A TRIGONOTARBID ARACHNID FROM THE UPPER SILURIAN OF SHROPSHIRE

by JASON A. DUNLOP

ABSTRACT. A trigonotarbid (Arachnida: Trigonotarbida) from the oldest known terrestrial ecosystem (Silurian, Přídolí Series) of Ludford Lane, Shropshire, UK is described as *Eotarbus jerami* gen. et sp. nov., and is the earliest known non-scorpion arachnid. This specimen predates Rhynie Chert and Gilboa trigonotarbids which show more plesiomorphic characters, and is similar to some Early Devonian trigonotarbids from Alken an der Mosel and other German localities of similar age. *Eotarbus jerami* is too poorly preserved to be assigned unequivocally to a family, but most closely resembles the Trigonotarbidae. *Eotarbus* is interpreted as a plesion and is probably a sister group to all trigonotarbids with triangular carapaces lacking lateral eyes.

TRIGONOTARBIDS are a group of spider-like arachnids which range from the late Silurian (Jeram *et al.* 1990) to the early Permian (Müller 1957), and are one of the most diverse and abundant groups of Palaeozoic terrestrial arachnids. Recent work (Shear and Selden 1986; Shear *et al.* 1987; Dunlop 1994*a*, 1994*b*) placed the trigonotarbids in the arachnid taxon Tetrapulmonata Shultz, 1990, as the plesiomorphic sister group of all the living tetrapulmonates (Araneae, Amblypygi, Uropygi and Schizomida) (Shear *et al.* 1987). Until recently, the oldest known examples of trigonotarbids were the exceptionally preserved Lower Devonian (Pragian) Rhynie Chert fauna (e.g. Hirst 1923; Shear *et al.* 1987). Jeram *et al.* (1990) made an initial report of some older terrestrial fossils macerated from Silurian (Přídolí Series) sediments from Ludford Lane, Shropshire. Among the arthropod and plant fragments recovered was a single specimen of an unnamed trigonotarbid arachnid (Jeram *et al.* 1990, fig. 1), and this is described herein, and compared with Devonian and Carboniferous trigonotarbids.

GEOLOGICAL SETTING

The specimen was recovered from an organic-rich horizon within the Ludlow Bone Bed Member of the Downton Castle Sandstone Formation, from Ludford Lane, Ludlow, Shropshire, UK. The precise horizon is unrecorded, but subsequent investigations suggested that the richest organic deposits are 1·6 m above the basal bone bed of the Ludlow Bone Bed Member, within the Platyschisma Shale Member (Manning 1993). The Ludford Lane sequence has been described by Bassett *et al.* (1982), and is interpreted as a near-shore deposit into which terrestrial plant and animal material was transported and then reworked during severe storms (Manning 1993; Manning and Dunlop 1995). It contains an assemblage of marine and terrestrial fossils. The former are predominantly eurypterids (Manning 1993), but also include aquatic scorpions, scolecodonts, thelodont denticles and, rarely, conodonts. The latter comprise vascular land plants, such as *Cooksonia* (Edwards *et al.* 1992), centipedes (Jeram *et al.* 1990), the arthropleurid *Eoarthropleura* (Shear and Selden 1995) and probable terrestrial scorpions (Manning (1993); A. Jeram, pers. comm.) Further arthropod material from this locality awaits description.

The Ludford Lane arthropod fossils are preserved as fragile fragments of cuticle, or, more rarely, nearly complete animals, as is the case with this trigonotarbid. The specimen is carbonized, which obscures morphological details of the cuticle, such as can be seen in the better preserved Gilboa trigonotarbids (Shear *et al.* 1987), and is compressed, but morphological features can be seen under low angle lighting.

MATERIALS AND METHODS

The material was originally prepared by A. Jeram using palaeobotanical hydrofluoric acid (HF) maceration techniques following methods described by Shear *et al.* (1987) and Manning (1993). The slide-mounted specimen, Ulster Museum K 25850, was examined and photographed under a binocular microscope with very low angle lighting to bring out the faint surface relief. Drawings were prepared using a *camera lucida*. Specimens of the trigonotarbids *Palaeocharinus* sp., from the Early Devonian (Pragian) of the Rhynie Chert, Aberdeenshire, and *Trigonotarbus johnsoni*, from the Upper Carboniferous of Coseley, West Midlands in the collections of the Natural History Museum, were examined in conjunction with the literature for comparative purposes.

