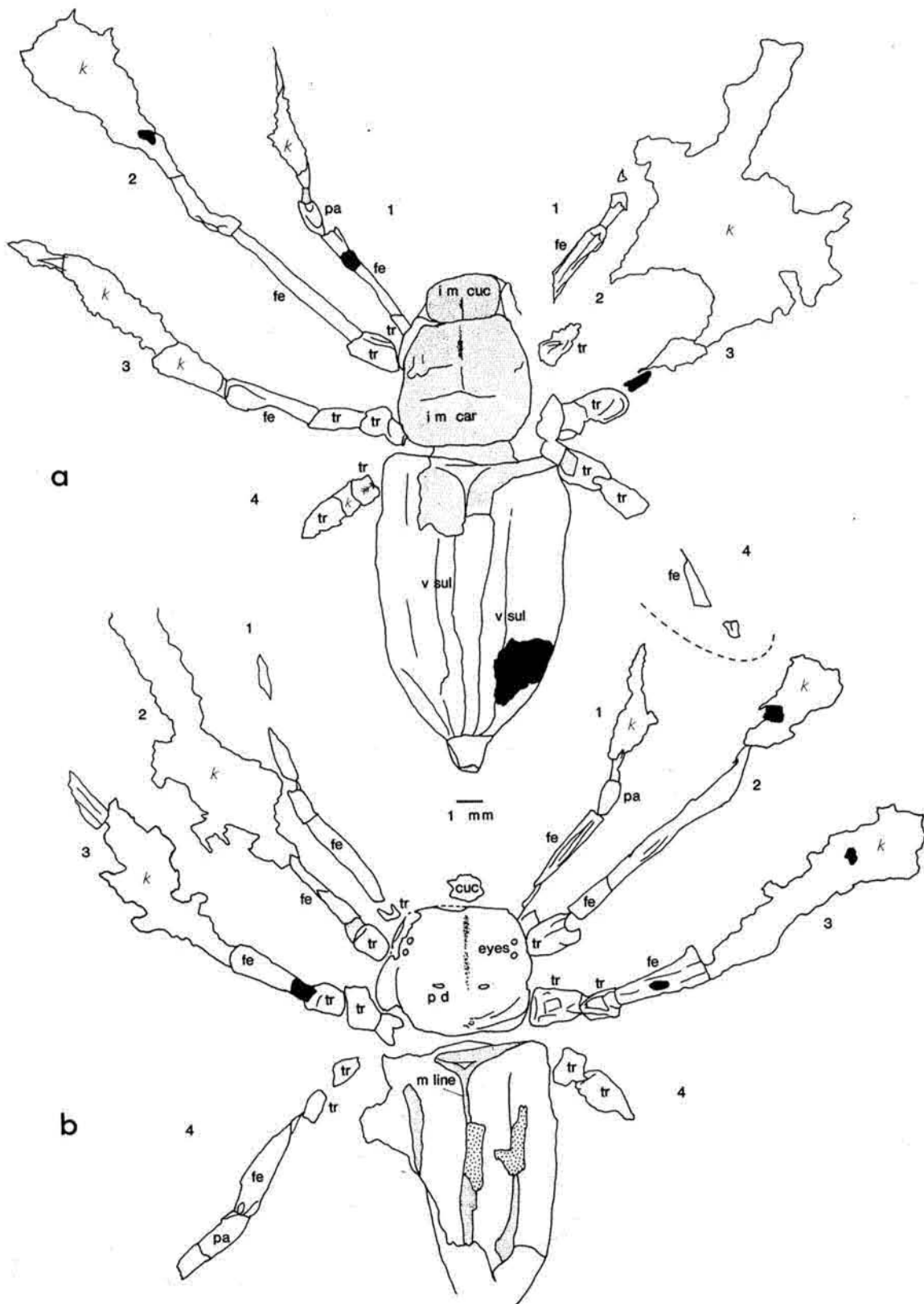


**Figure 4** Reconstructions of a range of fossil Ricinulei. (a) *Poliochera glabra*, based on UMMP 7223; (b) *Curculioides gigas*, based on PE 784; (c) *Poliochera punctulata*, based on USNM 37971 and PE 32206; (d) *Amarixys gracilis*, based on ISM 14862; (e) *Amarixys stellaris*, based on PE 32184; (f) *Curculioides mcluckiei*, based on USNM 440519; (g) *Terpsicroton alticeps*, based on In 31238.

at the anterior end of the median line on both part and counterpart a triangular sclerite is present. Lateral lines are present on the dorsal surface, about 1.8 mm on either side of the median line, and these lines curve outwards at the anterior end. The abdomen bears tubercles on the dorsal surface. The ventral abdomen surface is tuberculate except on the sulci. These sulci are 0.7 mm wide and 1.5 mm apart

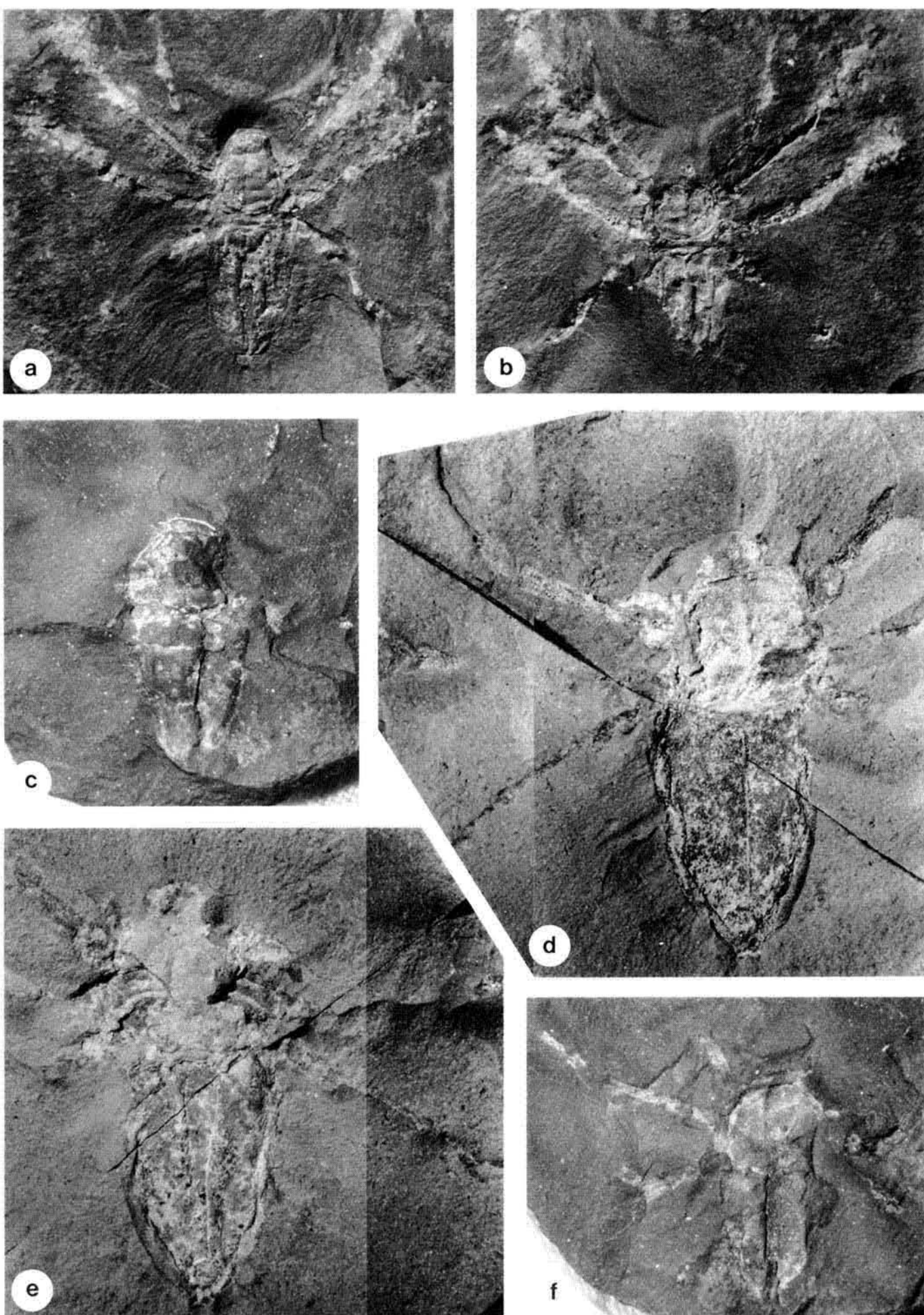
(between their inner margins) anteriorly, converging to 0.5 mm apart posteriorly. The surfaces of the sulci are smooth, but much of the ventral abdomen surface is obscured by fine mineralisation and large areas of pyrite. The pygidium is 1.4 mm long; its detailed structure is obscured by fine mineralisation.

No trace of the chelicerae or pedipalps is preserved. The



**Figure 5** *Curculioides ansticii* Buckland, 1837, camera lucida drawing of In 49323. (a) Ventral surface with internal mould of carapace; (b) dorsal surface. In this drawing, coarse stipple denotes areas of coarse mineralisation, black areas are solid pyrite, and *k* denotes patches of kaolinite.





**Figure 6** (a–e) *Curculioides ansticii* Buckland, 1837. (a, b) In 49323,  $\times 2.3$ , see Fig. 5; (a) ventral; (b) dorsal. (d, e) USNM 37973,  $\times 5.1$ , see Fig. 7; (d) dorsal; (e) ventral. (c, f) *Curculioides mcluckiei* sp. nov., PE 780,  $\times 3.0$ , see Fig. 8; (c) ventral; (f) dorsal.

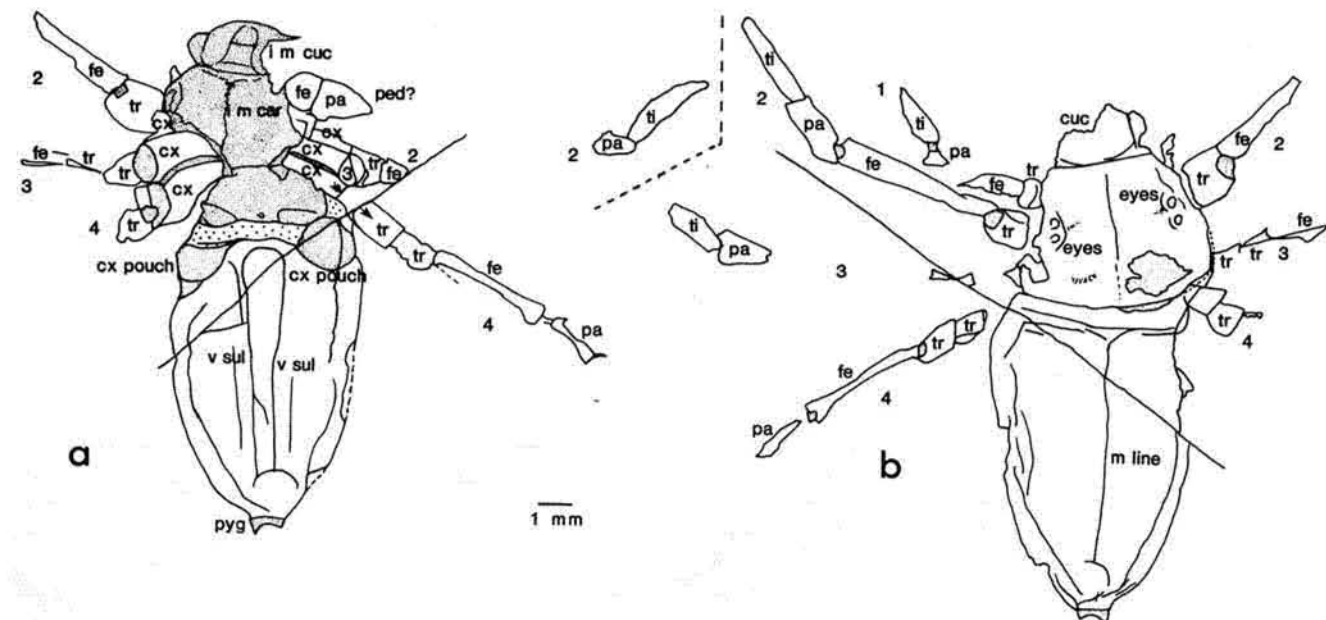
coxosternal region is obscured by the internal mould of the carapace on the counterpart. The distal parts of the walking legs deteriorate into amorphous patches of kaolinite. Attempts to scrape this material away revealed that there is no preserved morphology beneath. The proximal preserved parts of the legs measure, in mm, as follows: tr1,  $\geq 0.9$ ; fe1, 4.1; pa1, 1.5; tr2, 2.3; fe2, 6.5; tr<sup>1</sup>3, 2.0; tr<sup>2</sup>3, 1.6; fe3, 3.6; tr<sup>1</sup>4, 2.0; tr<sup>2</sup>4, 2.5; fe4, 4.5; pa4, 2.3.

**Description of USNM 37973.** The specimen is rather poorly preserved, being mostly covered with a film of minerals, and in parts with the internal mould as well. It is thus reminiscent of the type of preservation found in the holotype of *C. ansticii*. Ewing (1929) mentioned preparing out the second leg of a specimen of *C. ansticii*, and it is likely that this was the specimen he worked on.

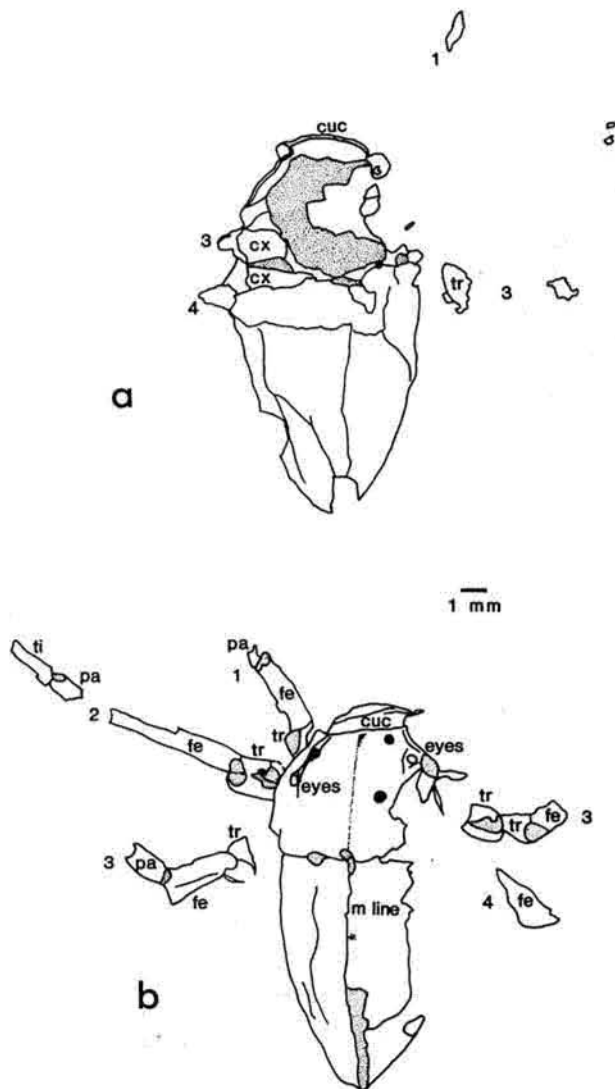
The cucullus is 1.8 mm long, and 3.4 mm wide; its outline is characteristic of that of the genus, but has a large median concavity on the dorsal surface. The carapace is 4.6 mm long and 6.1 mm wide; it is rounded subtrapezoidal in outline. The tuberculation is  $66 \text{ mm}^{-2}$ , and the tubercles are 0.071 mm in diameter. Eyes are present, though poorly preserved; the ocular axis is 1.8 mm from the anterior edge of the carapace (=ocular ratio of 0.39). The lateral crumpling has enhanced the relief of the ocular ridge, the ocular depressions, the median furrow, and the posterior depression (the latter on the left side of the part only, a piece is missing from the right side).

The abdomen is 8.9 mm long and 7.4 mm wide. The outline is slender elliptical. There is a median line dorsally, which finishes anteriorly in a small triangular sclerite; tuberculation is as on the carapace. The ventral abdomen has a pair of longitudinal, broad sulci, enclosing a median raised area, which run the length of the abdomen, converging slightly to the rear. At the anterior of the ventral abdomen, the raised area between the sulci, which increases in width from 0.5 mm to 1.25 mm towards the anterior, ends in a semicircle between the sacs for coxae 4. Only the basal segment of the pygidium is preserved.

Much of the ventral surface of the prosoma is obscured by the internal mould of the carapace. No trace of the chelicerae is preserved. The infracapitulum is obscured, but the femur and the base of the patella of the pedipalp can be



**Figure 7** *Curculioides ansticii* Buckland, 1837, camera lucida drawing of USNM 37973. (a) Ventral surface; (b) dorsal surface. In this drawing, coarse stipple denotes areas of coarse mineralisation.



**Figure 8** *Curculioides mcluckiei* sp. nov., camera lucida drawing of PE 780. (a) Ventral surface; (b) dorsal surface. In this drawing, black areas are clumps of pyrite.



made out on the right side of the counterpart. Only scraps of leg 1 are preserved, on the left side of the part, and consist of parts of the trochanter, femur, patella, and tibia. A small part of the triangular coxa of leg 2 is preserved on the left of the counterpart; tr2 is  $\geq 1.6$  mm long, fe2 is 5.2 mm long, pa2 is 2.2 mm long, and the proximal, preserved part of ti2 is 3.0 mm long. Coxa 3 is partly obscured by the internal mould of the carapace, and measures 2–3 mm in length; it is 1.2 mm wide. Tr<sup>1</sup>3 is 1.5 mm long; only scraps of the pa and ti of this leg are preserved. Coxa 4 is partly obscured by the internal mould of the carapace, and is 2–3 mm long, and 1.2 mm wide. Both trochanters of leg 4 are 1.5 mm long, fe4 is 4.0 mm long, and pa4 is 2.0 mm long.

**Remarks.** There is considerable similarity between the holotype and USNM 37973, but there are two exceptions. The density of the tubercles is  $54 \text{ mm}^{-2}$  in the holotype and  $66 \text{ mm}^{-2}$  in USNM 37973. This could be explained by the surface coating of fine mineralisation and kaolinite on the holotype, which needs to be scraped away before the tubercles are fully revealed in this specimen, in the process of which some information may have been lost. However, the same problem exists with USNM 37973, although in this case there is the addition of crumpling of the cuticle, which could be a factor acting to increase the tubercle density in this specimen. The ocular ratio also differs between the two specimens. This character might also be affected by different degrees of compression, and differs considerably between all the species of *Curculioides*. (It is most useful in distinguishing the species of *Poliochera*, in which genus the carapace is fairly flat and thus not subject to such a degree of distortion.)

*Curculioides mcluckiei* sp. nov.

(Figures 4f; 6c, f; 8; 9; 11a–e; 12; 13)

**Derivation of name.** After J. and L. McLuckie, whose fine collection of Mazon Creek fossils, now housed in the National Museum of Natural History, Washington DC, includes the holotype specimen.

- 1911 *Curculioides ansticii* Buckland: Pocock, pp. 39–40; text-figs 12, 13; pl. II, figs 7, 7a
- 1913 *Curculioides ansticii* Buckland: Petrunkevitch, p. 81, ref. to Pocock
- 1949 *Curculioides ansticii* Buckland: Petrunkevitch, p. 287, refs. to Pocock
- 1953 *Curculioides ansticii* Buckland: Petrunkevitch, p. 113, Coseley specimens
- 1963 *Curculioides gracilis* Petrunkevitch: Langford, p. 65; figs 104–5
- 1980 *Curculioides ansticii* Buckland: Morris, p. 34, Coseley specimens
- 1987 *Curculioides ansticii* Buckland: Brauckmann, p. 99
- 1991 *Curculioides ansticii* Buckland: Brauckmann, p. 47

**Diagnosis.** *Curculioides* with carapace tubercles with a diameter between 0.065 mm and 0.085 mm and a density of between  $65 \text{ mm}^{-2}$  and  $85 \text{ mm}^{-2}$ ; neither ventral sulci nor dorsal transverse lines on the abdomen.

**Material.** Holotype, USNM 440519, part and counterpart, J. and L. McLuckie Collection (collection No. 500-2.1), in the National Museum of Natural History, Washington DC, from the Westphalian D of Mazon Creek, Illinois. Other specimens: PE 780, part and counterpart, in the Field Museum of Natural History, Chicago, from the Westphalian D of Mazon Creek, Illinois; In 31246, part and counterpart, and In 31256, part and counterpart, in the British Museum (Natural History), London, from Coseley, Worcestershire,

probably Westphalian B, Lower Similis-Pulchra Zone, of Claycroft Openworks (SO 9372 9297; see Schram 1979). Neither of the American specimens have been described before; the British specimens were described by Pocock (1911) as *C. ansticii*, probably without reference to the holotype of this species.

**Description of the holotype.** This is a very well preserved specimen, exhibiting the morphology of a number of organs extremely well, although it has suffered lateral compression which gives it the appearance of a much narrower specimen. The cucullus is extended forwards, and the counterpart preserves its internal mould. It is 4.2 mm wide and 2.0 mm long. It is somewhat rectangular, with a bowed front, a pair of longitudinal furrows 2.8 mm apart, beyond which laterally the sides are bulbous. The carapace is 5.3 mm long and 6.1 mm wide, though it appears longer than wide due to the lateral compression. It is slightly rounded subtrapezoidal. The carapace tuberculation is  $79 \text{ mm}^{-2}$ , and the tubercles are 0.078 mm in diameter. There is a median furrow extending from the anterior border three-quarters of the length of the carapace, and at its termination, the posterior depressions occur, 1.6 mm apart, on either side of the midline. Ocular depressions are also present. Eyes are present, but somewhat hidden by folding; the ocular axis is 1.9 mm from the anterior border of the carapace (=ocular ratio of 0.36). The topography of the ocular ridge is enhanced by the folding.

