Evidence for a sister group relationship between Ricinulei and Trigonotarbida

Jason A. Dunlop
Department of Earth Sciences,
University of Manchester,
Manchester, M13 9PL

Summary

A review of previous phylogenetic placements of the arachnid order Ricinulei with particular reference to the fossil order Trigonotarbida, and comparison of the morphology of these two orders, has resulted in a revised scheme of opisthosomal segmentation for Ricinulei. Cladistic analysis suggests that Ricinulei are a sister group to Trigonotarbida, these two orders being the sister group of the extant tetrapulmonate arachnids (Araneae, Amblypygi, Uropygi and Schizomida). Suggested synapomorphies of Ricinulei and Trigonotarbida are: longitudinally divided tergites, fusion of tergites 2 and 3 into a diplotergite, a dorsal locking ridge and ventral recesses in the opisthosoma to accommodate the leg 4 coxae. Doubts still remain over the position of the Acari and Opiliones in this scheme.

Introduction

The extant arachnid order Ricinulei and the fossil order Trigonotarbida are two groups whose phylogenetic position has been subject to a variety of interpretations (see below), but which in earlier accounts have been placed together in the same higher taxon (see below). In this study the morphology and phylogeny of Ricinulei and Trigonotarbida are reviewed and have resulted in new synapomorphies of the two groups being proposed. A cladistic analysis suggests that Ricinulei and Trigonotarbida are sister groups, and the implications of this for arachnid phylogeny are discussed.

Background

Ricinuleids are strange and rather poorly known arachnids. They possess very thick cuticle, a movable cucullus or hood over the mouthparts, divided opisthosomal tergites, a locking mechanism between the prosoma and opisthosoma concealing the gonopore, and a sperm transfer device on leg 3 of the male (Millot, 1949; Pittard & Mitchell, 1972; van der Hammen, 1979). Additional characters of ricinuleids are discussed in further detail below. Their biology was discussed by Pollock (1967), Cooke (1967), Legg (1977) and Platnick & Pass (1982) among others. Ricinuleids have a fossil record extending back to the Upper Carboniferous (Namurian) (Selden, 1992) and have the distinction of having been described as fossils (though as beetles) before any living examples were recognised (Selden, 1986). The phylogenetic position of Ricinulei is uncertain and most recent authors placed them as the sister group of the Acari (mites and ticks) (see below). Extant ricinuleids were first classified as opilionids (e.g. Guérin-Méneville, 1838), and often allied to a group of extinct Palaeozoic arachnids, now recognised as a distinct order, the Trigonotarbida. Trigonotarbids ranged from

the Silurian (Přídolí) (Jeram et al., 1990) to Permian (Asselian?) periods (Müller, 1957) and are essentially spider-like arachnids, without spinnerets, characterised by a dorsal opisthosoma with tergites divided into median and lateral plates and the presence of a locking ridge between the prosoma and opisthosoma. Trigonotarbids have been placed in the arachnid taxon Tetrapulmonata as the sister group to the Araneae, Amblypygi, Uropygi and Schizomida (Shear et al., 1987; Selden et al., 1991). The possibility that ricinuleids are related to trigonotarbids has been previously considered (Ewing, 1930), but not explicitly investigated.

The first occurrence of ricinuleids and trigonotarbids was their description together as fossils from the British Coal Measures of Coalbrookdale by Buckland (1837), who interpreted them as beetles, naming them *Curculioides ansticii* and *Curculioides prestvicii* respectively. *C. prestivicii* was later identified as an arachnid and placed in a new genus, *Eophrynus*, by Woodward (1871), who thought it was a pseudoscorpion. A second trigonotarbid was described as a pseudoscorpion by Geinitz (1882). Karsch (1882) described a new trigonotarbid and erected a new order, Anthracomarti, for his, Geinitz's and Woodward's specimens. Scudder (1884) identified Buckland's *C. ansticii* as an arachnid and described the second fossil ricinuleid (see Selden (1992) for a fuller account of the history of ricinuleid research), placing both within Karsch's order Anthracomarti. Meanwhile, Guérin-Méneville (1838) described the first living ricinuleid, *Cryptostemma westermanni*, from West Africa and believed it to be an opilionid, partly because the cucullus resembles the non-movable hood of trogulid opilionids. It later emerged that an extant ricinuleid collected before 1799 existed unrecognised in Stockholm museum (see Selden, 1992). Westwood (1874) described a second extant ricinuleid from South America, still as an opilionid. Haase (1890) relegated Anthracomarti (still including the fossil ricinuleids) to a suborder of the Opiliones. Meanwhile, Thorell (1892) described the extant Stockholm ricinuleid using the name Ricinulei (a name he in fact coined in 1876 (Selden, 1992)), but still regarded it as an opilionid. Pocock (1902) retained the fossil anthracomartids within Opiliones and noted the similarity of the fossil *Curculioides* to the extant *Cryptostemma*. Frič (1904) proposed an extensive classification of fossil arachnids which misidentified some trigonotarbids as spiders and placed the rest within a taxon Meridogastra (a substitute name for Anthracomarti (Thorell & Lindström, 1885)), again as a suborder of Opiliones. The fossil ricinuleids were also placed as opilionids in Meridogastra in Frič's scheme.

The classic study of Hansen & Sørensen (1904) established the Ricinulei as a distinct order of arachnids and described their morphology in detail. These authors regard ricinuleids as rather primitive arachnids, a view which was to continue for some years, and they suggested an affinity with the Uropygi based on similar mouthparts. Pocock (1911) referred the fossil ricinuleids to Ricinulei and in the same monograph re-established Anthracomarti as a fossil order distinct from the Opiliones, regarding anthracomartids as somehow

bridging the gap between opilionids and more primitive orders of arachnids. Ewing (1930) suggested that ricinuleids were related to anthracomartids, since both have divided tergites, and that these orders bridged the gap between Araneae and Acari. No significant systematic revisions were made until Petrunkevitch (1949) arranged the fossil and extant arachnids into subclasses. The order Anthracomarti was split into a new order, Trigonotarbi, placed as the sole representative of a new subclass, Soluta, defined by a variable prosoma-opisthosoma junction. The remaining anthracomartids retained their ordinal name and with the fossil order Haptopoda were put into a new subclass, Stethostomata, defined by a broad prosoma-opisthosoma junction and downward-hanging chelicerae. The extant arachnid orders were split into the Latigastra, those with a broad prosoma-opisthosoma junction and forward-projecting chelicerae, and Caulogastra, those with a narrow prosoma-opisthosoma junction. Petrunkevitch (1949) placed the Ricinulei in the Caulogastra on account of their pedicel hidden beneath the prosoma-opisthosoma locking mechanism. Petrunkevitch's scheme proposed no relationships within or between subclasses and .has not been adopted by workers on extant arachnids, though Soluta and Stethostomata continued to be used until quite recently. Trigonotarbi and Anthracomarti became Trigonotarbida and Anthracomartida to fit current conventions (Petrunkevitch, 1955).

Millot (1945) argued against Hansen & Sørensen's (1904) contention that ricinuleids were primitive arachnids. Millot (1949) summarised ricinuleid anatomy and noted that some authors regarded ricinuleids as being derived from the extinct anthracomartids. Millot (1949) did not reference this remark to a particular author (presumably it was Ewing?) or state the arguments in favour of it. Millot (1949) himself regarded Ricinulei as a distinct order. Zachvatkin (1952) divided the Chelicerata into superorders and placed Ricinulei with Araneae, Amblypygi, Opiliones, the non-actinotrichid mites and Anthracomarti in a superorder Actinoderma. Zachvatkin (1952) therefore considered Acari to be diphyletic. Grandjean (1935) has been incorrectly credited with this diphyletic theory. While he recognised two broad divisions of the Acari, actinotrichid and anactinotichid mites, Grandjean still believed they formed a natural group (Lindquist, 1984). Various authors have recognised three main subgroups of the Acari: the Acariformes ("mites"), Parasitiformes (ticks) and Notostigmata (opilioacarids). The Acariformes are sometimes termed Actinotrichida and the other two are often grouped together to form the Anactinotrichida (Lindquist, 1984), and a recent account (Norton et al., 1993) recognised Acari as monophyletic, comprising two orders: Acariformes and Parasitiformes (the latter incorporating opilioacarids). Within the Actinoderma, Zachvatkin (1952) considered the parasitiform mites closest to Ricinulei and opilioacarid mites closest to Opiliones. Dubinin (1957) arranged the arachnids into classes: Trigonotarbida and Anthracomartida were placed along with spiders, Opiliones, Phalangiotarbida

and Haptopoda in the class Arachnides, while Ricinulei was placed with Eurypterida, Scorpiones, Pseudo-scorpiones, Palpigradi, Uropygi, Amblypygi and Kustarachnida (misinterpreted fossil opilionids (Beall, 1986)) in the class Scorpionomorpha. Zachvatin's and Dubinin's schemes were summarised by Lindquist (1984), but they have not been widely adopted by subsequent authors. Sharov (1966) placed Ricinulei along with Uropygi, Amblypygi, Palpigradi, Pseudo-scorpiones and Kustarachnida in a taxon Pedipalpida.

