# A TRIGONOTARBID ARACHNID FROM THE LOWER DEVONIAN OF TREDOMEN, WALES

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ABSTRACT. A new trigonotarbid (Arachnida: Trigonotarbida) *Arianrhoda bennetti* gen. et sp. nov. is described from the Lower Devonian (Lochkovian) of a quarry near Tredomen, Powys, mid Wales, UK. This relatively complete specimen is the first record of a pre-Carboniferous arachnid from Wales, one of only a handful of early Devonian arachnids, and the second oldest trigonotarbid recorded. Based on the rounded prosomal dorsal shield and the relatively narrow, elongate opisthosoma we refer this new fossil to the family Anthracosironidae. A distinct flange-like ornament on the leg 4 tibia in the new fossil is unique among trigonotarbids and is the primary autapomorphy for the new genus.

KEY WORDS: Brecon, Chelicerata, terrestrial.

TERRESTRIAL arachnids from the early Devonian are very rare. They are currently restricted to the famous Rhynie chert locality in Scotland (Hirst 1923; Hirst and Maulik 1926; Shear *et al*. 1987), to various localities in the Rhenish Slate Mountains of Germany (Størmer 1970; Brauckmann 1987, 1994; Schultka 1991; Dunlop and Poschmann 1997), of which Alken an der Mosel is the most famous, and to New Brunswick in Canada (Shear *et al*. 1996). A number of additional localities have yielded early Devonian scorpions, although at least some of these taxa may have been aquatic (Selden and Jeram 1989). Spiders, mites, and pseudoscorpions have been discovered at these early to mid-Devonian localities (Shear and Kukalová-Peck 1990; Selden *et al*. 1991) and there are further unpublished records of harvestmen (Opiliones) (Dunlop *et al*. 2003) and the extinct order Phalangiotarbida (Poschmann *et al*. in prep.). There is also an enigmatic early Devonian arachnid of uncertain affinities (Dunlop and Poschmann 1997). However, most of the Devonian non-scorpion arachnids belong to the diverse, extinct order Trigonotarbida, an unequivocally terrestrial group as shown by book-lungs in the Rhynie chert species (Claridge and Lyon 1961).

Trigonotarbids are spider-like arachnids, which lack the spider autapomorphies of opisthosomal silk glands and cheliceral venom glands, and which have usually been placed at the base of the so-called Tetrapulmonata group (Trigonotarbida (Araneae (Amblypygi (Uropygi, Schizomida)))) with which they share a number of synapomorphies such as two pairs of book-lungs in the ground pattern and details of the mouthparts (Shear *et al*. 1987; Selden *et al*. 1991). The most recent cladistic analysis resolved Trigonotarbida as sister group of the rare, Carboniferous–Recent arachnid order Ricinulei (Giribet *et al*. 2002, fig. 6), with this clade forming the putative sister group of the remaining tetrapulmonates. Trigonotarbids are characterized principally by their distinctive division of the opisthosomal tergites into median and lateral plates (Text-figs 1–2), a character shared with Ricinulei (Dunlop 1996*a*), which supports the relationship recovered by Giribet *et al*. As fossils, trigonotarbids and ricinuleids are easy to distinguish from each other. The dorsal opisthosoma of ricinuleids express either fusion into three large diplotergites (Selden 1992, fig. 28) or complete fusion with a median sulcus, whereas trigonotarbids typically express nine dorsal tergites in which tergites 2 and 3 are commonly fused into a single macrotergite. Petrunkevitch's (1949) division of the old order Anthracomarti into two separate and unrelated orders (Anthracomartida and Trigonotarbida) appears to be artificial (Shear *et al*. 1987; Shear and Kukalová-Peck 1990; Dunlop 1996*b*) and both have been reunited under the better defined name Trigonotarbida.

Trigonotarbids are known from the late Silurian (Jeram *et al*. 1990) to the early Permian (e.g. Rössler 1998) and have been recorded most frequently from the Upper Carboniferous Coal Measures of Europe

and North America (e.g. Petrunkevitch 1949, 1955). In this paper we describe a new trigonotarbid, the first fossil arachnid from the lower Devonian of Wales. To date, the only other Welsh arachnid fossils are trigonotarbids from the Coal Measures of South Wales (O'Conner 1896; Pocock 1911; Dix and Pringle 1930). The new fossil is quite distinct and differs from other Devonian trigonotarbids, most notably in the rather narrow abdomen and fairly elongate legs, the latter with a unique 'flaring' of the distal end of the tibia in leg 4. Lochkovian in age, it represents the second oldest trigonotarbid known.