The abdomen bears tuberculation similar to the carapace, on both dorsal and ventral sides, but the ventral side is, for the most part, obscured by the internal mould of the dorsal side. The abdomen is 9.5 mm long and 6.5 mm wide. It is slender elliptical; a median longitudinal line extends the length of the dorsal side of the abdomen; there are no lateral lines. The pygidium is well preserved, in the extended position. There are three segments, each narrower than the preceding, so that they could be telescoped in life. The anteriormost segment has a mid-dorsal notch, similar to that seen in many modern species. The posterior margins of each segment bears longitudinal striations which represent the positions of large setae in life. The pygidial cuticle is smooth, apart from a few tubercles at the posterior margin of the anteriormost segment.

The chelicerae are not preserved. The infracapitulum is trapezoidal in shape, with a basal pair of round concavities bearing tubercles, between which is a line that extends forwards to become the median groove. No more of the pedipalp is preserved. Leg 1 coxae are preserved as internal moulds lying above the pedipalp trochanter and femur; cx2 is triangular; it is impossible to determine whether a small tritosternum is present. Coxa 3 is 3.6 mm long and 1.7 mm wide; cx4 is 3.8 mm long and 1.7 mm wide. The more distal podomeres measure as follows, in mm: tr1, 1.1; fe1, 3.7; only the proximal part of pa1 is preserved; tr2, 2.5; fe2, 6.4; only the proximal 2.2 mm of pa2 is preserved; tr<sup>1</sup>3, 1.5; tr<sup>2</sup>3, 2.0; fe3, 3.2; only the proximal 2.2 mm of pa3 is preserved; tr<sup>1</sup>4, 1.6; tr<sup>2</sup>4, 2.0; fe4, 4.5; and only the proximal 1.5 mm of pa4 is preserved.

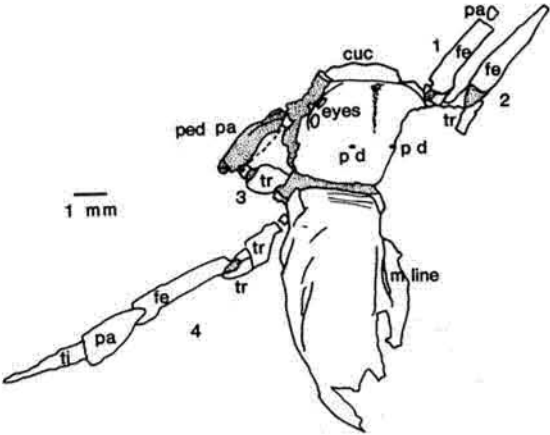
**Description of PE 780.** The cucullus is preserved part-closed, so that the proximal dorsal surface is on the dorsal part, and the ventral mould occurs on the counterpart. Also on the counterpart is a recurved slot in front of the carapace, where the cucullus dorsal and ventral moulds disappear into the rock matrix. The preserved area on the dorsal part is 1.0 mm long; the maximum width of the cucullus is 4.0 mm wide, and is 3.0 mm wide between the lateral grooves. The specimen is not crushed dorsoventrally in the nodule, and this has resulted in the carapace being

somewhat skewed. It is 5.2 mm long and 6.0 mm wide. The eye pairs are deformed by the lateral folding: only the posterior eye on the left of the part, and possibly the anterior eye on the right of the part, can be seen. The ocular ratio appears to be around 0.33, but this cannot be confirmed because of the distortion of the carapace. A median groove is present; posterior and ocular depressions are faint, but visible because of their finer tuberculation. The tubercles measure 0.080 mm in diameter and are present on the carapace at a density of 72 mm<sup>-2</sup>.

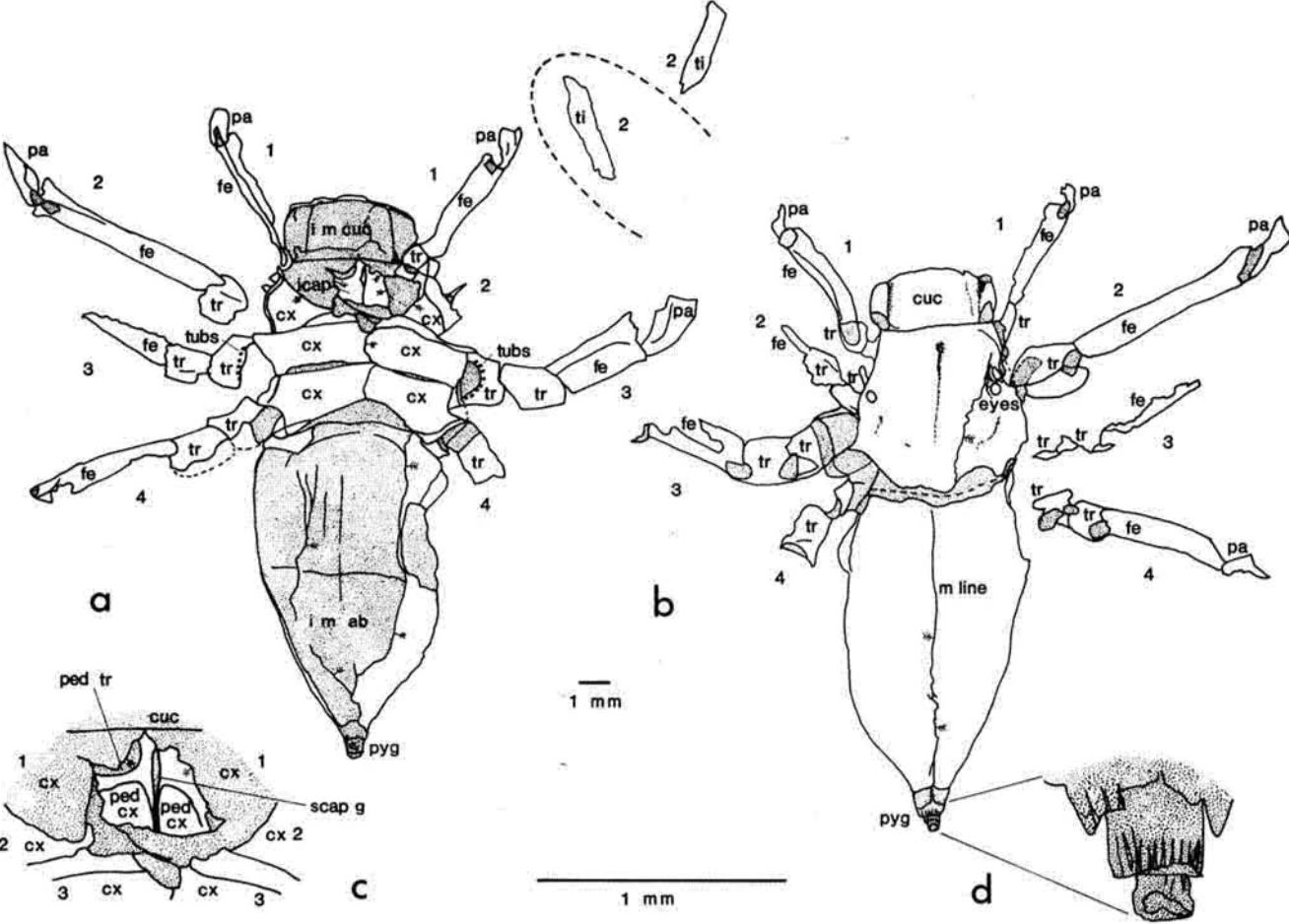
The abdomen is 9.0 mm long and 5.4 mm wide on the dorsal side; on the ventral side however, a figure of 7.3 mm is reached for the abdominal width. Tubercles are present on the abdomen, and these are finer on the ventral abdomen. A median line is present dorsally, and at the posterior a cylinder of internal mould material runs along just to the right of the line. On the ventral side, no sulci are present, but a faint lateral longitudinal line occurs on the left side of the counterpart, 3.9 mm from the midline anteriorly, and becoming half as close to the midline posteriorly.

The prosoma on the counterpart consists mainly of internal mould. In places, the coxae of legs 3 and 4 appear through breaks in the mould. The coxal pouches appear as a mass posterior to coxae 4. Fragments of the walking legs are present, and measure, in mm, as follows: tr1, ≥1.0; fe1, 3.3; tr2, 2.0; fe2, 6.0; pa2, 2.0; ti2, ≥2.0; tr13, 1.5; tr23, 1.5; fe3, 3.0; pa3, ≥1.7. Only scraps of other podomeres are preserved.

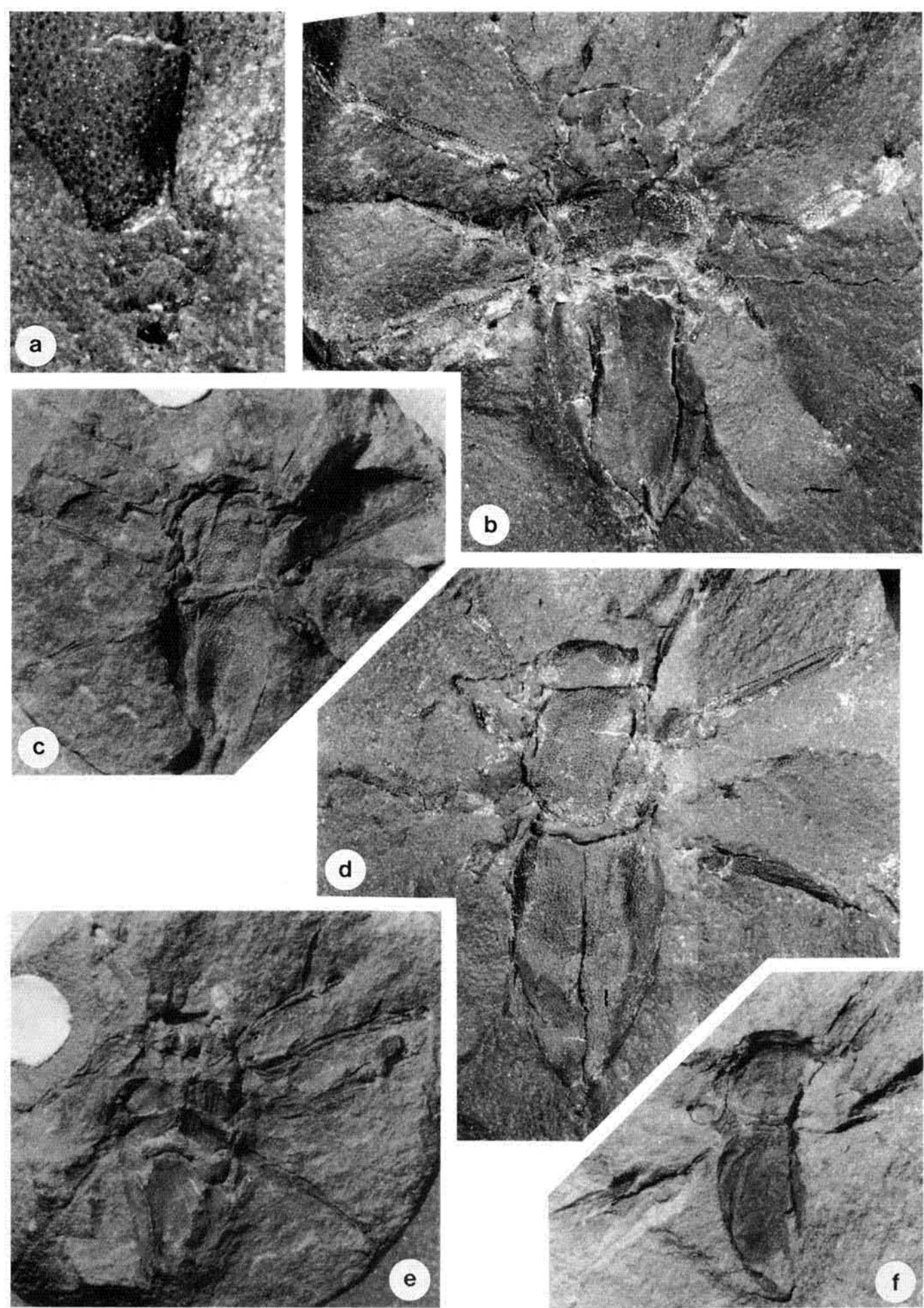
**Description of In 31246 and In 31256.** Two small specimens from Coseley, Worcestershire, In 31246 and In 31256, are preserved in small ironstone nodules. In 31246 is weathered to a bright yellow colour (limonite?), and has many fissures crossing the specimen; its preservation is poor. These two specimens are almost certainly the same species, being similar in shape, dimensions, and locality. In 31246 does not show any details not shown by In 31256, so the latter only is described below.



**Figure 10** *Curculioides pococki* sp. nov., camera lucida drawing of In 7885, dorsal surface.



**Figure 9** *Curculioides mcluckiei* sp. nov., camera lucida drawings of USNM 440519. (a) Ventral surface; (b) dorsal surface; (c) detail of infracapitulum from ventral surface; (d) detail of pygidium from dorsal surface. Upper scale bar refers to (a) and (b) lower scale bar to (c) and (d). On this specimen, the internal mould of the dorsal surface of the abdomen (Fig. 9a: i m ab) is not smooth but bears fine pits.



**Figure 11** (a–c) *Curculioides mcluckiei* sp. nov. (a, b, d) USNM 440519, see Fig. 9; a, detail of pygidium, dorsal aspect  $\times 26$ ; (b) ventral surface,  $\times 5.1$ ; (d) dorsal surface,  $\times 5.1$ . (c, e) In 31256,  $\times 4.7$ , see Fig. 12; (c) dorsal surface; (e) ventral surface. (f) *Curculioides pococki* sp. nov., In 7885,  $\times 4.9$ , see Fig. 10, dorsal surface.



In 31256 was buried in the nodule slightly rotated along its long axis to the right on the dorsal part. The cucullus is preserved in the part-closed position, and the preserved parts measure 0.7 mm long and 2.3 mm between the longitudinal grooves (which on this specimen form the lateral terminations). The carapace is 3.6 mm long and 4.7 mm wide. Eyes are visible, especially on the right side of the part, those on the left being involved in the folding of the lateral sides of the carapace. The eyes are 1.25 mm from the anterior edge of the carapace (=ocular ratio of 0.35). Ocular and posterior depressions and a median groove are present on the carapace. The tubercles on the carapace are 0.077 mm in diameter, and have a density of  $74 \text{ mm}^{-2}$  on the carapace.

The abdomen is 7.5 mm long and maximally 4.6 mm wide (6.0 mm wide if measured by doubling the greatest width of the best preserved half; because of the rotation, this may be an overestimate). There is a longitudinal median line on the dorsal side of the carapace. On the ventral side of the carapace, a pair of longitudinal depressions are present, with a V-shaped cross-section. These sulci are unlike those of *C. ansticii*, in which the sulcus is floored by smooth

cuticle, but are formed from the normal, tuberculate, ventral abdominal cuticle. At the anterior end the appearance of the sulci is strongly influenced by the large coxae 4 pouches: they are really lines on the abdomen which are enhanced into broad folds by the small size of the abdomen and the relatively large size of the coxal pouches. The lines are 2.4 mm apart anteriorly, and converge to 1.0 mm apart at the most posterior preserved part of the counterpart (the most posterior part of the ventral abdomen is not preserved on the counterpart). The pygidium is not preserved.

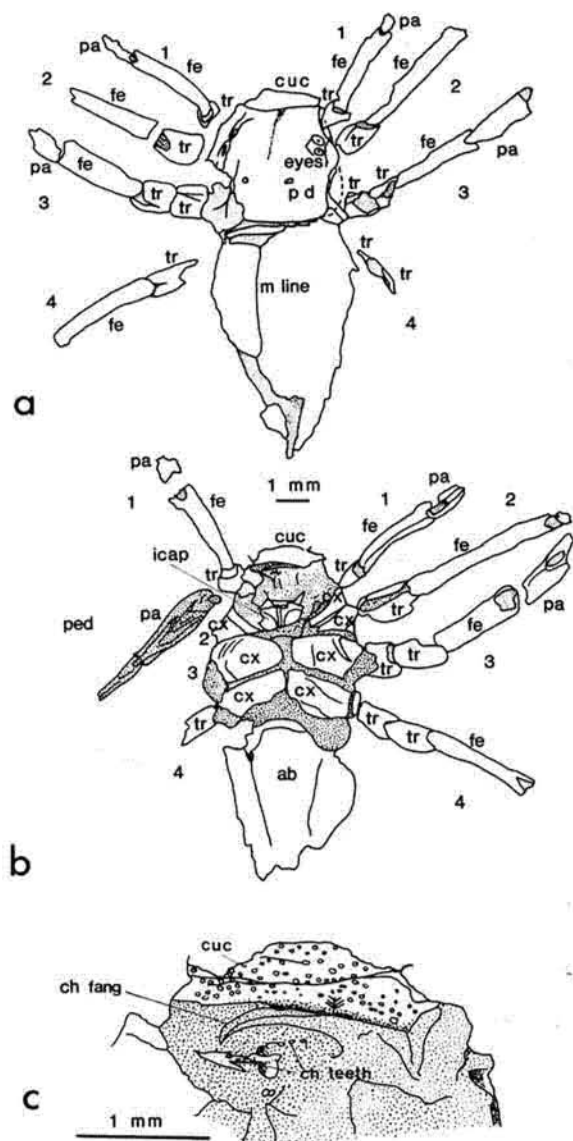
The cheliceral fang of the chelicera on the right side of the counterpart is preserved as a scimitar-shaped groove with a rectangular ridge running along its length. It is 1.0 mm long. Posterior to this, in the otherwise smooth external mould, two rows of at least three holes represent teeth on the main body of the left and right chelicerae. The infracapitulum is preserved on both In 31256 and In 31246; it is the normal subtrapezoidal shape, with a pair of finely tuberculate, shallow depressions in the posterior half and a median subcapitular gutter. The pedipalp trochanters and femora are preserved as internal moulds, thus their dimensions are not determinable. The pedipalp patella (3.1 mm long) and tibiotarsus ( $\geq 1.8$  mm long) are preserved on the left side of the counterpart. These podomeres are smooth apart from a few tubercles at the base of the patella. Coxa 1 is subrectangular; cx2 is subtriangular-kite-shaped; both are 1.4 mm long and neither coxa meets its opposite in the midline. Coxa 3 is 2.3 mm long and 1.3 mm wide; these coxae appear not to meet in the midline though no obvious tuberculate sternite can be discerned. Coxa 4 is 2.4 mm long, 1.3 mm wide and these coxae meet in the midline. Prominent pouches for the receipt of coxae 4 during locking of prosoma and abdomen are present on the ventral surface. The remaining podomeres measure, in mm, as follows: tr1, 1.0; fe1, 3.0; pa1,  $\geq 1.2$ ; tr2, 1.5; fe2, 5.1; tr'3, 1.1; tr'3, 1.3; fe3, 3.0; pa3, 1.9; tr'4, 1.4; tr'4, 1.5; fe4, 3.6. The remaining podomeres are preserved only as scraps.

*Curculioides eltringhami* Petrunkevitch, 1949

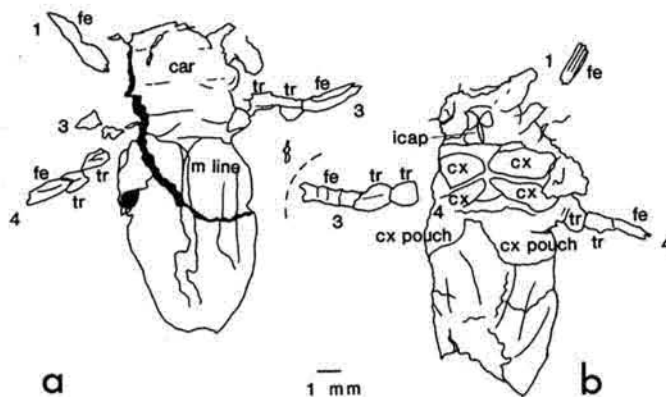
(Figures 14; 16g, h)

1949 *Curculioides eltringhami* Petrunkevitch, pp. 291–2; figs 167–9; pl. 83, figs 270–1

1953 *Curculioides eltringhami* Petrunkevitch, p. 113



**Figure 12** *Curculioides mcluckiei* sp. nov., camera lucida drawings of In 31256. (a) Dorsal surface; (b) Ventral surface; (c) detail of chelicerae and cucullus from ventral specimen.



**Figure 13** *Curculioides mcluckiei* sp. nov., camera lucida drawings of In 31246. (a) Dorsal surface; (b) ventral surface. Black areas on (a) represent deep cracks; the median line on the dorsal abdomen (m line in (a)) occurs as a ridge, which suggests that it was originally preserved as a line of mineralisation in this now heavily weathered specimen.