Savory (1971, 1977) regarded Ricinulei, Opiliones and Acari as forming a distinct group within the Arachnida, with Acari and Opiliones as a single cohort, Opilion-acea, and Ricinulei as a separate cohort, Ricinuliacea. All these orders, plus Phalangiotarbida, were placed by Savory (1971, 1977) in an infraclass Opilionomorphae. Savory (1977) further suggested that cyphophthalmid opilionids deserved separate ordinal status, as an order which gave rise to both the Ricinulei and the rest of the opilionids, but see Shear (1980) for a refutation of this. Firstman (1973) placed ricinuleids among his apul-monate arachnids (those lacking book-lungs), possibly close to Pseudoscorpiones and Solifugae. Yoshikura (1975) tentatively placed Ricinulei closest to Solifugae, Opiliones and Acari, but did not propose distinct characters to support this. The latter two authors did not attempt to place fossil taxa. Grasshoff (1978) placed Ricinulei closest to Pseudoscorpiones based on a grade of body organisation rather than synapomorphies of the two orders. Grasshoff (1978) placed Trigonotarbida close to spiders, Amblypygi and Uropygi while placing Anthracomartida as separate, early derivative arachnids.

The four most important recent considerations of extant arachnid phylogeny (van der Hammen, 1977, 1989; Weygoldt & Paulus, 1979; Lindquist, 1984; Shultz, 1989, 1990) have all placed Ricinulei as the sister group of the Acari. In general, none of these authors explicitly included the fossil arachnid orders in their schemes. Van der Hammen (1977, 1979, 1989) reinstated the split of the Acari into diphyletic actinotrichid and anactino-trichid mites and regarded Ricinulei as the sister group to the Anactinotrichida only, forming a taxon he called Cryptognomae. Van der Hammen (1979) referred the extinct arachnid order Phalangiotarbida to Crypto-gnomae, but later did not include phalangiotarbids (van der Hammen, 1989). Van der Hammen (1977, 1979, 1989) did not use strict cladistic methodology in his classification, but noted the following characters of both Ricinulei and Anactinotrichida: a gnathosoma (a movable segment bearing the mouthparts), no eyes or else one to three lateral eyes, one to four spiracles, no trichobothria, a palp without a free coxa and with the palpal tibia and tarsus tending to comprise a single segment, two trochanters ancestrally in walking legs 3 and 4 and the presence of a six-legged larva. Van der Hammen (1977, 1979, 1989) placed Cryptognomae as the sister group to what he regarded as the taxon Arachnida (=Tetrapulmonata, not all the "arachnids" as is the more typical interpretation).

Weygoldt & Paulus (1979), in their cladistic analysis of the arachnids, proposed a single synapomorphy,

possession of a six-legged larva, for Ricinulei + Acari, a taxon they called Acarinomorpha. Weygoldt & Paulus (1979) interpreted the Acari as monophyletic and regarded the gnathosoma as an autapomorphy of Acari only and not present in ricinuleids. These authors placed Opiliones as the sister group of Ricinulei + Acari, based on three synapomorphies: the second pair of walking legs being used as feelers, aflagellate spermatozoa with the acrosome located in an invagination, and an anteriorly located gonopore. In addition to these, it is worth noting other similarities of ricinuleids and opilionids such as tracheal respiration and walking leg 2 being longest (and used as feelers as noted above). Weygoldt & Paulus (1979) grouped Opiliones + (Ricinulei + Acari) in the taxon Cryptoperculata, a taxon quite distinct from the tetrapulmonates.

Lindquist (1984) reviewed a number of earlier arachnid classifications and interpreted Acari as monophyletic, considering the monophyletic and polyphyletic interpretations of the Acari in some detail. Lindquist (1984) proposed four synapomorphies of Acari and Ricinulei: a six-legged larva, a movable gnathosoma (rejecting Weygoldt & Paulus' (1979) use of this character as autapomorphic for Acari only), a scaly or denticulate labrum and a double trochanter in legs 3 and 4. Lindquist (1984) acknowledged the questionable status of the labrum character and Shultz (1990) regarded the double trochanter as symplesiomorphic. Lindquist (1984) discussed the possibility that Acari could be redefined to embrace Ricinulei if it emerged that one acarid group was the sister group of the Ricinulei with another acarid group as sister group to them both.

Shultz (1990) placed Ricinulei + Acari (the latter again interpreted as monophyletic) as sister groups forming a taxon Acaromorpha with the six-legged larva and subcapitulum (essentially the lower portion of the gnathosoma) as synapomorphies. He further noted the presence of tracheae, no coxal gland orifices associated with leg 3, a patellotibia joint with hinge articulations and broadly fused pedipalpal coxae as characteristics of Ricinulei and Acari (see Shultz (1990) for a discussion of convergences in these characters). Shultz (1990) placed Acaromorpha as the sister group to Megoperculata (Tetrapulmonata + Palpigradi) forming a broad taxon, Micrura, diagnosed principally on the presence of a pygidium (=postabdomen) (see Shultz (1990) for additional characters). Shultz (1990) suggested that Trigonotarbida, Kustarachnida and Phalangiotarbida may also belong in the Micrura.

Shear & Selden (1986), Shear et al. (1987) and Selden et al. (1991) made the most significant revision of trigonotarbid phylogeny, demonstrating that they are the sister group of the Araneae, Amblypygi, Uropygi and Schizomida: the extant Tetrapulmonata. Selden et al. (1991) discussed a range of synapomorphies for the Tetrapulmonata, the most important of which is two pairs of book-lungs, identified in some exceptionally preserved trigonotarbids (Claridge & Lyon, 1961), but also including two-jointed, clasp-knife chelicerae and a restricted prosoma-opisthosoma junction. Shear et al. (1987) rediagnosed Trigonotarbida as having opistho-

somal tergites divided into broad median plates and narrow lateral plates. Shear & Selden (1986), Shear et al. (1987) and Selden (1993) criticised Petrunkevitch's systematic work on fossil arachnids and the validity of the Soluta as a separate subclass for Trigonotarbida diagnosed on a variable character state. These authors also questioned the validity of the Stethostomata. Recent work supports this contention and suggests that Stethostomata is polyphyletic and that Trigonotarbida is synonymous with Anthracomartida (Dunlop, in press), though the more widely used name Trigonotarbida ought to be retained. Shear et al. (1987) commented on the fact that both trigonotarbids and ricinuleids have a prosoma-opisthosoma locking device and fusion of the second and third tergites, but that the developments were clearly not homologous, giving Selden (1986) as a reference. Selden (1986) did not actually mention this homology question between Ricinulei and Trigonotarbida.

Material and methods

A wide range of Devonian and Upper Carboniferous specimens referred to the Trigonotarbida and Anthracomartida were reviewed, principally from material in the British Museum (Natural History) (BMNH). Of this, the exceptionally preserved Lower Devonian Rhynie chert trigonotarbids (principally BMNH In 24671, In 24673, In 24674, In 24675, In 27756, In 27759, In 27762) were by far the most useful in determining the morphology of the trigonotarbids, though material referred to Anthracomartida was also examined (principally BMNH I. 7893, I. 13955, I. 15857, I. 15896, In 22841). BMNH specimens of fossil ricinuleids were also examined. Preserved specimens of the extant ricinuleid Ricinoides afzelii (Thorell) from Ghana were examined, as were slide-mounted, transverse serial sections through the prosoma and opisthosoma of Ricinoides sjostedti (Hansen & Sørensen) prepared by R. Dennell. Cladistic analysis was carried out using the MacClade 3.04 software package (Maddison & Maddison, 1992).

