

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

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## Abstract

Received 15 March 2013

Accepted 3 April 2013

Published 5 August 2013

## Key Words

Arachnida  
Trigonotarbida  
Fossil record  
Pyroclastics  
Sakmarian  
Saxony

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.

## 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 & Werneburg 2006); although precise geochronological ages are presently lacking. Here, we describe another Permian trigonotarbid this time from the Rotliegend of Chemnitz in the German state of Saxony (Fig. 1). At ca. 290 Ma (Sakmarian) 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

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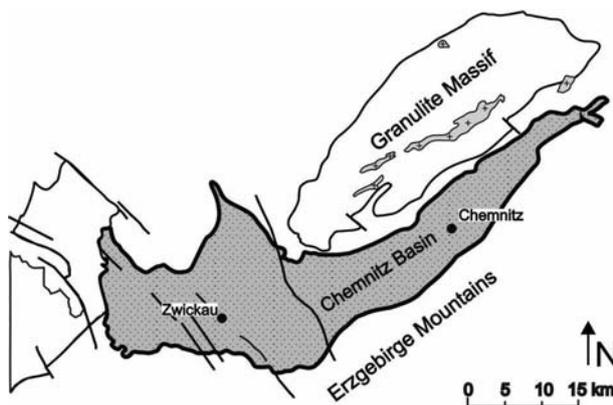
from the Late Carboniferous associated with numerous productive and often well-studied Coal Measures localities (Fig. 6). These in turn derive from industrial exploitation of coal seams (see Discussion). Trigonotarbids are notably rarer from after the time of the coal swamps. We discuss whether this is part of a genuine loss of diversity – part of a shift towards the eventual extinction of the Trigonotarbida – 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 volcanoclastics 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 associated automontage software for combining stacks of images at different focal planes (Leica Application Suite) 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



**Figure 1.** Location map of the fossil site in Chemnitz.

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 eryopid 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 Lagerstätte corresponds to the early Sakmarian and is thus dated at  $290.6 \pm 1.8$  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