- 1955 *Curculioides eltringhami* Petrunkevitch, pp. P159–60; fig. 115, 3a, b  
 1987 *Curculioides eltringhami* Petrunkevitch: Brauckmann, p. 99; fig 5  
 1991 *Curculioides eltringhami* Petrunkevitch: Brauckmann, p. 47; fig. 19

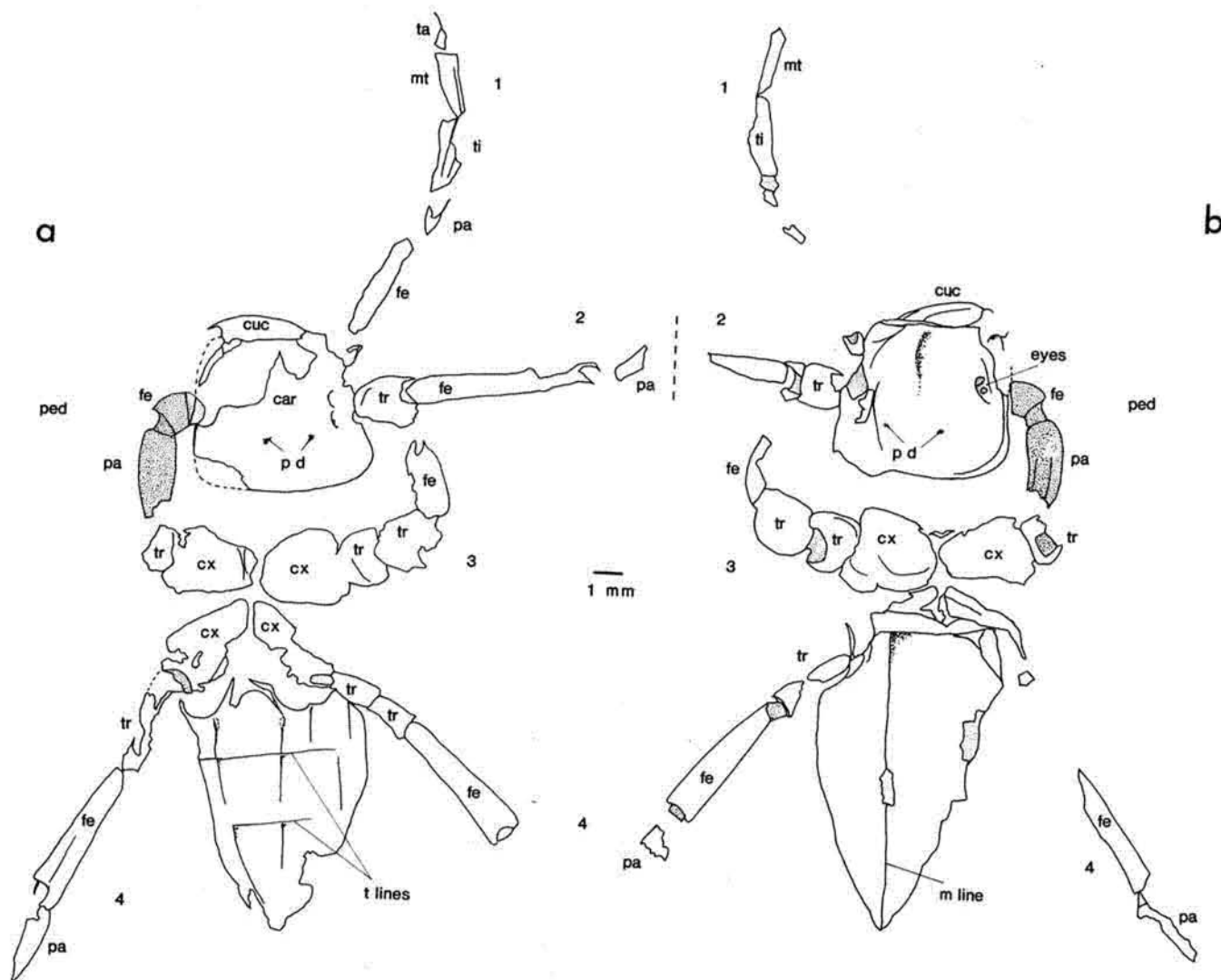
**Holotype and only known specimen.** In 39771, part and counterpart, in the British Museum (Natural History), London, from siltstones above the Hutton Coal, Upper Modiolaris Zone, Westphalian B, of Phoenix Brickworks, Crawcrook, Ryton-on-Tyne, Co. Durham (NZ 135628).

**Emended diagnosis.** *Curculioides* with carapace tubercles with a diameter between 0.065 mm and 0.085 mm and a density of less than 65 mm<sup>-2</sup>; neither ventral sulci nor dorsal transverse lines on the abdomen.

**Description.** The preservation of this specimen is slightly different from that of other fossil ricinuleids; the nodules from Ryton are somewhat larger and appear to be less iron-rich than those from elsewhere, so the specimen is more dorsoventrally compressed and its morphology is determined as much by tracing the darker colouration of its cuticle on the rock surface as by its relief. The specimen is preserved as an external mould of the dorsal surface (part) and a combination of external mould of the ventral abdomen and coxae, and internal mould of the carapace and

some anterior appendages (counterpart). The carapace appears to have come to rest at a slight angle to the horizontal, and is more crumpled on the left side of the part than on the right. The carapace is considerably detached forwards from the abdomen, revealing the coxae of legs 3 and 4. A narrow strip of cuticle, 0.9 mm long, at the anterior end of the specimen may represent the cucullus. The carapace is 5.3 mm long and 6.7 mm wide. Eyes are very difficult to make out on the specimen, but there is a suggestion of their presence (by smooth cuticle) about 4 mm apart and 2.1 mm from the anterior margin of the carapace (=ocular ratio of 0.40), on the part. A median groove and posterior depressions (1.8 mm apart and 1.8 mm from the posterior border) are present. The carapace tubercles are 0.072 mm in diameter and their density is 49 mm<sup>-2</sup>.

The abdomen is 10.4 mm long, but, since the pygidium is not preserved, this may not be the total length of the abdomen. It is 7.8 mm wide, and a median longitudinal line is present on the dorsal surface. The abdomen bears tubercles, which are fine in dorsal anterior and anterolateral areas. The ventral surface of the abdomen bears two faint transverse sutures representing sternite boundaries. The first two sternites bounded by these lines are 2.4 mm long, and the posterior one is 3.8 mm long, sagittally. A pair of longitudinal depressions occurs on each sternite, 2.2 mm apart, the posterior pair converging to the posterior. The



**Figure 14** *Curculioides eltringhami* Petrunkevitch, 1949, camera lucida drawings of In 39771. (a) Ventral surface; (b) dorsal surface.

ventral abdomen bears tubercles. Pouches for coxae 4 are prominent at the anterior of the ventral surface.

Coxae 3 and 4 are visible on both part and counterpart. Coxa 3 is 3.0 mm long and 2.5 mm wide, cx4 is 3.6 mm long and 2.3 mm wide. No trace of the chelicerae is visible. The pedipalp is represented by the femur (1.5 mm) and part of the patella ( $\geq 3.0$  mm) on the right side of the part, and the left side of the counterpart. The following parts of the walking legs are preserved and measure, in mm: tr1, 1.0; fe1, 4.0; pa1,  $\geq 1.7$ ; ti1, 2.8; mt1, 2.3; ta1,  $\geq 0.9$ ; tr2, 2.2; fe2, 6.7; pa2,  $\geq 1.9$ ; tr'3, 1.8; tr'3, 2.2; fe3, 2.7; tr'4, 2.0; tr'4, 1.6; fe4, 5.4; pa4,  $\geq 3.0$ .

*Curculioides granulatus* Petrunkevitch, 1949

(Figures 15; 16e, f)

- 1949 *Curculioides granulatus* Petrunkevitch, pp 287–91; figs 163–6; pls 81, fig. 266; 82, fig. 267  
 1953 *Curculioides granulatus* Petrunkevitch, 113  
 1955 *Curculioides granulatus* Petrunkevitch, p. P160; fig. 115, 2a, b (NB not from Penn., Ill.)  
 1980 *Curculioides granulatus* Petrunkevitch: Morris, p. 34  
 1987 *Curculioides granulatus* Petrunkevitch: Brauckmann, p. 99; fig. 7  
 1991 *Curculioides granulatus* Petrunkevitch: Brauckmann, p. 47; fig. 21

**Holotype and only known specimen.** In 18592, part and counterpart, in the British Museum (Natural History), London, from clays below the Top Hard Coal, Upper Modiolaris Zone, Westphalian B, of Shipley Manor Clay Pit, Ilkeston, Derbyshire (SK 4500 4410).

**Emended diagnosis.** *Curculioides* with carapace tubercles with a diameter less than 0.065 mm and a density of between 65 mm<sup>-2</sup> and 85 mm<sup>-2</sup>; neither ventral sulci nor dorsal transverse lines on the abdomen.

**Description.** The cucullus is preserved in the part-open position, the dorsal 1.4 mm is on the dorsal part, and on the ventral counterpart a recurved slot represents the external moulds (both dorsal and ventral) of the cucullus disappearing into the matrix in front of the chelicerae. Between the longitudinal grooves the cucullus measures 3.2 mm. The carapace is 4.3 mm long and 5.0 mm wide. A median groove, and ocular and posterior depressions are present on the carapace. The eyes are prominent, 3.6 mm apart, and the ocular axis is 1.6 mm from the anterior edge of the carapace (=ocular ratio of 0.37). The tubercles are 0.058 mm in diameter, and have a density of 79 mm<sup>-2</sup> on the carapace.

The abdomen is 8.4 mm long and 5.6 mm wide. The dorsal surface bears a median longitudinal line which terminates anteriorly in a small triangular sclerite. Tubercles are present over the surface of the abdomen. The ventral surface of the abdomen bears transverse lines which separate two anterior sternites of 2.5 mm long and a posterior sternite of 3.4 mm long, sagittally. In addition, a pair of longitudinal depressions occur, 1.9 mm apart on either side of the midline, on each sternite (they may converge towards the posterior, but are obscured by longitudinal folding here). Large pouches for the receipt of coxae 4 during locking are present anterolaterally. The pygidium consists of three telescoped segments. The total length, partly everted, is 1.2 mm. The anterior segment bears tubercles and is 0.7 mm long; the second and third segments are smooth and are 0.5 mm and 0.3 mm long, respectively.

On the counterpart, the hands of the chelicerae and the

coxae of legs 1 and 2, and the trochanters and femora of the pedipalps are represented by their internal moulds. The chelicerae are 1.1 mm long. A small piece of the pedipalp patella is present on the right side of the part. Coxae 1 are partly obscured by the trochanters and femora of the pedipalps, but the coxosternal region here is somewhat confused. The coxae of leg 2 are 2.5 mm long and triangular; they do not meet in the midline, but are separated by the infracapitulum which is subtrapezoidal in shape, with a median subcapitular gutter. The posterior half bears a pair of circular raised areas on either side of the gutter. Coxae 3 appear to be separated by a triangular sternite (the tritosternum). Coxa 3 is 2.9 mm long and 1.4 mm wide. Coxa 4 is 3.0 mm long and 1.1 mm wide. The remaining leg podomeres measure, in mm, as follows: tr1, 1.0; fe1, 3.2; pa1,  $\geq 1.9$ ; tr2, 1.7; fe2, 6.4; pa2, 2.0; ti2, 4.6; tr'3, 1.5; tr'3, 2.2; fe3, 2.8; pa3, 2.8; ti3,  $\geq 3.7$ ; tr'4, 1.4; tr'4, 1.2; fe4, 4.0; pa4, 2.0; ti4, 2.3.

*Curculioides scaber* (Scudder, 1890)

(Figures 16a, b; 17)

- 1890 *Geratarbus scabrum* Scudder, pp. 448–9; pl. 39, fig. 5  
 1913 *Curculioides scaber* (Scudder): Petrunkevitch, pp. 82–3; figs 47–8; pl. VII, figs 36–7  
 1949 *Curculioides scaber* (Scudder): Petrunkevitch, p. 287  
 1953 *Curculioides scaber* (Scudder): Petrunkevitch, p. 113  
 1955 *Curculioides scaber* (Scudder): Petrunkevitch, p. P160; fig. 116, 1a, b  
 1963 *Curculioides scaber* (Scudder): Laurentiaux-Vieira & Laurentiaux, p. 26  
 1987 *Curculioides scaber* (Scudder): Brauckmann, p. 99; fig. 8  
 1991 *Curculioides scaber* (Scudder): Brauckmann, p. 47; fig. 22

**Holotype and only known specimen.** USNM 37965, part and counterpart, in the National Museum of Natural History, Washington DC (ex R. D. Lacoe Collection, No. 1766; not 1765 as quoted by Petrunkevitch 1913), from the Westphalian D of Mazon Creek, Illinois.

**Emended diagnosis.** *Curculioides* with carapace tubercles with a diameter between 0.065 mm and 0.085 mm and a density greater than 85 mm<sup>-2</sup>; neither ventral sulci nor dorsal transverse lines on the abdomen.

**Description.** This specimen is generally well preserved, although on the dorsal part the right side is bent downwards and the left side is bent upwards; there are corresponding bends on the counterpart. The cucullus is poorly preserved, only scraps remaining on both part and counterpart. The carapace is 4.6 mm long and 6.6 mm wide. It is subtrapezoidal in outline, with a median furrow. The tuberculation is 90 mm<sup>-2</sup>, and the tubercles measure 0.075 mm in diameter. The eyes are well preserved on the right of the part; the ocular axis is about 1.6 mm from the anterior border of the carapace (=ocular ratio of 0.35; this is probably too low because of the compression at the front of the carapace). Ocular depressions occur adjacent to the ocular ridge, and the posterior depressions occur as transversely elongate furrows on either side of the median furrow about two-thirds of the way back from the anterior border.

The abdomen is 8.2 mm long and 7.5 mm wide. A median line is present, partly hidden by folding, which terminates anteriorly in a triangular sclerite. At the carapace–abdomen junction, there is a deep fold which is floored, in part, by finely tuberculate cuticle in a narrow band with a recurved



anterior margin and a straight posterior margin. The abdomen bears tubercles similar to those on the carapace. The ventral side of the abdomen is finely tuberculate, and divided into sternal fields; a very low angle illumination is necessary to see these faint features, but when recognised, a line of larger tubercles is noticeable just anterior to the dividing lines of the sternites. At the anterior end there is a recurved semicircular line between the ventral coxal sacs. Behind this line the mould is broken through into a circle, but at the posterior end of the semicircle there is a narrow sternite, 0.4 mm long. Two further transverse lines cross the ventral abdomen, dividing it into sternites 2 and 3, each 2 mm long, and a fourth sternite, 3.5 mm long. Shallow furrows run from the anterior border of each sternite, 1.5 mm apart, on either side of the midline. A further pair of furrows may be present laterally, but these are only faintly preserved on the right of the counterpart. The lateral edges of the abdomen are folded, suggesting the possibility of more flexible pleural cuticle. Only the most anterior segment of the pygidium is preserved.

The cheliceral fixed teeth are represented by a pair of holes in the counterpart behind the cucullus impression. The fangs are represented by a pair of larger holes lateral to these. The infracapitulum is subtrapezoidal, with a median groove. The trochanter of the pedipalp is subcircular; the rest of the appendage disappears into the matrix. Coxa 1 appears only as fragments of internal mould lying above the pedipalp trochanters. Coxa 2 is triangular, and is 2.5 mm long. Coxa 3 is 3.2 mm long and 2.1 mm wide. Coxa 4 is 3.9 mm long and 1.5 mm wide. Only the distal, horizontal pivot joint of tr1 can be seen on the part. The more distal podomeres measure as follows, in mm: fe1, 2.4; pa1, 1.6; ti1, 2.2; only the proximal part of mt1 is preserved; tr2, 1.9; tr'3, 1.6; tr'23, 1.3; fe3, 3.0; pa3, 2.9; ti3, 2.6; tr'4, 1.8; tr'24, 1.5; fe4, 4.9; pa4, 2.1; ti4, 3.9; mt4, only proximal 0.8 mm preserved.

*Curculioides pococki* sp. nov.

(Figures 10; 11f)

**Derivation of name.** After R. I. Pocock, who first saw the resemblance between fossil ricinuleids, until then placed in Anthracomarti, and the living forms.

1911 *Curculioides ansticii* Buckland: Pocock, pp. 39–40; text-figs 12, 13; pl. II, figs 7, 7a.

1913 *Curculioides ansticii* Buckland: Petrunkevitch, p. 81

1949 *Curculioides ansticii* Buckland: Petrunkevitch, p. 287; fig. 269

1953 *Curculioides ansticii* Buckland: Petrunkevitch, p. 113

1963 *Curculioides ansticii* Buckland: Laurentiaux-Vieira & Laurentiaux, p. 26

1987 *Curculioides ansticii* Buckland: Brauckmann, p. 99

1991 *Curculioides ansticii* Petrunkevitch: Brauckmann, p. 47

**Holotype and only known specimen.** I 7885, in the British Museum (Natural History), London; from Coseley, Worcestershire, probably Westphalian B, Lower Similis-Pulchra Zone, of Claycroft Openworks (SO 9372 9297; see Schram 1979). This specimen came from the W. Madeley Collection.

**Diagnosis.** *Curculioides* with tubercles less than 0.055 mm in diameter and a density of more than 95 mm<sup>-2</sup> on the carapace.

**Description.** This specimen is preserved only as the dorsal part, no counterpart is now available. The right side of the specimen is broken away. The cucullus is preserved in

the part-closed position, and only 0.5 mm of its length is present. It measures 2.5 mm between the grooves. The carapace is 3.3 mm long and 5.0 mm wide (the considerable convexity of the carapace in contrast to that of other specimens suggests that these measurements would be greater with more compression). Eyes occur on the left side, 1.0 mm from the anterior border of the carapace (=ocular ratio of 0.30, but again this measurement is affected by the carapace convexity). Ocular and posterior depressions and a median groove are present on the carapace. The tubercles are 0.05 mm in diameter and have a density on the carapace of 101 mm<sup>-2</sup>.

The abdomen is 7.6 mm long and 6.4 mm wide (determined by doubling the width of the preserved left side). A longitudinal median line occurs on the dorsal side of the abdomen. The ventral abdomen and the pygidium are not preserved.

The pedipalp patella on the left is preserved and is 2.7 mm long. Femur 1 is 2.7 mm long, tr2 is 1.3 mm long, fe2 is  $\geq 3.6$  mm long. The podomeres of leg 4 measure: tr<sup>1</sup>, 1.3 mm; tr<sup>2</sup>, 1.2 mm; fe, 3.5 mm; pa, 2.3 mm; ti,  $\geq 2.8$  mm. Other podomeres are preserved only as scraps.

**Remarks.** The small size of this specimen and its provenance from Coseley suggests conspecificity with *Curculioides mcluckiei*, but the high density of small tubercles sets this species apart from all other *Curculioides*. The high density of tubercles on the carapace could be related to its small size, because there is a tendency for tubercle density to decrease with increasing size in the genus, but the small size of the tubercles appears to be a real character.

*Curculioides gigas* sp. nov.

(Figures 4b; 19; 21a, d)

**Derivation of name.** Greek *gigas*, a giant.

**Holotype and only known specimen.** PE 784, part and counterpart, Field Museum of Natural History, Chicago; from the Westphalian D of Mazon Creek, Illinois.

**Diagnosis.** *Curculioides* with a pronounced bimodality in diameter of tubercles on body: larger are 0.073 mm in diameter, smaller are about one-sixth this diameter; two fine transverse lines present on dorsal side of abdomen in addition to median longitudinal line.

**Description.** This specimen is the largest ricinuleid known, fossil or living. The cucullus is preserved in the closed position, so that the dorsal surface occurs as an external mould on the ventral counterpart. It measures 1.8 mm long, and maximally 4.5 mm wide. The lateral grooves on the cucullus are 3.5 mm apart. The carapace is 5.8 mm long and 7.5 mm wide. It is subsemicircular in shape, its greatest width being close to the posterior border, which is slightly procurved, forming an angle of about 80° to the sagittal plane. The eyes are well preserved; they are 5.3 mm apart, and the ocular axis is 2.0 mm from the anterior border of the carapace (=ocular ratio of 0.35). The posterior depressions are well-defined, transversely elongate, 1.7 mm apart and 3.6 mm from the anterior border of the carapace. Ocular depressions are not as prominent as the posterior, and the median groove is represented by only a shallow pit in the midline 1.0 mm anterior to the posterior depressions. The large tubercles are 0.073 in diameter, and have a density of 87 mm<sup>-2</sup>. Small tubercles are present in profusion between the larger ones.

The abdomen is preserved as the external mould on the part, and mainly the internal mould on the counterpart. The abdomen is 12.2 mm long and 10.6 mm wide. The

abdominal cuticle surface bears tubercles which are bimodal in size, as on the carapace; the small tubercles are about one-sixth the diameter of the larger ones. The dorsal surface of the abdomen bears a median longitudinal line, which appears on the counterpart (internal mould) as a narrow sulcus. Two transverse lines occur on the dorsal surface, 1.0 mm and 6.4 mm from the anterior edge of the abdomen. They appear as slight ridges, and therefore grooves in life, on the external mould, and the anterior one also bears only fine tubercles. These lines are also reflected on the internal mould, and their symmetrical, right-angled relationship to the median line establishes them as real entities, not artefacts of preservation. The ventral surface of the abdomen is almost entirely concealed beneath the internal mould of the dorsal surface. The parts which emerge from beneath the overlying internal mould show no longitudinal sulci; lines may be present though lost in folding. The pygidium is not preserved. A subcircular depression in the midline between the pouches for the receipt of coxae 4 during prosoma–abdomen locking represents the genital apparatus, in life normally concealed during locking. It is not possible to sex the specimen because the structure of male and female genitalia in ricinuleids is not sufficiently different, and the depression in the fossil could have been produced by either penis or genital lips.