Ricinuleid morphology

Opisthosomal segmentation

Ricinuleid opisthosomal segmentation (Figs.1, 3) has been subject to a number of interpretations, the major problems being the number of segments constituting the pedicel, the position of the gonopore and whether or not there has been fusion of segments. The segmentation of the pedicel region has been investigated at length on numerous occasions (Hansen & Sørensen, 1904; Petrunkevitch, 1949; Millot, 1949; Pittard & Mitchell, 1972; van der Hammen, 1979). These are briefly reviewed here. The interpretations revolve around whether the membrane between the prosoma and opisthosoma bearing the gonopore comprises one or more segments and how many segments make up the sclerotised locking ridge which tucks under the carapace. Hansen & Sørensen (1904) and Petrunkevitch (1949) both rejected
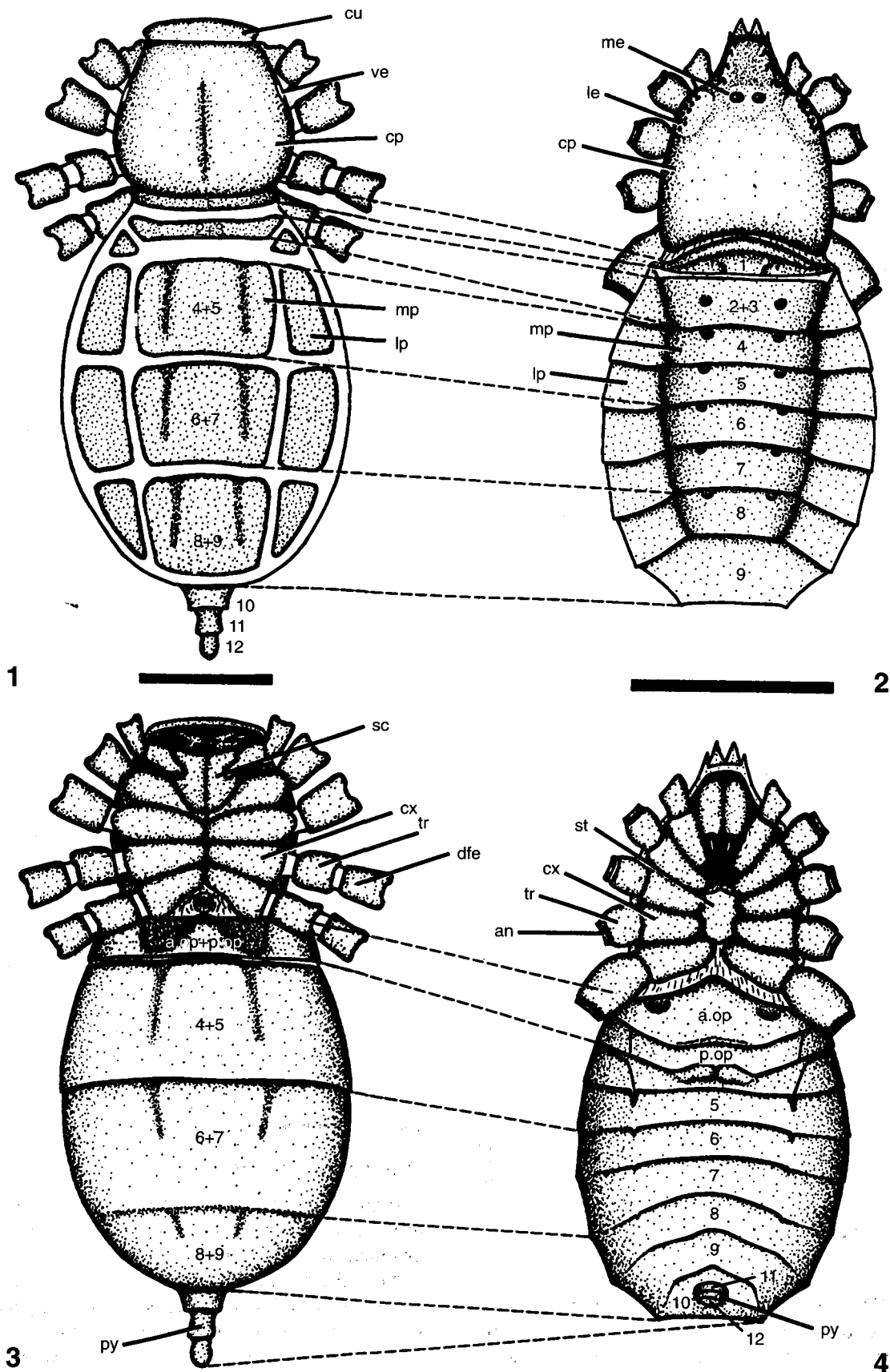
Figs. 1–4: Comparative opisthosomal segmentation in an extant ricinuleid, *Pseudocellus pelaezi*, mostly after Pittard & Mitchell (1972), and the trigonotarbid *Palaeocharinus hornei*, based on a composite of BMNH In 24671, In 24673 and In 24674. Both show the prosoma and opisthosoma decoupled to reveal the first tergite, and the ricinuleid pygidium is shown extended to show all the segments. **1** Dorsal view of *Pseudocellus*; **2** Dorsal view of *Palaeocharinus*; **3** Ventral view of *Pseudocellus*; **4** Ventral view of *Palaeocharinus*. See text for discussion of homology of segments. Opisthosomal tergites and sternites numbered appropriately. Other abbreviations: cp=carapace, cu=cucullus, ve=vestigial remnants of ricinuleid lateral eyes, me=trigonotarbid median eyes, le=trigonotarbid lateral eyes, sc=subcapitulum (fused palpal coxae), st=sternum, cx=coxa, tr=trochanter, an=trigonotarbid annulus, dfe=first podomere of the divided femur of ricinuleids, a.op=anterior operculum, p.op=posterior operculum; py=pygidium. Scale lines=1 mm.

the possibility that Ricinulei might have a unique pedicel anatomy among arachnids on the grounds that such a morphology would be unparalleled within Arachnida. Pittard & Mitchell (1972) rejected this circular logic and argued that a unique ricinuleid pedicel could simply represent an autapomorphy of the order. The presence of a gonopore on the inter-tagma membrane in Ricinulei has led authors to assume that the pedicel itself was at least one segment, and the possibility that this is just an inter-tagma membrane and not a true body segment has never been considered. Pittard & Mitchell (1972) noted the presence of a reduced sclerite between the leg 4 coxae which they interpreted as sternite 1, and they interpreted the anterior and posterior lips of the gonopore as sternites 2 and 3 (see also Fig. 9). It is worth noting that Hansen & Sørensen (1904) reported a faint sclerite in the dorsal surface of the pedicel membrane in their material, but that other authors have failed to locate this structure (Pittard & Mitchell, 1972).

The anteriormost tergites of the locking ridge have been interpreted as comprising 2 segments by both Pittard & Mitchell (1972) and van der Hammen (1979), though these authors and Millot (1949) differed in their interpretation of what was a separate sclerite (see below). Selden (1992) noted how the opisthosomas of some fossil ricinuleids have a single dorsal median sulcus, rather than transverse divisions. Selden (1992) regarded a medially divided opisthosoma as autapomorphic for the fossil family Curculioididae; a character not seen in any extant forms. Selden (1992; fig. 4g) also demonstrated that the three large dorsal tergites posterior to the locking structure in fossil ricinuleids each comprise 2 tergites fused together into diplotergites, since there are a pair of tergal apodemes on each tergite in the fossil species *Terpsicroton alticeps*. Extant ricinuleids also have these three large tergites (Fig. 1). Pittard & Mitchell (1972) did not regard these three large dorsal tergites as fused diplotergites, unlike van der Hammen (1979). Selden's (1992) observations also suggest that the three large sternites of ricinuleids correspond to the three large dorsal diplotergites. This implies that the three large ricinuleid sternites represent fused diplosternites (Fig. 3).

The anterior ventral region of the ricinuleid opisthosoma projects between the leg 4 coxae. This modified sclerite was interpreted as a single segment by Pittard & Mitchell (1972), but two segments by van der Hammen (1979). Most authors have recognised a three-segmented pygidium in ricinuleids (Fig. 3) (though Millot 1945) believed the pygidium to comprise four segments), comprising tubular segments, not divided into tergites and sternites. Pittard & Mitchell's (1972) scheme gave a total of 10 opisthosomal segments, rising to 13 if the three large tergites are assumed to be diplotergites as demonstrated by the fossil evidence, and van der Hammen's (1979) scheme also gave ricinuleids a total of 13 opisthosomal segments. Twelve opisthosomal segments is regarded as the normal groundplan in arachnids (Shultz, 1990); however, the possibility that ricinuleids have 13 cannot be immediately ruled out.