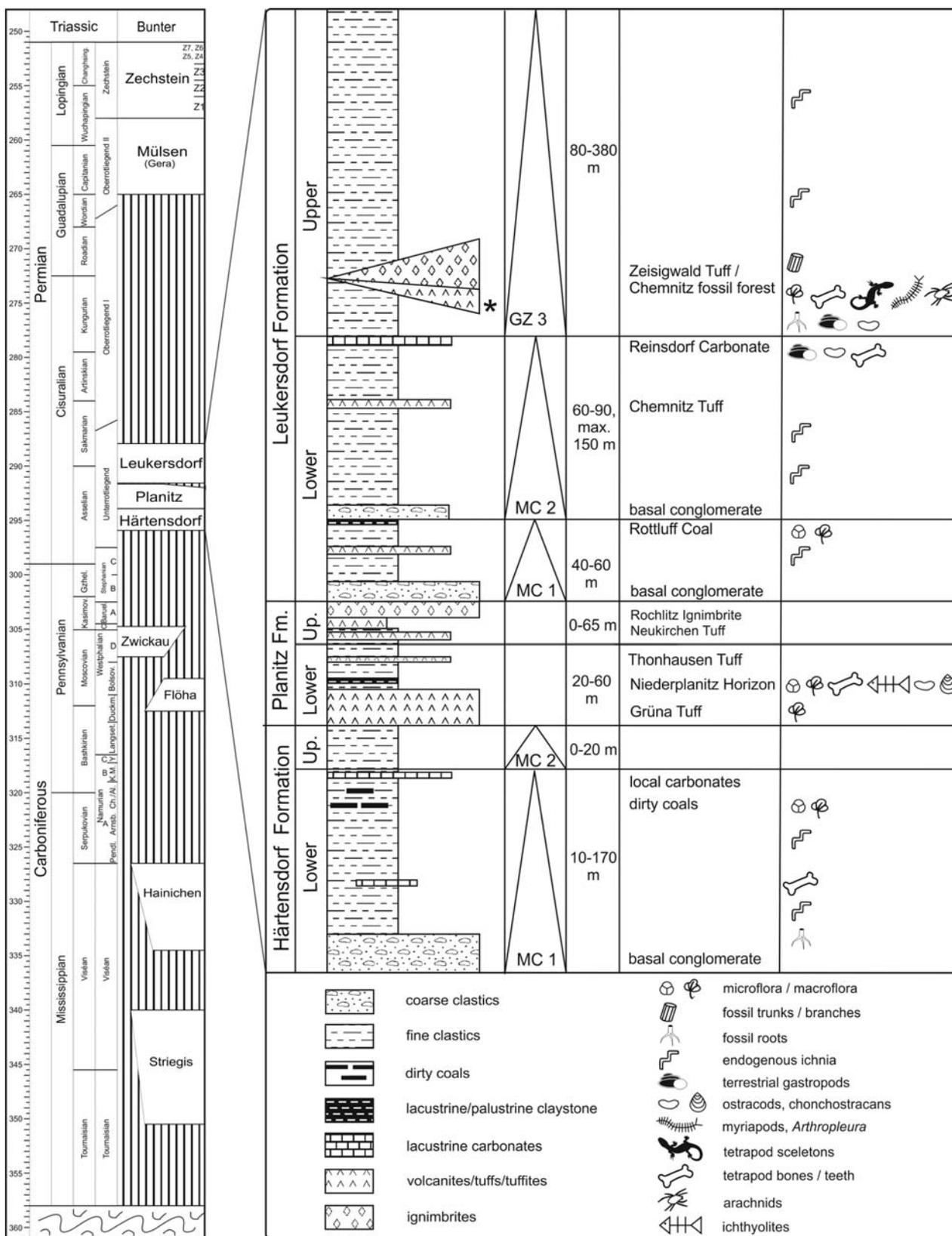
Family uncertain

### *Permotarbus* 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 medially 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 Anthracosironidae; 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*, *Kreischeriidae* and *Eophrynidae*. In terms of its overall outline and limb robust-



**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).

ness the new Chemnitz fossil resembles *Aphantomartida* (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