Two pieces of internal mould of the carapace obscure the posterior part of the infracapitulum, which is otherwise shaped as in other members of the genus, and a subcapitular gutter is present. The pedipalp trochanters and femora are present, though not entirely clear due to the adpression of the cucullus in front and the internal mould of the carapace behind. Just posterior to the pedipalp trochanter is the coxa of leg 1; this is rectangular, but the median edge is obscured (on both left and right sides) by the internal mould of the carapace. Coxa 2 is triangular to kite-shaped, with the most

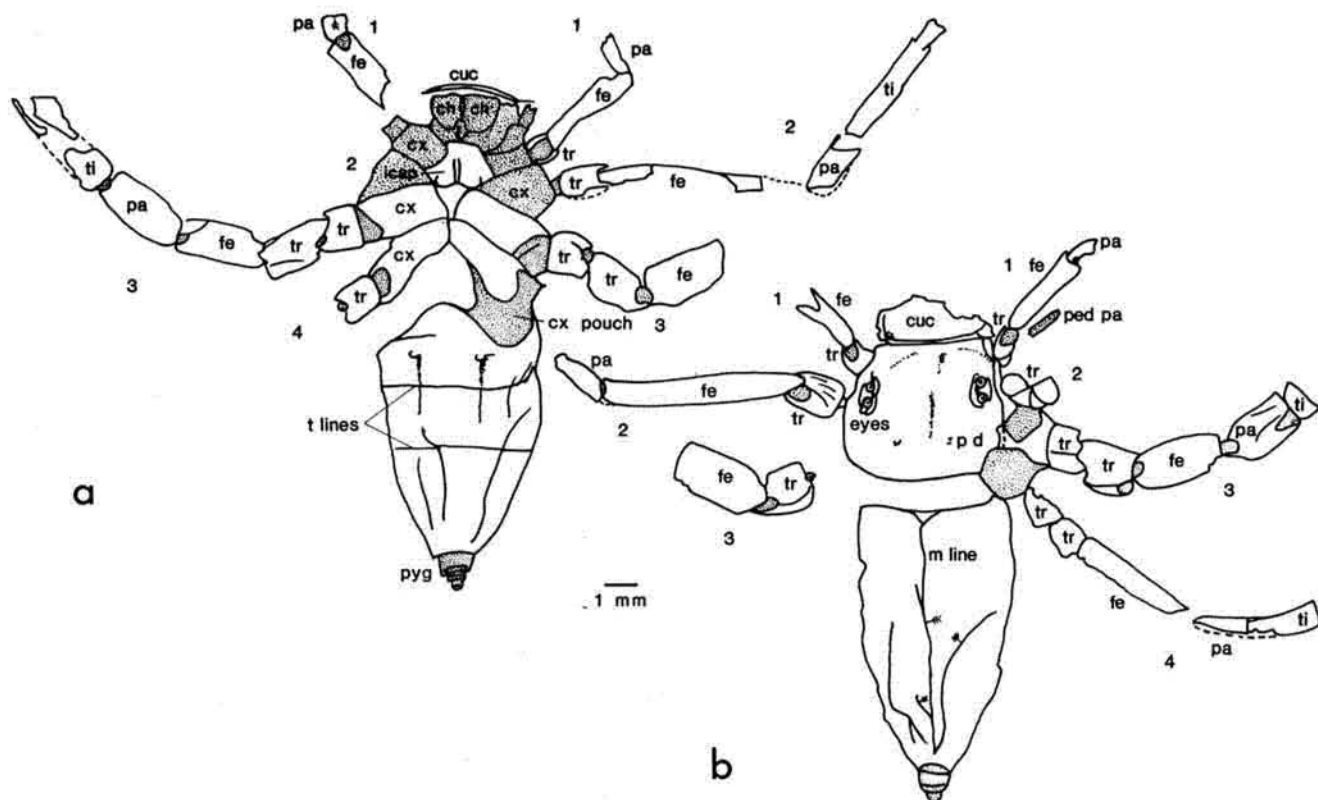
acute angle towards the median but not meeting the opposite cx2. Coxa 3 is 3.8 mm long, 2.6 mm wide, and subrectangular. Coxae 3 do not meet in the midline, but are separated by the tritosternum. Coxae 4 do meet in the midline, and are 4.3 mm long and  $\geq 1.6$  mm wide. Other podomeres measure, in mm, as follows: tr1, 1.4; fe1, 4.6; pa1, 2.5; tr2, 2.7; fe2, 8.0; pa2,  $\geq 3.2$ ; tr<sup>1</sup>3, 1.6; tr<sup>2</sup>3, 2.1; fe3, 4.7; pa3, 3.1; ti3, 3.4; mt3, 3.2; tr<sup>1</sup>4, 1.8; tr<sup>2</sup>4, 1.9; fe4, 5.7; pa4, 2.7; ti4, 4.0; mt4,  $\geq 3.6$ .

**Remarks.** The strongly bimodal size distribution of the tubercles in this species sets it apart from others in the genus. Fine tubercles do occur among the larger ones in other ricinuleids (though they are not so obviously bimodal in size), and this feature can be effaced by poor preservation or hard preparation. It is also possible that the fine transverse lines on the dorsal abdomen, not found in any other *Curculioides*, are enhanced by preservation or develop as a recapitulation of ancestral tergites only in larger specimens such as *C. gigas*. Further evidence will be required before either of these hypotheses can be tested. Nevertheless, on present evidence, this specimen is readily distinguished by these features, and in addition, the effacement of the median groove on the carapace and the shape of the carapace add weight to its placement in a new species.

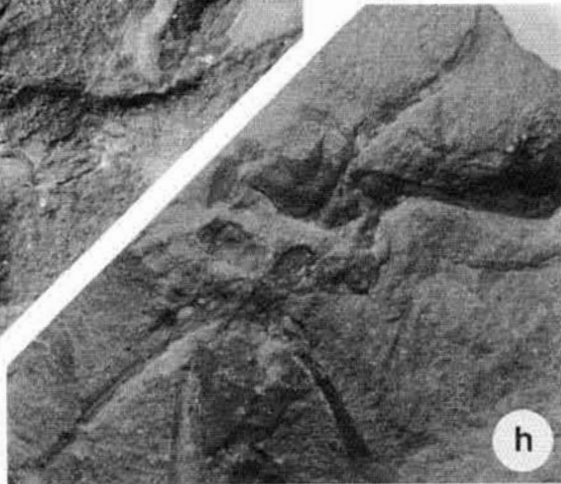
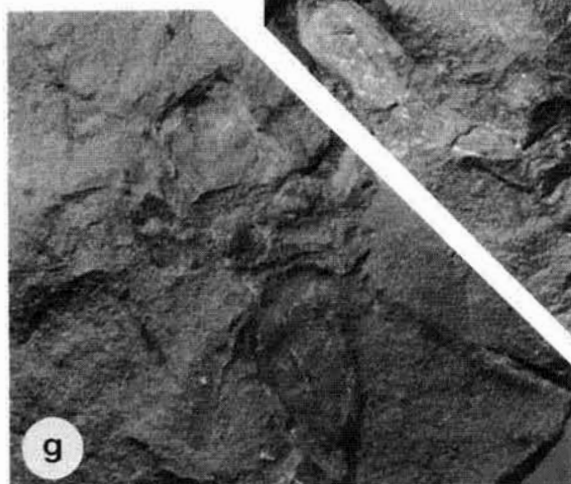
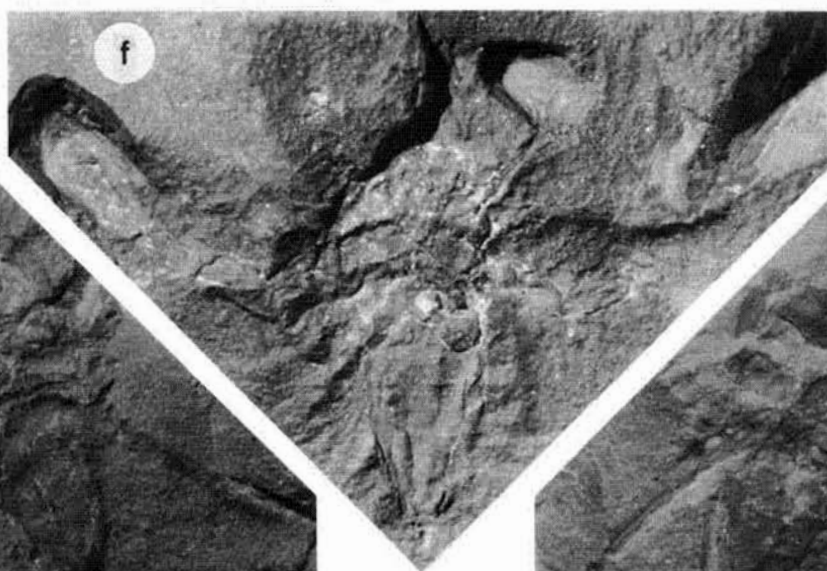
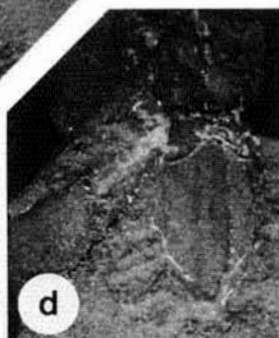
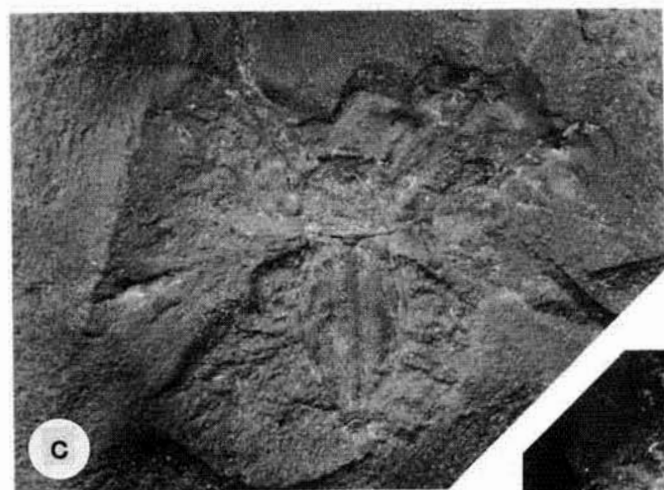
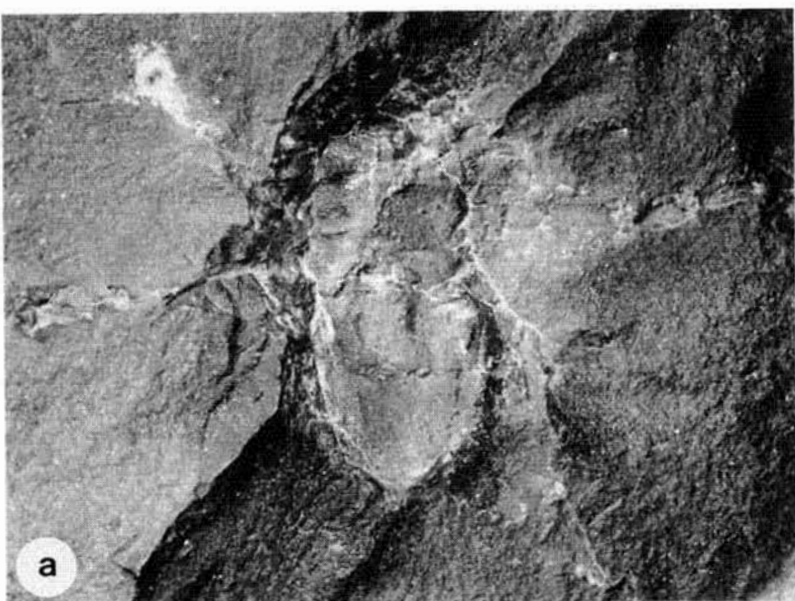
*Curculioides adompha* Brauckmann, 1987

1991 *Curculioides adompha* Brauckmann, p. 49; fig. 17

**Remarks.** This species, described by Brauckmann (1987, 1991), is represented by a single specimen (No. 1054 in the W. Sippel collection, Fuhlrott Museum, Wuppertal, Germany) which comes from the Vorhalle Schichten, upper Namurian B (R2c) of Ziegeli-Grube Hagen-Vorhalle, NW Hagen Westphalia. The holotype was not examined for the



**Figure 15** *Curculioides granulatus* Petrunkevitch, 1949, camera lucida drawings of In 18592. (a) Ventral surface; (b) dorsal surface.



**Figure 16** (a, b) *Curculioides scaber* (Scudder, 1890), USNM 37965,  $\times 3.6$ , see Fig. 17; (a) ventral surface; (b) dorsal surface. (c, d) *Amarixys sulcata* (Melander, 1903), UC 9235,  $\times 2.3$ ; (c) dorsal surface, see Fig. 18a; (d) ventral surface, NB: the piece of rock bearing legs 1–3 on the right side has been glued onto the remainder of the specimen incorrectly, see Fig. 18b for correct position, (e, f) *Curculioides granulatus* Petrunkevitch, 1949, In 18592; (e) dorsal surface,  $\times 2.9$ ; (f) ventral surface,  $\times 3.4$ ; see Fig. 15. (g, h) *Curculioides eltringhami* Petrunkevitch, 1949, In 39771,  $\times 2.3$ , see Fig. 14; (g) dorsal surface; (h) ventral surface.



present study, so the comments here are based on the published description.

This is the oldest ricinuleid so far described, all other fossil Ricinulei being Westphalian in age. It is preserved as an external mould of the dorsal surface with the outline of ventral surface features, such as the pouches for coxae 4 and the coxosternal region, superimposed. Unique in this specimen, among fossil ricinuleids, is the preservation of the tarsal region of walking legs 2–4. It is impossible to see the detail of the tarsi on the photographs in Brauckmann (1987), but the reconstruction shows 5 tarsomeres beyond the metatarsus in legs 2 and 4, but in leg 3 only 3 tarsomeres appear to be present, the most proximal bearing a short spine. Important diagnostic features of the specimen are: the density of tubercles on the carapace of  $90\text{ mm}^{-2}$ , and a dorsal median longitudinal line, not a sulcus, on the abdomen. The ocular ratio, estimated from the published figures, is about 0.33.

Three tarsomeres is characteristic of the third leg in the protonymph stage of *Ricinoides hanseni* (Legg 1976a) and *Cryptocellus pelaezi* (Pittard & Metcchell 1972). No other leg of any other instar possesses three tarsomeres, but one, two, four, or five occur. This suggests that *C. adompha* could be a protonymph, which seems unlikely given its large size. Three could be the true number present in this species, or there may have been a miscount. The small spine on tarsal segment 1 of leg 3 is interesting because this leg bears

genital modifications in the male. The pre-adult male shows a slight modification of these segments in *Ricinoides hanseni* (Legg 1976a), but a small spine could also occur in a female. Therefore, assuming a similar genital modification occurred in *Curculioides* as is seen in living ricinuleids, this specimen represents either an immature or a female.

The median longitudinal line on the dorsal side of the abdomen, but no sulcus, places this specimen in *Curculioides*. The carapace tubercle density of  $90\text{ mm}^{-2}$  suggests a relationship closer to *C. scaber* or *C. gigas* than any other species. The species characteristics of *C. gigas* of transverse dorsal lines on the abdomen and a bimodal size range of carapace tubercles was not mentioned for *C. adompha* by Brauckmann (1987), so it can be assumed that, of these two American species, *C. scaber* is more closely related to *C. adompha*.

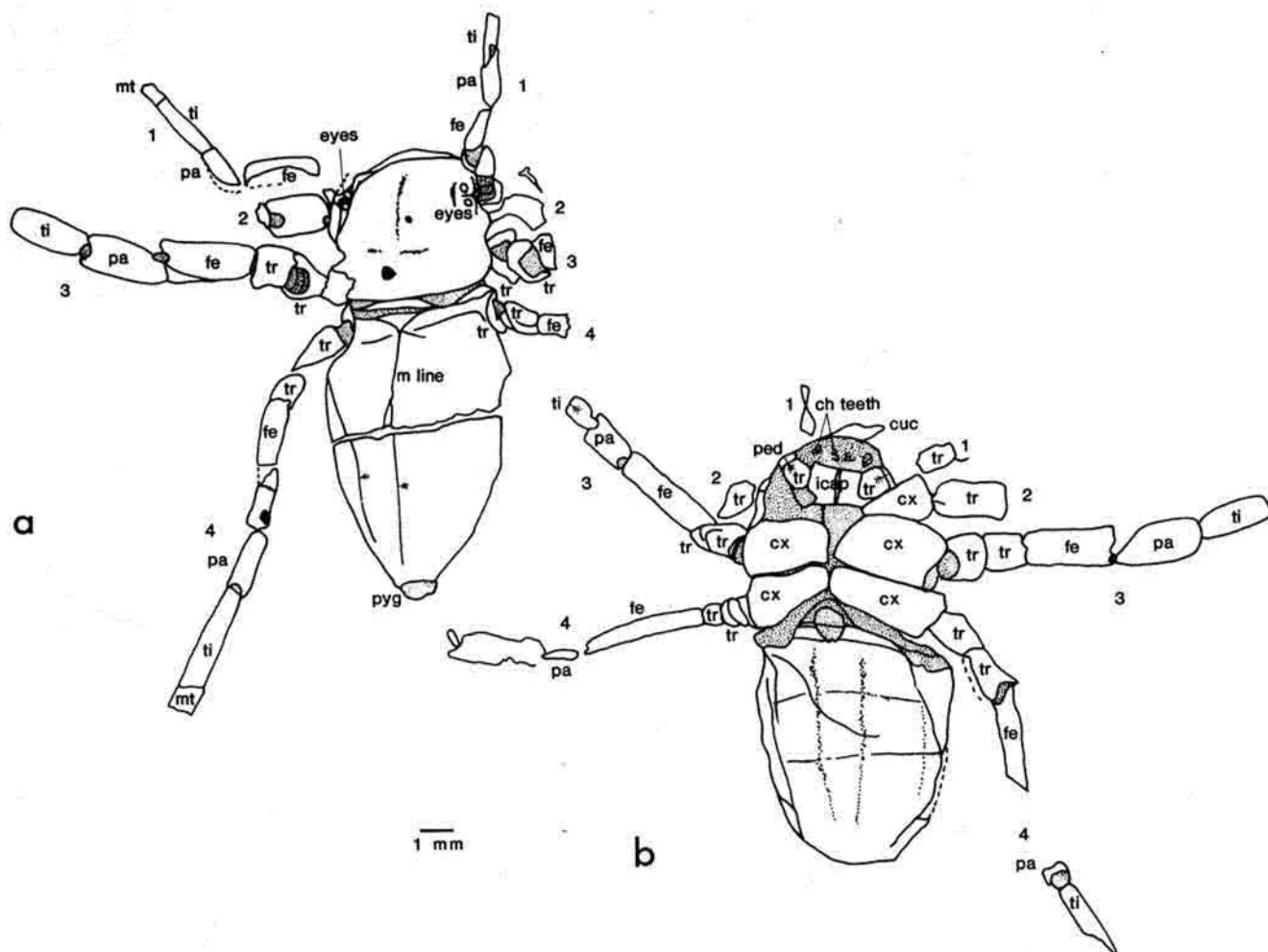
#### *Genus Amarixys* gen. nov.

**Type species.** *Kustarachne sulcata* Melander, 1903

**Derivation of name.** Greek *amara*, a trench, and *ixys*, the loins, lower part of the back; referring to the longitudinal sulcus running down the dorsal abdomen.

**Diagnosis.** Curculioidids with dorsal median sulcus, which lacks tubercles, on abdomen.

**Included species.** In addition to the type species, the following are included in the genus: *Curculioides gracilis* (Petrunkévitch, 1945), and *Amarixys stellaris* sp. nov.



**Figure 17** *Curculioides scaber* (Scudder, 1890), camera lucida drawings of USNM 37965. (a) dorsal surface; (b) ventral surface. Black spots are clumps of pyrite. The considerable relief on this nodule adjacent to the right side of the body of (a) and the left side of (b) has produced foreshortening of the podomeres in these parts of the drawing.

**Remarks.** Study of the fossil ricinuleids shows that one group of specimens, previously included within *Curculioides*, is distinctly different in having a broad, median sulcus, which lacks tubercles, in place of the median line which characterises the type and remaining species. The specimens with a sulcus are therefore removed from *Curculioides*, and placed in the new genus *Amarixys*. Additionally, this genus appears to have a subrectangular carapace, rather than the broadly pyriform shape which is typical of *Curculioides*.

There are great differences in tubercle size and density between the two species placed in *Amarixys*. These characters do not correlate with any others, such as size, so that there is little doubt that, pending the availability of much more material of *Amarixys*, they must be considered as separate species.

*Amarixys sulcata* (Melander, 1903)

(Figures 16c, d; 18)

- 1903 *Kustarachne sulcata* Melander, pp. 181–2; pl. V, fig. 5; pl. VII, fig. 4  
 1913 *Curculioides sulcatus* (Melander): Petrunkevitch, pp. 83–4; text-figs. 49, 50; pl. VII, fig. 38  
 1949 *Curculioides sulcatus* (Melander): Petrunkevitch, p. 287  
 1953 *Curculioides sulcatus* (Melander): Petrunkevitch, p. 113  
 1955 *Curculioides sulcatus* (Melander): Petrunkevitch, p. P160; fig. 116, 3a, b  
 1987 *Curculioides sulcatus* (Melander): Brauckmann, pp. 99, 102; fig. 9  
 1991 *Curculioides sulcatus* (Melander): Brauckmann, p. 48; fig. 23

**Holotype and only known specimen.** UC 9235, part and counterpart, in the Field Museum of Natural History, Chicago; from the Westphalian D of Mazon Creek, Grundy Co., Illinois. The specimen was originally housed in the Gurley Collection of the Walker Museum of the University of Chicago (Melander 1903)

**Emended diagnosis.** *Amarixys* with large ( $>0.095$  mm diameter), sparse ( $<45$  mm<sup>-2</sup>) tubercles on carapace.

