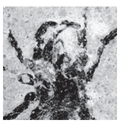
# A new species of trigonotarbid arachnid from the Pilsen Basin of the Czech Republic

Ivana Hradská, Stanislav Opluštil, Paul A. Selden & Jason A. Dunlop



A new genus and species of trigonotarbid (Arachnida: Trigonotarbida) is described from the late Carboniferous (Middle Pennsylvanian, Moscovian) of the Pilsen Basin in the Czech Republic. *Doubravatarbus krafti* gen. et sp. nov. is assigned to the family Aphantomartidae and is principally diagnosed by its relatively long and gracile legs compared to other trigonotarbids such as for example Eophrynidae and Anthracomartidae. The specimen is preserved in pale grey volcanic ash fall deposits, a type of entombment which is presumably responsible for the instant burial and nearly complete preservation of the trigonotarbid's body. Its possible habitat in the original ecosystem is discussed in relation to the associated flora and its taphonomic implications. • Key words: collection, new species, palaeoecology, Pennsylvanian, taxonomy, trigonotarbids.

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Trigonotarbids (Arachnida: Trigonotarbida Petrunkevitch, 1949) are representatives of an extinct group of somewhat spider-like arachnids known from the upper Silurian (Přídolí) to the lower Permian (Sakmarian); see Dunlop & Rößler (2013) for a summary of their localities and stratigraphic distribution. Trigonotarbids are usually resolved in the arachnid clade Pantetrapulmonata (*e.g.* Garwood & Dunlop 2014) as the sister-group of Tetrapulmonata, *i.e.* the orders Araneae (spiders), Amblypygi (whip spiders), Thelyphonida (whip scorpions) and Schizomida (schizomids). Trigonotarbids also share characters with the order Ricinulei (hooded tick spiders), such as an opisthosoma with longitudinally divided tergites, a locking mechanism between the prosoma and opisthosoma and a small claw at the tip of the pedipalp (*e.g.* Dunlop *et al.* 2009). Trigonotarbid fossils are characterised by a segmented opisthosoma with eight or nine dorsally visible tergites, most of which are, as noted above, divided longitudinally into median and lateral plates. These animals evidently had mouthparts modified for biting in the form of 'clasp-knife' chelicerae (Garwood & Dunlop 2010; Haug 2018, 2020) and were presumably predators in Palaeozoic terrestrial ecosystems.

Around a hundred species of trigonotarbid have been described in the literature, of which 70 are currently considered valid (Dunlop *et al.* 2020). Fourteen of them are known from the Czech Republic, and historical descriptions can be found in Stur (1877), Kušta (1883, 1884), Frič (1901, 1904), Petrunkevitch (1953) and Přibyl (1958). More recent summaries and species descriptions can be found in Opluštil (1985, 1986), with a revision of three genera by Dunlop (1995) and the description of a further new species by Hradská & Dunlop (2013). Here, we describe a new genus and species of an unusually gracile trigonotarbid from the Pennsylvanian (early Moscovian) Radnice Member of the Pilsen Basin.

## Material and methods

The specimen described here is stored in the collections of the Centre of Paleobiodiversity of the West Bohemian Museum in Pilsen, under the catalogue numbers M00762A (part) and M00762B (counterpart). The specimen was studied and photographed under incident light using an Olympus SZ12 binocular microscope and immersion in 70% alcohol was used to improve contrast and detection of morphological details. Photographs were taken with an Olympus E410 camera and drawings were made with the aid of a *camera lucida*. For scanning electron microscopy (SEM) a JEOL model JSM-6380LV at the Institute of Geology and Paleontology, Charles University, Prague was used. All measurements were taken from dorsal view and are given in millimetres.