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 subtriangular 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 morphol-

ogy. 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

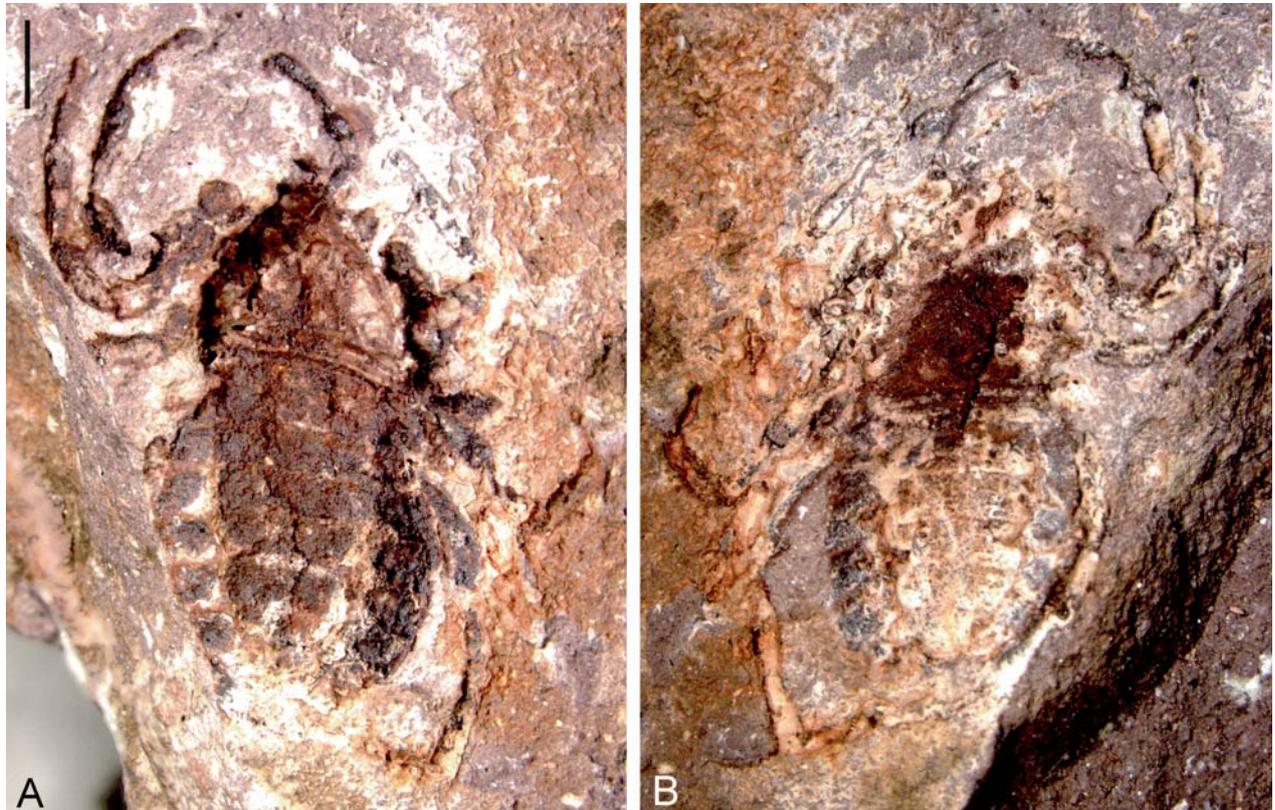
*Derivation of the name.* In honour of Dr. Peter Schubert, who was involved in the financial support which made the Chemnitz-Hilbersdorf excavation (2008–2011) both possible and successful.