**Description.** Both the dorsal part and the ventral

counterpart are preserved, but much of the prosoma is absent from the counterpart. The carapace is subrectangular; it is 3.8 mm long and 5.2 mm wide. Eyes are prominent, the pairs lie 3.9 mm apart, and the ocular axis is 1.4 mm from the anterior border of the carapace, which gives an ocular ratio of 0.37. Ocular and posterior depressions are present, and in addition, depressions are present at 0.8 and 1.8 mm from the anterior border along the median groove. The tubercle density is 40 mm<sup>-2</sup>, and the tubercles are 0.097 mm in diameter. Only the proximal 1.0 mm of the cucullus is preserved on the part.

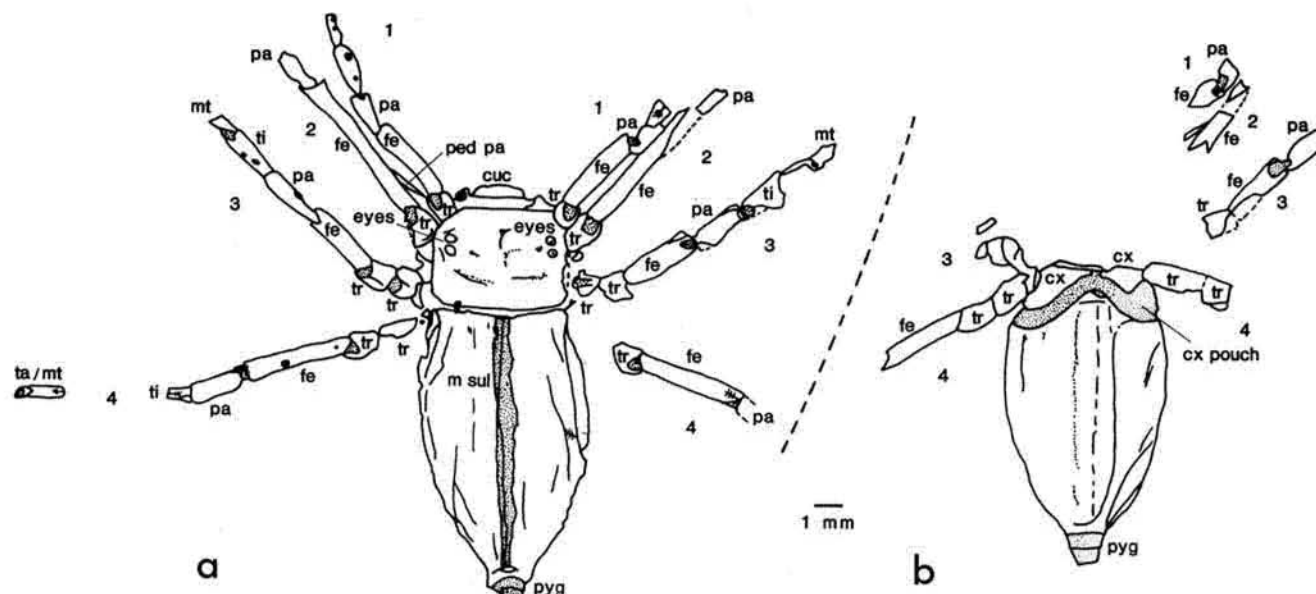
The abdomen is 10.8 mm long and 6.5 mm wide; it bears tubercles which are slightly smaller than those on the carapace. The dorsal surface bears a median sulcus, 0.8 mm wide, which is devoid of tubercles and bears a fine median ridge along its length. The ventral abdomen bears tubercles, which are slightly smaller than those of the dorsal surface, over the left and right sides; the median one-third consists of a broad, shallow sulcus which bears fine tubercles. The pouches for receiving coxae 4 during locking are situated anterolaterally on the ventral surface, and lack tubercles. The pygidium consists of three segments; it is 1.2 mm long and 1.8 mm wide in total, and each segment measures, axially, 0.45 mm. The first pygidial segment bears tubercles, and the posterior two segments lack them.

The anterior part of the ventral prosoma is missing. Coxae 4 are preserved, however, and the left cx4 on the counterpart measures 3.0 mm long. The chelicerae are not preserved, and a 1.6 mm sliver of the pedipalp patella occurs on the left side of the part. The following podomeres, and their measurements in mm, are preserved on specimen UC 9235: tr1, 1.1; fe1, 3.6; pa1, 1.7; ti1, 2.1; mt1,  $\geq 1.3$ ; tr2, 1.6; fe2, 6.5; pa2,  $\geq 1.9$ ; tr<sup>1</sup>3, 1.1; tr<sup>2</sup>3, 1.4; fe3, 3.2; 2.4; ti3, 2.4; mt3,  $\geq 2.4$ ; tr<sup>1</sup>4, 1.7; tr<sup>2</sup>4, 1.5; fe4, 4.4; pa4, 2.3; ti4,  $\geq 0.9$ . Additionally, part of the fourth metatarsus or tarsus is preserved on the left side of the part.

*Amarixys gracilis* (Petrunkevitch, 1945)

(Figures 4d; 20; 21b, c)

- 1945 *Curculioides gracilis* Petrunkevitch, pp. 68–70; text-fig. 34; pl. II, figs 8–10



**Figure 18** *Amarixys sulcata* (Melander, 1903), camera lucida drawings of UC 9235. (a) Dorsal surface; (b) ventral surface, with legs 1–3 on right rotated to correct position. On this specimen, black areas denote clumps of pyrite.

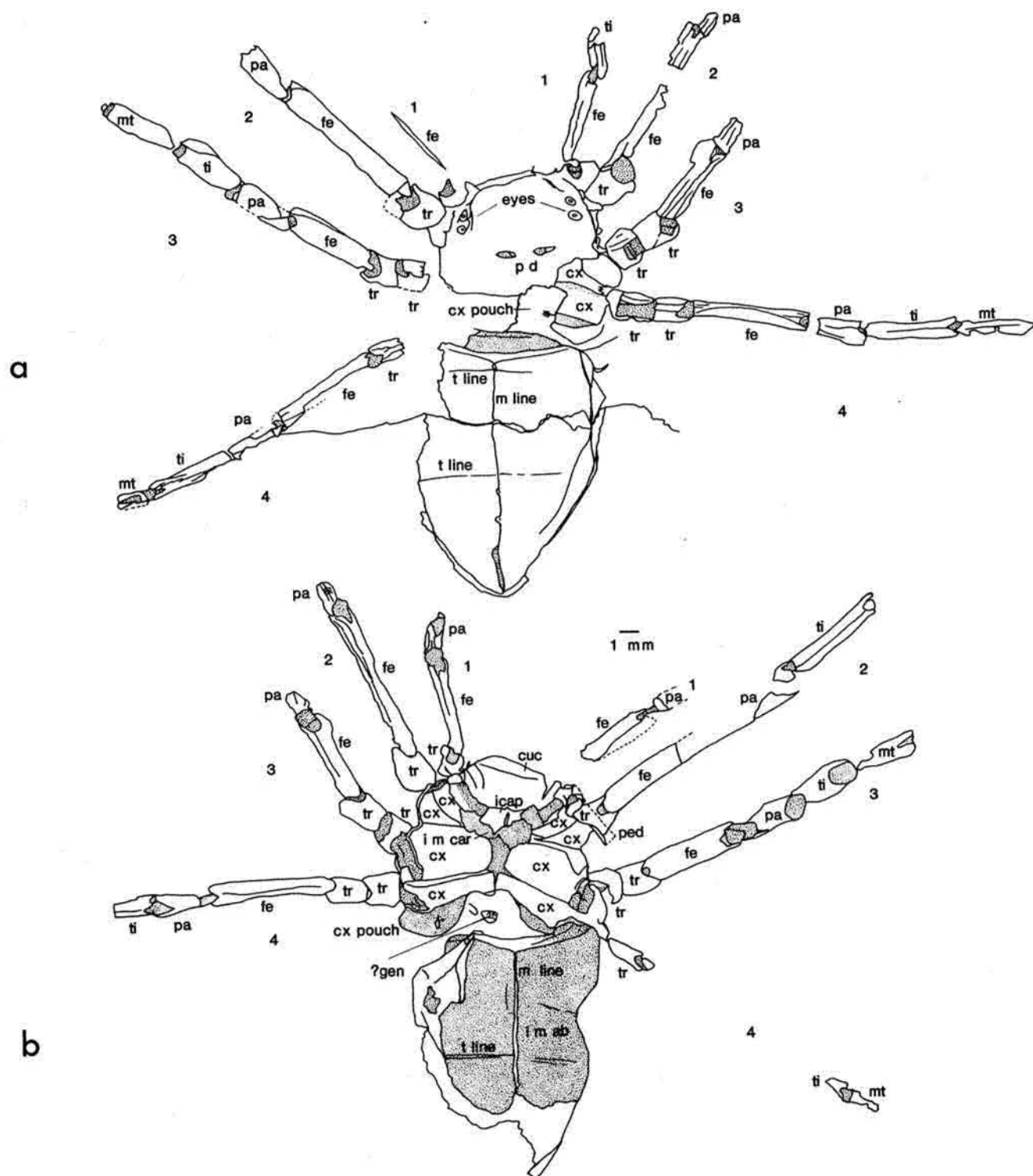
- 1949 *Curculioides gracilis* Petrunkevitch, p. 287  
 1953 *Curculioides gracilis* Petrunkevitch, p. 114  
 1955 *Curculioides gracilis* Petrunkevitch, p. P160; fig. 116, 2a, b  
 1963 *Curculioides gracilis* Petrunkevitch: Langford, p. 65; figs 101–3; not p. 65; figs 104–5, McLuckie specimen  
 1987 *Curculioides gracilis* Petrunkevitch: Brauckmann, p. 99; fig. 6  
 1991 *Curculioides gracilis* Petrunkevitch: Brauckmann, p. 47; fig. 20

**Material.** Holotype, ISM 14862, part and counterpart, in

the Langford Collection, Illinois State Museum, Springfield, Illinois; from the Westphalian D of Mazon Creek, Illinois. Additional specimen, MCP 548, part and counterpart, in the collection of the Mazon Creek Project, Northeastern Illinois University, Chicago, from a strip mine tip in Westphalian rocks, north-west of Morris, Okmulgee County, Oklahoma (map reference: NE 1/4, NE 1/4, sec. 1, T13N, R13E).

**Emended diagnosis.** *Amarixys* with tubercles on carapace less than 0.07 mm in diameter, and with a density of more than  $60 \text{ mm}^{-2}$ .

**Description of the holotype.** The cucullus is preserved in the part-closed position, so that 1.3 mm of its length is



**Figure 19** *Curculioides gigas* sp. nov., camera lucida drawings of PE 784. (a) Dorsal surface; (b) ventral surface. On this specimen, the internal mould of the dorsal surface of the abdomen (Fig. 19b: i m ab) is not smooth but bears fine pits.



present on the dorsal part, and on this part the width of the cucullus can be seen to be 4.0 mm. Grooves occur on the cucullus, about 3.0 mm apart. The carapace is 3.9 mm long and 5.2 mm wide. It is subrectangular in shape, but narrows slightly towards the anterior. The eyes are well preserved; they are situated 3.9 mm apart, with the ocular axis 1.6 mm from the anterior border (=ocular ratio of 0.41). The tubercles are 0.064 mm in diameter, and  $68 \text{ mm}^{-2}$  in density. Ocular and posterior depressions are present on the carapace, and in addition, a line of depressions forms the median groove in the anterior half of the carapace.

The abdomen is 9.8 mm long and 6.2 mm wide. It has been compressed to the right on the dorsal part, so that the median dorsal sulcus is offset to the right. The sulcus is 0.8 mm wide and lacks tubercles (the rest of the abdomen bears tubercles), except along the median line which runs down the length of the sulcus where fine tubercles are present. On the left side of the dorsal abdomen surface is a longitudinal line, situated 2.1 mm from the edge of the median sulcus. The ventral abdomen surface bears tubercles, and these are fine on the broad, median sulcus which is 2.0 mm wide. Fine transverse lines across the ventral surface, at about 2.7 mm and 5.7 mm from the anterior edge, represent the sutures of the sternites. The pygidium is partly telescoped, but the split of the nodule and the mode of preservation reveals that the first and second segments bear tubercles except at their junction with the following segment. The third segment lacks tubercles. The pygidium is 1.2 mm long in its telescoped state, the individual segments measuring, in mm: 1, 1.0; 2, 0.5; 3, 0.4.

The external mould of a cheliceral fang, probably of the left side, is preserved on the counterpart; it is 0.9 mm long, and behind it is the impression of a fixed tooth. The infracapitulum is subtrapezoidal in shape, with a prominent subcapitular gutter. The pedipalp trochanter is about 1.5 mm long, and femur is about 1.0 mm long. Parts of the left pedipalp patella is present on the counterpart, and the right pedipalp patella is 4.5 mm long; only a proximal fragment of the tibiotarsus is preserved. The pedipalp podomeres lack tubercles. The coxae of legs 1 and 2 occupy a triangular area on the left side of the counterpart, measuring 2.5 mm in length. Only parts of the right coxae 1 and 2 are present, but show that these coxae of the left and the right do not meet in the midline. Coxa 3 is 2.9 mm long, and cx4 is 3.4 mm long. The remaining podomeres measure, in mm, as follows: tr1,  $\geq 0.9$ ; fe1, 3.7; pa1, 1.6; ti1, 2.3; mt1,  $\geq 1.2$ ; (of leg 2, only a fragment of tr2 is preserved); tr'3, 1.2; tr'3, 1.6; fe3, 3.2; pa3, 2.4; ti3, 2.5; tr'4, 1.6; tr'4, 1.7; fe4, 4.0; pa4, 2.3; ti4,  $\geq 1.1$ .

**Description of MCP 548.** This specimen is preserved as internal and external moulds of the ventral prosoma and the dorsal abdomen. Only the abdomen, some indeterminate pieces of coxosternal region, and scraps of a leg are preserved. The abdomen is 11.0 mm long and 6.7 mm wide. The median dorsal sulcus is 1.2 mm wide; it lacks tubercles but has a median line. The rest of the abdomen bears tubercles. The tubercles on the abdomen have a diameter of 0.052 mm, and a density of  $68 \text{ mm}^{-2}$ . A parallel line occurs on each side of the dorsal abdomen, about 1.8 mm from the edge of the median sulcus. Fragments possibly representing coxae 2–4 and parts of two podomeres of a walking leg are preserved.

**Remarks.** There is no doubt that this specimen belongs in *Amarixys*. The prominent median sulcus on the dorsal abdomen is distinctive. The specimen lacks a carapace, so strictly, it should not be assigned to a species, because the species characters in this genus and carapace features.

However, the tubercle size and density on the abdomen match those of *A. gracilis* and are quite unlike those of the other two species, so it is considered that MCP 548 belongs in *A. gracilis*.

*Amarixys stellaris* sp. nov.

(Figures 4e; 21e, f; 22)

**Derivation of name.** Latin *stellaris*, starred; referring to the radial arrangement of elongate depressions and raised areas on the carapace.

**Holotype and only known specimen.** PE 32184, part and counterpart, in the Field Museum of Natural History, Chicago; from the Westphalian D of Mazon Creek, Illinois.

**Diagnosis.** *Amarixys* with tubercles on carapace between 0.07 mm and 0.09 mm in diameter and a density of between  $45 \text{ mm}^{-2}$  and  $60 \text{ mm}^{-2}$ ; radial pattern of raised and depressed areas on carapace.

**Description.** The preserved parts of the cucullus, on the dorsal part, measure 1.5 mm long and 3.8 mm wide, and bear longitudinal grooves 2.3 mm apart. The carapace is 4.6 mm long and 6.1 mm wide. It appears to be somewhat circular, but the overhanging parts of the posterior coxae are obscuring the corners of the carapace in the dorsal part. The eyes lie 4.5 mm apart; the ocular axis is 1.5 mm from the anterior border, which gives an ocular ratio of 0.33. The eyes are noticeably convergent towards the anterior. The tubercles are 0.079 mm in diameter and have a density of  $50 \text{ mm}^{-2}$  on the carapace. In addition to the transversely elongate ocular and posterior depressions, the carapace bears two pairs of longitudinal oval depressions on either side of the midline just anterior to the ocular axis. A small depression lies on the midline almost centrally. Subtriangular raised areas are present at the anterior and posterior ends of the midline, and a circular raised area occurs where the midline and ocular axis cross. Additional, elongate raised areas occur in front of the ocular depressions, and behind the posterior depressions; the latter raised areas converge forwards and meet in the midline, from where they run forwards and diverge around the central depression. The overall impression which arises from these low ridges and shallow furrows is of a radial pattern on the carapace; there is no doubt, however, that compression during fossilisation has enhanced these features.

The abdomen is 8.6 mm long and 6.0 mm wide. The median dorsal sulcus is 0.7 mm wide. It is devoid of tubercles, which are present on the rest of the abdomen, except for a row of fine tubercles along its median line. About 1.5 mm on either side of the median sulcus is a line, which turns outwards at the anterior end. The broad, shallow, median sulcus on the ventral side of the abdomen is less pronounced than in other species, though this may be a preservational difference. The sulcus bears rather finer tubercles than on the rest of the abdomen. Only one sternite suture, 3.5 mm from the posterior end of the abdomen, can be seen on the ventral surface. The pygidium measures 1.2 mm in its telescoped state. The first segment bears fine tubercles, the remainder of the preserved parts are smooth. The first pygidial segment bears a broad depressed median area on the ventral surface. The last pygidial segment bears a transverse ridge, and a circular pit immediately behind this. The lengths, sagittally in mm, of the pygidial segments are: 1, 0.56; 2, 0.36; 3, 0.4. At the anterior end of the ventral abdomen, the pouch for reception of coxa 4 during locking is well exposed on the right side of the counterpart. Where this pouch extends into the midline, a subcircular depression represents the genital apparatus, in life normally

concealed by the locking of abdomen and carapace. However, it is not possible to sex the specimen because the structure of male and female genitalia in ricinuleids is not sufficiently different, and the depression in the fossil could have been produced by either penis or genital lips.

On the counterpart, the cheliceral area is concealed beneath a piece of the internal mould of the cucullus, and there is a piece of internal mould of the carapace on the right side which obscures the trochanter and femur of the pedipalp on that side. The infracapitulum is preserved, and shows the subcapitular gutter. A small triangular tritosternum is apparent behind the infracapitulum. Coxae 1 and 2 are triangular and widely spaced; each is 2.2 mm long. Coxa 3 is 3 mm long and 1.6 mm wide. Coxa 4 is 3.5 mm long and 1.3 mm wide. A small part of the pedipalp patella is present on the left side of the counterpart. The walking leg podomeres measure, in mm, as follows: tr1, 1.2; fe1, 3.0; tr2, 1.9; fe2,  $\geq 4.3$ ; tr<sup>1</sup>3, 1.5; tr<sup>2</sup>3, 1.9; fe3, 2.2; pa3, 2.0; ti3,  $\geq 1.3$ ; tr<sup>1</sup>4, 2.2; tr<sup>2</sup>4, 1.7; fe4, 4.0; pa4, 2.0; ti4,  $\geq 2.4$ .

#### Family Poliocheridae Scudder, 1884

**Emended diagnosis.** Palaeoricinulei with dorsal abdomen divided into transverse tergites, as in modern Ricinulei; and not divided longitudinally by a median line or sulcus.

#### Genus *Poliochiera* Scudder, 1884

**Type species.** *Poliochiera punctulata* Scudder, 1884

**Emended diagnosis.** Poliocheridae with tuberculate cuticle on carapace, abdomen, and legs; median tergal fields of dorsal abdomen with elongate depressions, not circular pits.

