The youngest trigonotarbid *Permotarbus schuberti* n. gen., n. sp. from the Permian Petrified Forest of Chemnitz in Germany

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**Abstract**

A new trigonotarbid (Arachnida: Trigonotarbida) is described as *Permotarbus schuberti* n. gen., n. sp. from the Early Permian Petrified Forest (Rotliegend) of Chemnitz in Saxony (Germany). At ca. 290 Ma it represents the youngest record of this extinct arachnid order discovered to date. Its familial affinities are uncertain, but may lie close to the Aphantomartidae. The distribution of the trigonotarbid genera through time is summarised, together with a list of their seventy-seven fossil-yielding localities. Together they offer a broad overview of the group’s fossil record, which is heavily biased towards the Moscovian Stage (ca. 307–312 Ma) of the Late Carboniferous in Europe and North America. This is due in no small part to numerous localities associated with coal mining districts, and trigonotarbids are found less frequently after this stage. While it is tempting to associate this with biological events – such as a putative ‘Carboniferous Rainforest Collapse’ dating to ca. 305 Ma – it is difficult to differentiate the effects of genuine extinction patterns from artefacts caused by fewer appropriate localities in the economically less relevant latest Carboniferous and Early Permian strata. Nevertheless, trigonotarbids became extinct at some point after the Early Permian and loss of the Coal Measures forests remains one of the most likely possible causes.

**Key Words**

Arachnida
Trigonotarbida
Fossil record
Pyroclastics
Sakmarians
Saxony

**Introduction**

Trigonotarbids are an extinct order of arachnids with an essentially spider-like appearance, albeit characterised by an opisthosoma in which the dorsal tergites are divided into median and lateral plates; a feature which they share with the rare order Ricinulei. Including *incertae sedis* taxa, sixty-five valid species of trigonotarbid in thirty-four genera are currently recognised in the literature (Dunlop et al. 2013), and as a group they ranged from the late Silurian through to the Early Permian. While trigonotarbids can be diverse and abundant in the Late Carboniferous across a range of European and North American Coal Measures localities (see e.g. Petrunkevitch 1953), Permian records are extremely rare. They are presently restricted to the Carboniferous–Permian boundary of Bajo de Véliz in Argentina (Pinto & Hünicken 1980), and a number of localities in the Rotliegend of Thuringia in eastern Germany (Scharf 1924; Müller 1957; Rößler 1998; Rößler et al. 2003). These German records date to about 295 Ma (Asselian) based on biostratigraphic considerations (Schneider & Wernerburg 2006); although precise geochronological ages are presently lacking. Here, we describe another Permian trigonotarbid this time from the Rotliegend of Chemnitz (Fig. 1). At ca. 290 Ma (Sakmarians) it is the stratigraphically youngest record of a trigonotarbid arachnid to date (Fig. 2). Although its rather coarse state of preservation (Figs 3–4) and the absence of certain details preclude its unequivocal assignment to a family, we tentatively name it as a new genus and species with probable affinities to the family Aphantomartidae.

In the broader context of trigonotarbid geological history, we document visually (Fig. 5) the stratigraphic ranges of the known genera and list localities by age which have yielded fossils of these arachnids (Table 1). Unsurprisingly, this reveals a concentration of records...
from the Late Carboniferous associated with numerous productive and often well-studied Coal Measures localities (Fig. 6). These in turn derive from industrial exploitation of coal seams (see Discussion). Trigonotarbids are notably rarer from after the time of the coal swamps. We discuss whether this is part of a genuine loss of diversity – part of a shift towards the eventual extinction of the Trigonotarbidia – or an artefact of less accessible and/or less intensively mined rock sequences suitable for their preservation.