## MATERIAL AND METHODS

The new fossil has been deposited in the National Museum of Wales, Cardiff (NMW) with the repository number 2003.15G.1a–b (part and counterpart). The specimen was compared to other Devonian trigonotarbids, principally specimens of *Palaeocharinus* Hirst, 1923 in the collections of The Natural History Museum, London (NHM) and *Alkenia* Størmer, 1970 and *Archaeomartus* Størmer, 1970 in the Senckenberg Institute, Frankfurt am Main, Germany (SMF) and specifically to specimens of the Carboniferous genus *Anthracosiro* Pocock, 1903 in the NHM collections.

The specimen was studied and drawn using Wild M7S and Olympus MZ5 microscopes with camera lucida drawing attachments. Photographs were taken with a Nikon D1X digital camera attached to the Wild microscope and all illustrations were processed using Adobe Photoshop 7 software on an Apple PowerBook G4 computer running Mac OS X.

All measurements are in mm. Abbreviations: 1, 2, 3, 4, walking legs 1–4; car, carapace; cx, coxa; fe, femur; mt, metatarsus; pa, patella; Pd, pedipalp; pyg, pygidium; ta, tarsus; ti, tibia; tr, trochanter.

## GEOLOGICAL SETTING

The new fossil comes from a working quarry near the village of Tredomen, Powys, mid Wales (National Grid reference: SO 117304). The locality is a few kilometres north-east of Brecon, and north of the Llangorse lake. The specimen was discovered in a plant bed which is dated to early Devonian (Lochkovian) on palynological evidence; work is currently under way in Cardiff to more accurately date the plant bed, which contains an unusual palynoflora (Dianne Edwards, pers. comm. 2003). The matrix is a greenish grey, rusty weathering siltstone with fine (≤ 1 mm), irregular laminations. Associated with the plants, eurypterid and scorpion fragments have been recorded, as well as an undescribed myriapod (possibly a kampecarid). The geological setting, sedimentology and associated fauna suggest that the arachnid was derived from a terrestrial environment.

## MORPHOLOGICAL INTERPRETATION

The specimen consists of part and counterpart, both preserved as dark brown cuticle fragments on a paler matrix. The part preserves more of the original cuticle than the counterpart. The latter more clearly shows the pattern of opisthosomal segmentation. The animal is almost 9 mm long and is clearly an arachnid, with two distinct tagmata: prosoma and opisthosoma, together with a number of partially preserved prosomal appendages. The posterior appendages are more complete than the anterior ones. The specimen is preserved almost entirely in dorsal view, but the posterior end of the carapace and the anterior of the opisthosoma are partly missing, revealing the underlying leg coxae. Some sternal elements also appear to be superimposed through onto the tergites as diagonal elements converging towards the midline, and the pygidium, which is clearly a ventral element in well-preserved, three-dimensional trigonotarbids (e.g. Hirst 1923), is superimposed here onto the dorsal surface at the posterior end of the specimen.

The prosomal dorsal shield, or carapace, is semicircular in outline and, like many trigonotarbids, bears a short, blunt, anterior projection, usually called the clypeus. The dorsal shield expresses a slightly flatter anterior marginal rim which merges into the clypeus. The dorsal shield is raised towards the centre and there is some indication for radiating lines around this raised area implying a lobed pattern. This raised

area may bear eyes on the dorsal midline, but these are not preserved unequivocally. There is, however, a clear V-shaped depression immediately behind the putative eyes which could conceivably be a muscle attachment area. The posterior margin of the dorsal shield is poorly preserved with patchy cuticle; thus it is difficult to reconstruct the entire dorsal shield shape accurately. Confusing the morphology in this region, the dorsal surface at the back of the prosomal shield has been lost and impressions of the paired leg 4 coxae can be seen as slightly hollowed-out subtriangular structures bearing little or no cuticle. Other ventral elements of the prosoma are not preserved.