#### *Poliochiera punctulata* Scudder, 1884

(Figures 4c; 23; 25c-f; 26)

1884 *Poliochiera punctulata* Scudder, p. 16

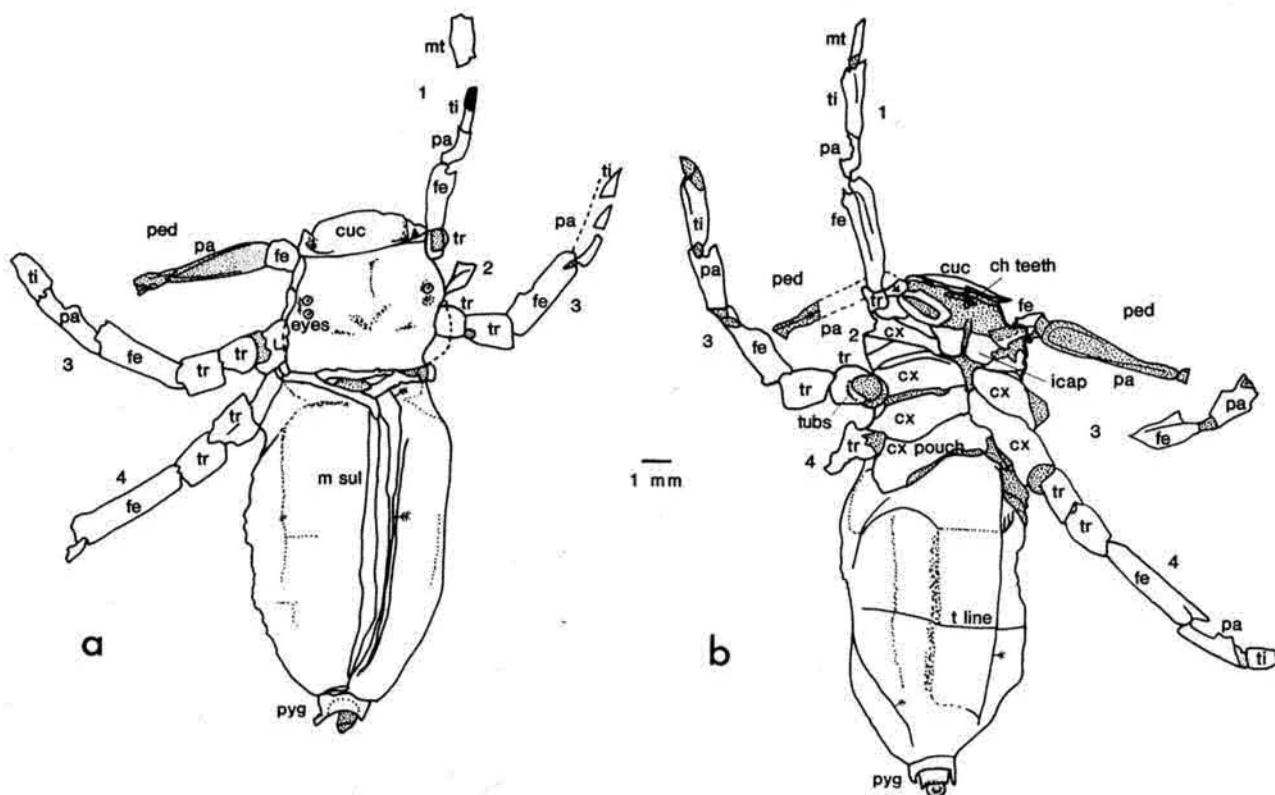
- 1890 *Poliochiera punctulata* Scudder, p. 444; pl. 39, figs 2, 6  
 1904 *Poliochiera punctulata* Scudder: Fritsch, pp. 31-3  
 1913 *Polyochera punctulata* Scudder: Petrunkevitch, pp. 78-80; Figs 44, 45; Pl. VIII, figs 41, 42 *not* p. 80, L. E. Daniels specimen  
 1929 *Polyochera punctulata* Scudder: Ewing, pp. 586-8  
 1949 *Polyochera punctulata* Scudder: Petrunkevitch, pp. 285, 286 *not* p. 286, L. E. Daniels specimen  
 1953 *Poliochiera punctulata* Scudder: Petrunkevitch, p. 112  
 1955 *Poliochiera punctulata* Scudder: Petrunkevitch, p. P159; fig 115, 1a, b

**Holotype.** USNM 37971, part and counterpart, in the National Museum of Natural History, Washington DC (*ex* R. D. Lacoe Collection, No. 1745), from the Westphalian D of Mazon Creek, Illinois.

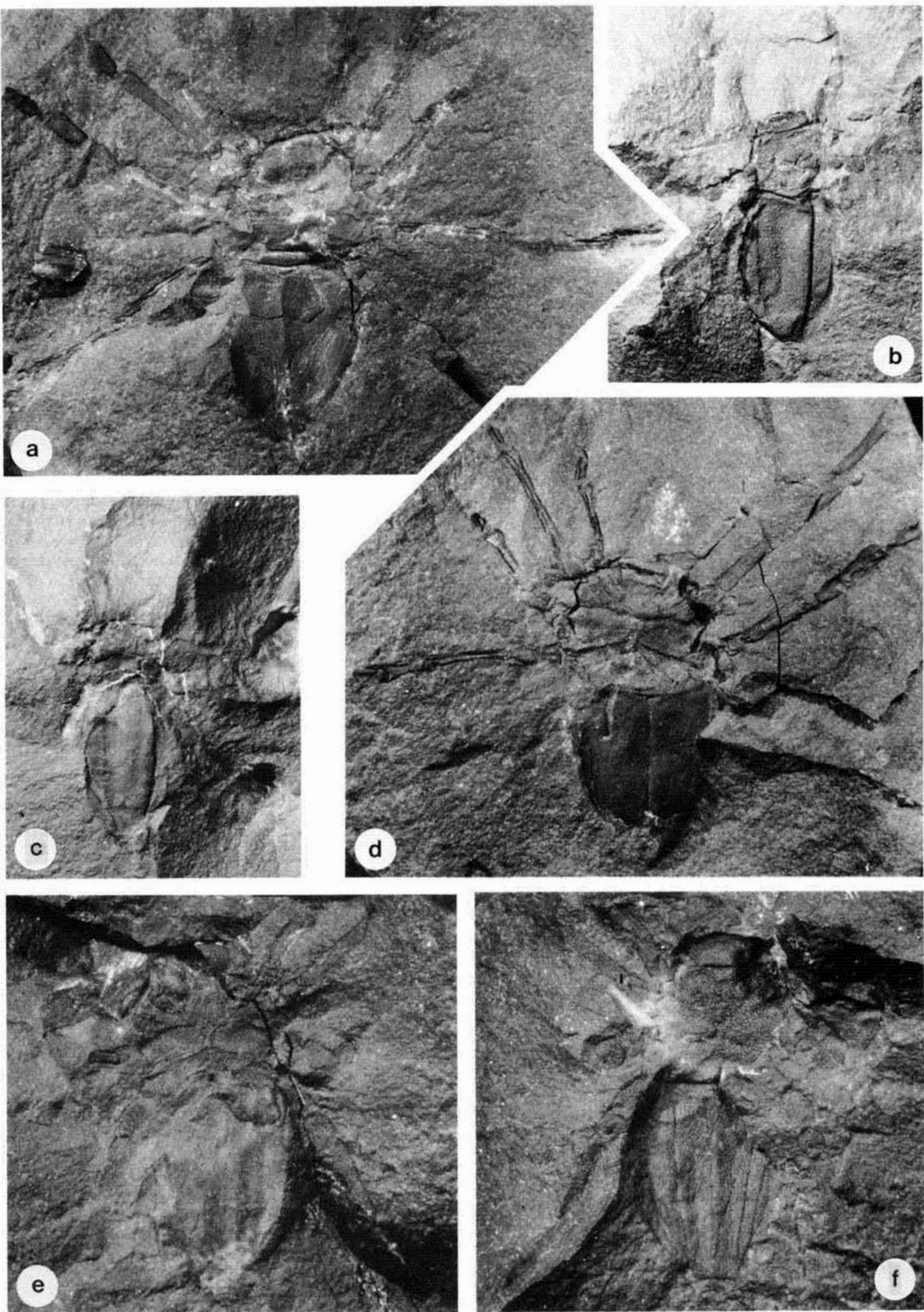
**Other material.** PE 32206, part and counterpart, in the Field Museum of Natural History, Chicago; from the Westphalian D of Mazon Creek, Illinois.

**Emended diagnosis.** *Poliochiera* with ocular axis closer to anterior edge of carapace than one-third of carapace length; carapace tubercles more than 0.055 mm in diameter.

**Description of the holotype.** The cucullus is preserved compressed in the half-open position, with the dorsal part on the part and the ventral on the counterpart, so its outline cannot be determined. The lateral edges are not preserved, but it approached 4 mm in width; tubercles cover the dorsal surface. The carapace is 4.4 mm long and 5.8 mm wide. The anterior edge is straight, and the remaining edges describe a subtrapezoidal outline. There is little relief on the surface, apart from a general declivity forwards from the eyes, a slight median groove, and only the faintest indication of ocular and posterior depressions. The eyes are low in relief; those of the left side of the part can be seen well, and include an ocular ridge. The ocular axis lies 1.3 mm from the



**Figure 20** *Amarixys gracilis* (Petrunkevitch, 1945), camera lucida drawings of ISM 14862. (a) Dorsal surface; (b) ventral surface. The coxal pouch labelled on (b) is revealed by an area of rock matrix; the corresponding pouch on the right is preserved, but crumpled.



**Figure 21** (a, d) *Curculioides gigas* sp. nov., PE 784,  $\times 3.0$ , see Fig 19; (a) dorsal surface; (d) ventral surface. (b, c) *Amariyys gracilis* (Petrunkévitch, 1945), ISM 14862,  $\times 2.8$ , see Fig. 20; (b) dorsal surface; (c) ventral surface. (e, f) *Amariyys stellaris* sp. nov., PE 32184,  $\times 4.2$ , see Fig. 22; (e) ventral surface; (f) dorsal surface.



anterior edge of the carapace (ratio 0.295 of carapace length). The tubercle density is  $103\text{ mm}^{-2}$ , and the tubercles measure 0.062 mm in diameter, though they are smaller in size around the eyes.

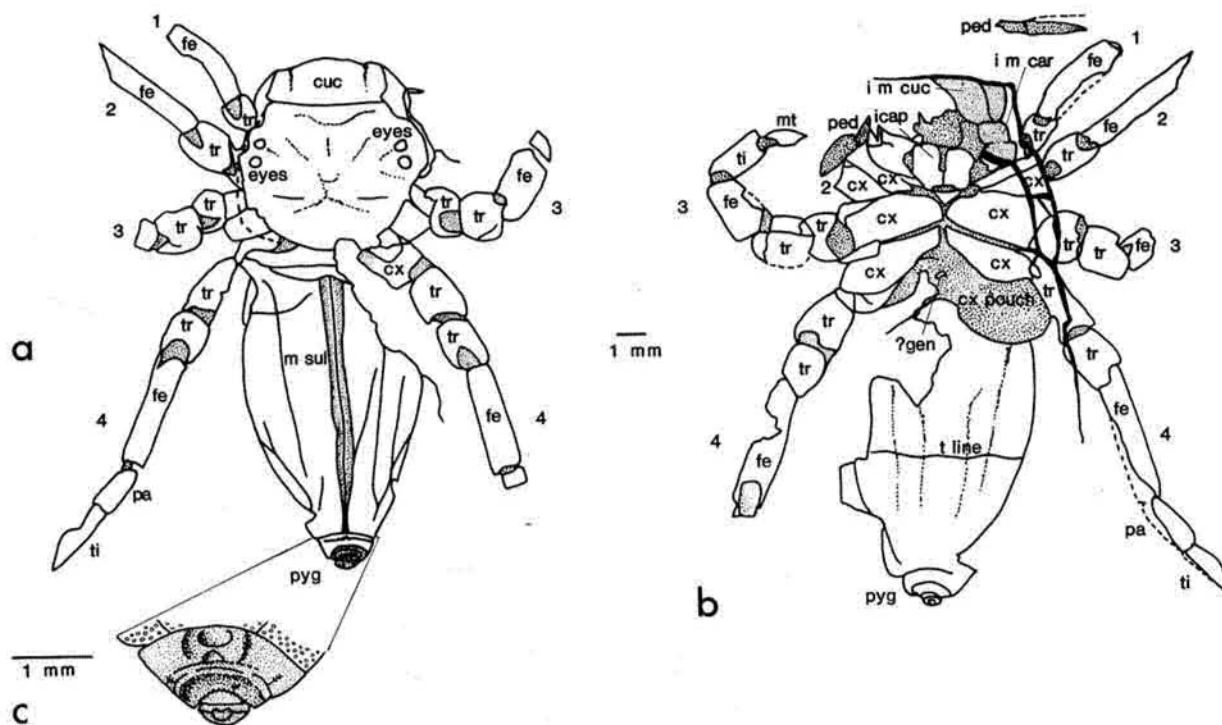
The abdomen is oval apart from a straight anterior border; it is 8.7 mm long and 7.1 mm wide. The first, narrow tergite measures 0.25 mm long, the second and third are each about 2.0 mm long, and the fourth tergite is 2.9 mm long. The longitudinal lateral lines which divide tergites 2, 3, and 4 into median and lateral fields, are difficult to make out in this specimen and are rather complicated by the folding of the abdomen sides. Longitudinal, elongate depressions occur on either side of the midline, 1.7 mm apart, on tergites 2, 3, and 4. These depressions on tergite 2 are positioned about half-way down the tergite, whilst those of tergites 3 and 4 extend from the anterior border of the tergite. The lateral sides of the abdomen are strongly folded, suggesting very flexible cuticle in life. The tubercles on the dorsal abdomen are variable in size; a row of large tubercles occurs at the posterior edge of each tergite. Tubercles are also present on the flexible cuticle of the sides of the abdomen. The ventral side of the abdomen is almost identical to the dorsal in the arrangement of tergites and their pattern of longitudinal depressions; however, the tubercles on the ventral side are smaller than on the dorsal surface. Anteriorly, there is a procurved semicircular line, the ends of which align with the rows of depressions, which lies between the ventral sacs which accommodate coxae 4 during locking. The pygidium lies within the matrix and cannot be seen.

The cheliceral fixed teeth are represented by holes in the counterpart behind the cucullus. The exposed part of the infracapitulum is trapezoidal in shape, with a median groove; the subcircular trochanter of the pedipalp and the proximal part of the pedipalp fe are preserved, but no other parts of this appendage. Coxa 1 cannot be made out with certainty, and it is presumed that it is mostly obscured by

the pedipalp tr and fe. Coxa 2 is subtriangular, cx3 is 3.5 mm long and 1.6 mm wide, cx4 is 3.7 mm long and 1.4 mm wide. The more distal parts of the legs measure as follows, in mm: tr1, 1.2; fe1, 3.0; pa1, 2.0; ti1, 1.8; tr2, 1.6; fe2, 5.4; pa2, 2.4; ti2, 4.1; tr3, 0.7; tr3, 1.4; fe3, 2.6; pa3, 2.5; ti3,  $\geq 2.5$ ; tr4, 1.0; tr4, 1.4; fe4, 4.0; ti4,  $\geq 3.0$ .

**Description of PE 32206.** This specimen has not been described before. The cucullus is preserved only in part, as a fragment attached to the anterior edge of the carapace. The carapace is 5.5 mm long and 7.4 mm wide. Eyes are not preserved, but from the configuration of the preserved parts of the carapace, it can be assessed that the ocular axis was situated about 1.7 mm behind the anterior margin of the carapace, thus giving a ratio of 0.31 to the length of the carapace. The tuberculation is difficult to determine due to the rather rubbed appearance of the specimen surface, but is about  $92\text{ mm}^{-2}$ . The tubercles are 0.060 mm in diameter. The lateral parts of the carapace are generally poorly preserved, nevertheless, the carapace can be seen to have been particularly broad, and the posterior margin was straight, thus the outline would have been somewhat rectangular.

The abdomen is 8.5 mm long and 9.0 mm wide. The dorsal surface is rather confusing because some of the ventral sutures have been impressed upon it, and similarly, some dorsal lines appear on the ventral surface. The specimen is important in this respect, because it reveals the nature of the ventral sternites, which are obscured in other specimens. Tergite 1 is 0.5 mm long, tergites 2 and 3 are each 2.0 mm long, and tergite 4 is 2.9 mm long. The paired depressions are shaped and situated as in the type specimen, though are less well preserved. The lateral edge of the median field on the left side of the dorsal part is well preserved. The lateral edges are folded, and the extreme lateral parts bear no tubercles. The rest of the dorsal surface of the abdomen is tuberculate; the tubercles appear to vary in size, but, like the carapace, the tuberculation appears to



**Figure 22** *Amarixys stellaris* sp. nov., camera lucida drawings of PE 32184. (a) Dorsal surface; (b) ventral surface; (c) detail of pygidium. Large cracks shown in black at right of (b).

be smoothed almost away. Impressions of the edges of the ventral sternites appear as little transverse scarps between the anterior and posterior edges of the tergites. The pygidium is preserved in the extended position; it appears on both part and counterpart. The anterior part of the first pygidial segment is tuberculate; the rest of the pygidium appears smooth, apart from some faint striations at the posterior end of the middle segment. No median dorsal notch is apparent on the anteriormost segment, but its absence cannot be proven.

Few appendage fragments are preserved. The infracapitulum is trapezoidal, with a median groove, and the pedipalp trochanter, femur, and the base of the patella are preserved on the left side of the counterpart. The pedipalp tr is 1.0 mm long and wide, and the pedipalp fe is 0.7 mm long. Only the proximal part of the pedipalp pa is preserved, and a fragment of the pa of the other pedipalp may be present in front of the coxae. Coxae 1 and 2 are poorly preserved. A fragment of fe1 occurs on the left side of the part. Tr2 is 2.3 mm long. Only the proximal 4.8 mm of fe2 is preserved. Coxa 3 is 4.0 mm long and 1.4 mm wide; a fragment of the distal part of tr<sup>2</sup>3 is preserved. Femur 3 is 3.2 mm long, pa3 is 2.6 mm long, and ti3 is 2.8 mm long. Only the coxa of leg 4 is preserved; it is 3.8 mm long and 1.9 mm wide.

*Poliochera glabra* Petrunkevitch, 1913

(Figures 4a; 24; 25a, b; 27; 29d, f)

- 1913 *Polyochera glabra* Petrunkevitch, pp. 78, 81; fig. 46; pl. VII, figs 39, 40  
included here L. E. Daniels specimen, p. 80  
1949 *Polyochera glabra* Petrunkevitch, pp. 285, 286  
included here L. E. Daniels specimen, p. 286  
1953 *Poliochera glabra* Petrunkevitch, p. 112  
1955 *Poliochera glabra* Petrunkevitch, p. P159; fig. 115, 5  
1963 *Polyochera glabra* Petrunkevitch: Langford, p. 64, figs 99, 100  
1963 *Poliochera glabra* Petrunkevitch: Laurentiaux-Vieira & Laurentiaux, p. 26

**Holotype.** USNM 37981, part and counterpart, in the National Museum of Natural History, Washington DC (ex R. D. Lacoe Collection, No. A5, 6), from the Westphalian D of Mazon Creek, Grundy Co., Illinois.

**Other material.** UMMP 7223, part and counterpart, from the Westphalian D, Mazon Creek, Illinois (ex L. E. Daniels Collection).

**Emended diagnosis.** *Poliochera* with ocular axis more than one-third carapace length from anterior edge of carapace; carapace tubercles less than 0.055 mm in diameter.

**Description of the holotype.** The cucullus is preserved as a fragment in front of the carapace, and measured at least 4.0 mm wide when complete. The carapace has a rounded subtrapezoidal outline with a straight anterior margin; it is 4.2 mm long and 5.2 mm wide. The eyes are preserved, but faint; they are 1.6 mm from the anterior border, which gives an ocular ratio of 0.38. There is a slight median groove, but no indication of ocular or posterior depressions. The carapace tubercles are 0.046 mm in diameter, and have a density of 103 mm<sup>-2</sup>.

The abdomen is 7.5 mm long, 6.0 mm wide, and has an oval outline. The short first tergite is 0.25 mm long, tergites 2 and 3 are each 1.8 mm long, tergite 4 is 2.3 mm long. The paired depressions on the tergites run from the anterior edges of the tergites and are about 1.6 mm apart. The lateral

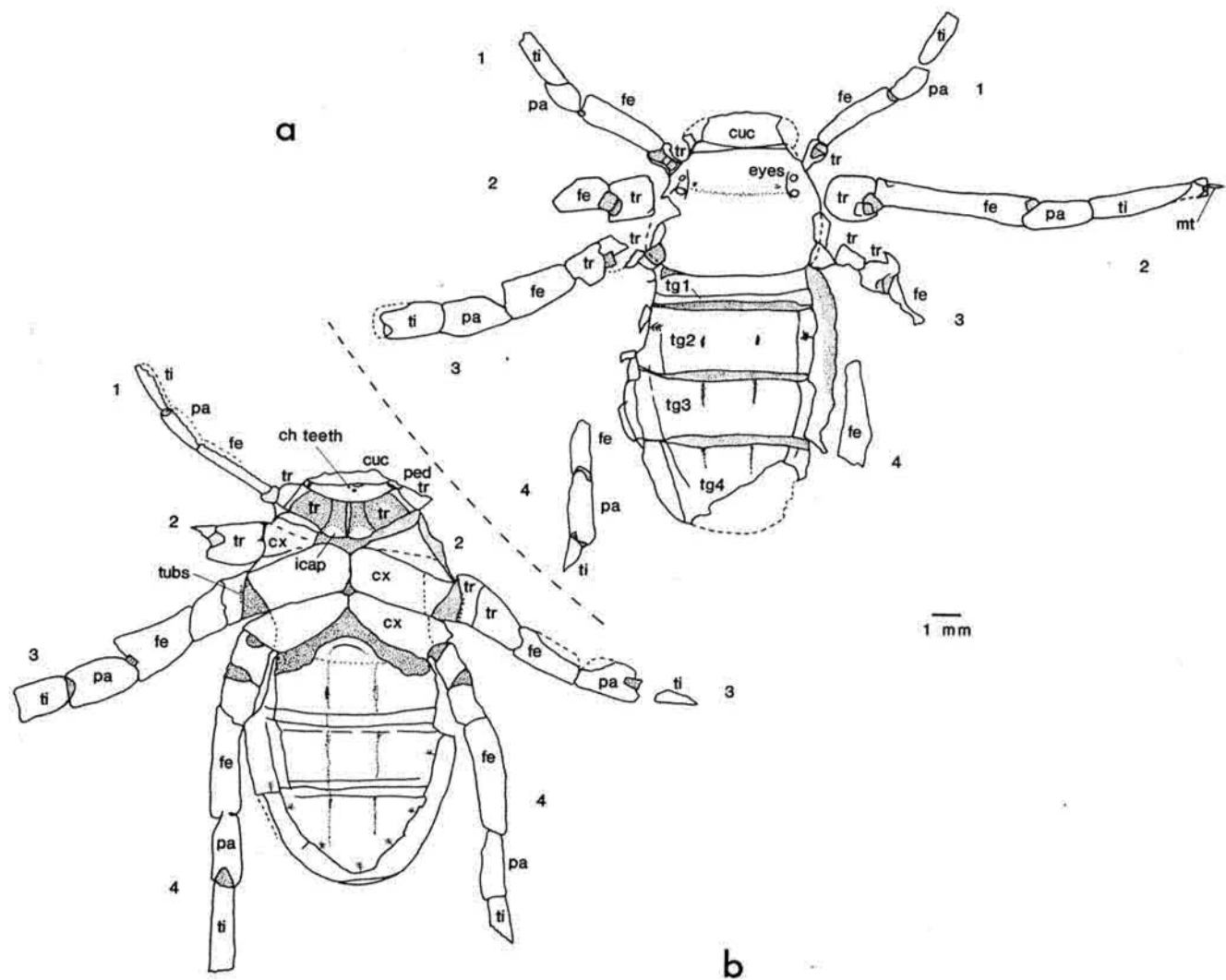
edges of the median fields, and the flexible cuticle at the lateral edges of the abdomen, are poorly preserved. The pygidium is not preserved. The ventral side is covered with fine mineral coating; there are faint impressions of transverse lines and lateral lines, and a semicircular impression between the sacs for locking coxae 4.