## Geological background

The specimen is preserved in a volcanic ash bed called the Bělka. It was found in one of the coal mines, which operated in the vicinity of Doubrava, a village located along the western edge of the Nýřany coalfield in the southern part of the Pilsen Basin, about 7 km west of Pilsen. Coal mining in this area started in the mid-19th century and the last coal mine was closed in 1956 (Bureš *et al.* 2013). Thus we presume the discovery of the arachnid dates back to the first half of the 20th century, but details of a collector and/or date are lacking. The Bělka is a whitish to pale grey layer of vitrocrystalic tuff of sand grain size with a clayey kaolinite matrix (Orlov 1942, Opluštil *et al*. 2014, Tomek *et al*. 2021). It is followed by a usually thicker bed of redeposited and laminated volcaniclastics with a siliciclastic admixture called the Whetstone. Together they form the Whetstone Horizon, which can be up to a few meters thick and is sandwiched between the Lower and Upper Radnice seams. These together make up the Radnice group of extensively mined seams in the Pilsen Basin. The age of this coal group was recently constrained by U–Pb CA-ID TIMS radioisotopic dating of zircon crystals present in the Bělka and in another volcaniclastic bed intercalated in the Upper Radnice Seam (Opluštil *et al.* 2016). It is about 313.9 Ma old, which corresponds to the late Duckmantian regional substage or the middle Moscovian stage of the global chronostratigraphic chart. The Radnice group of seams is a part of the wider Radnice Member. This in turn makes up the lower part of the Kladno Formation, the oldest lithostratigraphic unit of the Pilsen Basin and other Late Palaeozoic continental basins in the western and central part of Bohemia (Pešek 1994, Opluštil 2005).

## Floral and faunal associations

The Nýřany coalfield is renowned for rich vertebrate and invertebrate fossils collected in the past in sapropelic coal of the slightly younger (Asturian or late Moscovian) Main Nýřany Seam; see Bureš *et al*. (2013) for an overview. Less known are the remains of plant fossils found in the Bělka bed in the roof of the Lower Radnice Seam. The Bělka was formed by volcanic ash fall which buried a peat-forming forest *in situ* (Opluštil *et al.* 2009a, 2014). The distribution of plant remains in the tuff bed therefore reflects the structure of the former forest. Much less frequent are findings of animals, mostly arthropods like insects and arachnids. For example, the Nýřany locality has yielded thirteen myriapods, ten blattid cockroaches and five chondrichthyan fish (Štamberg & Zajíc 2008). Most of them are quite complete, again presumably thanks to their rapid burial *in situ*.

Plant assemblages preserved in the Bělka tuff bed represent the peat-forming vegetation of the Lower Radnice Seam, which could be characterised as lycopsid – a *Cordaites*-dominated forest with a well-developed understory and ground cover (Opluštil *et al.* 2009a, b, 2014). The overall diversity is estimated to be about 40 species Opluštil *et al*. (2007, 2014). Dominant components of the tree storey are arborescent lycopsids (e.g. *Lepidodendron simile* sensu Němejc *non* Kidston, *L. lycopodioides* Sternberg, *Lepidofloios* cf. *acerosus* Lindley & Hutton (Opluštil *et al.* 2009a, b) together with cordaitalean trees identified as *Cordaites borassifolius* (Sternberg) Unger (Šimůnek *et al*. 2009). The shrubby understorey and ground cover are dominated by the subarborescent lycopsid *Spencerites havlenae* Drábková, Bek & Opluštil (Drábková *et al*. 2004), the medullosan pteridosperm *Laveineopteris loshii* (Brongniart) Cleal, Shute & Zodrow, several lyginodendrid pteridosperm species comprising *Sphenopteris mixta* Shimper, *Eusphenopteris nummularia* (Gutbier) Novik, *Palmatopteris furcata* (Brongniart) Potonie, *Dicksonites irregularis* (Sternberg) Němejc, and a sphenopsid of the genus *Calamites* Brongniart. Zygopterid, eusporangiate and leptosporangiate ferns are common.

Eusporangiate ferns are represented by the genus *Psaronius* of tree habitus with the foliage *Lobatopteris aspidioides* Sternberg (Wagner) and *L. miltonii* (Artis) (Pšenička *et al*. 2009). *Corynepteris angustissima* (Sternberg) Němejc, *C. essinghii* (Andrae), *Desmopteris longifolia* (Sternberg *in* Goeppert) Stur and *Rhodeites gutbieri* (Ettingsahusen) belong to the zygopterid ferns (Pšenička & Schultka 2009). These zygopterid species had a creeping/climbing growth habit. Leptosporangiate ferns are represented by several species of *Oligocarpia* Goeppert, *Discopteris* Stur and *Senftenbergia* Corda, which are all interpreted as lianas (Opluštil *et al*. 2014). Sphenopsids, represented by subarborescent (by habit) calamitalean plants and several small herbaceous species of the genus *Sphenophyllum* Brongniart, were locally common (Libertín & Bek 2004, Libertín *et al*. 2008). Epiphytes, represented by two *Selaginella* (Beauvoir) species, were also identified (Pšenička & Opluštil 2013). The arachnid described here is associated with the creeping/climbing zygopterid fern *Desmopteris longifolia* (Sternberg *in* Goeppert) Stur, which occupied the understory, but could also apparently climb other trees or shrubs in its proximity (Opluštil *et al*. 2009a, 2014).