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

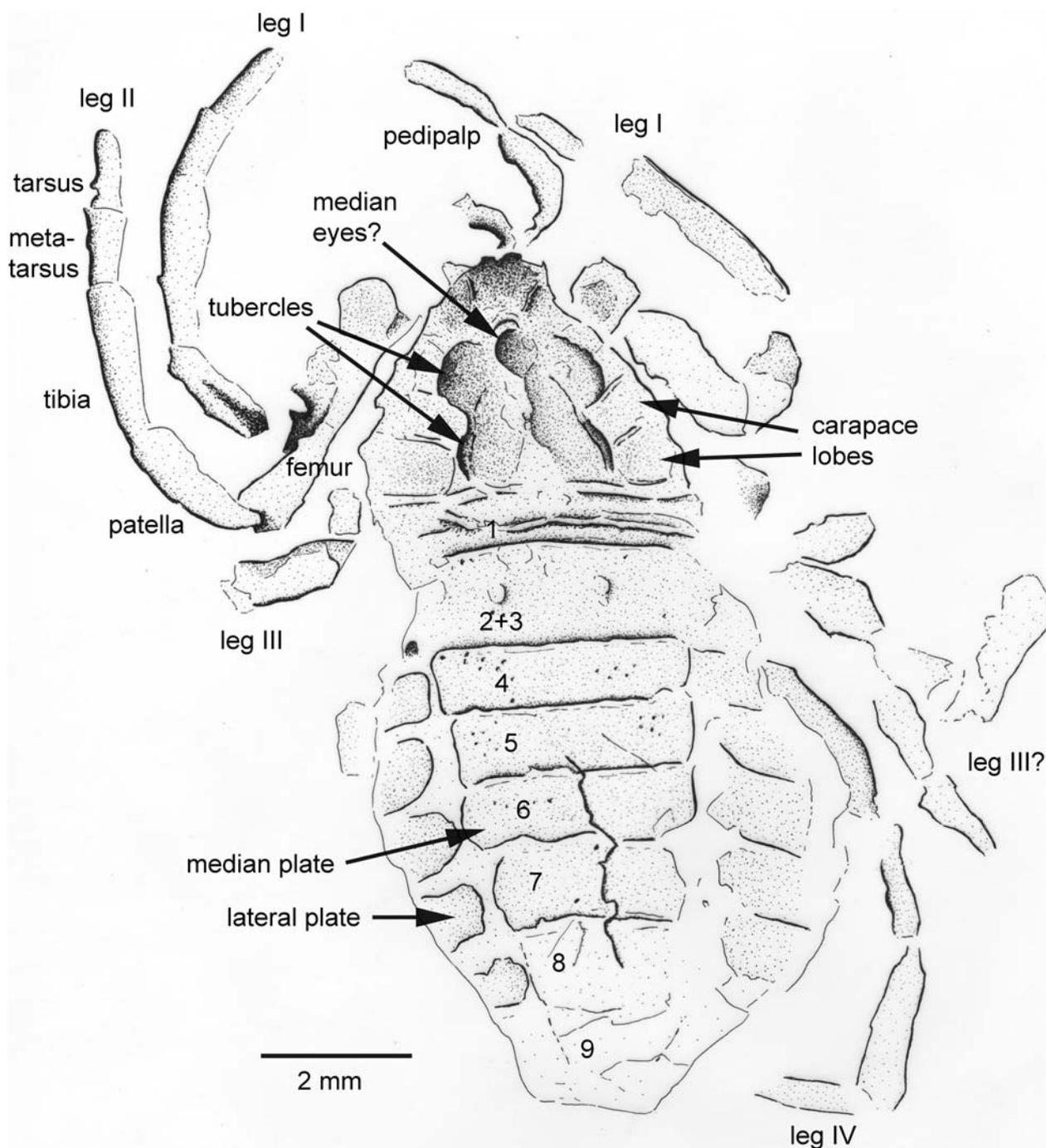
*Type locality and horizon.* Coordinates SSP-60; leg. Sandra Mehlhorn, 05.11.2010. From the Zeisigwald Tuff horizon, Petrified Forest of Chemnitz, Saxony, Germany. Early Permian (Sakmarian).