Materials and methods

The holotype and only known specimen of the new trigonotarbid was collected from Early Permian volcanioclastics of the Zeisigwald Tuff horizon, Petrified Forest of Chemnitz, Saxony, Germany (50.85262° N, 12.94616° E) (Fig. 1). The specimen has been deposited in the Museum für Naturkunde Chemnitz under the repository number TA0932. It was photographed using a Leica stereomicroscope with a camera lucida and drawn using a Leica MZ12 stereomicroscope with a camera lucida attachment. All measurements are given in millimetres. Stratigraphic and locality data for trigonotarbids in general were assembled directly from the primary literature (Table 1). In general the oldest published record from a given locality is presented here as the source reference, although it should be borne in mind that subsequent specimens from these fossil sites may have been described. Stage names and approximate absolute dates in millions of years (Table 1) are based on the 2012 ‘International Chronostratigraphic Chart’ provided by the International Commission on Stratigraphy <http://www.stratigraphy.org>.

Preservation and geological setting

The new fossil is preserved in a purple-red matrix of an approximately 15–20 cm thick, weakly horizontally-bedded and moderately sorted fine to medium-grained ash-tuff (Fig. 2). The pyroclastic material is nonwelded, rich in altered blocky shards and composed of several normal-graded units. Light grey to green mottling frequently occurs in the vicinity of organic inclusions. This deposit rests sharply upon a variegated palaeosol, and represents a succession that resulted from low-concentration pyroclastic density currents and accompanying fallout during an early stage of volcanic activity in the investigation area. The bed from which the new trigonotarbid came represents the lowermost deposit of the Zeisigwald Tuff horizon, Leukersdorf Formation.

Caused by an explosive magmatic to phreatomagmatic eruption, volcanic ashes covered the standing vegetation and were deposited. As a result, many trees shed their leaves, which are found embedded in a layer near the basis of Unit S5 sensu Rößler et al. (2012). Along with leafy shoots, pinnate fronds, detached whole and fragmentary leaves, this horizon has yielded the first outstanding faunal remains. Among them are vertebrates – comprising five reptile skeletons, aistopod microsaurians, and remains of an euryopid amphibian – as well as such invertebrates as diplopods, chilopods, remains of the giant arthropod Arthropleura, various arachnids including trigonotarbids, one uropygid, and many gastropods. Thus, the Chemnitz Petrified Forest provides a window into an almost complete Permian forest ecosystem, preserved in-situ in a geological instant (Rößler et al. 2012). The stratigraphic position of this fossil Lagerstaette corresponds to the early Sakmarian and is thus dated at 290.6 ± 1.8 Ma (Stanek, personal communication, 2009). Stratigraphic, geological and taphonomic details were reported in Kretzschmar et al. (2008) and Rößler et al. (2009, 2010, 2012).

Systematic palaeontology

Order Trigonotarbida Petrunkevitch, 1949
Family uncertain

Permotoarbus n. gen.

Derivation of name. After the stratigraphic occurrence of the type species in the Early Permian Rotliegend of Chemnitz, Germany.

Diagnosis. Trigonotarbids with a subtriangular carapace, raised medi ally and with lobation of the lateral margins. Unlike the similar-looking Aphantomartus, dorsal body surface without obvious ornament of tubercles or pustules.

Remarks. The coarse nature of the sediment and the equivocal nature of some details – e.g. the complete morphology of the carapace, whether the ninth tergite is divided or entire, and whether the dorsal cuticle was finely ornamented – renders a formal assignment of the new Chemnitz fossil to one of the existing trigonotarbid families difficult. The apparent presence of lateral lobes (Figs 3–4) on a subtriangular carapace tends to rule out most of the (presumably) more basal families, i.e. Palaeocharinidae, Archaeomartidae, Anthracomartidae and Anthracosorionidae; none of which have a lobed or subtriangular carapace. Trigonotarbidae also has a subtriangular carapace, which is also medially raised similar to the condition seen in our fossil, but lacks these lateral lobes. Indeed, a distinctly lobed carapace is one of the characters seen in the ‘eophrynid assemblage’ sensu Dunlop & Brauckmann (2006) which includes Aphantomartidae, Kreischeridae and Eophrynidae. In terms of its overall outline and limb robust-
ness the new Chemnitz fossil resembles Aphantomartidae (cf. figures in Rößler 1998). However, all the eophrynid-related trigonotarbids were heavily armoured creatures with distinct pustules, granules or tubercles ornamenting the dorsal body surface. As noted above, the hosting sediment is not conducive to picking up

Figure 2. Stratigraphic framework of the fossiliferous horizon, which yielded *Permotarbus schuberti* n. gen., n. sp.; star indicates the stratigraphic position of the find (adapted from Berger & Junghanns 2010).
fine details of surface structure in the new fossil, but we see no compelling evidence for a highly ornamented dorsal body surface as in the three latter named families.