Trigonotarbids have an opisthosoma of 12 segments (Figs. 2, 4), not 11 as reported by Shear *et al.* (1987). In trigonotarbids tergite 1 forms a locking ridge, tergites 2 and 3 are fused into a single diplotergite with a single pair of muscle apodemes (Shear *et al.*, 1987), though a few Carboniferous trigonotarbids appear to have undergone a reversal of this fusion. Tergites 4–9 are not fused into diplotergites and comprise the dorsal surface of the opisthosoma. Tergites 2–8 (2–9 in some trigonotarbids) are divided into median and lateral plates (see below). The exceptional preservation of the Rhynie chert trigonotarbid material allowed tergites to be matched to their corresponding sternites. Ventrally, somite 1 is represented by a membrane between the prosoma and opisthosoma (BMNH In 24673, In 24675, Fig. 10). There is no evidence for a gonopore in this membrane as in Ricinulei. The "sternites" 2 and 3 in trigonotarbids are interpreted as representing modified appendages bearing the book-lungs, as has been demonstrated in uropygids by Shultz (1993) where they are termed the anterior and posterior opercula respectively (Fig. 4). The most anterior visible true sternite in trigonotarbids is therefore sternite 4 (Fig. 4), and sternites 4–9 are not fused into diplosternites. The gonopore in Trigonotarbida is assumed to lie beneath the anterior operculum (see also Pocock (1911)) as it does in Uropygi (Shultz, 1993), but this cannot be demonstrated in the fossils. The posterior operculum bears a pair of ventral sacs similar to those seen in Amblypygi. The last three segments of the trigonotarbid opisthosoma, 10–12, are not divided into tergites and sternites. Segments 10–12 form a pygidium, with segment 10 comprising a plate surrounding the tubular segments 11–12 (Dunlop, in prep.).

Working to the typical arachnid groundplan of twelve opisthosomal segments, I homologise the 3 segments of the ricinuleid pygidium with segments 10–12 in Trigonotarbida, which are likewise not divided into tergites and sternites (Figs. 3–4). The three large tergites preceding the pygidium, each a fused diplotergite of 2 segments in Ricinulei, can therefore be homologised with segments 4 and 5, 6 and 7, and 8 and 9 respectively of trigonotarbids (Figs. 3–4). This leaves the locking ridge of ricinuleids. Millot (1949) figured *Ricinoides* as having the locking ridge and the tergite following it fused into a single tergite, and van der Hammen proposed a similar fused tergite for *Cryptocellus*. However, Pittard & Mitchell (1972) demonstrated in *Pseudocellus* that the locking ridge is separate from the tergite which follows it (Figs. 1, 7). This tergite following the locking ridge has lateral tergites in some extant ricinuleids such as *Pseudocellus* (see below).

I believe the ricinuleid and trigonotarbid locking ridges to be homologous expressions of opisthosomal tergite 1, with the following tergite in ricinuleids and trigonotarbids representing diplotergite 2+3 (Figs. 1–2). However, it is conceivable that if Hansen & Sørensen's (1904) dorsal pedicel sclerite is genuine (though I could not find it in the material I examined) then this structure may be homologous with tergite 1 in trigonotarbids and the ricinuleid locking ridge would be homologous with diplotergite 2+3 only. Ventrally, sternites 4 and 5, 6 and 7, and 8 and 9 of trigonotarbids are interpreted as being

homologous with the three large ventral sclerites of ricinuleids (Figs. 3–4). The anteriormost region of the ricinuleid ventral opisthosoma is not formed into distinct sclerites, but could be homologised with the fused anterior and posterior opercula respectively of trigonotarbids. This region in ricinuleids, and the trigonotarbid anterior operculum, both have a median projection between the leg 4 coxae and are modified to accommodate the leg 4 coxae (see below, Figs. 9–10). The ricinuleid gonopore could represent sternite 1, sternite 1 could have been lost as in trigonotarbids (perhaps representing a synapomorphy of Trigonotarbida + Ricinulei), or the triangular plate identified between the leg 4 coxae by Pittard & Mitchell (1972) could be sternite 1. The sclerotised gonopore lips of ricinuleids (Fig. 9) could even represent displaced and highly modified true sternites 2 and 3.

The position of the gonopore remains one of the most controversial points in this present scheme, as it implies a gonopore opening on opisthosomal somite 1 which would be different from all other arachnids where it opens on somite 2. Even in Opiliones and Acari, with an anteriorly located gonopore, it is somite 2 which has migrated forwards bearing the genital opening. There is no embryological evidence for Ricinulei to demonstrate how the gonopore and neighbouring somites develop, but since the anterior ventral opisthosoma of ricinuleids (and probably other arachnids) comprises a complex and rather derived mixture of true sternal and appendicular elements, I prefer to leave the question of the ricinuleid gonopore's somite position open and refer to Pittard & Mitchell (1972) for a discussion. A summary diagram of the proposed homologisation of dorsal and ventral segmentation in trigonotarbids and ricinuleids is shown in Figs. 1–4. The opisthosomal segmentation of trigonotarbids is, I believe, well constrained, but the anterior opisthosomal segmentation of Ricinulei is less so. The model presented here provides a logical homology of these structures within the framework of a twelve-segmented opisthosoma and so is preferred over Pittard & Mitchell's (1972) and van der Hammen's (1989) schemes.

Divided tergites

Alone among arachnids, the tergites of both Ricinulei and Trigonotarbida are longitudinally divided into median and lateral plates (Figs. 1–2, 5–6), though in trigonotarbids neither tergite 1, nor tergite 9 in earlier forms, is divided. The pygidium in both groups is discussed above. The anteriormost diplotergite in ricinuleids shows lateral plates in some species (e.g. Pittard & Mitchell (1972) for Pseudocellus and van der Hammen (1989) for Cryptocellus) but not others (e.g. Millot (1949), pers. observation, for Ricinoides). The tergites of the trigonotarbid family Anthracomartidae are further subdivided, giving five plates across each tergite. The functional significance of tergites divided into median and lateral plates in either group is unclear, but this feature has not been recorded in any other arachnid order (some pseudoscorpions have tergites divided medially into two plates). Divided tergites is
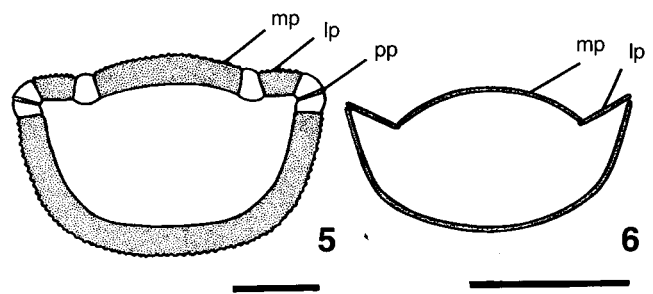
Figs. 5–6: Transverse sections through the opisthosomas of 5 the ricinuleid *Ricinoides sjostedti* and 6 the trigonotarbid *Palaeocharinus hornei* based on BMNH In 27762, showing the division of the tergites into median plates (mp) and lateral plates (lp) and the presence of pleurites (pp) in ricinuleids. The diagram shows the concavo-convex shape of the opisthosoma in both groups. Scale lines = 1 mm.

not an autapomorphic character for either Ricinulei or Trigonotarbida, contrary to previous diagnoses (e.g. Shear et al., 1987). Pittard & Mitchell (1972) noted the presence of highly reduced "pleurites" in Ricinulei, narrow sclerotised elements in the membrane between the tergites and sternites (Fig. 5). Whether these are true pleurites in the sense of primitively lateral sclerites is debatable; pleurites are also observed in tetrablemmid, pacullid, and some theridiid and araneid spiders, nemastomatid and trogulid opilionids and some pseudoscorpions (W. A. Shear, pers. comm.). J. Shultz (pers. comm.) suggested that there is no evidence for truly primitive pleurites in Arachnida. In all the groups with pleurites these sclerites probably sutured off from either the tergites or sternites. Trigonotarbids do not show such pleurites, though the divided tergites on anthracomartids noted above provide an interesting parallel whereby each somite comprises a sternite and five dorsal/dorso-lateral sclerites, though whether this is phylogenetically significant is unclear. The opisthosoma of both Ricinulei and Trigonotarbida shows a similar concavo-convex shape in transverse section (Figs. 5–6) which supports the overall similarity of these animals.

Prosoma-opisthosoma locking mechanism

Alone among arachnids, both ricinuleids and trigonotarbids have a locking mechanism between the prosoma and opisthosoma. Dorsally in both groups there is a modification of the anteriormost tergite(s) which slots into a fold in the posterior margin of the carapace (Figs. 7–8). This locking ridge is more strongly developed in early trigonotarbids (unpublished observations) and is shown particularly well in BMNH 24674, but becomes reduced in some later trigonotarbids (unpublished observations). The ricinuleid locking mechanism is complemented by a ventral component (see below). The arthrodial membrane between the body tagmata folds up like a concertina within the locking mechanism in ricinuleids (van der Hammen, 1989) and presumably a similar situation existed in trigonotarbids. Ricinuleids unlock to mate, since the gonopore is on the ventral membrane between the tagmata, and presumably they must unlock to moult; though moulting has not been

observed in these animals (Cooke, 1967). As noted above, the trigonotarbid gonopore is thought to lie beneath the anterior operculum, but this interpretation remains equivocal.