*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.



**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.

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 rather 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.

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.

Opisthosoma 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. Opisthosoma 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 opisthosoma equivocal. A few depressions hint at a slight granulation of the cuticle in life, but in general the dorsal opisthosomal 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 *Elaverimartus* Petrunkevitch, 1953 are now regarded as *nomen dubium* – 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 'eophrynid assemblage' (see also above) of Kreisleriidae–Eophrynidae–Aphantomartidae, postulated by Dunlop & Brauckmann (2006) on the basis of the putative synapomorphies of a strongly lobed carapace and robust dorsal tuberculation.

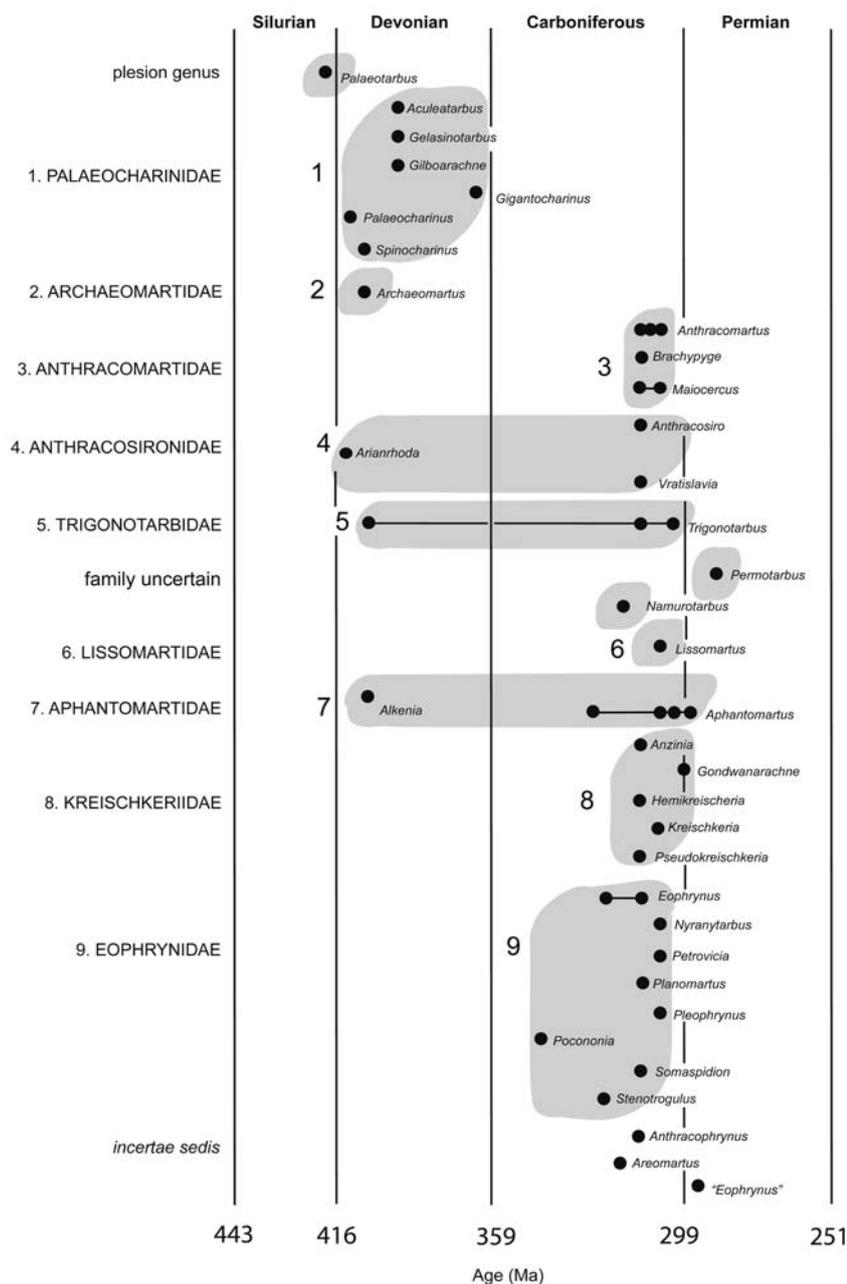
## Silurian records

The oldest trigonotarbid genus – *Palaeotarbus* 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 Trigonotarbitidae, but details are lacking and it is currently treated as a plesion genus (Fig. 5).

## Devonian records

Stratigraphically, the next trigonotarbid genus is *Arianrhoda* 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 *Palaeocharinus* Hirst, 1923 (Palaeocharinidae) from the Early Devonian (Pragian: ca. 410 Ma) Rhynie and Windyfield cherts of Scotland (Hirst 1923; Hirst & Maulik 1926; Fayers et al. 2005). These silicified fossils are unequivocally of terrestrial animals since they exhibit the oldest evidence for air-breathing book lungs (Claridge & Lyon 1961).

Slightly younger is a further palaeocharinid genus, *Spiniocharinus* 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* Størmer, 1970 and *Archaeomartus* Størmer, 1970 from Alken an der Mosel (Størmer 1970; Poschmann & Dunlop 2010). Of these, *Alkenia* was recently reassigned to Aphantomartidae and *Archaeomartus* 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 (Trigonotarbitidae) 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-



**Figure 5.** Stratigraphic distribution of the valid trigonotarbid genera recorded in the literature (data derived from Dunlop et al. 2013). Grey boxes highlight taxonomic groups (families numbered) as they are currently recognised. The Late Carboniferous evidently yields the greatest number of genera. By contrast, only a few taxa have been recorded from the (early) Permian. Compare this data with the localities in Table 1 and see text for details.

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, *Gelasinotarbus* 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) *Gigantocharimus* 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 trigonotarbids 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’.