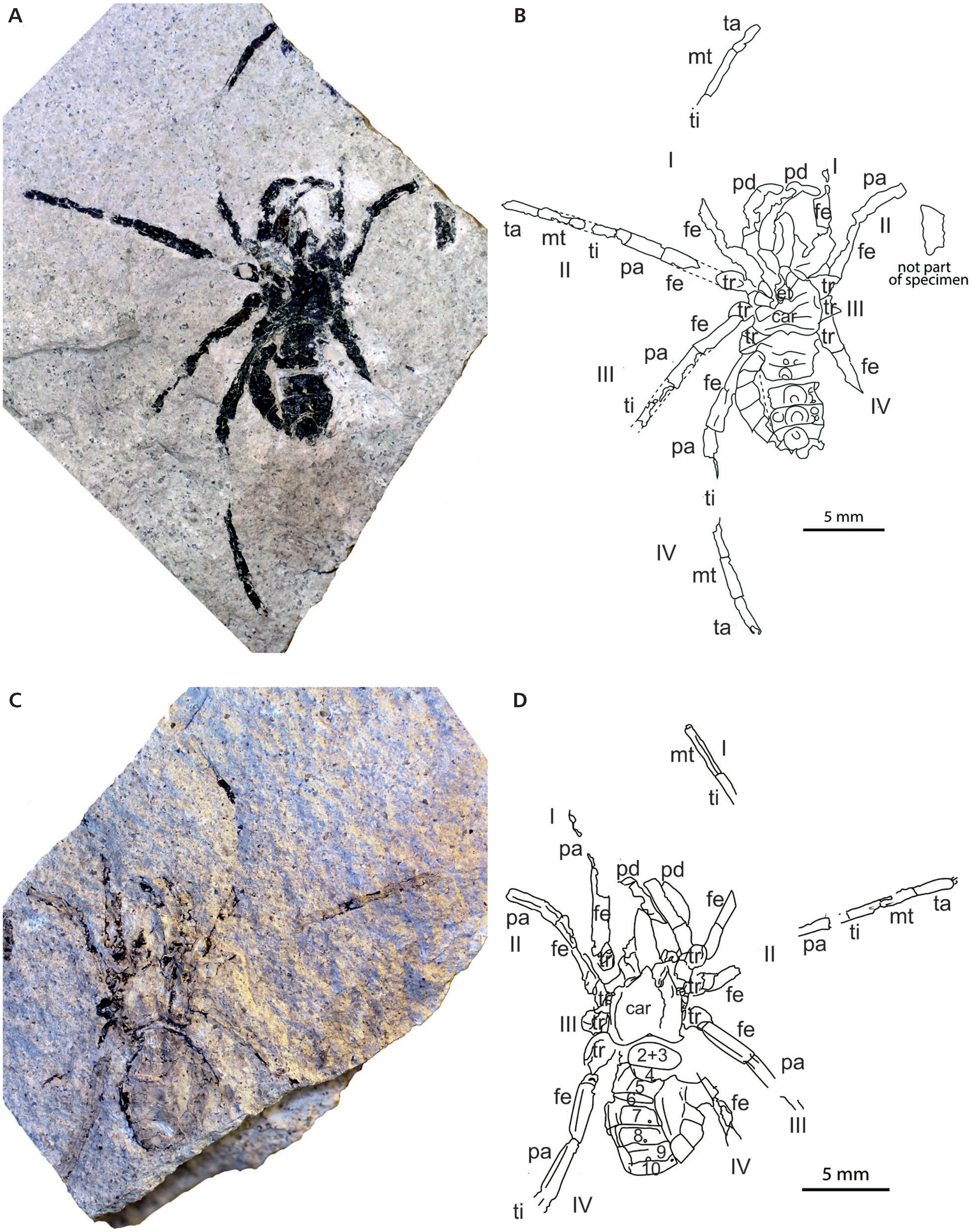


**Figure 1.** *Doubravatarbus krafti* gen. et sp. nov. (Arachnida: Trigonotarbida: Aphantomartidae) from the Pennsylvanian (Duckmantian) of Doubrava near Nýřany in the Pilsen Basin, West Bohemia, Czech Republic. A – part; B – camera lucida drawing; C – counterpart; D – camera lucida drawing. Abbreviations: I–IV – numbered legs; car – carapax; et – eye tubercle; fe – femur; mt – metatarsus; pa – patella; Pd – pedipalp; ta – tarsus; ti – tibia; tr – trochanter. Scale bar = 5mm