Ventrally, the anterior opisthosomas of both ricinuleids and trigonotarbids have a median projection which fits snugly between the leg 4 coxae, abutting the sternum in trigonotarbids and the leg 4 coxae only in ricinuleids (Figs. 9–10) (the sternum is absent in the latter order). The anteriormost ventral plate is interpreted as the anterior operculum in trigonotarbids (see above), though whether this is homologous with the projection in ricinuleids is unclear since the segmentation here in ricinuleids is not distinct. The coxae of leg 4 in Ricinulei are actively movable and provided with distinct keels which lock into corresponding grooves in the opisthosoma (Fig. 9). This provides a ventral com-

ponent to the dorsal locking ridge in ricinuleids described above. The Rhynie chert trigonotarbids show a pair of depressions in the anterior opisthosoma (BMNH 27762, see also Pocock (1911: fig. 29) on an anthracomartid) which accommodate the coxae of leg 4 (Fig. 10). While there are no specific keels on the leg 4 coxae of trigonotarbids to slot into these depressions, there is a modification of the opisthosoma in both groups to accommodate the coxa of leg 4. It is not clear whether coxa 4 of trigonotarbids was mobile as in Ricinulei, though this seems likely on anatomical grounds (W. A. Shear, pers. comm.).

Mouthparts

Tetrapulmonate chelicerae are two-segmented (though there is some evidence for a vestigial third
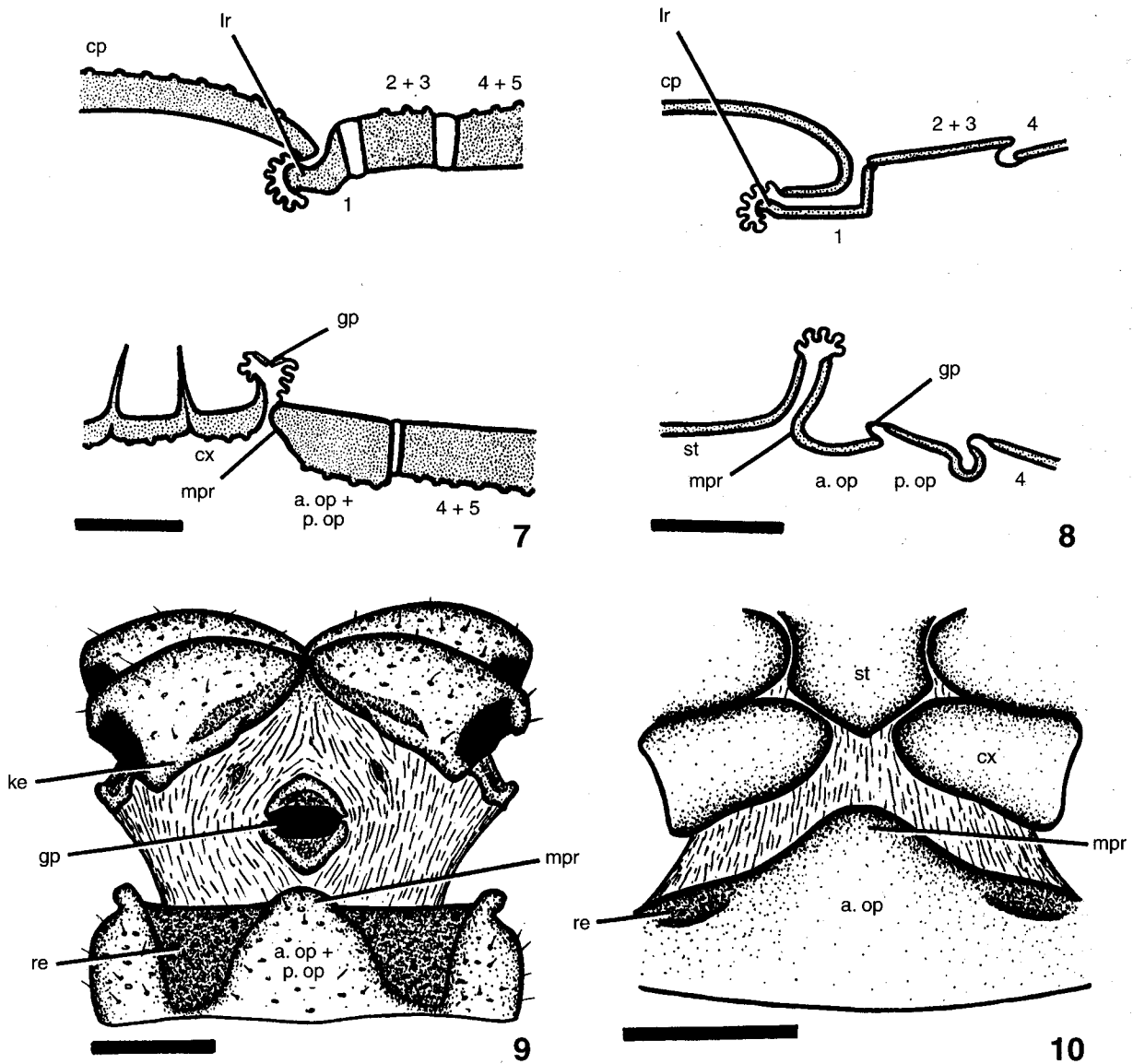
Figs. 7–10: Comparison of the prosomal-opisthosomal locking mechanism in an extant ricinuleid, *Pseudocellus pelaezi*, mostly after Pittard & Mitchell (1972), and the trigonotarbid *Palaeocharinus hornei*, based on BMNH In 24673, In 24674 and In 27759 and In 27762. **7** Longitudinal section along midline of *Pseudocellus*; **8** Longitudinal section along midline of *Palaeocharinus*; **9** Ventral view of *Pseudocellus*; **10** Ventral view of *Palaeocharinus*. Both ventral views show the prosoma and opisthosoma eased apart to show the function of the leg 4 coxa in the coupling mechanism. Abbreviations: lr=locking ridge, mpr=median projection of opisthosoma, gp=gonopore, ke=keel on ricinuleid coxa 4; re=recess to accommodate coxa 4. Other abbreviations and numbering of tergites and sternites as in Figs. 1–4. Scale lines=0.25 mm.

segment in some Rhynie chert trigonotarbids (Dunlop, in prep.)) and of the clasp-knife type. Ricinuleid chelicerae are also two-segmented, though whether they are clasp-knife or chelate in nature is debatable since they appear to present an intermediate morphology between the two extremes. The movable finger (the fang) is somewhat longer than the opposing fixed finger (Fig. 11), giving chelicerae not unlike those of Uropygi and Amblypygi which are interpreted as being of clasp-knife type (Selden et al., 1991), but which have a strongly developed tooth row opposing the fang. I see no convincing grounds for interpreting ricinuleid chelicerae as fundamentally different from those of the Tetrapulmonata.

A movable subcapitulum is present in ricinuleids (Fig. 11) in the form of fused palpal coxae, and has been widely reported for Acari (Lindquist, 1984; van der Hammen, 1989; Shultz, 1990). Movable coxae are probably plesiomorphic for arachnids (Shultz, 1990) and it might be argued that the subcapitulum in both Acari and Ricinulei simply represents retained plesiomorphic mobility in coxae which happen to have fused, rather than a secondarily derived, functional adaptation, as believed by van der Hammen (1989). The dorsal surfaces of the fused coxae in Ricinulei form a setae-lined preoral conduit very similar to that seen in Uropygi (e.g. Dunlop, 1994) where it filters particles from the food (see also Hansen & Sørensen (1904) who noted this ricinuleid-uropygid similarity). The Acari show a great diversity of mouthpart structures associated with their different modes of feeding, and determining unequivocally which is the groundplan of the order is questionable. The possibility therefore remains that the subcapitulum is not a functional synapomorphic adaptation of Acari and Ricinulei, but a convergent fusion of palpal coxae (perhaps to give more stability for palpal movements). That said, the presence of similar mouthparts in Ricinulei and Acari should not be ignored. The palpal coxae of trigonotarbids are unfused (Dunlop, 1994), but were quite possibly mobile like those of many spiders (Foelix, 1982) since they do not abut the sternum or a large labium and bear endites which may have had a masticatory function (Dunlop, 1994).