The chelicerae are not preserved, being typically held completely beneath the body in trigonotarbids (see e.g. Hirst 1923). The pedipalps are incomplete, but appear to have been pediform appendages, slightly more slender than the legs. Some setae-like structures near the base of the pedipalps in the part appear to be plant fragments and not part of the animal. Legs 1 and 2 are fragmentary; legs 3 and 4 are more complete and suggest relatively robust appendages. Leg 4 has an estimated leg length of at least 8 mm, but the terminal claws are not preserved.

A unique and remarkable feature of this new fossil is the flaring of the distal end of the tibia in leg 4. This distal tibial margin is about twice the width of both the proximal end of the tibia and of the adjacent metatarsus (= basitarsus in some teminologies). This flaring is seen in both the left and right legs and provides a valuable diagnostic character for the genus (see Systematic Palaeontology). It is difficult to say whether this morphology is restricted only to leg 4 or whether it was also a feature of the other walking legs too which are less completely preserved. What also remains unclear is whether leg 4 is preserved in purely dorsal view, in which case the flaring is a lateral extension of the podomere, or whether the leg has been preserved flattened on its side such that the extension is in a dorso-ventral or superior-inferior axis.

The anterior part of the opisthosoma is poorly preserved. The cuticle present implies that the anteriormost tergite is broad posteriorly and narrows anteriorly, although in comparison to better preserved taxa this morphology would be unusual. In most trigonotarbids the first opisthosomal tergite is not divided into median and lateral plates and is a modified locking ridge which tucks into a corresponding pocket at the back of the prosomal dorsal shield (Hirst 1923; Dunlop 1996a), locking the prosoma and opisthosoma together. This character may be reduced or lost in some Carboniferous genera (pers. obs.), but cannot be assessed in this fossil. Petrunkevitch (1955) reported a degree of variability in the number of opisthosomal segments in trigonotarbids; however, a typical feature of this group is the $2 + 3$ diplotergite (see above), which makes the posteriormost tergite seen in dorsal view consistently the ninth. This segmentation pattern is seen in the well-preserved Rhynie material (Hirst 1923; Dunlop 1996a) and has been assumed in assigning tergites to segments in this new material in which we regard tergite 1 as equivocal and tergite $2 + 3$ as poorly preserved. The first unequivocal tergite preserved across its entire width in the fossil is number 4 in this scheme (Text-fig. 1).

From tergite 4 backwards, the characteristic trigonotarbid character of divided tergites is apparent with a broad median plate and narrower lateral plates. The lateral plates on the left side of the part are not as wide as those on the right, which suggests that the animal has been slightly compressed to one side and that it may have had a slightly wider opisthosoma in life. On the right side of the part there is cuticle extending beyond the normal margin of the opisthosoma which may represent ventral sternites which have been translocated laterally during compression. The posterior margins of the tergites begin straight, but start to curve more towards the posterior. The posteriormost (ninth) tergite is also divided into median and lateral plates, although the orientation is at something of an angle compared to the preceding tergites. In some trigonotarbid taxa tergite 9 is undivided, in others it is divided like the preceding tergites; see e.g. Shear (2000) for a discussion of the potential significance and polarity of this character.

Overall, the opisthosoma itself is lozenge-shaped, and is nearly twice as long as wide. Unusually for trigonotarbids (see below), it retains a relatively constant width along most of its length with almost parallel lateral margins. The posterior end of the opisthsoma is bluntly rounded. As in many trigonotarbid fossils preserved in shales, the two-segmented postabdomen, or pygidium, is superimposed through onto the dorsal surface as an oval element close to the posterior margin of the opisthosoma. There is no evidence for a postanal structure such as a telson.

TEXT-FIG. 1. *Arianrhoda bennetti* gen. et sp. nov. Trigonotarbid arachnid from the early Devonian (Lochkovian) deposits at Tredomen, Wales; NMW 2003.15G.1a, part; ×10.

SYSTEMATIC PALAEONTOLOGY

Order TRIGONOTARBIDA Petrunkevitch, 1949
Family ANTHRACOSIRONIDAE Pocock, 1903

*Emended diagnosis*. Trigonotarbids with an elongate opisthosoma, at least 1·5 times as long as broad, lacking two rows of large tubercules as in *Alkenia*; posteriormost (ninth) tergite divided into median and lateral plates. Prosomal dorsal shield rounded, not (sub)triangular, or box-shaped as in other trigonotarbids. (Emended from Petrunkevitch 1955).

*Type genus*. *Anthracosiro* Pocock, 1903.