The chelicerae are represented by holes, which are the external moulds of the fixed fingers, at the anterior of the counterpart. The infracapitulum is approximately trapezoidal, with a median groove; faint curved impressions mark the outlines of the proximal edges of the pedipalp trochanters. The pedipalp on the right side of the part is preserved, with a trochanter, femur, and patella (2.7 mm long); these podomeres lack tubercles. Coxa 1 is poorly preserved, cx2 is triangular, and 2.5 mm long. Coxae 3 and 4 are better preserved, with tuberculation showing through the mineralisation. Both coxae are 2.5 mm long, cx3 is 1.5 mm wide, and cx4 is 1.3 mm wide. The more distal podomeres measure as follows, in mm: tr2, 1.2; fe2, 4.8; pa2, 1.6; ti2, 2.2; tr<sup>1</sup>3, 0.7; tr<sup>2</sup>3, 1.0; fe3, 2.3; tr<sup>1</sup>4, 1.1; tr<sup>2</sup>4, 1.0; fe4,  $\geq 1.9$ .

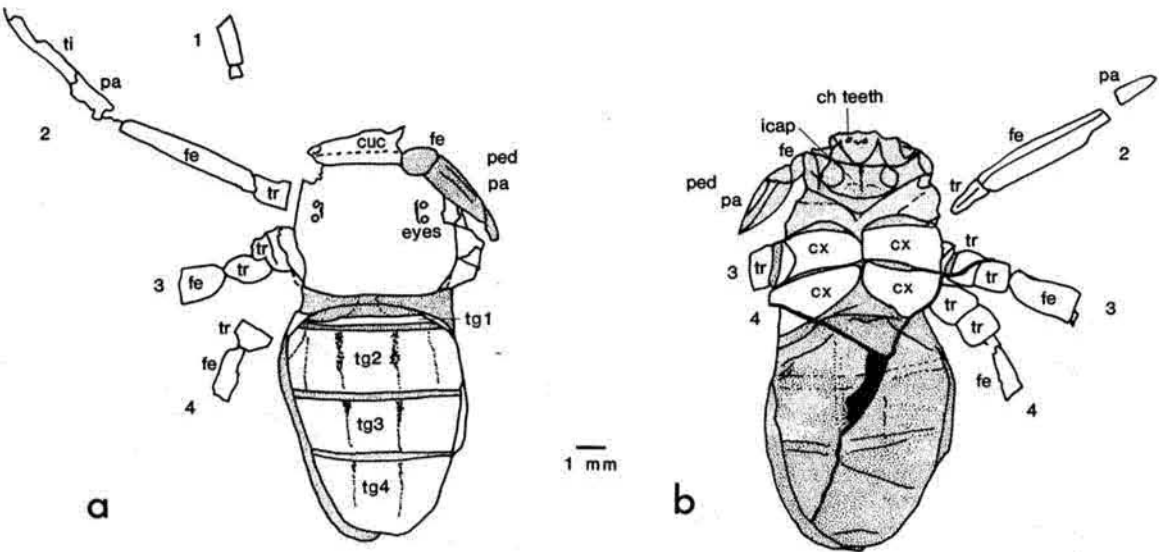
**Description of UMMP 7223.** The cucullus is outstretched horizontally, thus providing a near-perfect view of its morphology. It is 3.4 mm wide and 2.1 mm long. Broadly curved in front, the sides are parallel or slightly diverging to the anterior. The longitudinal grooves are deepest half-way along their length. The cucullus is covered in tubercles dorsally, similar to the carapace. The ventral side of the cucullus is preserved on the counterpart; it is smooth apart from a submarginal groove.

The carapace has a straight anterior margin, the remaining edges are rounded subtrapezoidal in outline. It measures 4.6 mm long and 5.2 mm wide, and was gently domed in life, with a slight median groove. No other depressions are observed on the carapace. The eyes are not well preserved, but discernible, especially on the left side of the specimen; the ocular ridge is present on both sides. The eyes are 1.7 mm from the anterior border of the carapace, giving an ocular ratio of 0.37. The carapace tuberculation is 97 mm<sup>-2</sup>, the tubercles are 0.052 mm in diameter.

The abdomen is 9.0 mm long and 7.6 mm wide. The lateral sides consisted of flexible cuticle in life, the dorsal being divided into a number of transverse tergites. The first, narrow, tergite is 0.2 mm long, tergites 2 and 3 are each 2.0 mm long, and the fourth is 2.8 mm long. Tergite 1 is gently anteriorly procurved, the second and third are rectangular, and the fourth is subtriangular in outline. The line dividing the tergites into a median and a pair of lateral fields is well preserved on the left side of the part, but on the right, this line is lost among the cuticular folds. This, together with the presence of a well defined pair of grooves on tergites 2 to 4, gives the specimen the appearance of having a median groove and two lateral lines. The paired, elongate depressions on tergites 2 to 4 run from the anterior border of the tergite but do not reach the posterior border. The tergites are tuberculate but the abdominal tubercles are smaller than those of the carapace. Between and around the tergites the cuticle is smooth or very finely tuberculate. The ventral side of the abdomen is covered with fine mineralisation, so it is difficult to discern the morphological details. No longitudinal lines can be made out, but transverse grooves, as on the dorsal side (they may, indeed, be reflections of dorsal morphology) can be seen. Anteriorly, the ventral abdomen projects in a convex curve between the fourth coxal sacs. The most anterior segment of the pygidium is preserved, the more distal parts disappear into the matrix.

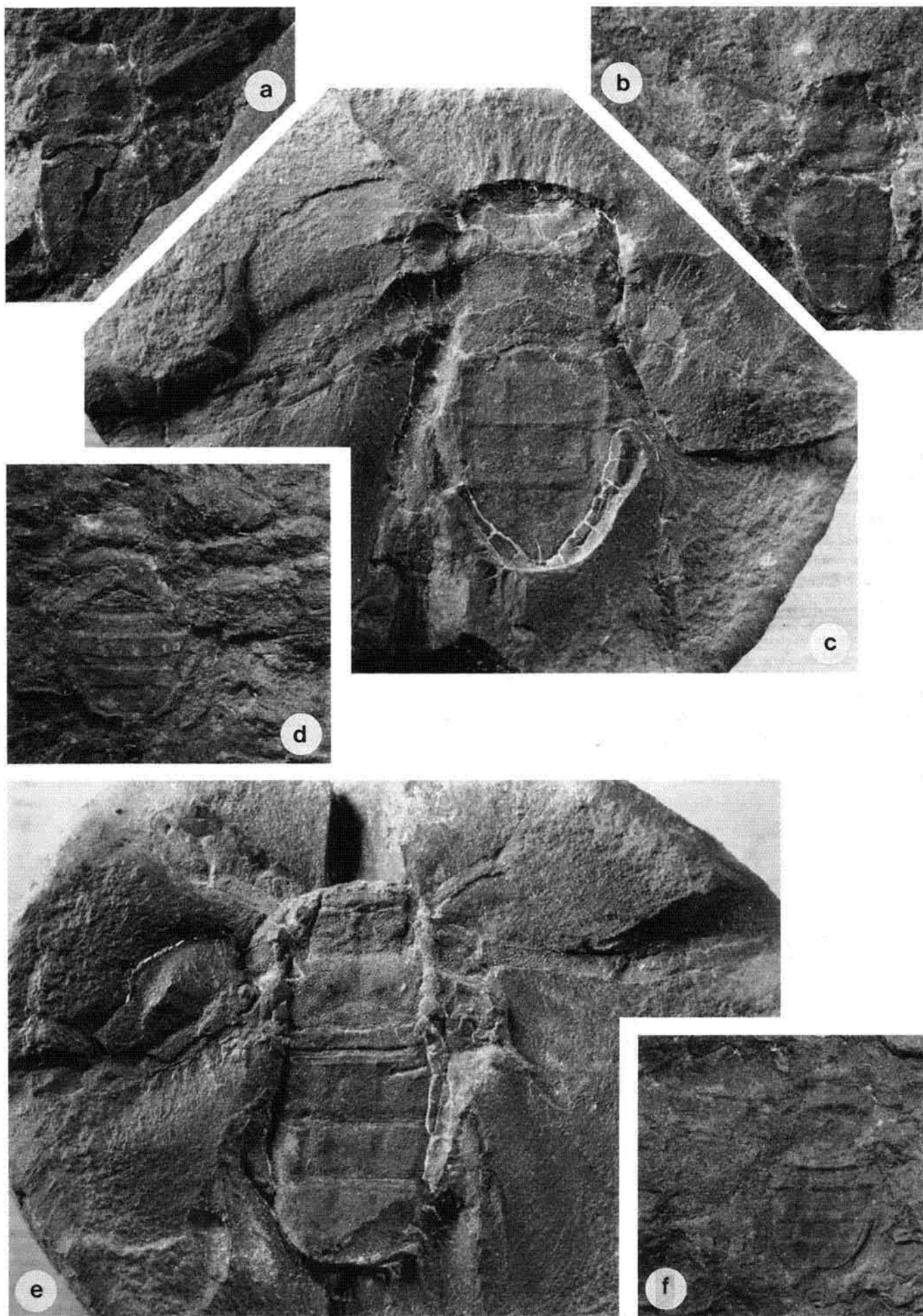


**Figure 23** *Poliochera punctulata* Scudder, 1884, camera lucida drawings of USNM 37971. (a) Dorsal surface; (b) ventral surface.



**Figure 24** *Poliochera glabra* Petrunkevitch, 1913, camera lucida drawings of USNM 37981. (a) Dorsal surface; (b) ventral surface. A large, Y-shaped crack is shown in black on (b).





**Figure 25** (a, b) *Poliochera glabra* Petrunkevitch, 1913, USNM 37981,  $\times 3.5$ , see Fig. 24; (a) dorsal surface; (b) ventral surface. (c–f) *Poliochera punctulata* Scudder, 1884. (c, e) USNM 37971,  $\times 5.3$ , see Fig. 23; (c) ventral surface; (e) dorsal surface. (d, f) PE 32206,  $\times 2.7$ , see Fig. 26; (d) ventral surface; (f) dorsal surface.

The appendages are generally poorly preserved. Two holes behind the ventral mould of the cucullus represent the fixed teeth of the chelicerae, and an external mould of a fang is preserved on the right side of the counterpart. The infracapitulum is trapezoidal with a median groove, and there is evidence, in the form of finely striated matrix, of much anterior setation. The pedipalp trochanters and femora are poorly preserved, but the patella and part of the tibiotarsus is preserved on the left side of the part. These podomeres lack tuberculation. The leg coxae are difficult to differentiate because of the mineralisation obscuring them. Trochanter 1 is 0.9 mm long, and the proximal part of fe1 is preserved; tr2 is 2.0 mm long; fe2 is 4.8 mm long. Podomeres of more posterior legs are very fragmentary.

*Poliochera gibbsi*, sp. nov.

(Figures 29a, b; 30)

**Derivation of name.** After Tom Gibbs, the collector of the holotype specimen.

**Holotype and only known specimen.** PE 29176, part and counterpart, in the Field Museum of Natural History (ex Tom Gibbs Collection), from the Westphalian D, Francis Creek Shale, Pit 11, Peabody Coal Co., Will-Kankakee Counties, Illinois.

**Diagnosis.** *Poliochera* with ocular axis less than one-third of carapace length from anterior edge of carapace; carapace tubercles less than 0.055 mm in diameter; carapace tubercle density exceeding  $150\text{ mm}^{-2}$ .

**Description.** This specimen is described here for the first time. It consists of dorsal part and ventral counterpart in a haematitic nodule. The specimen is skewed, particularly at the right anterior part. The carapace is 3.0 mm long and about 4.4 mm wide. The eyes on the left are well preserved, and are 0.78 mm from the anterior edge of the carapace, giving a ratio of 0.26 of carapace length. The right eye-pair is not preserved, being hidden by folding of the right anterior side of the carapace. The carapace tubercles are well preserved, so that the great variability between the

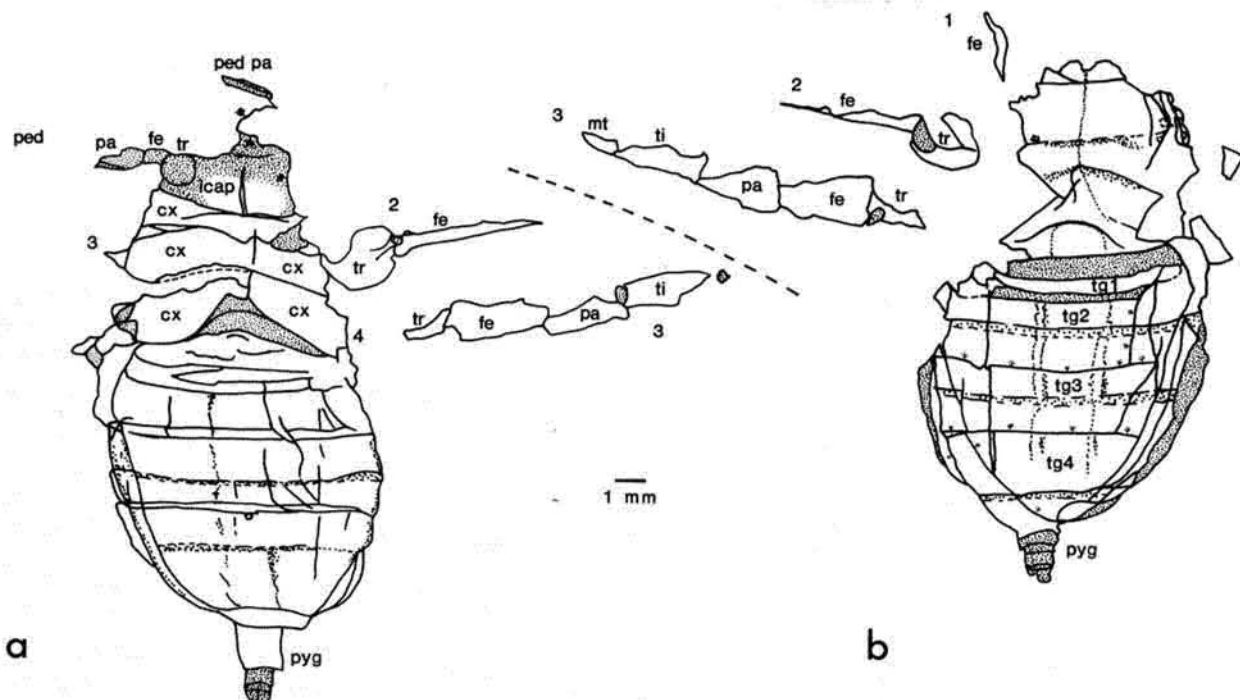
larger ones (0.041 mm diameter) and the numerous, smaller subsidiary tubercles is apparent. The tubercle density is thus difficult to determine, particularly since the carapace is also distorted, but that of the major tubercles is about  $190\text{ mm}^{-2}$ . The carapace shows little original relief.

The abdomen is 7.0 mm long and 5.5 mm wide. The first tergite is 0.16 mm long, the smooth areas between the tergites are this length also; tergites 2 and 3 are each 1.75 mm long, and the fourth tergite is 2.8 mm long. The tergites are 3.9 mm wide between the folded lateral sides. A faint pair of longitudinal sulci occur 2.6 mm apart on tergites 2 to 4.

The counterpart bears numerous cracks which make morphological interpretation difficult. The ventral surface bears tubercles of variable sizes, similar to those which occur on the dorsal surface. The infracapitulum and pedipalp trochanters together describe a procurved crescent which encloses an area of slightly coarser tubercles to the anterior, which represents the external surface of the closed cucullus. Posterior to the infracapitulum the coxae are poorly outlined, although the anterior edge of the left coxa 3 is well preserved.

The pedipalp patellae (3.1 mm long) on both right and left sides are well preserved on the counterpart, and the tibiotarsi (maximum preserved length together: 2.6 mm) can be traced by their smooth cuticle lining the floor of cracks in the specimen. Trochanter 1 is 1.5 mm long, fe1 is 4.1 mm long, and pa1 is 2.0 mm long; tr2 is 1.6 mm long, and 2.4 mm of fe2 is preserved on the left side of the counterpart. Parts of tr<sup>1+2</sup>3 and tr<sup>1</sup>4 are preserved, as is the proximal 2.5 mm of fe3. The pygidium is not preserved.

**Remarks.** In his key to the species of *Poliochera*, Petrunkevitch (1913, p. 81) gave as the distinguishing characters for *P. glabra*: (1) a distinct constriction between the cephalothorax and abdomen (i.e. the edges of the carapace and abdomen did not appear to align directly), (2) body smooth (cf. tuberculate), and (3) abdominal tergites divided into 3 fields, and not 5, by parallel lines. The constriction is produced by a lesser degree of flatness of



**Figure 26** *Poliochera punctulata* Scudder, 1884, camera lucida drawings of PE 32206. (a) Ventral surface; (b) dorsal surface. On this specimen, impressions of the dorsal surface occur on the ventral, and vice versa.

*P. glabra* than *P. punctulata*, thus the groove between the carapace and abdomen of *P. glabra* is more pronounced. The dorsal surface of the carapace and abdomen is normally tuberculate in *P. glabra*; that the carapace, at least, is tuberculate was recognised later by Petrunkevitch (1949, p. 285), when he used the couplet "tergites smooth" to distinguish *P. glabra*; nevertheless, the tergites are also tuberculate. The ventral side of *P. glabra* is actually covered with fine mineralisation, like UMMP 7223, which could be mistaken for a smooth appearance. Lastly, the arrangement of tergites in *P. glabra* is no different from that of *P. punctulata*, though only the inner row of elongate depressions on the median tergal fields are seen well, the outer lines separating off the lateral fields are poorly represented. The major distinguishing features separating *P. glabra* from *P. punctulata* are: (a) the position of the eyes on the carapace; in *P. glabra* they are more than one-third of the length of the carapace from the anterior border (ratio about 0.37) whereas in *P. punctulata* they are less than one-third of the distance from the anterior edge of the carapace (ratio about 0.30), and (b) the carapace tubercles are smaller (<0.55 mm) in *P. glabra* than in *P. punctulata* (>0.55 mm). Additionally, the carapace of *P. punctulata* is somewhat more rectangular than that of *P. glabra*, and the paired grooves on the second abdominal tergite of *P. punctulata* does not reach the anterior edge of the tergite whereas it does in *P. glabra*. However, the latter two features may not be definitive. The new species, *P. gibbsi*, is distinctly smaller than the other two species, so it could conceivably represent the immature of one of them. However, a number of features distinguish this form: it resembles *P. glabra* in having small tubercles (<0.55 mm), but is similar to *P. punctulata* in eye position; uniquely however, the carapace tubercles are more densely arranged than on any other fossil ricinuleid, exceeding  $190\text{ mm}^{-2}$  on the holotype. Until more specimens of this rare and interesting genus are discovered, the true relationships between these forms will remain obscure.

*Poliochera incertae sedis*

(Figures 29c, e; 31)

One specimen, PE 29375, from the Westphalian D of Mazon Creek, Illinois, and kept in the collections of the Field Museum of Natural History, Chicago, is insufficiently preserved to show the distinguishing features of the species, but definitely belongs in *Poliochera* because of the transverse tergites with tubercles, but lack of prominent pits which characterise *Terpsicrpton* gen. nov.

**Description of PE 29375.** No traces of the carapace or cucullus are preserved in this specimen. The abdomen is 8.8 mm long and 7.4 mm wide. Tergite 2 is 5.2 mm wide (between the flexible lateral borders) and 2.0 mm long; tergite 3 is 1.8 mm long and 4.8 mm wide; tergite 4 is at least 2.5 mm long and maximally 4.5 mm wide. The tergites bear a sculpture of tubercles of various sizes, this is lacking over much of the specimen because of the rubbed surface. The inter-tergite cuticle is up to 0.4 mm long and lacks sculpture. The prominent, everted pygidium is maximally 1.4 mm wide, and the lengths of the segments are: 1, 0.9 mm, 2, 0.9 mm, and 3, 0.3 mm. Vague outlines of the coxae are apparent on the counterpart (Fig. 31b), though sternite boundaries are obscured by impressions of the tergite boundaries on the counterpart.

Only a part of leg 2 is preserved. Femur 2 measures  $\geq 5.5$  mm, pa2 is 2.0 mm long, and ti3 is  $\geq 2.8$  mm long.

Genus *Terpsicrpton*, gen. nov.

**Type and only known species.** *Poliochera alticeps* Pocock, 1911.

**Derivation of name.** Greek *terpsis*, gladdening, delighting, and *croton*, a tick or bug.

**Diagnosis.** Palaeoricinuleid lacking tubercles over entire body surface; with well-defined pits in a regular arrangement on carapace and abdomen.