Cladistic analysis

Included taxa

In the past ricinuleids have been placed in a higher taxon with nearly every other arachnid order at one time or another, and to give consideration to each model would result in a revision of all the Arachnida, beyond the scope of this present work. As discussed above, the principal recent models proposing distinct shared characters (Weygoldt & Paulus, 1979; Lindquist, 1984; van der Hammen, 1989; Shultz, 1990) have considered Ricinulei to be similar to either the Acari and/or Opiliones while Ewing (1930) noted their similarity to the Trigonotarbida. I limit this analysis to these principal contenders for the sister group of the Ricinulei: i.e. the Trigonotarbida (in addition to which I have
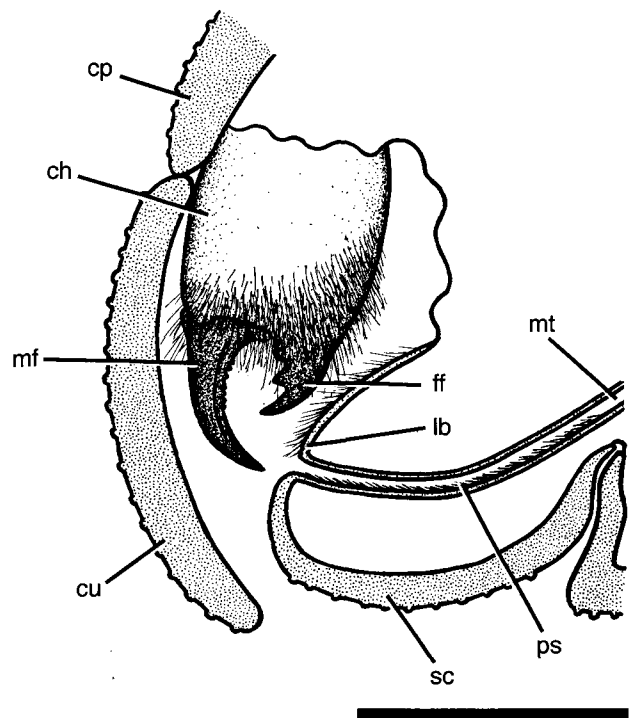

Fig. 11: Transverse section of the mouthparts of a ricinuleid, *Ricinoides afzelii*, showing the subcapitulum bearing preoral setae and the chelicera with its resemblance to the clasp-knife chelicera of the tetrapulmonate arachnids. Abbreviations: ch=chelicera, mf=movable finger (fang), ff=fixed finger, lb=labrum, mt=mouth, ps=preoral setae. Other abbreviations as in Figs. 1–4. Scale line=0.5 mm.

included the extant tetrapulmonates as a single group) and the Acari and Opiliones. Acari are assumed to be monophyletic in this study, following Norton et al. (1993). Van der Hammen (1979) likened Ricinulei to the fossil order Phalangiotarbida. The character states and phylogenetic relationships of the Phalangiotarbida are poorly known and a revision of this order would be necessary before it could be included in any analysis. Since this analysis is essentially reinterpreting Shultz's (1990) taxon Micrura the order Palpigradi is included for completeness.

Characters and character polarities

The characters used and their polarities are listed in Table 1 and the data matrix is given in Table 2. Characters resolving the subgroups of the Acari and the extant Tetrapulmonata are not included since they are not relevant to this study. Autapomorphies of the various orders are excluded since they are of no use in resolving phylogenetic relationships. The characters and character polarities are as follows:

Character 1: Three-segmented, chelate chelicerae are seen in arachnid outgroups such as Xiphosura and Eurypterida and are also present in Palpigradi, Opiliones and early derivative Acari (van der Hammen, 1989; Shultz, 1990). This is interpreted as the plesiomorphic state. Two-segmented, essentially "clasp-knife" chelicerae are interpreted as the apomorphic condition and are seen in Ricinulei and the Tetrapulmonata,

though some Acari have two-segmented chelicerae (W. A. Shear, pers. comm.).

Character 2: A plagula ventralis is reported as a synapomorphy of all the Tetrapulmonata, including Trigonotarbida (Shear *et al.*, 1987), though it is certainly not present in all Araneae and could not be found in the theraphosid *Brachypelma smithi* (F. O. P.-Cambr.) (pers. observation).

Character 3: A movable subcapitulum comprising the palpal coxae is present in Ricinulei and Acari (Shultz, 1990) where it was considered the derived state.

Character 4: Leg 2 being longer than leg 1 and used as a feeler is seen in Ricinulei and Opiliones and is interpreted as the derived state. Weygoldt & Paulus (1979) claimed this character was also present in Acari, but this is not borne out by examination of a range of Acari figured in the literature.

Character 5: Ricinulei and early derivative Acari have a divided femur on legs 3 and 4, while Trigonotarbida have an annulus around the coxa-trochanter joint of all walking legs. Shultz (1990) regarded these structures as homologous and plesiomorphic. Extant Tetrapulmonata, Palpigradi and Opiliones are coded as having the derived state of all leg femora undivided.

Character 6: The tritosternum or labium is recorded as present in extant Tetrapulmonata, Trigonotarbida (Dunlop, 1994), Ricinulei, Palpigradi and Acari (though it is considerably reduced in some groups). There is no tritosternum in Opiliones (Shultz, 1990) and this absence was regarded by Shultz (1990) as the plesiomorphic state.

Character 7: A pedicel constituting a reduced prosoma-opisthosoma junction is seen in all Tetrapulmonata, Ricinulei and Palpigradi and was regarded by Selden *et al.* (1991) as the derived state for Tetrapulmonata.

Character 8: A locking ridge formed from the first opisthosomal tergite undertucking the carapace and indentations in the anterior ventral opisthosoma to receive the leg 4 coxae (see above for a discussion of ricinuleid opisthosomal segmentation) is present in Ricinulei and Trigonotarbida only. Its presence is interpreted as the derived state.

Character 9: Fusion of tergites 2+3 into a diplotergite is interpreted as the derived state in both Ricinulei and Trigonotarbida only, as it is not seen in arachnid outgroups such as Xiphosura and Eurypterida. In Ricinulei other tergites have also fused into diplotergites and this would be autapomorphic for the order.

Character 10: Tergites with lateral plates are present in Ricinulei and Trigonotarbida only and their presence is interpreted as the derived state since they are not seen in outgroups such as Xiphosura and Eurypterida.

Character 11: A pygidium is present in Tetrapulmonata, Ricinulei and Trigonotarbida, but is absent in Acari and Opiliones (Shultz, 1990). I regard the presence of a pygidium as the plesiomorphic state as it is seen in eurypterids (though here it comprises 5 segments).

Character 12: An anteriorly located gonopore is seen in Ricinulei, Acari and Opiliones and is interpreted as the derived state, following Weygoldt & Paulus (1979).

Characters	Plesiomorphic state	Apomorphic state
1. Cheliceral segmentation	3-segmented	2-segmented
2. Plagula ventralis	absent	present
3. Subcapitulum	absent	present
4. Leg 2	unmodified	elongate
5. Leg femora	some/all divided	all undivided
6. Tritosternum	absent	present
7. Pedicel	absent	present
8. Locking ridge	absent	present
9. Tergites 2+3 fused	absent	present
10. Divided tergites	absent	present
11. Pygidium	present	absent
12. Anterior gonopore	absent	present
13. Ovipositor	absent	present
14. Sperm axoneme	free	1, coiled 2, absent
15. Hexapodal larva	absent	present
16. Trichobothria	absent	present

Table 1:   Characters and character states used in the phylogenetic analysis.

As noted above the precise segmental position of the gonopore in Ricinulei is uncertain. In Tetrapulmonata (and all other extant arachnids) the gonopore is on the second opisthosomal somite. The gonopore has not been observed in Trigonotarbida and this character is coded as uncertain.

Character 13: An ovipositor is present only in Acari and Opiliones among arachnids and was interpreted as the derived condition by Shultz (1990). No ovipositor is known in Trigonotarbida and this character is coded as uncertain.

Character 14: The sperm axoneme is coiled in extant Tetrapulmonata, Ricinulei and Opiliones, but absent in Acari and Palpigradi (Shultz, 1990). These two character states were interpreted as alternative apomorphies from a plesiomorphic free axoneme by Shultz (1990). The status of this character in Trigonotarbida is uncertain.

Character 15: A six-legged larva is seen only in Ricinulei and Acari and is interpreted as the derived condition (Shultz, 1990). Extant Tetrapulmonata and Opiliones have instars with the full complement of appendages, though a full ontogenetic sequence in Trigonotarbida is unknown.

Character 16: Trichobothria are present in extant Tetrapulmonata, Acari and Palpigradi (Selden *et al.*, 1991), but not in Trigonotarbida, Ricinulei and Opiliones. Selden *et al.* (1991) regarded absence of

									1						
Taxon	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6
Extant Tetrapulmonata	1	1	0	0	1	1	1	0	0	0	0	0	0	1	0	1
Trigonotarbida	1	1	0	0	0	1	1	1	1	1	0	?	?	?	?	0
Ricinulei	1	0	1	1	0	1	1	1	1	1	0	1	0	1	1	0
Palpigradi	0	0	0	0	1	1	1	0	0	0	0	0	0	2	0	1
Acari	0	0	1	0	0	1	0	0	0	0	1	1	1	2	1	1
Opiliones	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	0

Table 2:   Data matrix used in the phylogenetic matrix. 0=plesiomorphic state, 1=apomorphic state, 2=alternative apomorphic state, ?=character state uncertain. See text for details.

trichobothria as the derived state, though since tri-
chobothria are not found in the arachnid outgroups
Xiphosura or Eurypterida I regard their absence as
plesiomorphic and their presence as derived; the impli-
cation being that they are convergent adaptations to
terrestrial life.