The leaves the genus *Namurotarbus* Poschmann & Dunlop, 2010 from Hagen-Vorhalle in Germany, currently unplaced at family level, and the genus *Lissomartus* Petrunkevitch, 1949 placed in its own family, Lissomartidae, from Mazon Creek in Illinois, USA; both Late Carboniferous. Although a formal phylogeny of the trigonotarbids is lacking, it is possible that these two genera somehow bridge the morphological gap between the fairly simple-looking Trigonotarbidae and the more heavily armoured eophrynid-like families. In detail, *Namurotarbus* is a squat and compact animal with a lobed and distinctly triangular carapace, but no tuberculation (Dunlop & Brauckmann 2006, fig. 2). *Lissomartus* also has a medially raised carapace and no tuberculation, but the carapace lobation is only hinted at by faint demarcation lines (Dunlop 1995, fig. 3) – as if in the process of first evolving.

Thus although imperfect, our fossil does appear to express a character combination different to what is known from other trigonotarbids; i.e. a lobed and sub-triangular carapace, but no pustulate dorsal body ornament (see also Diagnosis). For this reason we name it, with reservations, as a new genus and species and hope that future material will confirm details of its morphology. We suspect that, like *Namurotarbus* and *Lissomartus*, our new fossil probably resolves somewhere towards the base of the ‘eophrynid assemblage’, but this needs to be formally tested cladistically. Pending this, we are reluctant to create a monotypic family and prefer to leave the position of this genus and species open.

**Permotarbus schuberti** n. gen., n. sp.

Figures 3–4

**Derivation of the name.** In honour of Dr. Peter Schubert, who was involved in the financial support which made the Chemnitz-Hilbersdorf excavation (2008–2011) both possible and successful.

**Holotype.** Museum für Naturkunde Chemnitz, no. TA 0932 (part and counterpart).

**Type locality and horizon.** Coordinates SSP-60; leg. Sandra Mehlhorn, 05.11.2010. From the Zeisigwald Tuff horizon, Petrified Forest of Chemnitz, Saxony, Germany. Early Permian (Sakmarian).

**Diagnosis.** As for the genus.

**Description.** Part (Fig. 3) and counterpart of an almost complete animal, largely in dorsal view but with ventral elements of the prosoma visible in the (generally less well preserved) counterpart. All measurements in mm. Total preserved length 11.8. Carapace subtriangular in outline, length 3.8, maximum width at base ca. 4.0. Carapace with a raised central region, approximately in

*Figure 3. Permotarbus schuberti* n. gen., n. sp. Holotype and only known specimen, Museum für Naturkunde Chemnitz, no. TA 0932. A. Part. B. Counterpart. Scale bar equals 2 mm.
the form of a broad ‘hour-glass’, maximum width ca. 2.0. Raised area slightly depressed along the midline towards the posterior end. Raised area bears an oval to diamond-shaped tubercle on the midline, length 0.6, situated in the anterior half of the carapace ca. 1 mm from the anterior tip; probably the median eye tubercle, but individual lenses not well preserved. Lateral margins of raised, central region seem to merge into depressions in the matrix suggesting the presence of raised, perhaps elongate tubercles here in life. Anterior end of carapace (clypeus) apparently with a pair of longitudinal, slightly splaying grooves; carapace tip apparently bilobed. Carapace laterally with evidence of at least two (probably three) pairs of subtriangular lobe-like divisions flanking the raised central area. Carapace cuticle lacks obvious ornament in the form of tubercles or pustules.

Chelicerae equivocal but one pedipalp perhaps represented by a small fragment in front of the carapace. Coxo-sternal region poorly preserved, but appears to show a series of subtriangular coxae surrounding a fairly wide sternal region; sternal plate itself equivocal.