MORPHOLOGICAL INTERPRETATION

The carbonized preservation of this specimen makes interpretation difficult, but its overall body shape, with a triangular prosoma and rounded opisthosoma, and its division of the opisthosomal tergites into median and lateral plates shows that it is a trigonotarbid (Text-figs 1–2).
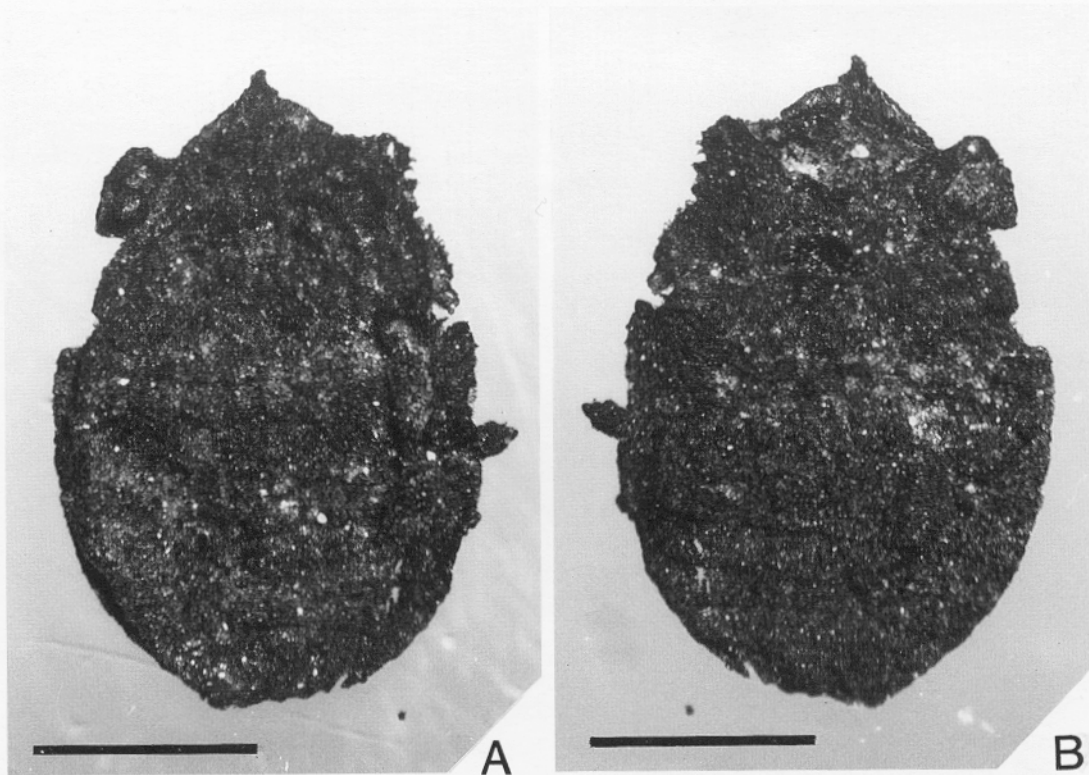

TEXT-FIG. 1. *Eotarbus jerami* gen. et sp. nov. Silurian (Přídolí), Ludford Lane, Shropshire. Ulster Museum No. K 25850. A, dorsal surface. B, ventral surface. Scale bar represents 0·5 mm. Photographs courtesy of Dr A. Jeram.