Discussion

Using these 16 characters the two most parsimonious
cladograms have a tree length of 24 and a consistency
index of 0.67. Both suggest that Ricinulei are the sister
group of the Trigonotarbida and that these two are
sister group to the rest of the Tetrapulmonata (Araneae,
Amblypygi, Uropygi and Schizomida). Palpigradi
emerge as the sister group to Tetrapulmonata (including
ricinuleids), as they were in Shultz's (1990) scheme
forming a taxon Megoperculata. The analysis does
not differentiate between Acari as sister group to the
Opiliones or sister group to the other orders in the
analysis, since these alternatives produce the same con-
sistency index. The latter model is adopted as this is
closer to Shultz's (1990) analysis, and this second clado-
gram is presented in Fig. 12. Retaining Acari as the
sister group of Ricinulei in their position as sister group
to Trigonotarbida in this analysis reduces the consist-
ency index to 0.55. Ricinulei as the sister group to Acari
with both as the sister group to Megoperculata as in
Shultz's (1990) scheme reduces the consistency index to
0.57. The placement of Trigonotarbida as the sister
group of the extant Tetrapulmonata by Shear et al.
(1987) and Selden et al. (1991) is supported by a range of
characters, including the pedicel, two-segmented cheli-
cerae and a pygidium. Trigonotarbida and Tetrapulmo-
nata also have two pairs of book-lungs (this character
was omitted from the analysis owing to the difficulties of
homologising the various tracheal systems in arachnids
with either book-lungs or even each other), though
this condition appears to be symplesiomorphic for
non-scorpion arachnids.

This analysis suggests that Ewing (1930) was correct
to suggest that trigonotarbids and ricinuleids are related.
Synapomorphies identified in this study for Ricinulei +
Trigonotarbida are: (1) tergites longitudinally divided
into median and lateral plates, (2) fusion of at least
tergites 2 and 3 into a diplotergite, and (3) a locking
ridge between the prosoma and opisthosoma involving
tergite 1 and the accommodation of the leg 4 coxae into
a recess in the opisthosoma. Loss of sternite \1 might
represent a further synapomorphy of these orders, but
this character is equivocal. The overall opisthosomal
segmentation pattern of nine dorsally visible tergites
plus a pygidium of three segments and the con-
cavo-convex opisthosomal shape (Figs. 1–6) represent
additional similarities between Ricinulei and Trigono-
tarbida, though ones which are hard to code into a
cladistic analysis. Other shared characters of ricinuleids
and trigonotarbids which are interpreted as symplesio-
morphic are lack of trichobothria and retention of an
additional proximal joint in at least walking legs 3 and
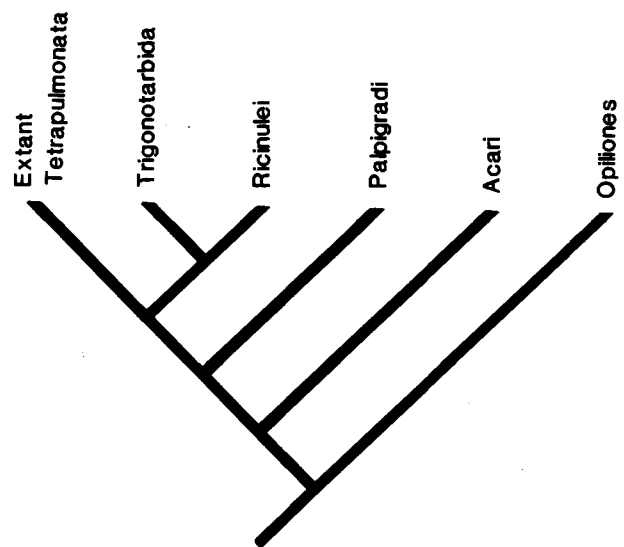4 (Figs. 1–2). Of the Trigonotarbida, Ricinulei most

Fig. 12: Cladogram of the relationships of the arachnid taxa
discussed in this account of ricinuleid phylogeny (see text
for details). The cladogram has a tree length of 24 and a
consistency index of 0.67.

closely resemble the families Palaeocharinidae and
Anthracomartidae (see also Millot (1949)), though there
is no evidence to derive ricinuleids from any particular
trigonotarbid group and Ricinulei are regarded as a
sister group of Trigonotarbida. Since trigonotarbids are
recorded from the Upper Silurian, this model implies a
split of Trigonotarbida and Ricinulei before this time.

Ricinuleids can, according to this analysis, be re-
garded as the sister group of the Trigonotarbida and
as early derivative, but highly derived, members of
the Tetrapulmonata (Fig. 12). The principal criticism of
this hypothesis is that ricinuleids lack book-lungs, but
then not all tetrapulmonates have two lung pairs,
schizomids have one pair and many spiders have
only one pair or even none at all (Foelix, 1982). The
characters which link Ricinulei to the rest of the
Tetrapulmonata (and may represent better diagnostic
characters of the order) would be 2-segmented, essen-
tially clasp-knife chelicerae, a pedicel between the pro-
soma and opisthosoma, and a pygidium. In this model
(Fig. 12) ricinuleids are assumed to have undergone
reversals to lose the book-lungs, other major differences
between Ricinulei and the rest of the tetrapulmonates
(e.g. the cucullus, leg 3 sperm transfer device, extremely
thick cuticle) being autapomorphic and of no use in
reconstructing phylogeny.

An alternative model would be to retain Acari and
Ricinulei as sister taxa, this clade itself being the sister
group to Trigonotarbida. This model overcomes the
problem of acarid and ricinuleid synapomorphies and
virtually recreates Shultz's (1990) taxon Micrura (arach-
nids with a pygidium) with the inclusion of Trigono-
tarbida, a slightly different arrangement of the extant
taxa. This model would be controversial by also placing
Acari in the Tetrapulmonata and assumes that Acari are
monophyletic and have undergone reversals to lose the
locking mechanism and divided tergites as well as other
tetrapulmonate characters such as the pedicel. More-
over, the presence of three-segmented, chelate chelicerae

in many Acari argues against this model. As noted above, placing Acari in this position lowers the consistency index and so the model presented in Fig. 12 is preferred. In any case, Acari are a highly specialised group of arachnids and determining their origins, or even whether they are monophyletic, is difficult (Lindquist, 1984).

In the models presented above there seems no way of resolving the similarities of Ricinulei and Opiliones, e.g. an anterior gonopore and leg 2 longer than leg 1, except by assuming convergence. The alternative would be to assume that opilionids also are highly derived tetrapulmonates, though the presence of 3-jointed, chelate chelicerae in opilionids (see above) argues strongly against this. Placing Opiliones + Ricinulei as sister group to the Trigonotarbida in the analysis reduces the consistency index to 0.55 * and is therefore rejected. (Opiliones + Acari) + Ricinulei as sister group to the Trigonotarbida has a consistency index of 0.59. Opilionids and acarids share a number of potentially synapomorphic characters such as an ovipositor, and a broader re-study of the phylogenetic significance of the opilioacarids and the similar-looking cyphophthalmid opilionids may help resolve the position of the Acari.

Acknowledgements

References

BEALL, B. S. 1986: Reinterpretation of the Kustarachnida (Abstract). *Am. Arachnol.* **34**: 4.

BUCKLAND, W. 1837: *The Bridgewater treatises on the power, wisdom and goodness of God as manifested in the creation. Treatise IV. Geology and mineralogy considered with reference to natural theology.* 2nd ed. William Pickering, London.

CLARIDGE, M. F. & LYON, A. G. 1961: Lung-books in the Devonian Palaeocharinidae (Arachnida). *Nature, Lond.* **191**: 1190–1191.

COOKE, J. A. L. 1967: Observations on the biology of Ricinulei (Arachnida) with descriptions of two new species of *Cryptocellus. J. Zool., Lond.* **151**: 31–42.

DUBININ, V. B. 1957: A new system of the superclass Chelicerata. *Bull. Soc. Mosc. exp. Nat.* **62**: 25–33. [In Russian.]

DUNLOP, J. A. 1994: Filtration mechanisms in the mouthparts of the tetrapulmonate arachnids (Trigonotarbida, Araneae, Amblypygi, Uropygi, Schizomida). *Bull. Br. arachnol. Soc.* **9**: 267–273.

DUNLOP, J. A. In Press. Systematics of the fossil arachnids. *Revue suisse Zool.*

EWING, H. E. 1930: A fossil arachnid from the Lower Carboniferous shales (Pocono formation) of Virginia. *Ann. ent. Soc. Am.* **23**: 641–643.