## Systematic palaeontology

Order Trigonotarbida Petrunkevitch, 1949
Family Aphantomartidae Petrunkevitch, 1945

*Remarks*. – Although superficially resembling a spider, such as the Silesian fossil described by Roemer (1866), see also Selden (2021) for an overview, the presence of a single pair of median eyes that are situated towards the centre of the prosomal dorsal shield in conjunction with what appears to be divided opisthosomal tergites indicate that the new fossil belongs in Trigonotarbida. Nine families of this order are currently recognised. For details of their systematics and geographical and stratigraphic distribution see Dunlop *et al*. (2020). The lobes at the margins of the dorsal shield together with the heavily ornamented opisthosomal tergites point towards a group of trigonotarbids informally referred to as the eophrynid assemblage (Dunlop & Brauckmann 2006, Jones *et al*. 2014). This includes the families Kreischeriidae Haase, 1890 Eophrynidae Karsch, 1882 and Aphantomartidae Petrunkevitch, 1945, with some currently unplaced genera (*e.g*. Dunlop & Rößler 2013, Hradská & Dunlop 2013) possibly resolving close to, or within, this assemblage too.

The *ca*. 20 mm long body and overall habitus of the new fossil is most consistent with Aphantomartidae Petrunkevitch, 1945; *e.g*. reconstructions in Jones *et al*. (2014: fig. 1). In Kreischeriidae and Eophrynidae (*e.g*. Dunlop 1995) the prosomal dorsal shield tends to be more triangular and less rounded to subpentagonal, and is often drawn into an anterior spine, while the opisthosoma in these two families is typically larger and more circular in relation to the prosoma. Notable in the new fossil are the relatively elongate and gracile legs in which the patella is of similar length to the femur. In most trigonotarbids (and in tetrapulmonate arachnids in general) the patella is usually less than half the length of the adjacent femur, forming a small knee joint in the leg. Interestingly, several examples of the Carboniferous genus *Aphantomartus* Pocock, 1911 also have a patella which was about as long as the femur (*e.g*. Rößler 1998: figs 1, 7–8; Dunlop 1999: fig. 2); something also reflected in the reconstruction in Jones *et al*. (2014) which showed an aphantomartid with quite long legs, including a long patella.

Based on this combination of limb and body characters, we suggest the new fossil is best placed in Aphantomartidae. A possible problem here is the presence of marginal spines towards the back of the opisthosoma. Spination of this form is typical for both eophrynids and kreischeriids, but not aphantomatids; at least not the three species assigned to *Aphantomartus*.

***Doubravatarbus* gen. nov.**

*Type species*. – *Doubravatarbus krafti* sp. nov.

*Etymology*. – From the type locality of Doubrava in West Bohemia and the typical trigonotarbid suffix -*tarbus*, derived from the Greek "tarbos" meaning fear/alarm.

*Diagnosis*. – Trigonotarbid arachnids from the eophrynid-assemblage characterised by long and gracile legs. Like other members of this assemblage, prosomal dorsal shield divided laterally into lobes and ornamentation of dorsal cuticle tuberculate, but differs from members of the similarly tuberculate families Eophrynidae and Kreischeriidae by a more subtriangular prosomal dorsal shield not drawn into an anterior spine and legs in which the patella is about as long as the femur. Within Aphantomartidae it differs from *Alkenia* Størmer, 1970, which has rows of small discrete opisthosomal dorsal tubercles, and from both *Alkenia* and *Aphantomartus* by the presence of marginal opisthosomal spines and legs which are proportionally longer and more slender.

***Doubravatarbus krafti* sp. nov.**
Figure 1

*Holotype*. – Part and counterpart housed in the Centre of Paleobiodiversity of the West Bohemian Museum in Pilsen, Czech Republic under the numbers M 00762A and M00762B respectively.

*Type horizon and locality*. – Whetstone Horizon of the Radnice Member, Kladno Formation; early Moscovian (= Duckmantian in the regional stratigraphy, *ca*. 313.9 Ma), middle Pennsylvanian; Doubrava village near Nýřany, Pilsen Basin (Carboniferous of Central and Western Bohemia).

*Material*. – Holotype only.

*Etymology*. – In honor of Jaroslav Kraft, a great Czech paleontologist who renewed the Department of Paleontology (now Centre of Paleobiodiversity) of the West Bohemian Museum in Pilsen.

*Diagnosis*. – As for the genus.