Figure 4. Camera lucida drawing of the holotype of *Permotarbus schuberti* n. gen., n. sp. part shown in Figure 3A. Scale bar equals 2 mm.
Legs partially complete; left legs 1 and 2 more or less entire. Legs generally fairly short and robust; trochanters rounded. Articles not always clearly defined, but approximate lengths as follows. Leg 1: femur 1.9; patella 1.6; tibia 2.2; metatarsus 1.2; tarsus 0.7 (total preserved length 7.6). Leg 2: femur 1.4; patella 1.7; tibia 2.0; metatarsus 1.3; tarsus 0.9 (total preserved length 7.3). Legs 3 and 4 probably with similar overall lengths and proportions, but details poor.

Oviposithosoma oval, widest more or less in the middle, maximum preserved length 8.0, maximum preserved width 5.9. Tergite 1 present as a short, ca. 0.3 long, element apparently modified into a locking ridge tucked under the carapace ventral margin in life. Remaining tergites clearly divided into median and lateral plates. Tergite 2 + 3 larger than the others, length 1.3, and thus implicitly a fused ‘diplotergite’; as in most other trigonotarbids. Paired indents either side of the midline here probably represent muscle apodemes. Tergites 4–6 shorter, length ca. 0.9, tergite 7 slightly longer, ca. 1.1. Median plates generally range in width from about 4.0 to 5.0; lateral plates may not be preserved at their maximum width (those on the left appear narrower than those on the right) but could be up to ca. 1.3. Tergites 8–9 poorly defined and boundary between them obscure. Unclear whether tergite 9 is also divided into median and lateral plates, but hints of such a division are preserved. Oviposithosoma terminates posteriorly in a somewhat pointed end, but given the incompleteness of the preserved morphology we cannot rule out that this is an artefact. Ventral oviposithosoma equivocal. A few depressions hint at a slight granulation of the cuticle in life, but in general the dorsal oviposithosomal cuticle lacks obvious ornament in the form of large tubercles or pustules (sensu Aphantomartus), although here and for the carapace we would caution that the coarse nature of the tuffaceous matrix could mask any fine ornament originally present in this fossil.

Discussion

Thirty-four trigonotarbid genera, distributed across nine family groups, are currently recognised as valid in the literature. Note that recent work has recognised numerous generic synonyms among the Anthracomartidae (Garwood & Dunlop 2011) and future revisions are likely to reduce the total number of genera still further. For completeness, Eurymartus Matthew, 1895 and Elavermartus Petrunkevitch, 1953 are now regarded as nomina dubia — see Dunlop & Miller (2007), and Rößler (1998) and Dunlop et al. (in press) for respective explanations. They are excluded from Fig. 5, but as bone-fide trigonotarbids their localities are still included in Table 1. A comprehensive cladistic study of relationships among trigonotarbids is lacking, but the sequence of genera presented in this figure reflects recently published ideas on their phylogeny. These include a Palaeocharinidae–Archaeomartidae–Anthracomartidae group elucidated by Poschmann & Dunlop (2010, fig. 9), which retain well-developed lateral eye tubercles on a subquadrate, box-like carapace. Another is the ‘cophynnid assemblage’ (see also above) of Kreischerididae–Eophrynidae–Aphantomartidae, postulated by Dunlop & Brauckmann (2006) on the basis of the putative synapomorphies of a strongly lobed carapace and robust dorsal tuberculation.

Silurian records

The oldest trigonotarbid genus – Palaecorbus Dunlop, 1999 – hails from the late Silurian (Pridoli: 419–423 Ma) of Ludford Lane in England (Jeram et al. 1990; Dunlop 1996a, 1999a). This remains the oldest non-scorpion arachnid and, assuming that trigonotarbids were all terrestrial, one of the oldest land-living animals known to date. Its triangular carapace may suggest affinities with the younger family Trigonotarbidae, but details are lacking and it is currently treated as a pleion genus (Fig. 5).