*Terpsicrpton alticeps* (Pocock, 1911)

(Figures 4g; 28; 29g, h)

- 1911 *Poliochera alticeps*: Pocock, pp. 40–1; text-fig. 14; pl. II, fig. 6.
- 1913 *Polyochera alticeps* Pocock: Petrunkevitch, p. 78.
- 1949 *Polyochera alticeps* Pocock: Petrunkevitch, p. 286
- 1953 *Poliochera alticeps* Pocock: Petrunkevitch, p. 113; figs. 114, 177.
- 1955 *Poliochera alticeps* Pocock: Petrunkevitch, p. P159; fig. 115, 6.
- 1980 *Polyochera alticeps* Pocock: Morris, p. 45
- 1987 *Poliochera alticeps* Pocock: Brauckmann, p. 99.

**Holotype and only known specimen.** In 31238, in the British Museum (Natural History), London (*ex* collection of Mr Walter Eggington (Pocock 1911)), from the Lower Similis-Pulchra Zone, Westphalian B of Coseley, Worcestershire, probably from the Ten Foot Measures above the Thick Coal, at Claycroft Open Works, Coseley (SO 9372 9297) (Schram 1979).

**Description.** The specimen is preserved as the external mould of the dorsal surface (part) and the external mould of the ventral surface of the abdomen together with the internal mould of the carapace and cucullus (counterpart). The cucullus is preserved extended out forwards on the counterpart. Only the area between the parallel, longitudinal grooves is preserved; this is 1.0 mm wide and 0.67 mm long, and is rectangular in outline. There is a transverse gutter just inside the posterior edge, observable on the part. The carapace is 2.35 mm wide and 1.8 mm long. It has a straight anterior border and is broadly pyriform in shape behind. Prominent subcircular pits occur on the carapace surface in the following positions: a pair of shallow pits at the anterolateral corners (seen on the internal mould); a pair close to the lateral borders a short distance behind the first pair; a pair 1.1 mm apart just anterior to the centre of the carapace (the ocular depressions); a single central pit; and a pair of pits 1.1 mm apart in the posterior half of the carapace (the posterior depressions). A median groove is present, which is preserved on the internal mould as a line of small depressions (i.e. as small internal projections). Eyes cannot be seen, but are presumed to have been present because of the large, reniform lobes which are evident on the internal mould in the position where eyes occur in other genera. If these lobes do represent the eyes, then the distance of the ocular axis from the anterior border of the carapace is 0.7 mm, which gives an ocular ratio of 0.39.

The abdomen is 2.9 mm wide and 3.5 mm long. The first tergite is 0.3 mm long and tergites 2, 3, and 4 are each 1.05 mm long. The tergites are maximally 2.35 mm wide. Subcircular pits occur close to the anterior border of tergites 2, 3, and 4, about 1.5 mm apart; these are prominent on tergite 2, but less so on tergites 3 and 4. In the positions occupied in *Poliochera* by a pair of longitudinal depressions on tergites 2, 3, and 4, on *Terpsicrpton* two confluent subcircular pits occur; these are situated half-way down each

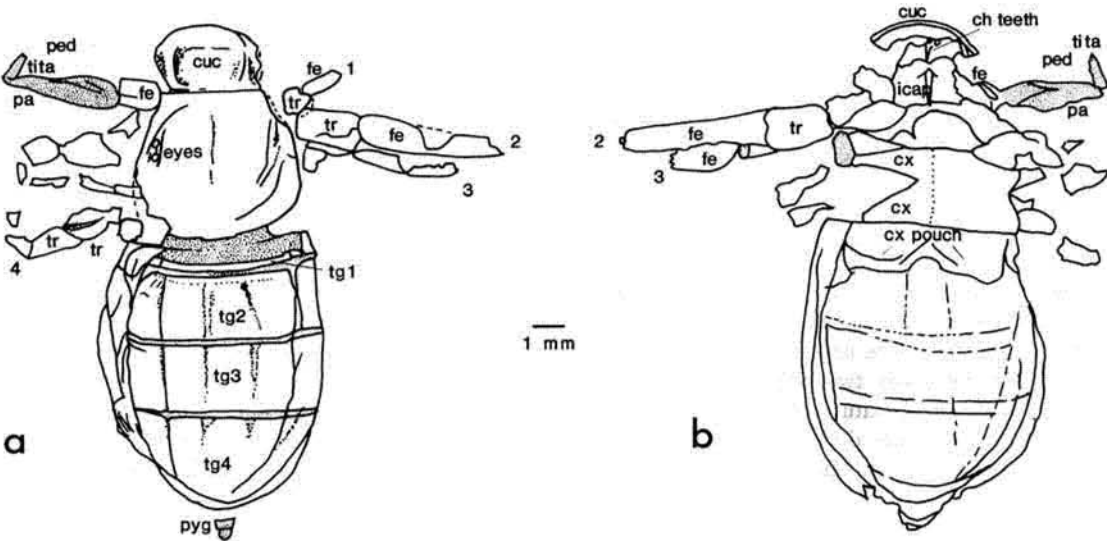


tergite and about 0.85 mm apart. The edges of the abdomen, outside the tergite boundaries, are composed of folded cuticle. The ventral abdomen is also composed of flexible cuticle, as evidenced by the thin longitudinal folds. Two transverse lines divide the ventral abdomen into 3 sternites, and anteriorly there is a transverse groove which separates off a narrow first sternite. This is mainly obscured from dorsal view by the internal mould of the carapace. The pouches which receive the coxae of legs 4 are inconspicuous, and widely spaced on this sternite. Sternites 2 and 3 are 1.15 mm long, and sternite 4 is 1.375 long. Pits occur on the three large sternites in the following positions: a pair about 1 mm apart just anterior to the half-way line, another pair in an anterolateral position; in addition to these, on sternites 3

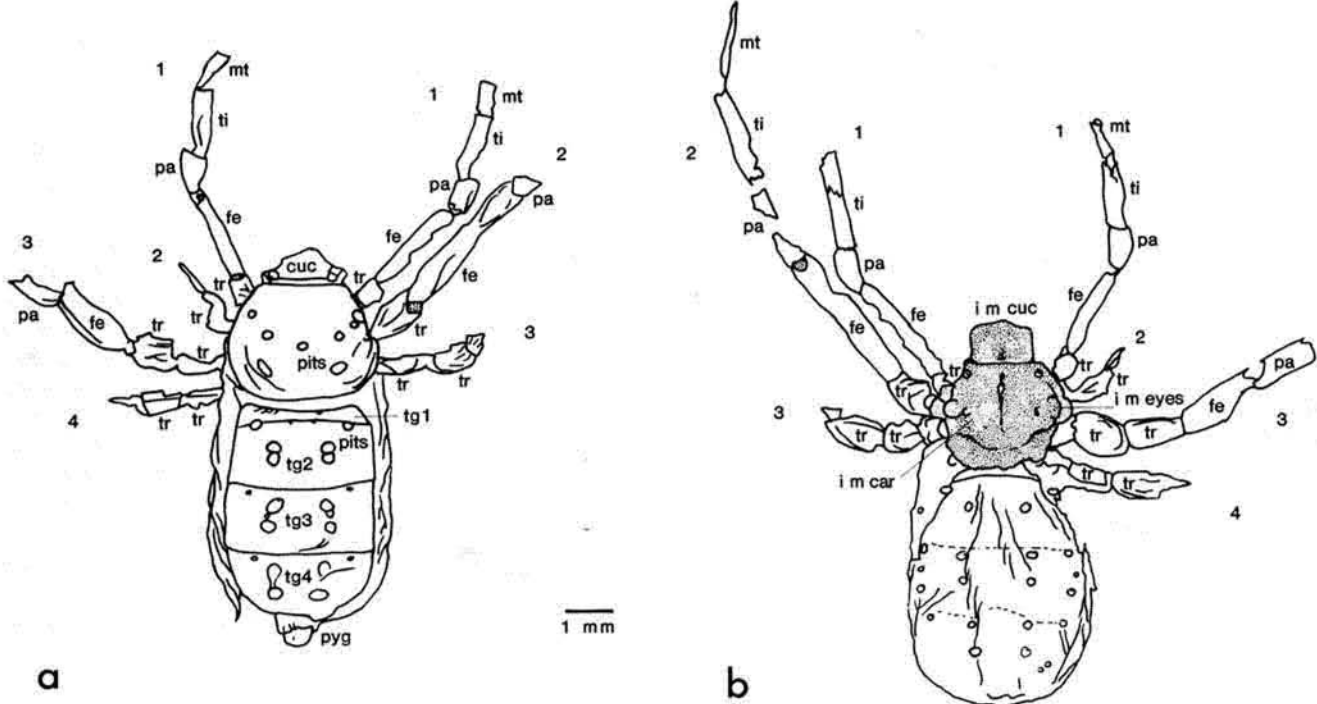
and 4 (and possibly present but not conspicuous on sternite 2), a pair of pits occurs about 1 mm apart at the anterior border of the sternite, and another pair about half-way down the sternite at the lateral sides. The pygidium is 0.55 mm long, the first segment is 0.35 mm long, and the partly retracted posterior segments total 0.325 mm.

The chelicerae and pedipalps are not preserved. The internal mould of the carapace on the counterpart obscures the coxosternal region. Podomere measurements, in mm, are as follows: tr1, 0.475; fe1, 1.6; pa1, 0.625; ti1, 1.075; mt1,  $\geq 0.7$ ; tr2, 0.85; fe2, 2.45; pa2, 1.35; ti2, 1.675; mt2,  $\geq 1.35$ ; tr<sup>1</sup>3, 0.8; tr<sup>2</sup>3, 0.8; fe3, 1.35; pa3,  $\geq 1.15$ ; tr<sup>1</sup>4, 0.8; tr<sup>2</sup>4, 0.8; fe4,  $\geq 1.25$ .

**Remarks.** This specimen is the smallest of all the fossil



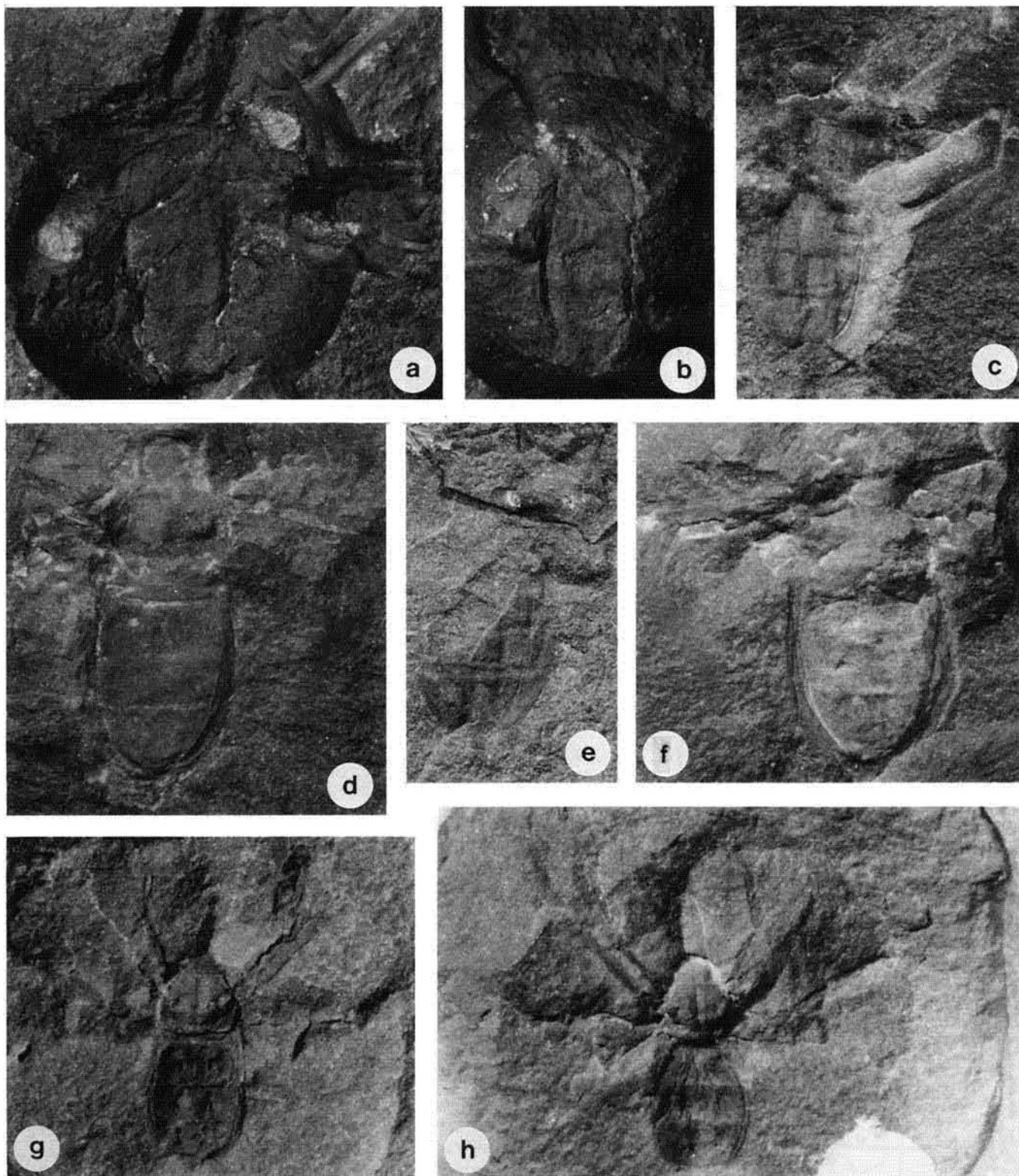
**Figure 27** *Poliochera glabra* Petrunkevitch, 1913, camera lucida drawings of UMMP 7223. (a) Dorsal surface; (b) ventral surface.



**Figure 28** *Terpsicroton alticeps* (Pocock, 1911), camera lucida drawings of In 31238. (a) Dorsal surface; (b) ventral surface with interior mould of carapace. The pits on the carapace and abdomen appear as circular lumps on the external moulds.

ricinuleids, although it is the same size as the adults of most living forms. Nevertheless, the possibility exists that it is the immature of another fossil genus. *Terpsicroton* cannot be a larva because it has four pairs of legs whereas ricinuleid larvae bear only three pairs. Supporting the hypothesis that *Terpsicroton* could be a nymph is the poor development of

the pouches on the abdomen which receive coxae 4 during locking; these pouches are but shallow depressions in the larva of *Cryptocellus pelaezi* (Pittard & Mitchell 1972). However, the distinctive lack of tubercles of *Terpsicroton* contrasts with the abundance of randomly arranged tubercles in living ricinuleid nymphs (Pittard & Mitchell



**Figure 29** (a, b) *Poliochera gibbsi* sp. nov., PE 29176,  $\times 4.2$ , see Fig. 30; (a) ventral surface; (b) ventral surface. (c, e) *Poliochera incertae sedis*, PE 29375,  $\times 2.6$ ; see Fig. 31; (c) ventral surface; (e) dorsal surface. (d, f) *Poliochera glabra* Petrunkevitch, 1913, UMMP 7223,  $\times 3.9$ ; see Fig. 27; (d) dorsal surface; (f) ventral surface. (g, h) *Terpsicroton alticeps* (Pocock, 1911), In 31238,  $\times 5.9$ ; see Fig. 28; (g) dorsal surface; (h) ventral surface.

1972). This latter feature, together with the conspicuous pits of *Terpsicroton*, are considered important characters sufficient for its separation as a distinct genus.

*Palaeoricinulei incertae sedis*

(Figure 32)

A latex peel of a specimen in the collection of Mr Pohl, and brought to my attention by Bret Beall, Curatorial Assistant at the Field Museum of Natural History, represents the internal mould (part) and external mould (counterpart) of the ventral abdomen, together with an anterior sclerite, of a palaeoricinuleid. The ventral surfaces of *Curculioides* and *Poliochera* are very similar, and the latex mould examined does not show the details of the dorsal surface,

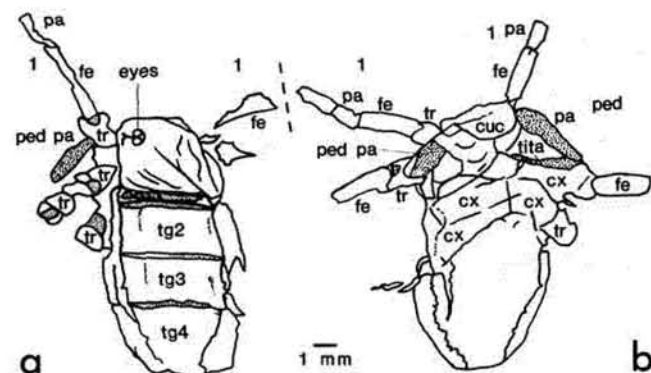


Figure 30 *Poliochera gibbsi* sp. nov., camera lucida drawings of PE 29176. (a) Dorsal surface; (b) ventral surface.

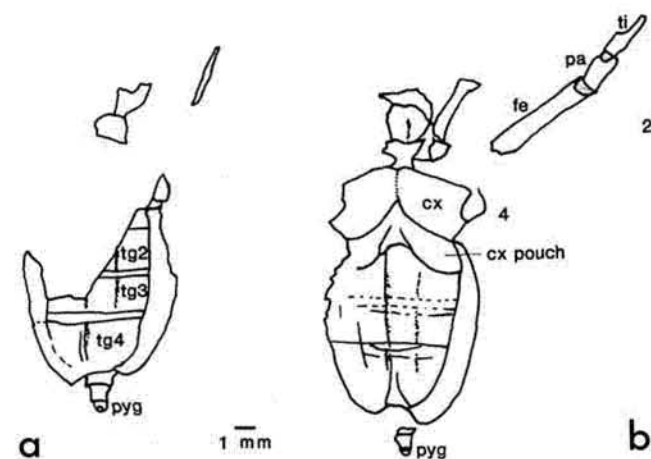


Figure 31 *Poliochera incertae sedis*, camera lucida drawings of PE 29375. (a) Dorsal surface; (b) ventral surface.

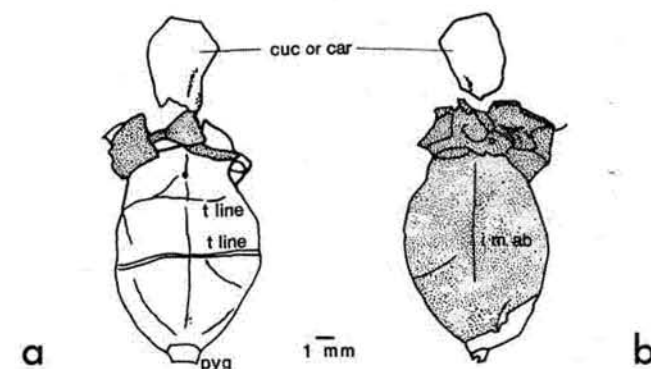


Figure 32 *Palaeoricinulei incertae sedis*, camera lucida drawings of Pohl specimen. (a) Ventral surface; (b) dorsal surface.

tuberculation, etc. which might allow identification, so it is impossible to assign this specimen to a genus.

**Description.** The specimen is preserved rotated so that a ventrolateral view of the animal is presented. A 4.3 mm long hexagonal plate at the anterior of the specimen could represent the carapace or the cucullus; no features are present on the latex mould which would allow identification. The abdomen measures 9.9 mm long, and the preserved part is 6.8 mm wide. The ventral abdomen is traversed by fine lines (sternite sutures) at 2.5 and 5.2 mm from its anterior edge. The fine longitudinal line running the length of the abdomen does not lie in the median but represents one of a pair of fine longitudinal lines on the ventral abdomen. The proximal segment of the pygidium is preserved. Only internal moulds of parts of the coxal area are preserved. The counterpart preserves the internal mould of the ventral surface.

*non Ricinulei*

- 1963 (*Poliochera* Scudder, 1884 vel *Curculioides* Buckland, 1837) *pustulatus*, Laurentiaux-Vieira and Laurentiaux, pp. 25–6; fig. 3  
1987 (*Poliochera* vel *Curculioides*) *pustulatus* Laurentiaux-Vieira & Laurentiaux: Brauckmann, p. 99.

**Only specimen.** No. 51, part only, in the collection of F. F. Mathieu, Institut Royal des Sciences Naturelles de Bruxelles, Belgium; from the upper Westphalian of Kaiping, China.

**Remarks.** This specimen, which has not been examined for the present study, consists of a subelliptical fragment, about 9 mm long, bearing tubercles of very variable size arranged in rows, attached to which is a small piece with patches of small tubercles and a row of larger tubercles (Laurentiaux-Vieira & Laurentiaux 1963, fig. 3). The authors interpreted the large piece as the carapace of a ricinuleid, and the smaller piece as the attached cucullus. In my opinion, there is no evidence whatsoever that this fossil is part of a ricinuleid; indeed, the shape of the fragments and the size and distribution of the tubercles are so unlike those of ricinuleids, living or fossil, that a ricinuleid origin for the fossil can clearly be ruled out. The tuberculation is more suggestive of crustacean or scorpion, among the arthropods.

## 9. Acknowledgements

I am grateful to Fred Collier (US National Museum), Dan Fisher (University of Michigan), Catherine Forster (Field Museum), Richard Leary (Illinois State Museum), and Sam Morris (British Museum (Natural History)), for the loan of specimens in their care. I thank Bret Beall for kind hospitality in Chicago, Bill Shear for providing facilities for the part of this work which was carried out at Hampden-Sydney College, Virginia, John Kennaugh for providing extant ricinuleid material and for discussion on the cuticle, Carsten Brauckmann for useful correspondence on the Namurian ricinuleid, and John Dalingwater for bringing a live specimen from Panama. I had helpful discussions with John Dalingwater and Bill Shear. Additional help was given by Gerald Legg and Peter Gabbutt. Particular thanks is extended to all those collectors who entrusted their fine specimens to the care of institutions, thereby making this study possible.



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