*Description*. – Relatively large arachnid (Fig. 1); total preserved length 20, estimated length prior to deformation during entombment in matrix *ca*. 22. Prosomal dorsal shield (or carapace) rounded to subtriangular in outline, length 7, maximum width 7; strongly deformed on right side, but left side well-preserved and slightly cambered in shape. Ocular tubercle, probably bearing two eyes, present on midline slightly anterior to the midpoint of the dorsal shield. Dorsal shield bordered by a *ca*. 1 mm wide margin and sub-divided into at least three visible lobes, each lobe roughly corresponding to emergence of

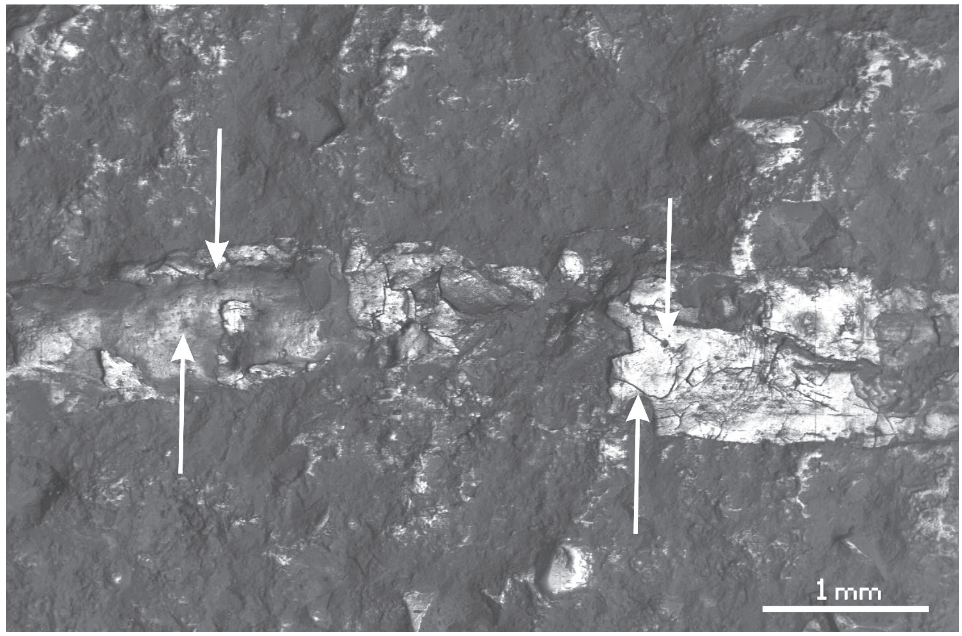


**Figure 2.** Scanning electron microscopy image of the first left leg of *Doubravatarbus krafti* gen. et sp. nov. (Arachnida: Trigonotarbida: Aphantomartidae). Arrowed are the spines visible on tibia and metatarsus. Scale bar = 1 mm.

a leg. Chelicerae equivocal. Pedipalps well-preserved, apparently quite long with preserved length of 6 and 7 mm respectively, although terminal article (tarsus) of both pedipalps missing. Legs also relatively well-preserved (see Tab. 1 for measurements) with spines visible on tibia and metatarsus I of a left leg (Fig. 2). Legs generally long and gracile in comparison with most other trigonotarbids, giving the fossil a more spider-like appearance. Coxosternal region equivocal.

Connection between prosoma and opisthosoma narrowed, but not well preserved. Length of opisthosoma 13, maximum width 7; dimensions in life perhaps *ca.* 15 and 9 respectively. Opisthosoma broadly oval, slightly cambered with a noticeable marginal border. Fossil shows evidence of lateral compaction as a result of lying somewhat on the right side of its body in the matrix. Thus border on right side of opisthosoma equivocal. Tergites ornamented with rounded tubercles (diameter *ca.* 1.3), clearly traceable across entire width of each tergite, becoming indistinct on last tergite where impression of rounded pygidium from ventral surface is superimposed. In addition to larger tubercles, tergites also sparsely covered with smaller granules *ca*. 0.1–0.3 in diameter. Anterior part of opisthosoma somewhat deformed, but outline of nine tergites (of which 2 and 3 are fused) can be distinguished. Distinction into median and lateral plates less obvious due to deformation. Margins of tergites smooth except for last four, each of which bear a small spine; length *ca*. 1 basal width *ca*. 0.5. Marginal spines only visible on the left side of opisthosoma due to orientation in the matrix.