Devonian records

Stratigraphically, the next trigonotarbid genus is Ariathoda Dunlop & Selden, 2004 from the Lochkovian (ca. 411–419 Ma) of Tredomen in Wales. It was placed in the family Anthracosironidae. This is followed by some exquisitely preserved and three-dimensional fossils assigned to Palaecorcharinus Hirst, 1923 (Palaeocharinidae) from the Early Devonian (Pragian: ca. 410 Ma) of Ludford Lane in England (Jeram et al. 1990; Dunlop 1996a, 1999a). This remains the oldest non-scorpion arachnid and, assuming that trigonotarbids were all terrestrial, one of the oldest land-living animals known to date. Its triangular carapace may suggest affinities with the younger family Trigonotarbidae, but details are lacking and it is currently treated as a pleion genus (Fig. 5).

Slightly younger is a further palaeocharinid genus, Spinotherenus Poschmann & Dunlop, 2011, recently described from Bürdenbach in the German Rhineland and which may also date to the late Pragian. Near contemporary, but perhaps a little younger at Lower Emsian (ca. 405 Ma) are a series of further Rhineland genera, namely Alkenia Störmer, 1970 and Archaeomartidae Störmer, 1970 from Alken an der Mosel (Störüer 1970; Poschmann & Dunlop 2010). Of these, Alkenia was recently reassigned to Aphantomartidae and Archaeomartidae to a new family Archaeomartidae; the latter with characters intermediate between palaeocharinids and anthracomartids (Poschmann & Dunlop 2010). Further adjacent localities in the German Rhineland, such as Konderbachtal (Brauckmann 1987) and Waxweiler (Brauckmann 1994), have also yielded Alken-type trigonotarbids. The oldest record of Trigonotarbus Pocock, 1911 (Trigonotarbidae) comes from a less clearly defined locality in this region given as the ‘Rhenish Slate Mountains’ [Rheinisches Schiefergebirge] (Schultka 1991). However, there are some differ-
ences compared to the Carboniferous type species of the genus and restudy of the original specimen would be welcome to confirm its familial affinities.

Middle Devonian (Givetian: ca. 385 Ma) sediments have yielded three palaeocharinid trigonotarbid genera as cuticle macerates from the Gilboa Mudstones of New York, USA: namely Aculeatarbus Shear, Selden & Rolfe, 1987, Gelasinocharinus Shear, Selden & Rolfe, 1987 and Gilboarachne Shear, Selden & Rolfe, 1987. The only record from the Late Devonian is also from the USA. The late Famennian (ca. 365 Ma) Gigantocharinus Shear, 2000 comes from Red Hill in Pennsylvania. Although originally assigned to Palaeocharinidae, its tuberculate dorsal surface and lobed carapace suggest that it may be better placed in a more derived family, perhaps Aphantomartidae; see also comments in Dunlop & Brauckmann (2006).

Carboniferous records

Early Carboniferous trigonotarbs are rare. Pocononia Petrunkevitch, 1953 derives from the Pocono Formation of Virginia, USA (Ewing 1930; Dunlop 1996b). Its age is usually given as “early Mississippian” – perhaps about 345 Ma? – whereby Pocononia represents the oldest record of the family Eophrynidae. Additionally, Rößler (1998, fig. 17) documented two finds from the late Viséan (ca. 330 Ma) of the Erzgebirge Basin of Chemnitz in Germany and Kamienna Gora (Intrasudetic Basin) in Poland. Both could be assigned to Aphantomartus Pocock, 1911 (Aphantomartidae) and represent the youngest record of this important, and long-lived genus (see also Correia et al. 2013) which can be traced right through into the Permian (Fig. 5).
Table 1. The seventy-seven localities known to have yielded trigonotarbid fossils, arranged stratigraphically from youngest (above) to oldest (below). Note the concentration of records from the Late Carboniferous Coal Measures associated with coal mining districts; particularly in the Moscovian (ca. 307–312 Ma) of Europe and North America (see also Figure 6). Stage names and absolute dates derived from the 2012 edition of the ‘International Stratigraphic Chart’.