Carapace

The carapace is broadly triangular, with a slight anterior projection and a straight posterior margin. It is folded and pitted, but shows some original surface detail. It appears raised close to the assumed
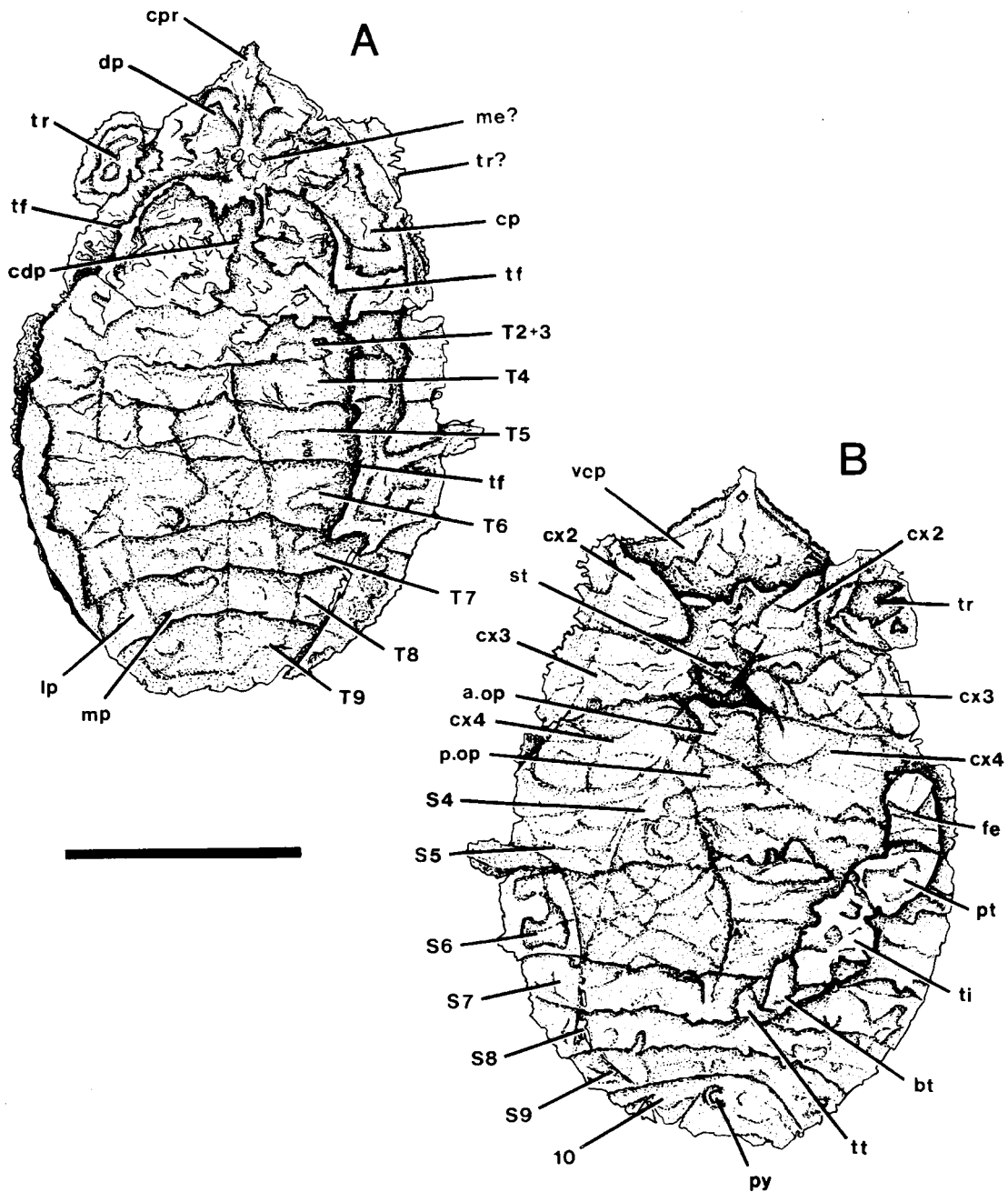
TEXT-FIG. 2. *Camera lucida* drawing of the specimen shown in Text-figure 1. A, dorsal surface, B, ventral surface, a.op = anterior operculum; bt = basitarsus; cdp = central (?taphonomic) depression of carapace; cp = carapace; cpr = anterior projection of carapace; cx = coxa, with number; dp = anterior depressions of carapace; fe = femur; lp = lateral plate; me? = probable position of median eyes; mp = median plate; p.op = posterior operculum; pt = patella; py = pygidium; S = sternite, with number; st = sternum; T = tergite, with number; tf = taphonomic folding of cuticle; ti = tibia; tr = trochanter; tt = telotarsus; vcp = ventral surface of carapace. See text for details. Scale bar represents 0·5 mm.
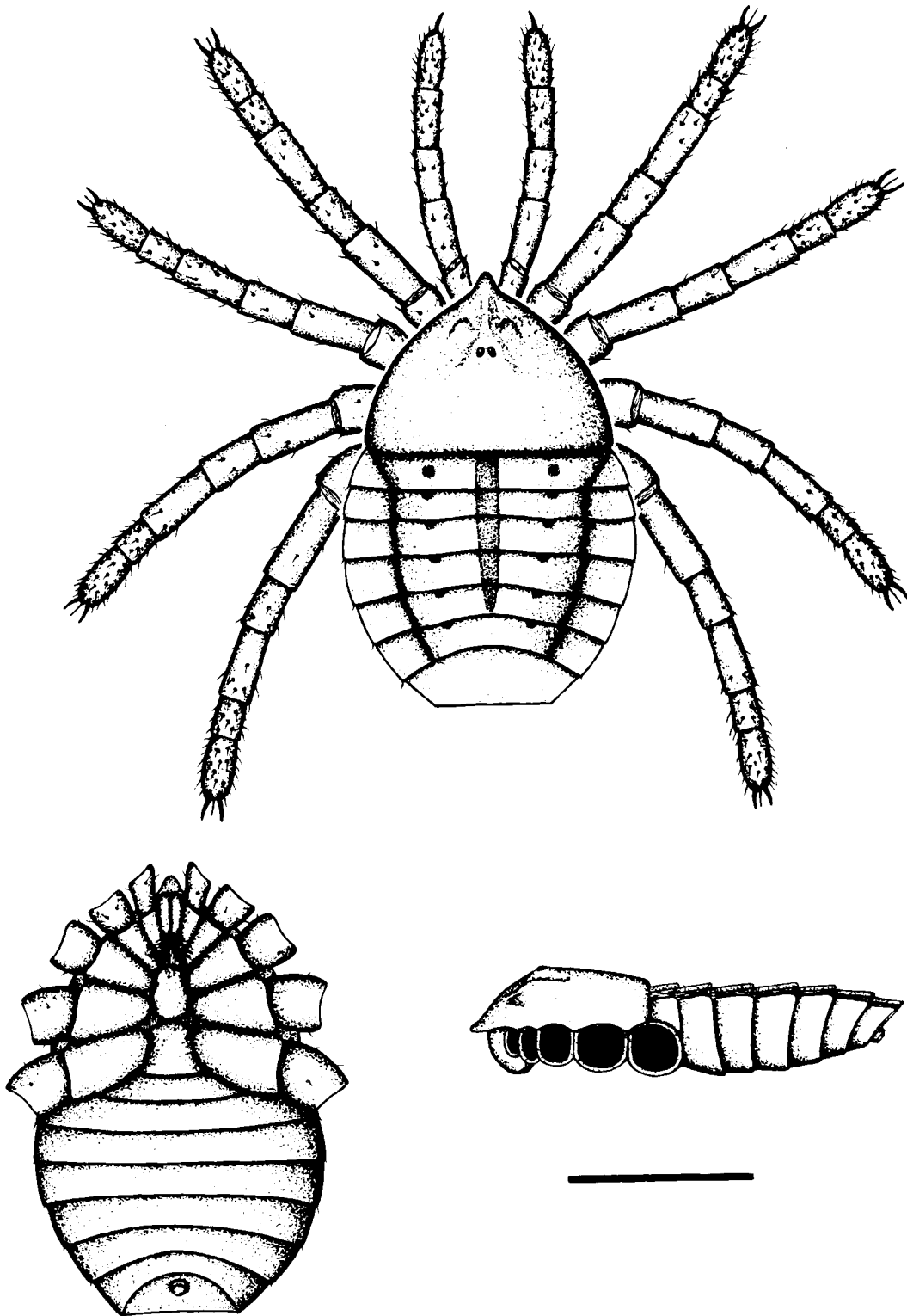
TEXT-FIG. 3. For caption see opposite.