**Table 1.** Lengths of leg segments of *Doubravatarbus krafti* gen. et sp. nov. (Arachnida: Trigonotarbida: Aphantomartidae). Abbreviations: L – left leg; R – right leg.

| Leg segment | (L) I. | (R) I. | (L) II. | (R) II. | (L) III. | (R) III. | (L) IV. | (R) IV. |
|---|---|---|---|---|---|---|---|---|
| Coxa | ? | | 1 | | ? | | | |
| Trochanter | ? | | 2 | | 2 | | 2 | |
| Femur | 5 | | 6 | | 5 | | 10 | |
| Patella | ? | | 5 | | 5 | | 3 | |
| Tibia | 5 | | 9 | | ? | | 9 | |
| Metatarsus | 3 | | 4 | | 2 | | 4 | |
| Tarsus | ? | | ? | | ? | | ? | |
| Total | 13 | 10 | 27 | 12 | 14 | 3 | 28 | |

## Discussion

Several trigonotarbids have been reported previously from Nýřany. Anthracomartidae is represented by *Anthracomartus bohemica* (Frič, 1901), *A. carcinoides* (Frič, 1901), *A. elegans* Frič, 1901 and *A. nyranensis* (Petrunkevitch, 1953). Anthracomartids can be easily differentiated from our new fossil by the fact that there are five plates across the opisthosoma, as opposed to three, and the legs are rather short and stubby (Garwood & Dunlop 2011). Eophrynidae is represented by *Nyranytarbus hofmanni* (Frič, 1901) and *N. longipes* (Frič, 1901). As noted above, eophrynids differ from the new fossil in having a more triangular prosomal dorsal shield, which is often drawn into an anterior spine, and a more rounded opisthosoma. *Tynecotarbus tichaveki* Hradská & Dunlop, 2013 is unplaced at family level, but may be close to the eophrynid assemblage (see above). It has a similar habitus to our fossil, but differs in having only a lightly granulated dorsal cuticle (Hradská & Dunlop 2013), as opposed to discrete tubercles, and also lacks any terminal opisthosomal spines.

*Doubravatarbus krafti* gen. et sp. nov. contributes towards the wider observation that representatives of Aphantomartidae were relatively common and widespread faunal elements in the Coal Measures of North America and Europe. Representatives of this family have previously been reported from the USA, Canada, the United Kingdom, Portugal, Spain, France, Austria, Germany, Poland, and from Libušín and Ostrava in the Czech Republic (Rößler 1998, Rößler & Brauckmann 2000, Correia *et al.* 2013). Our present find is the first record of an aphantomartid from the Nýřany region of the Czech Republic and also suggests, by virtue of its terminal spines, that the morphological diversity may have been greater within the aphantomartids than previously recognised.

With respect to the palaeoenvironment of the new trigonotarbid, the vertical distribution of plant fossils in the Bělka tuff layer reflects the growth habit of the original plant species (Burnham 1994, Opluštil *et al*. 2014). Plant litter on the surface of the peat swamp was presumably buried by an initial load of volcanic ash and preserved through contact between a coal seam and the tuff. Small herbaceous plants like ferns and sphenophylls were initially buried under a load of volcanic ash a few centimetres thick and, after the tuff's compaction, were preserved as the 1–2 cm thick basal part of the Bělka tuff bed. Here, the concentration of fossils is usually high. By contrast, larger shrubby and arborescent plants probably survived a heavier ash load and, after the limits of their strength was exceeded, their branches broke off and were buried around the parent stem together with smaller plant remains of a liana-type habit. This would explain why remains of thick branches are accompanied by much more slender plant axes of ferns and pteridosperms that are assumed to have climbed the trees. Such an assemblage is observed throughout the middle and even into the upper part of the tuff bed (Opluštil *et al.* 2014).

Although the precise position of *Doubravatarbus krafti* within the Bělka tuff layer is unknown, the fact that the specimen is associated with remains of liana-like ferns suggests that at the time of the volcanic eruption the animal inhabited either the shrubby or the tree storey part of the original peat swamp forest. The implication is that this habitat may have been where the animal lived and hunted its prey, probably other terrestrial arthropods such as the cockroaches noted above. The gracile limbs of this trigonotarbid may also be consistent with an animal more used to clambering through the vegetation, rather than being purely cursorial and hunting on the forest floor. We also note that in spiders, males often have somewhat longer legs compared to females; however we do not have a clear suite of secondary sexual characters for trigonotarbids which would allow us to confidently assign this (or other fossils) to a particular gender.