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Trigonotarbids are found most frequently in the Late Carboniferous Coal Measures of Europe and North America. Stratigraphically, the oldest of these include the Czech genus *Stenotrogulus* Fricˇ, 1904 (Eophrynidae) from the ‘Namurian A’ (ca. 325 Ma) corresponding to the Serpukhovian Stage. Another specimen, recognised as an aphantomartid (Rölßler & Brauckmann 2000), comes from rocks of a similar age at Nötsch in the Austrian Alps. Slightly younger material comes from the ‘Namurian B’ (ca. 318 Ma) of Hagen-Vorhalle in Germany. This includes the first record of the genus *Eophrynus* Woodward, 1871 (Eophrynidae), as well as

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<td>Ludford Lane</td>
<td>UK</td>
<td>419–423</td>
<td>Jeram et al. (1990)</td>
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Namurotarbus Poschmann & Dunlop, 2010 erected for a fossil originally described under another genus name by Dunlop & Brauckmann (2006) and currently unplaced at family level.

Numerous trigonotarbid fossils also stem from the Bashkirian, which is more or less equivalent to (or overlaps with) the ‘Westphalian A’/Lanssettian of traditional European terminology. Notable localities here include Klodzko [= Glatz] and Nowa Ruda [= Neurolde] in Silesia, Poland (Römer 1878; Karsch 1882). These produced, respectively, Vratislavia Frick, 1904 (Anthracosironidae) and the oldest example of Anthracomartus Karsch, 1882 (Anthracomartidae). The other two anthracomartid genera, Maiocercus Pocock, 1911 and Brachypyge Woodward, 1878, also appear in the Bashkirian in England and Belgium respectively. Note that Maiocercus also occurs in continental Europe too and at some slightly younger sites (e.g. van Essen et al. 1997). Contemporary records from further Bashkirian Belgian localities were elucidated by de Dorlodot (1922), Pruvost (1922, 1930) and van der Heide (1951). The incertae sedis genus Areomartus Petrunkevitch, 1913 from West Virginia, USA may also be Bashkirian in age (cf. Dunlop 2010), but its stratigraphy is not well constrained and was only given as “lower Kanawah Formation”.

Perhaps the greatest concentration of fossils comes from the Moscovian, roughly equivalent to the Westphalian B–D of the older literature. Important studies covering this fauna include Scudder (1884, 1893), Fricˇ phalian B’ (or Duckmantian) sites such as Aachen (2011, 1930) and other contemporaries outcroppings of the British Middle Coal Measures (e.g. Gill 1909; Moysey 1911) – and other contemporaneous outcrops in the British Middle Coal Measures (e.g. Gill 1909; Moysey 1911) – together with Anzinia in northern France (Pruvost 1919) and the Jerusalemberg in eastern Slovakia (Vaňovská 1987; Hyžný et al. 2013). Genera first recorded from this time period include Anthracosiro Pocock, 1903 (Anthracosironidae), Anzinia Petrunkevitch, 1953 and Pseudokreischeria Petrunkevitch, 1953 (both Kreischeriidae) and Somaspidion Jux, 1982 (Eophrynidae).

The ‘Westphalian C’ (or Bolsovian) includes outcrops in the Variscan foreland basin, such as the drilling core ‘Rehden 21’ in northern Germany, but more frequently, various outcrops in the intermontane area provided trigonotarbid finds. Among these are the Saar Basin of Germany (e.g. Guthörl 1938; Brauckmann 1984) as well as Rakonik, Kladno (summaries in Opluštil 1985, 1986) and the recently discovered Týnee site (Tichávek & Bureš 2010) in the Central Bohemian Basin of the Czech Republic. The genus Planomartus Petrunkevitch, 1953 (Eophrynidae) appears in rocks of this age in Bohemia.

The ‘Westphalian D’ includes important localities such as Nyřany in the Czech Republic, a series of German outcrops (see below), parts of the South Wales coalfield (Pocock 1911), Kilmersdon and the adjacent Writhlington Geological Nature Reserve in south-western England (Ambrose & Romano 1972), and Rhode Island and Mazon Creek in the USA (Scudder 1884, 1893; Petrunkevitch 1913). Taxa appearing in this stage include the Czech genera Nyrantrarius Harvey & Selden, 1995 and Petirovicia Frick, 1904 (both Eophrynidae), the German genus Kreischeria Geinitz, 1882 (Kreischeriidae) from Zwickau, the Mazon Creek genus Lissomartus (Lissomartidae), and the more widely distributed Pleophyurus Petrunkevitch, 1945 (Eophrynidae) found in both Europe and the USA. Other German records from this regional substage include aphantomartids from Oelsnitz (Barthel & Rößler 1998) as well as numerous specimens of Aphantomartus from the classic open cast mine of Piesberg near Osnabrück, northern Germany.