position of the eyes and the two notches anterior to these 'eyes' appear to be genuine, rather than taphonomic features, since they are approximately symmetrical about the midline of the animal (Text-fig. 2). There are two strong lateral folds on the carapace (Text-fig. 2), but these are not in the same position on each side, and the stronger right hand fold continues onto the opisthosoma. This suggests that the folds are principally taphonomic, perhaps caused by crushing of the central region (Text-fig. 2). This interpretation is preferred over one in which the folds indicate a raised median region to the carapace, which might be expected to produce strong, symmetrical folds on either side of the midline. The carapace shows some evidence for a pair of median eyes (Text-fig. 2), but none for lateral eye tubercles, such as those seen on the carapaces of the palaeocharinid trigonotarbids from the Rhynie Chert and Gilboa (Shear et al. 1987). If lateral eye tubercles were present in life, it might be expected that crushed remnants of these could be detected as paired, slightly raised structures on the anterior half of the carapace of this specimen, even if individual lenses could not be resolved. I believe it is more parsimonous, though admittedly equivocal, to interpret the carapace as a moderately high, dorsally flattened structure, slightly raised around the apparent position of the median eyes than to reconstruct it with a more complex morphology, the evidence for which would be equally equivocal.

Appendages

The preserved coxae radiate around the sternum in a typical trigonotarbid pattern. Two of the coxal pairs are clearly evident and are labelled as coxae 2 and 3, but the pair interpreted as coxae 4 are not distinct (Text-fig. 2) and may have been compressed against the opisthosoma. The alternative interpretation would be that the coxa labelled 3 is in fact coxa 4, and this would indicate a situation different from that in other trigonotarbids, where coxae 4 often attach just behind the sternum (Dunlop 1994a) rather than against its lateral sides. Also, the coxa labelled 3 is directed laterally, whereas in most arachnids coxa 4 is directed posterolaterally (and coxa 3 is directed laterally) so that leg 4 is directed backwards to improve the stability of the animal during walking. The interpretation shown in Text-Figures 2–3 is further supported by the fact that only the leg 1 coxae, the palpal coxae and the chelicerae have to be fitted into the space beneath the carapace in which the chelicerae and coxae are not preserved (Text-fig. 2). If the coxa interpreted as coxa 3 is in fact coxa 4, then two leg coxae, the palpal coxae and the chelicerae would have to be squeezed into this space, which appears too small to accommodate the basal podomeres of eight additional appendages. I therefore favour the interpretation shown in Text-figures 2–3, although the imperfect preservation leaves this open to question. The coxo-sternal region and prosoma-opisthosoma junction of the better preserved Rhynie Chert material will be investigated more fully in a subsequent publication.

The entire limb series is not preserved in this specimen, but an incomplete leg is preserved bent across the opisthosoma, comprising a partial femur, the patella, tibia, basitarsus and a partial telotarsus. This leg may represent leg 3 since the incomplete femur rests over what is interpreted as the leg 4 coxa and would probably have extended back to about the position of the leg 3 coxa, though it could conceivably be a displaced leg 4. Knowledge of the podomere proportions of the femur and telotarsus in other early trigonotarbids (e.g. Hirst 1923; Shear et al. 1987) allows its total length to be estimated at a little over 1 mm. In most trigonotarbids all the walking legs are approximately the same length, with legs 1 and 4 being a little longer (Dunlop 1994a). On this basis, a tentative reconstruction of the limb series of this animal can be made (Text-fig. 3). The size of the pedipalps in this reconstruction is hypothetical, and based on analogies with the Rhynie Chert material (Hirst 1923).

TEXT-FIG. 3. Reconstruction of Eotarbus jerami gen. et sp. nov. Majority of legs, part of coxosternal region and position of opisthosomal heart and muscle apodemes hypothetical, and reconstructed in comparison with more complete trigonotarbids from the Rhynie Chert, and Recent arachnids. Scale bar represents 0·5 mm.

Opisthosoma

The dorsal opisthosoma shows clear transverse divisions under low angle lighting which are assumed to represent tergite boundaries. The specimen is interpreted as showing seven visible dorsal tergites (Text-fig. 2). In comparison with the opisthosoma in the Rhynie Chert and Gilboa trigonotarbids (Shear *et al.* 1987), these are assumed to represent a fused diplotergite 2 + 3 (tergite 1 being a modified locking ridge tucked under the carapace in palaeocharinids (Shear *et al.* 1987)), and then sequentially tergites 4–9. The only concern with this interpretation is tergite 6 (Text-fig. 2) which seems rather long on the left-hand side, and possibly even subdivided here which would suggest an 'extra' tergite. If this were true then tergites 2 and 3 would be interpreted as unfused, with no diplotergite, giving eight dorsally visible tergites. The opisthosoma posterior to tergite 5 has rotated slightly anticlockwise which confuses the morphology of this region. Subsegmentation of tergite 6 cannot be traced all the way across the opisthosoma, and so the interpretation shown in Text-figures 2–3 is preferred, with reservations. The pattern of segmentation shown in Text-figure 2 with tergites 2 and 3 fused into a diplotergite seems to characterize the majority of trigonotarbids (Dunlop 1994*a*), the exception being the rather derived Carboniferous family Eophrynidae (Dunlop 1994*b*). The left side of the opisthosoma shows, faintly, the division into median and lateral plates which characterizes trigonotarbid tergites. A major fold on the right hand side (Text-fig. 2) may be associated with the division into lateral plates, but could be taphonomic since it continues on to the carapace as discussed above. There is no obvious tuberculation and/or spination on the opisthosoma, unlike in some geologically younger trigonotarbids (Dunlop 1994*b*). Overall, the dorsal opisthosoma seems to follow the pattern of tergites 2 + 3 fused and tergite 9 not divided into median and lateral tergites, which is also seen in the Rhynie Chert palaeocharinids and all other Devonian trigonotarbids studied by the author (Dunlop 1994*a*).