*Included genus*. *Arianrhoda* gen. nov.

*Remarks*. Previous Devonian trigonotarbids have been assigned to one of two families: Palaeocharinidae

TEXT-FIG. 2. Counterpart (NMW 2003.15G.1b) of specimen in Text-figure 1; ×10.

(e.g. Hirst 1923; Shear *et al*. 1987; Shear 2000) or Trigonotarbidae (e.g. Størmer 1970; Brauckmann 1987, 1994; Schultka 1991). There is also the unusual *Alkenia mirabilis* Størmer, 1970 from Alken an der Mosel. It was originally referred on stratigraphic grounds to Palaeocharinidae, was assigned with reservations to Aphantomartidae (Brauckmann 1994), but was not included in the aphantomartid revision of Rössler (1998). The Palaeocharinidae were originally diagnosed on the retention of multifaceted lateral eyes, but this is clearly a plesiomorphic character for arachnids and Shear (2000) rediagnosed palaeocharinids on the putative autapomorphy of fusion of the divided ninth tergite into a single sclerite. Both this fused tergite 9 character, and the lateral eye tubercles, are absent from the new fossil and exclude it from Palaeocharinidae. It should be added that Shear's late Devonian palaeocharinid closely resembles the Carboniferous aphantomartids (see especially figures in Rössler 1998) in the lobation of the carapace and tuberculation of the opisthosoma; thus Palaeocharinidae may not be monophyletic as it currently stands.

The Devonian–Carboniferous Trigonotarbidae are compact animals, recognisable by their essentially triangular carapace and an almost circular opisthosoma, which lacks the tuberculation and/or spines seen in many other Carboniferous groups. The shape of both the carapace and opisthosoma in the new fossil excludes Trigonotarbidae. The German species *Alkenia mirabilis* is more like our material in having a less
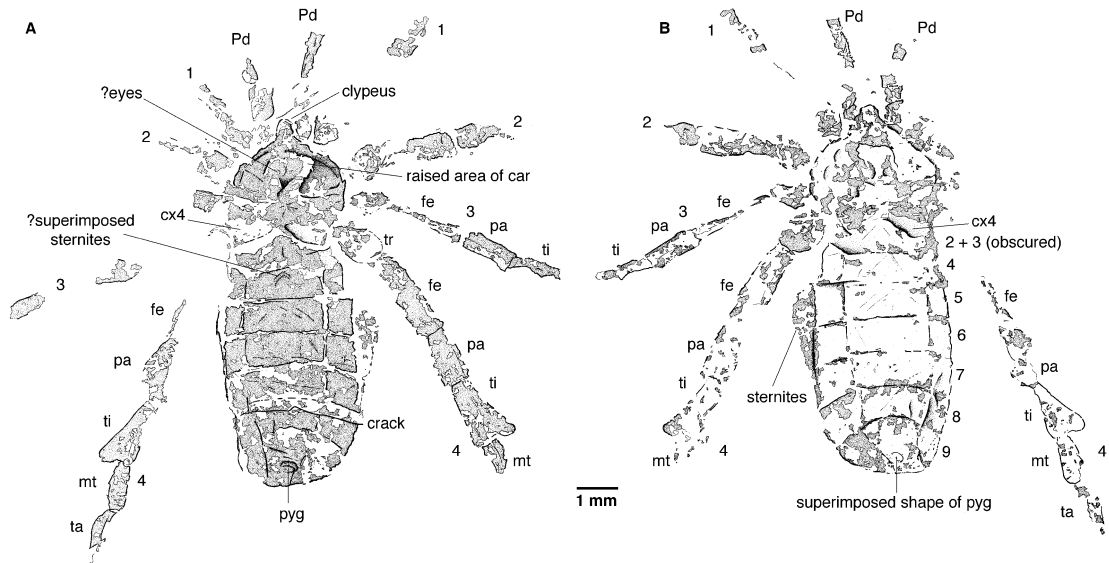
TEXT-FIG. 3. Camera lucida drawing of the specimen shown in Text-figures 1–2.

rounded and more elongate opisthosoma, but this unique and remarkable taxon has a much more elongate carapace and an autapomorphic pattern of tuberculation (Størmer 1970; Brauckmann 1994) in which each opisthosomal tergite bears two rows of discrete tubercles. The complete lack of a tubercular ornament in the new fossil also excludes the heavily armoured Carboniferous families Eophrynidae, Kreischeriidae and Aphantomartidae.