Latest Carboniferous records are, by contrast, rather sparse (Table 1) and the only Kazimovian record is of Anthracomartus sp. from Kansas, USA (Wright & Selden 2011). Slightly younger (Gzhelian) finds – corresponding to the Stephanian in traditional stratigraphic terminologies (ca. 299–304 Ma) – include a Trigono- martus from Decazeville in France (cf. Petrunkevitch 1955) and examples of Anthracomartus from near Brücken in Germany (Ammon 1901) and Radvanice in the Czech Republic (Opluštil 1985). Aphantomartus was recorded by Selden and Romano (1983) from León Province in Spain, by Correia et al. (2013) from Portugal, by Rößler (1998) from the Saale Basin at Plötz near Halle, Germany, and by Dunlop (1999b) from Montceau-les-Mines in France. In a conference abstract Eskov (1998) noted further trigonotarbids from the Kazimovian stage, at least one euphrynid from Chunya in the Tungsuska Basin and one aphantomartid from Zhet-tyi Yar in the Kuznetsk Basin (both Russia). Additional arachnids of this age, probably trigonotarbids, were documented from the Saale Basin by Aue & Rohrlack (2007), but identified under the rather questionable name Orthotarbus longipes Simon, 1971 which implies a different arachnid order: Phalangiobouridae.

Permian records

The only South American trigonotarbid genus, Gondwanarachne Pinto & Hünicken, 1980 comes from Bajo de Véliz, San Luiz Province in Argentina. The precise age of this locality has been disputed (see Martins-Neto et al. 2007), but the current consensus seems to be that it is either on (or near) the Carboniferous–Permian boundary. The youngest trigonotarbids are unequivocally Permian in age, but these records are comparatively rare. Some material from the Czech Republic was originally interpreted as Permian (e.g. Frick 1901), although subsequent dating placed all these Bohemian
localities within the Carboniferous (summarised by Opšušil 1986: fig. 1). Thus the only unequivocal Permian records are those noted in the Introduction from Thuringia (Ilfeld, Manebach, several new, still unidentified ones from Sperbersbach and Cabarz (Stephan Brauner, pers. comm. 2012) and Chemnitz; all associated with the Rotliegend of eastern Germany. Although not yet described, Eskov & Selden (2005) mentioned a poorly preserved trigonotarbid from the Chekarda locality of the Kungurian stage. Nevertheless, at ca. 290 Ma, our new fossil is the youngest recorded trigonotarbid to date (Table 1) and extends their fossil record to approximately 130 million years (i.e. from 420–290 Ma).

Extinctions

Trigonotarbida is one of four arachnid orders which, on current evidence, did not survive beyond the Paleozoic. The others are Phalangiotarbida (Devonian–Permian), Haptopoda (Carboniferous) and the recently recognised and spider-like Uraraneida (Devonian–Permian). Trigonotarbids are the most species-rich of these extinct orders, with sixty-five currently valid species; as compared to thirty-one phalangioteids, one haptopodid and two uraraneid species respectively (cf. Dunlop et al. 2013). Also in terms of raw numbers of fossils, and fossil localities hosting these specimens (Table 1), the general impression is of trigonotarbids having been a fairly common and widespread group; particularly in the Late Carboniferous Coal Measures environments of Europe and North America (Figs 5, 6). They are certainly discovered more frequently as fossils than diverse modern arachnids of at least medium body size like spiders (Araneae) and harvestmen (Opiliones) today. To what extent this reflects genuine palaeodiversity patterns or ecological and/or taphonomic factors is a matter for further discussion. For example most Palaeozoic spiders appear to belong to a clade whose modern representatives (Mesothelae) spend most of their life cycle concealed in burrows today, which would obviously confer a lower fossilisation potential.