The ventral opisthosoma shows segmentation, but not as distinctly as the dorsal surface, so the reconstruction of segmentation in Text-figures 2–3 is partly hypothetical, Posteriorly, a pygidium (segments 11 and 12, not 10 and 11 as reported by Shear *et al.* (1987)) can be made out surrounded by a plate interpreted as segment 10, not divided into tergites and sternites, with sternite 9 (which connects to the corresponding tergite 9) surrounding this segment. Trigonotarbids appear to have lost sternite 1 (Dunlop 1994*a*) and in comparison with studies of uropygids (Shultz 1993) the next two sclerites ('sternites' 2 and 3 in trigonotarbids) are interpreted not as true sternites, but as highly modified appendages bearing the respiratory organs. Following Shultz's (1993) terminology, these are termed the anterior and posterior operculae respectively, and their probable position is noted on Text-figure 2. This pattern of ventral opisthosomal segmentation in trigonotarbids differs from that given in previous accounts (e.g. Petrunkevitch 1949; Shear *et al.* 1987) in the recognition of operculae, and is being explored more fully by the author in the much better preserved Rhynie Chert material.

The reconstruction (Text-fig. 3) shows the suggested appearance of *E. jerami* in life based on the above interpretation and draws partly on comparison with the exceptionally preserved Rhynie Chert material for the distribution of chelicerae, setae, muscle apodemes, etc. This animal was probably a predator on some of the other early terrestrial arthropods in the Ludford Lane ecosystem.

PHYLOGENETIC RELATIONSHIPS

The poor preservation of the Ludford Lane trigonotarbid and the equivocal status of many of its morphological details makes its phylogenetic placement difficult. Its small size and weak sclerotization are reminiscent of the Devonian family Palaeocharinidae Hirst, 1923, redefined by Shear *et al.* (1987) as trigonotarbids retaining lateral eyes. There is nothing to support the presence of lateral eyes in *Eotarbus*, though the evidence is not conclusive for or against their presence. All other trigonotarbids with a triangular carapace lack lateral eyes (Dunlop 1994*a*). The best preserved Rhynie Chert material shows these palaeocharinids to have a box-like carapace with subparallel lateral sides, distinct oval lateral eye tubercles and an anteriorly projecting clypeus (e.g. Hirst 1923,

TEXT-FIG. 4. Reconstruction of the carapace of *Trigonotarbus johnsoni*, based on Natural History Museum no. I. 15897, showing the prominent median ridge which differentiates it from *Eotarbus jerami*. Scale bar represents 1 mm.
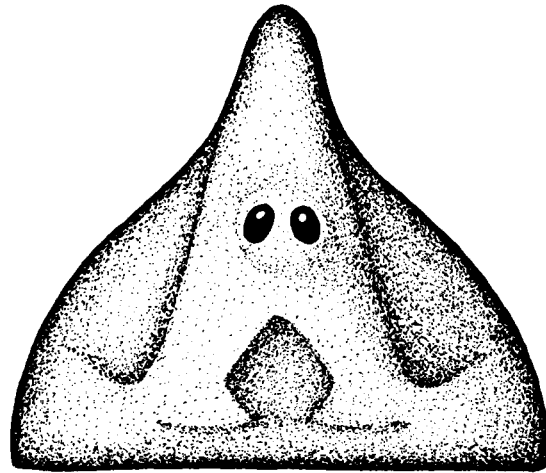
pls 12–14; Dunlop 1994*a*). This is significantly different from the triangular carapace of *Eotarbus* and on these grounds of carapace morphology I believe that *Eotarbus* should not be referred to the Palaeocharinidae.

The triangular carapace and rounded body of the Ludford Lane trigonotarbid are most reminiscent of the family Trigonotarbidae Petrunkevitch, 1949. Specimens of *Trigonotarbus johnsoni* from the British Middle Coal Measures were examined, and considering this, and other material referred to the Trigonotarbidae, a revision of this family is required. Petrunkevitch (1949, 1953) diagnosed it as having eight opisthosomal segments. However, Petrunkevitch's morphological interpretations of fossil arachnids and their segmentation have been questioned (e.g. Shear *et al.* 1987; Selden 1993). Examination of the type material of *T. johnsoni* (unpublished observations) suggests errors in Petrunkevitch's description of this specimen, making his diagnosis of the family unreliable.