The new fossil most closely resembles the Upper Carboniferous family Anthracosironidae. This family is represented by a single European genus, *Anthracosiro*, and although a number of species have been erected since Pocock's initial description (see Petrunkevitch 1953 for synonyms) only two are currently recognised, and even these are differentiated mostly by size and might conceivably be part of an ontogenetic sequence. Putative synapomorpies of the new fossil and *Anthracosiro* are the general shape of the body and in particular the rounded carapace coupled with a rather narrow, elongate opisthosoma. In most other trigonotarbids the carapace is more triangular and the opisthosoma tends to be oval or round (see above). The depression on the carapace behind the likely position of the eyes is also paralleled by a deep, diamond-shaped depression in *Anthracosiro*.

## Genus ARIANRHODA gen. nov.

*Derivation of name*. From *Arianrhod*, a female figure in the Welsh mythological cycle the Mabinogion, who is thought to be associated with spiders.

*Type and only species*. *Arianrhoda bennetti* sp. nov.

*Diagnosis*. Anthracosironid with almost parallel sides to the opisthosoma, not becoming wider posteriorly as in *Anthracosiro*, and with a unique flaring of the distal end of the tibia of at least leg 4.

*Remarks*. Our new genus can be differentiated from *Anthracosiro* by the shape of the leg 4 tibia and the fact that in *Arianrhoda* the opisthosoma is lozenge-shaped and does not expand to become widest about three-quarters of the way along its length. Although the anteriormost legs of *Arianrhoda* are poorly preserved they do not appear to have been especially robust. In *Anthracosiro*, in contrast, the anterior legs are heavily built, preserved with their prolateral side uppermost and express tooth-like projections on the

inner (ventral) margins (Pocock 1903, 1911; Petrunkevitch 1955). These were probably used for prey capture in an analogous way to modern crab spiders (Thomisidae). The distinctly projecting clypeus is another difference between *Arianrhoda* and *Anthracosiro*, although even in Pocock's (1911, figs 35–37) illustrations there are hints of a small clypeus in the Carboniferous genus that were not picked up in later illustrations (e.g. Petrunkevitch 1955, fig. 71).

### *Arianrhoda bennetti* sp. nov.

Text-figures 1–3

*Derivation of name*. In honour of Phil Bennett of Brecon, the amateur collector who discovered the fossil and made it available to us for study.

*Holotype and only specimen*. NMW 2003.15G.1a–b (part and counterpart) from a quarry near Tredomen, Powys, mid Wales, UK; early Devonian (Lochkovian).

*Diagnosis*. As for the genus.

*Description*. Moderate-sized trigonotarbid arachnid. Total length 8·9. Prosoma-opisthosoma boundary not clearly preserved, but carapace length *c*. 2·7. Carapace rounded, maximum width 2·8, with blunt clypeus anteriorly, length 0·5; with narrow (0·2) marginal rim and raised median region, possibly bearing eyes. Median raised area surrounded by at least two sets of radiating lines and with V-shaped depression behind putative eye region. Coxo-sternal region mostly not preserved, but subtriangular cx4, length 1·1, preserved. Pedipalps fragmentary, but appear pediform. Leg podomere lengths: fe2 2·1, pa2 1·2, ti2 1·2; tr4 1·0, fe4 2·3, pa4 1·4, ti4 1·6, mt4 1·1, ta4 $\geq$ 1·0. Tarsal claws not preserved. Tibia of leg 4 with distinctly flared shape, maximum width at distal end 1·1. Flaring begins about half-way along the length of the podomere.

Opisthosoma length *c*. 6·2, maximum width 3·4. Opisthosomal lateral margins almost parallel, becoming bluntly rounded posteriorly. Expected tergite 1 not preserved, putative diplotergite 2 + 3 incomplete. Tergites 4–9 clearly preserved. All tergites, including the ninth, divided into median and lateral plates. Tergites 4–7 increase successively in length slightly from 0·7 to 0·9; median plates with straight posterior margins. Tergite 8 length 0·7, and with more procurved margins. Tergite 9 length 1·4. Impressions of pointed ventral structures superimposed on tergites 4 and 5. Impression of pygidium, diameter 0·5, superimposed on tergite 9.

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