Period	Age/Stage	Locality	Country	Ma	Reference
PERMIAN	Sakmarian	Chemnitz	Germany	290–295.5	this study
	Asselian	Ottostollen near Ilfeld	Germany	295.5–299	Scharf (1924)
	Asselian	Manebach	Germany	295.5–299	Müller (1957)
	Asselian	Sperbersbach	Germany	295.5–299	unpublished, pers. comm. Brauner, 2012
	Asselian	Cabarz	Germany	295.5–299	unpublished, pers. comm. Brauner, 2012
	?Asselian	Bajo de Véliz	Argentina	295.5–299	Pinto & Hünicken (1980)
CARBON.	Gzhelian [Stephanian]	Radvanice	Czech Republic	299–304	Opluštil (1985)
	Gzhelian [Stephanian C]	Plötz near Halle	Germany	299–304	Rößler (1998)
	Gzhelian	Steinbach near Brücken	Germany	299–304	Ammon (1901)
	Gzhelian	Montceau-les-Mines	France	299–304	Dunlop (1999b)
	Gzhelian	São Pedro da Cova	Portugal	299–304	Correia et al. (2013)
	Gzhelian	Guardo, León	Spain	299–304	Selden & Romano (1983)
	Gzhelian	Decazeville	France	299–304	Petrunkévitch (1955)
	Gzhelian	Commentry	France	299–304	Thevenin (1902)
	Kasimovian	Lawrence, Kansas	USA	304–307	Wright & Selden (2011)
	Kasimovian	Chunya, Tunguska Basin	Russia	304–307	Eskov (1998)
	Kasimovian	Zheltiy Yar, Kusnezsk Basin	Russia	304–307	Eskov (1998)
	Moscovian [Asturian]	San Giorgio, Sardinia	Italy	307–315	Selden & Pillola (2009)
	Moscovian	Merlebach	France	307–315	Waterlot (1934)
	Moscovian	Kilmersdon / Writhlington	UK	307–315	Ambrose & Romano (1972)
	Moscovian	Glyn-coch	UK	307–315	Pocock (1911)
	Moscovian	Maes-y-cwmmer	UK	307–315	Pocock (1911)
	Moscovian	Nýřany	Czech Republic	307–315	Frič (1901)
	Moscovian	Mazon Creek, Illinois	USA	307–315	Scudder (1884)
	Moscovian	Pawtucket, Rhode Island	USA	307–315	Scudder (1893)
	Moscovian	Piesberg near Osnabrück	Germany	307–315	Rößler (1998)
	Moscovian	Oelsnitz	Germany	307–315	Barthel & Rößler (1998)
	Moscovian	Zwickau	Germany	307–315	Geinitz (1882)
	Moscovian [Bolsovia]	Týnec	Czech Republic	307–315	Tichávek & Bureš (2010)
	Moscovian	Libušín and Vinařice near Kladno	Czech Republic	307–315	Opluštil (1985, 1986)
	Moscovian	Ovčín near Pilsen	Czech Republic	307–315	pers. comm. Opluštil, 2012
	Moscovian	Rakovník	Czech Republic	307–315	Kuřta (1883)
	Moscovian	New Brunswick	Canada	307–315	Miller & Forbes (2001)
	Moscovian	Drilling Rehden 21	Germany	307–315	Rößler (1995)
	Moscovian	Drilling Stangenmühle, Saar	Germany	307–315	Guthörl (1938)
	Moscovian [Duckmantian]	Ibbenbüren	Germany	307–315	van Essen et al. (1997)
	Moscovian	Aachen	Germany	307–315	Guthörl (1940)
	Moscovian	Drilling Kuhl 2 near Dinslaken	Germany	307–315	Jux (1982)
Moscovian	Jerusalemsberg	Slovakia	307–315	Vaňová (1987)	

**Table 1.** (continued)

Period	Age/Stage	Locality	Country	Ma	Reference
CARBON.	Moscovian	Lens	France	307–315	Pruvost (1912)
	Moscovian	Aniche	France	307–315	Pruvost (1912)
	Moscovian	L'Escarpelle	France	307–315	Thevenin (1902)
	Moscovian	Anzin	France	307–315	Pruvost (1919)
	Moscovian	Shipley	UK	307–315	Moysey (1911)
	Moscovian	Crawcrook	UK	307–315	Gill (1909)
	Moscovian	Ty'nybedw	UK	307–315	O'Connor (1896)
	Moscovian	Coseley	UK	307–315	Woodward (1871)
	Moscovian	Coalbrookdale	UK	307–315	Buckland (1837)
	Bashkirian [Langsettian]	Westhoughton	UK	315–323	Gill (1911)
	Bashkirian	Ellismuir	UK	315–323	Pocock (1911)
	Bashkirian	'Fern Ledges', New Brunswick	Canada	315–323	Matthew (1895)
	Bashkirian	Joggins, Nova Scotia	Canada	315–323	Petrunkovitch (1913)
	Bashkirian	Limbourg	Belgium	315–323	van der Heide (1951)
	Bashkirian	Mariemont-Bascoup	Belgium	315–323	Pruvost (1922)
	Bashkirian	Rieu-du-Coer	Belgium	315–323	Dorlodot (1922)
	Bashkirian	Near Mons	Belgium	315–323	Woodward (1878)
	Bashkirian	Nowa Ruda	Poland	315–323	Karsch (1882)
	Bashkirian	Kłodzko	Poland	315–323	Römer (1878)
	Bashkirian?	Cotton Hill, West Virginia	USA	315–323	Petrunkovitch (1913)
	Serpukhovian [Namurian B]	Hagen-Vorhalle	Germany	323–331	Brauckmann et al. (1985)
	Serpukhovian [Namurian A]	Nötsch	Austria	323–331	Röbber & Brauckmann (2000)
	Serpukhovian	Ostrava-Karviná	Czech Republic	323–331	Stur (1877)
Serpukhovian	Fayetteville, Arkansas	USA	323–331	Scudder (1884)	
late Visean	Drilling Delitzsch 9/64	Germany	331–347	Kahlert (1998)	
Visean	Kamienna Gora	Poland	331–347	Röbber (1998)	
Visean	Chemnitz	Germany	331–347	Röbber (1998)	
Tournaisian?	Pocono, Virginia	USA	347–359	Ewing (1930)	
DEVONIAN	Famennian	Red Hill, Pennsylvania	USA	359–372	Shear (2000)
	Givetian	Gilboa, New York	USA	383–388	Shear et al. (1987)
	Emsian	'Rheinisches Schiefergebirge'	Germany	393–408	Schultka (1994)
	Emsian	Waxweiler	Germany	398–408	Brauckmann (1994)
	Emsian	Konderbachtal	Germany	398–408	Brauckmann (1987)
	Emsian	Alken	Germany	398–408	Störmer (1970)
	Pragian?	Bürdenbach	Germany	408–411	Poschmann & Dunlop (2010)
	Pragian	Windyfield, Scotland	UK	408–411	Fayers et al. (2005)
	Pragian	Rhynie, Scotland	UK	408–411	Hirst (1923)
Lochkovian	Tredomen	UK	411–419	Dunlop & Selden (2004)	
SILURIAN	n/a	Ludford Lane	UK	419–423	Jeram et al. (1990)