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## References

Bureš, J., Opluštil, S., Pšenička, J. & Tichávek, F. 2013. Brouskový obzor (bolsov) s autochtonní zachovalou flórou na lokalitě Kamenný Újezd u Nýřan (plzeňská pánev). *Zprávy o geologických výzkumech v roce 2012*, 12–19.

Burnham, R.J. 1994. Plant deposition in modern volcanic environments. *Transactions of the Royal Society of Edinburgh, Earth Sciences 84*, 275–281. DOI 10.1017/S026359330000609X

Correia, P., Murphy, J.B., Sá, A.A., Domingos, R. & Flores, D. 2013. First Palaeozoic arachnid from Portugal and implications for Carboniferous palaeobiogeography. *Geological Journal 48*, 101–107. DOI 10.1002/gj.2443

Drábková, J., Bek, J. & Opluštil, S. 2004. The first compression fossils of *Spencerites* (Scott) emend., and its isospores, from the Bolsovian (Pennsylvanian) of the Kladno-Rakovník and Radnice basins, Czech Republic. *Review of Palaeobotany and Palynology 130*, 59–88. DOI 10.1016/j.revpalbo.2004.01.004

Dunlop, J.A. 1995. A redescription of two eophrynids (Arachnida Trigonotarbida) from the Coal Measures (Carboniferous), of Ostrava, Czech Republic. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1995(8)*, 449–461. DOI 10.1127/njgpm/1995/1995/449

Dunlop, J.A. 1999. A new specimen of the trigonotarbid arachnid *Aphantomartus areolatus* Pocock, 1911 from the Stephanian of Montceau-les-Mines, France. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1999(1)*, 29–38. DOI 10.1127/njgpm/1999/1999/29

Dunlop, J.A. & Brauckmann, C. 2006. A new trigonotarbid from the Coal Measures of Hagen-Vorhalle, Germany. *Fossil Record 9*, 130–136. DOI 10.1002/mmng.200600004

Dunlop, J.A. & Rößler, R. 2013. The youngest trigonotarbid *Permotarbus schuberti* n. gen., n. sp. from the Permian Petrified Forest of Chemnitz in Germany. *Fossil Record 16*, 229–243. DOI 10.5194/fr-16-229-2013

Dunlop, J.A., Kamenz, C. & Talarico, G. 2009. A fossil trigonotarbid with a ricinuleid-like pedipalpal claw. *Zoomorphology 128*, 305–313. DOI 10.1007/s00435-009-0090-z

Dunlop, J.A., Penney, D. & Jekel, D. 2020. A summary list of fossil spiders and their relatives. In *World Spider Catalog*. Natural History Museum Bern, online at *http://wsc.nmbe.ch, version 20.5*, accessed September 8th 2021.

Frič, A. 1901. *Fauna der Gaskohle und der Kalksteine der Permformation Böhmens. Myriopoda pars II. Arachnoidea, Vol IV, part 2*. 64 pp. Selbstverlag: In Commission bei Fr. Řivnáč, Prague.

Frič, A. 1904. *Palaeozoische Arachniden*. 85 pp. Privately published, Prague.

Garwood, R.J. & Dunlop, J.A. 2010. Fossils explained 58. Trigonotarbids. *Geology Today 26*, 34–37. DOI 10.1111/j.1365-2451.2010.00742.x

Garwood, R.J. & Dunlop, J.A. 2011. Morphology and systematics of Anthracomartidae (Arachnida: Trigonotarbida) *Palaeontology 54*, 145–161. DOI 10.1111/j.1475-4983.2010.01000.x

Garwood R.J. & Dunlop, J.A. 2014. Three-dimensional reconstruction and the phylogeny of extinct chelicerate orders. *PeerJ 2*, e641. DOI 10.7717/peerj.641

Haase, E. 1890. Beiträge zur Kenntnis der fossilen Arachniden. *Zeitschrift der Deutschen Geologischen Gesellschaft 42*, 629–657.