FIRSTMAN, B. 1973: The relationshiop of the chelicerate arterial system to the evolution of the endosternite. *J. Arachnol.* **1**: 1–54.

FOELIX, R. F. 1982: *Biology of Spiders.* Harvard University Press, Cambridge, Mass.

FRIČ, A. 1904: *Palaeozoische Arachniden.* Privately published by Anton Frič, Prague.

GEINITZ, H. B. 1882: *Kreischeria wiedei* H. B. Gein, ein Pseudoskorpion aus der Steinkholenformation von Zwickau. *Z. dt. geol. Ges.* **34**: 238–242.

GRANDJEAN, F. 1935: Observations sur les Acariens (1re série). *Bull. Mus. natn. Hist. nat. Paris* **7**: 119–126.

GRASSHOFF, M. 1978: A model of the evolution of the main chelicerate groups. *Symp. zool. Soc. Lond.* **42**: 273–284.

GUÉRIN-MÉNEVILLE, M. 1838: Note sur l'*Acanthodon* et sur le *Cryptostemme*, nouveaux genres d'Arachnides. *Revue Zool. Soc. Cuvier.* **1**: 10–12.

HAASE, E. 1890: Beiträge zur Kenntniss der fossilen Arachniden. *Z. dt. geol. Ges.* **42**: 629–657.

HAMMEN, L. VAN DER 1977: A new classification of Chelicerata. *Zool. Meded. Leiden* **51**: 307–319.

HAMMEN, L. VAN DER 1979: Comparative studies in Chelicerata I. The Cryptognomae (Ricinulei, Architarbi and Anactinotrichida). *Zool. Verh. Leiden* **174**: 1–62.

HAMMEN, L. VAN DER 1989: *An Introduction to Comparative Arachnology.* The Hague: SPB Academic Publishing.

HANSEN, H. J. & SØRENSEN, W. 1904: *On two orders of Arachnida.* Cambridge: Cambridge University Press.

JERAM, A. J., SELDEN, P. A. & EDWARDS, D. 1990: Land animals in the Silurian: arachnids and myriapods from Shropshire, England. *Science, N. Y.* **250**: 658–661.

KARSCH, F. 1882: Ueber einige neues Spinnenthier aus der Schlesischen Steinkohle und die Arachnoiden der Steinkohlenformation überhaupt. *Z. dt. geol. Ges.* **34**: 556–561.

LEGG, G. 1977: Sperm transfer and mating in *Ricinoides hanseni* (Arachnida: Ricinulei). *J. Zool., Lond.* **182**: 51–61.

LINDQUIST, E. E. 1984: Current theories on the evolution of major groups of Acari and on their relationships with the other groups of Arachnida, with consequent implications for their classification. *In* D. A. Griffiths & C. E. Brown (eds.), *Acarology* **VI**: 28–62. New York: John Wiley.

MADDISON, W. P. & MADDISON, D. R. 1992: *MacClade version 3.04.* Sunderland, Mass: Sinauer Associates Incorporated Publishers.

MILLOT, J. 1945: Les Ricinulei ne sont pas des arachnides primitifs. *Bull. Soc. ent. Fr.* **70**: 106–108.

MILLOT, J. 1949: Ordre des Ricinuléides. *Trait. Zool.* **6**: 744–760.

MÜLLER, A. H. 1957: Ein Arachnidenrest (*Brachylycosa manebachensis* n.sp.) aus dem Unteren Rotligenden (Manebacher Schichten) von Thüringen. *Geologie* **6**: 95–98.

NORTON, R. A., KETHLEY, J. B., JOHNSTON, D. E. & O'CONNER, B. M. 1993: Phylogenetic perspectives on genetic systems and reproductive modes of mites. *In* D. L. Wrensch & M. A. Ebbert (eds.), *Evolution and diversity of sex ratio in insects and mites:* 8–99. London: Chapman and Hall.

PETRUNKEVITCH, A. I. 1949: A study of Palaeozoic Arachnida. *Trans. Conn. Acad. Arts Sci.* **37**: 69–315.

PETRUNKEVITCH, A. I. 1955: Arachnida. *In* R. C. Moore (ed.), *Treatise on Invertebrate Paleontology, Part P, Arthropoda* **2**: 42–162. Boulder Colorado and Lawrence, Kansas: Geological Society of America and University of Kansas Press.

PITTARD, K. & MITCHELL, R. W. 1972: Comparative morphology of the life stages of *Cryptocellus pelaezi* (Arachnida, Ricinulei). *Grad. Stud. Texas Tech Univ.* **1**: 1–77.

PLATNICK, N. I. & PASS, G. 1982: On a new Guatemalan *Pseudocellus* (Arachnida, Ricinulei). *Am. Mus. Novit.* **2733**: 1–6.

POCOCK, R. I. 1902: *Eophrynus* and allied Carboniferous Arachnida. Part 1. *Geol. Mag.* **4**: 487–493.

POCOCK, R. I. 1911: *A monograph of the terrestrial Carboniferous Arachnida of Great Britain.* Monographs of the Palaeontographical Society, London.

POLLOCK, J. 1967: Notes on the biology of the Ricinulei (Arachnida). *Jl W. Afr. Sci. Ass.* **12**: 19–22.

SAVORY, T. H. 1971: *Evolution in the Arachnida.* Merrow, Watford: Merrow Monographs.

SAVORY, T. H. 1977: *The Arachnida.* 2nd edn. London: Academic Press.

SCUDDER, S. H. 1884: A contribution to our knowledge of Palaeozoic Arachnida. *Proc. Am. Acad. Arts Sci.* **20**: 13–22.

SELDEN, P. A. 1986: Ricinuleids—living fossils? *Actas X congreso internacional de aracnologia, Jaca, 1986* **1**: 425.

SELDEN, P. A. 1992: Revision of the fossil ricinuleids. *Trans. R. Soc. Edinb.* (Earth Sci.) **83**: 595–643.

SELDEN, P. A. 1993: Fossil arachnids—recent advances and future prospects. *Mem. Qd Mus.* **33**: 398–400.

SELDEN, P. A., SHEAR, W. A. & BONAMO, P. M. 1991: A spider and other arachnids from the Devonian of New York, and reinterpretations of Devonian Araneae. *Palaeontology* **34**: 241–281.

SHAROV, A. G. 1966: *Basic arthropodan stock with special reference to insects.* Oxford: Pergamon Press.

SHEAR, W. A. 1980: A review of the Cyphophthalmi of the United States and Mexico, with a proposed reclassification of the suborder (Arachnida Opiliones). *Am. Mus. Novit.* **2705**: 1–34.

SHEAR, W. A. & SELDEN, P. A. 1986: Phylogenetic relationships of the Trigonotarbida, an extinct order of arachnids. *Actas X congreso internacional de aracnologia, Jaca, 1986* **1**: 393–397.

SHEAR, W. A., SELDEN, P. A., ROLFE, W. D. I., BONAMO, P. M. & GRIERSON, J. D. 1987: New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida). *Am. Mus. Novit.* **2901**: 1–74.

SHULTZ, J. W. 1989: Morphology of locomotor appendages in Arachnida: evolutionary trends and phylogenetic implications. *Zool. J. Linn. Soc.* **97**: 1–56.

SHULTZ, J. W. 1990: Evolutionary morphology and phylogeny of Arachnida. *Cladistics* **6**: 1–38.

SHULTZ, J. W. 1993: Muscular anatomy of the giant whipscorpion *Mastigoproctus giganteus* (Lucas) (Arachnida: Uropygi) and its evolutionary significance. *Zool. J. Linn. Soc.* **108**: 335–365.

THORELL, T. 1892: On an apparently new arachnid belonging to the family Cryptostemmoidae. *Bih. K. svenska VetenskAkad. Handl.* **17**: 1–18.

THORELL, T. & LINDSTRÖM, G. 1885: On a Silurian scorpion from Gotland. *K. svenska VetenskAkad. Handl.* **21**: 1–33.

WESTWOOD, J. O. 1874: *Thesaurus Entomologicus Oxoniensis.* Oxford: Clarendon Press.

WEYGOLDT, P. & PAULUS, H. F. 1979: Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. *Z. Zool. Syst. EvolForsch.* **17**: 85–200.

WOODWARD, H. 1871: On the discovery of a new and very perfect arachnide from the ironstone of the Dudley Coal-field. *Geol. Mag.* **8**: 383–387.

YOSHIKURA, M. 1975: Comparative embryology and phylogeny of Arachnida. *Kumamoto J. Sci.* (Biol.) **12**: 71–142.

ZACHVATKIN, A. A. 1952: Razdeleniye kleshchei (Acarina) na otryady i ikh polozheniye v sisteme Chelicerata. *Parazit. Sb. Inst. zool. Akad. Nauk* **14**: 5–46.