Trigonotarbid 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* Frič, 1904 (Eophryniidae) from the 'Namurian A' (ca. 325? Ma) corresponding to the Serpukhovian Stage. Another specimen, re-

cognised as an aphantomartid (Röbber & 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 (Eophryniidae), as well as

*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'/Langsettian of traditional European terminology. Notable localities here include Kłodzko [= Glatz] and Nowa Ruda [= Neurode] in Silesia, Poland (Römer 1878; Karsch 1882). These produced, respectively, *Vratislavia* Frič, 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), Frič (1901, 1904), Pocock (1911) and Petrunkevitch (1913, 1949, 1953). This ca. 307–315 Ma time frame encompasses many of the classic trigonotarbid localities and, presumably because of this, the highest levels of reported species diversity. These include from the 'Westphalian B' (or Duckmantian) sites such as Aachen (Guthörl 1940) or Ibbenbüren (van Essen et al. 1997) in the Variscan foreland basin; Coseley in the English West Midlands (Pocock 1911) – and other contemporary outcroppings of the British Middle Coal Measures (e.g. Gill 1909; Moysey 1911) – together with Anzin in northern France (Pruvost 1919) and the Jerusalemberg in eastern Slovakia (Vaňová 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 Rakovník, Kladno (summaries in Opluštil 1985, 1986) and the recently discovered Týnec 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 Nýřany 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 *Nyranytarbus* Harvey & Selden, 1995 and *Petrovicia* Frič, 1904 (both Eophrynidae), the German genus *Kreischeria* Geinitz, 1882 (Kreischeriidae) from Zwickau, the Mazon Creek genus *Lissomartus* (Lissomartidae), and the more widely distributed *Pleophrynus* 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 *Trigonotarbus* 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 Kasimovian stage, at least one eophrynid from Chunya in the Tunguska Basin and one aphantomartid from Zheltyi 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: Phalangiotarbida.

### 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. Frič 1901), although subsequent dating placed all these Bohemian

localities within the Carboniferous (summarised by Opluštil 1986: fig. 1). Thus the only unequivocal Permian records are those noted in the Introduction from Thuringia (Ilfeld, Manebach, several new, still undescribed 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 Palaeozoic. 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 phalangiotarbid, 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, disco-

vering 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 ecologic 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 Euafrican ‘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 Euafrican CRC event by up to 15 million years (Fig. 5; Table 1). Also, the last recorded species in the Early



**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).

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).

## Acknowledgements

We thank the excavation team of the Chemnitz Museum of Natural History, particularly Ralph Kretzschmar, Mathias Merbitz, Volker Annacker and Sandra Mehlhorn. We gratefully acknowledge both the enthusiastic field work help from, and scientific discussions with, Jörg W. Schneider (Freiberg), Ralf Werneburg and Georg Sommer (Schleusingen) and Stephan Brauner (Friedrichroda). We are also indebted to Thorid Zierold for her professional project management and thank the reviewers for helpful comments on the typescript. This research was funded by the Volkswagen Foundation (Az: I/84638).

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