The Ludford Lane specimen appears to differ from *T. johnsoni* in one important character. The carapace of the latter has a raised median ridge bearing a single eye tubercle, widening posteriorly and then curving back on itself on each side, to merge with the rest of the carapace, with a diamond-shaped depression in the median ridge posterior to the eyes (Text-fig. 4). This morphology may represent a better diagnostic character for the Trigonotarbidae. The carapace of *Eotarbus* shows no evidence of such a strong median ridge and is interpreted as being a relatively flat structure (Text-fig. 3), though the evidence for this is equivocal. I am reluctant to refer *Eotarbus* to Trigonotarbidae since there are apparent differences in carapace morphology between *Eotarbus* and *Trigonotarbus* and the diagnostic characters of Trigonotarbidae are poorly constrained. *Eotarbus* might represent a new, monotypic, family, but owing to its poor preservation and equivocal diagnostic characters I prefer to leave its familial status open and regard *Eotarbus* as a plesion as discussed below.

Devonian trigonotarbids

In addition to the Palaeocharinidae discussed above, there are four other Devonian trigonotarbid species. Of these, *Alkenia mirabilis* from the Lower Devonian (Emsian) of Alken an der Mosel, Germany, is a relatively large, tuberculated form with an oval carapace lacking lateral eyes (Størmer 1970; Shear *et al.* 1987) which does not appear to be closely related to *Eotarbus*. Of the other three, all referred to the Trigonotarbidae (see above), *Archaeomartus levis* from the Emsian of Alken an der Mosel and the Rheinisches Schiefergebirge (Størmer 1970; Brauckmann 1987) and *Trigonotarbus stoermeri* from the Rheinisches Schiefergebirge (Schultka 1991) both show a triangular prosoma and rounded opisthosoma and are thus superficially similar to *Eotarbus*.

Archaeomartus tuberculatus, also from Alken an der Mosel, is known only from an isolated opisthosoma (Størmer 1970). Brauckmann's (1987, pl. 2) specimen of *A. levis* represents a ventral opisthosoma and the internal surface of the carapace, which does not show a strong median lobe as in *T. johnsoni*. Schultka's *T. stoermeri* is poorly reconstructed (Shulkta 1991, fig. 1) and he interpreted many ventral structures as dorsal, but figured a triangular carapace (Schulkta 1991, fig. 11) with a raised median region. This carapace is therefore reminiscent of that of *T. johnsoni* (Text-fig. 4) and supports Schulkta's placement of *T. stoermeri* in the Trigonotarbidae. Because the diagnostic characters of Trigonotarbidae are equivocal, the position of all the Devonian taxa requires revision. Study of the opisthosomal segmentation of taxa referred to this family may further refine the phylogeny of this group.

Trigonotarbid phylogeny

Shear *et al.* (1987) regarded the presence of lateral eyes as representing the plesiomorphic state in both trigonotarbids and arachnids in general. *Eotarbus*, apparently lacking lateral eyes, therefore appears to be more derived than the younger palaeocharinids. Outgroup comparison with eurypterids, most of which have a rectangular carapace bearing a pair of lateral eye tubercles (carapaces similar to those of palaeocharinids in some respects), also suggests that a triangular carapace is an apomorphic character. Although the oldest trigonotarbid (and the oldest tetrapulmonate arachnid), *Eotarbus jerami*, apparently lacking lateral eye tubercles, appears not to be the most 'primitive' trigonotarbid; the younger Rhynie Chert trigonotarbids show more plesiomorphic characters (Dunlop 1994*a*). *Eotarbus* provides evidence for an early split of the Trigonotarbida into two major lineages: an earlier one retaining more plesiomorphic characters such as lateral eyes, i.e. the Palaeocharinidae (and perhaps also the Anthracomartidae and Anthracosironidae (Dunlop 1994*a*)) and a more derived one, with triangular and subtriangular carapaces, in which the lateral eyes are lost, i.e all other families (see below). This split must therefore have occurred prior to the late Silurian and predicts the presence of even older palaeocharinids. Whether these trigonotarbids were aquatic or terrestrial is unknown. *Eotarbus* cannot be referred confidently to any existing family and shows no strong autapomorphies. If the carapace could be demonstrated unequivocally to lack a median lobe this might represent a diagnostic character, but outgroup comparison with eurypterids, which also lack a median lobe, suggests this would be a plesiomorphic character rather than an apomorphic one, and therefore a poor diagnostic character. On these grounds, I believe that *Eotarbus* should be regarded as a plesion. *Eotarbus* may represent a sister group for all triangular- and subtriangular-carapaced trigonotarbids lacking lateral eyes, i.e. the Trigonotarbidae, Lissomartidae, Dunlop 1995, Aphantomartidae and Eophrynidae.