In discussing broader diversity patterns among trigonotarbids, and contemporary fossil arachnids, we should also bear in mind that the Carboniferous—and the Coal Measures in particular—were economically significant and intensively mined. Accordingly, the chance of finding specimens was comparatively high both in the coal mines and many years later on the mining spoil heaps. Hence the majority of Palaeozoic arachnid finds are more or less connected with coal exploration or mining and this is strongly reflected in the distribution and nature of the localities seen in Table 1 and Figure 6. By contrast, Permian strata were not of the same level of industrial interest as those of the Carboniferous. A few occurrences with coal were also mined, and these sites have also yielded fossil arachnids (e.g. Ilfeld and Manebach in Germany). Nevertheless, discovering arachnid fossils in the Permian was always a rather random event.

It is also worth remarking that trigonotarbids have not (yet) been found in the Early Permian coal deposits of China. In this geographical region the ‘European’ type of Carboniferous Coal Measures forest persists even into the upper Permian where it yields many typical swamp plants, like the arboreal lycopsids—the majority of which became extinct in Euramerica at the end of the Carboniferous—or calamitaleans. These floral elements probably migrated into Asia towards the end of the Palaeozoic and survived in China much longer; see e.g. Wang (2010). Unlike in Europe, fossil plants are abundant in China throughout the entire Permian and are found even just below the Permian–Triassic boundary where they formed coal beds. The latter are currently being heavily mined (and may continue to be mined in the future). In general, the late Palaeozoic is characterised by major climatic changes, such as the transition from an icehouse to a greenhouse world. The floral provincialism starting in the Carboniferous culminated in the Permian during which four major floral provinces can be recognised; all of which are represented in China. We might predict that typical Carboniferous arachnids, including trigonotarbids, may yet be discovered at Asian localities of Permian age which maintained something akin to the typical Coal Measures floras.

A further point to note is that the available sequences belonging to Permian deposits—although reaching considerable thickness—are very rich in hiatuses (Kerp 2000). Thus the sediments rarely reflect the classical arachnid biotopes and exhibit a high amount of extrabasinal material. The Permian is generally characterized by rapid vertical and lateral facies changes and the fossil remains originate from different types of environments and habitats. A large portion of the sediments developed in red bed facies. The preservation potential of organic remains is considerably reduced in an environment prone to erosion, seasonality and overall drying. All things considered, the apparent sudden decline of the trigonotarbids (Fig. 5) may also be a consequence of a chain of different geotectonic processes causing large-scale climatic and ecological changes resulting in different environments, smaller basins and thus a rather limited fossil record.

Nevertheless, trigonotarbids are no longer with us and it is interesting to speculate about the eventual biological causes of their extinction. For example a Euanamerican ‘Carboniferous Rainforest Collapse’ (CRC) dating to about 305 million years ago has been postulated, at least for tetrapods (e.g. Sahney et al. 2010). This immediately follows the last time period (the Moscovian: ca. 307–315 Ma) from which trigonotarbid fossils are frequently recovered. However, we should stress that at least four trigonotarbid genera (Anthracomartus, Aphantomartus, Trigonotarbus and the southern hemisphere Gondwanarachne) postdate this putative Euanamerican CRC event by up to 15 million years (Fig. 5; Table 1). Also, the last recorded species in the Early
Permian does not seem to coincide with any particular mass extinction. The next one would be the massive loss of biodiversity at the End Permian event. In any case the current dataset is probably too small for a meaningful statistical analysis. On present data, the most important factor may simply have been the loss of the coal swamps and a general drying of the environment during the Permian. It begs the question why groups like spiders survived these changes and subsequently radiated so spectacularly in the Mesozoic (cf. Selden & Penney 2010, fig. 2).

Figure 6. Geographic distribution of the known trigonotarbid localities. A. Global distribution. B. Details for Europe. Note the preponderance of Carboniferous sites – strongly correlating to areas of intensive coal production in the 19th and 20th centuries such as the Saar region, Silesia, Bohemia, the British midlands, etc. – as compared to the relative paucity of Permian sites (Argentina and Germany only).

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