SYSTEMATIC PALAEONTOLOGY

Class ARACHNIDA Lamarck, 1801
TETRAPULMONATA Shultz, 1990
Order TRIGONOTARBIDA Petrunkevitch, 1949

Emended diagnosis. Tetrapulmonate arachnids with 12 opisthosomal somites. Tergite 1 forming a ridge associated with a locking device with the prosoma, reduced in some families. Tergites 2–8 (2–9 in some) divided into median and lateral plates, tergites 2–3 fused in some families, tergites 4–9 not fused. Sternite 1 absent. Terminal three segments not divided into tergites and sternites, terminal two segments forming a pygidium. Pedipalps and walking legs pediform. Chelicerae two segmented and of the clasp-knife type.

Remarks. The above definition differs from that given by Shear *et al.* (1987) in recognizing a 12-segmented opisthosoma and the lack of fusion among tergites 4–9 which is seen in ricinuleids. Ricinuleids also have tergites divided into median and lateral plates and a prosoma-opisthosoma

locking device. The arachnid order Trigonotarbida was erected by Petrunkevitch (1949) from material originally placed in the order Anthracomartida. This division into two orders is almost certainly invalid and Anthracomartida should be synonymized with a revised Trigonotarbida (Dunlop 1994a). A formal account of this synonymy is currently in preparation.

Plesion (Genus) EOTARBUS gen. nov.

Derivation of name. From the Latin, *Eo*, dawn, and the suffix, *tarbus*, fear.

Type and only known species. *Eotarbus jerami* gen. et sp. nov.

Diagnosis. Tiny trigonotarbid with a triangular carapace lacking an obvious median ridge.

Remarks. This diagnosis is not entirely satisfactory given the preservation of this specimen and the lack of obvious autapomorphies. *Eotarbus* is regarded as a plesion, representing the sister group of the triangular- and subtriangular-carapaced trigonotarbid families lacking lateral eye tubercles.

Eotarbus jerami gen. et sp. nov.

Text-figures 1–3

1990   Trigonotarbid; Jeram *et al.*, p. 658, fig. 1a–d.

Holotype and only specimen. Ulster Museum, Belfast, K 25850. Slide labelled as De.3.42/113.

Derivation of name. For Dr Andrew Jeram in recognition of his discovery of the specimen, and his work on fossil arachnids.

Diagnosis. As for the family.

Description. Holotype 1·35 mm long. Carapace 0·60 mm long with a basal width of 0·77 mm. Opisthosoma 0·75 mm long with a maximum width of 0·9 mm. Carapace triangular, lacking a strongly defined raised median region along the length of the carapace, but with a slight anterior projection. Posterior margin of carapace straight. Right hand margin of carapace better preserved than left. Probable median eyes present on slight raised tubercle 0·23 mm from the anterior tip of the carapace. Distinct pair of inverted 'V'-shaped grooves anterior to the eyes, either side of this raised area.

Coxosternal region partly complete with leg coxae 2–4 preserved and subtriangular in shape. Chelicerae, palpal coxae and leg coxae 1 absent. Coxae 2 and 3 arranged around a sternum, coxae 4 not distinct, but appear to attach to the body posterior to the sternum. Lengths of coxae in mm: 2, 0·25; 3, 0·31; 4, 0·36. Appendages generally not preserved. Trochanter of leg 2 present, 0·12 mm long, but apparently compressed. A single, fragmentary walking leg, probably leg 3 or 4, preserved, bent back beneath the ventral opisthosoma. Podomere lengths in mm as follows: femur (incomplete) 0·18; patella 0·18; tibia 0·20; basitarsus 0·15. Telotarsus not preserved.

Opisthosoma broadly oval. Division into median and lateral tergites present, but not distinct. Tergite 9 apparently lacking division into median and lateral plates. Approximate lengths of tergites along the midline in mm: macrotergite 2+3, 0·11; 4, 0·08; 5, 0·11; 6, 0·13; 7, 0·10; 8, 0·09; 9, 0·16. Posterior margins of anterior tergites straight, posterior margins of tergites 6–8 increasingly curved, though posterior margin of tergite 9 straighter. Posterior tergites 6–9 slightly displaced relative to the rest of opisthosoma with slight anticlockwise rotation. Ventral opisthosomal segmentation less distinct than dorsal. Segment 10 surrounding a pygidium present.

Remarks. *Eotarbus jerami* is the smallest trigonotarbid known, although it is impossible to determine whether or not it is a juvenile.

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