Haug, C. 2018. Feeding strategies in arthropods from the Rhynie and Windyfield cherts: ecological diversification in an early non-marine biota. *Philosophical Transactions of the Royal Society B 373*, 20160492. DOI 10.1098/rstb.2016.0492

Haug, C. 2020. The evolution of feeding within Euchelicerata: data from the fossil groups Eurypterida and Trigonotarbida illustrate possible evolutionary pathways. *PeerJ 8*, e9696. DOI 10.7717/peerj.9696

Hradská, I. & Dunlop, J.A. 2013. New records of Pennsylvanian trigonotarbid arachnids from West Bohemia, Czech Republic. *Journal of Arachnology 41*, 335–341. DOI 10.1636/Ha12-41.1

Jones, F.M., Dunlop, J.A., Friedman, M. & Garwood, R.J. 2014. *Trigonotarbus johnsoni* Pocock, 1911, revealed by X-ray computed tomography, with a cladistic analysis of the extinct trigonotarbid arachnids. *Zoological Journal of the Linnean Society 172*, 49–70. DOI 10.1111/zoj.12167

Karsch, F. 1882. Ueber ein neues Spinnenthier aus der Schlesischen Steinkohle und die Arachnoiden der Steinkohlenformation überhaupt. *Zeitschrift der Deutschen Geologischen Gesellschaft 34*, 556–561.

Kušta, J. 1883. *Anthracomartus krejcii*, eine neue Arachnide aus dem Böhmischen Karbon. *Sitzungsberichte der Königlich Böhmischen Gesellschaft der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse 1883*, 7.

Kušta, J. 1884. Neue Arachniden aus der Steinkohlenformation von Rakonitz. *Sitzungsberichte der Königlich Böhmischen Gesellschaft der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse 1884*, 398–401.

Libertín, M. & Bek, J. 2004. *Huttonia spicata* (Sternberg) emend. and its spores, the Radnice Basin (Bolsovian), Carboniferous continental basins of the Czech Republic. *Review of Palaeobotany and Palynology 128*, 247–261. DOI 10.1016/S0034-6667(03)00136-2

Libertín, M., Bek, J. & Drábková, J. 2008. Two new Carboniferous fertile sphenophylls and their spores from the Czech Republic. *Acta Palaeontologica Polonica 53*, 723–732. DOI 10.4202/app.2008.0414

Němejc, F. 1932. Stratigrafické výzkumy konané z hlediska paleobotanického v uhelných revírech jižní části plzeňské pánve v letech 1928–1932. *Hornický Věstník 14*, 417–466.

Opluštil, S. 1985. New findings of Arachnida from the Bohemian Upper Carboniferous. *Věstník Ústředního ústavu geologického 60*, 35–42.

Opluštil, S. 1986. *Promygale janae* sp. n., the new anthracomartid (Arachnida) from the Upper Carboniferous of central Bohemia. *Věstník Ústředního ústavu geologického 61*, 287–292.

Opluštil, S. 2005. Evolution of the Middle Westphalian river valley drainage system in central Bohemia (Czech Republic) and it palaeogeographic implication. *Palaeogeography Palaeoclimatology Palaeoecology 222*, 223–58. DOI 10.1016/j.palaeo.2005.03.016

Opluštil, S., Pšenička, J., Libertín, M. & Šimůnek, Z. 2007. Vegetation paterns of Westphalian and Lower Stephanian mire assemblages preserved in tuff beds of the continental basins of Czech Republic. *Review of Palaeobotany and Palynology 143*, 107–154. DOI 10.1016/j.revpalbo.2006.06.004

Opluštil, S., Pšenička, J., Libertín, M., Bashforth, A.R., Šimůnek, Z., Drábková, J. & Dašková, J. 2009a. A Middle Pennsylvanian (Bolsovian) peat-forming forest preserved in situ in volcanic ash of the Whetstone Horizon in the Radnice Basin, Czech Republic. *Review of Palaeobotany and Palynology 155*, 234–274. DOI 10.1016/j.revpalbo.2009.03.002

Opluštil, S., Pšenička, J., Libertín, M., Bek, J., Dašková J., Šimůnek, Z. & Drábková, J. 2009b. Composition and structure of an in situ Middle Pennsylvanian peat-forming plant assemblage in volcanic ash, Radnice Basin (Czech Republic). *Palaios 24*, 726–746. DOI 10.2110/palo.2008.p08-128r

Opluštil, S., Pšenička, J., Bek, J., Wang. J., Feng, Z., Libertín, M., Šimůnek, Z., Bureš, J. & Drábková, J. 2014. $T^0$ peat-forming plant assemblage preserved in growth position by volcanic ash-fall: A case study from the Middle Pennsylvanian of the Czech Republic. *Bulletin of Geosciences 89*, 773–818. DOI 10.3140/bull.geosci.1499

Opluštil, S., Schmitz, M., Cleal, C.J. & Martínek, K. 2016. A review of the Middle-Late Pennsylvanian west European regional substages and floral biozones, and their correlation to the Global Time Scale based on new U-Pb ages. *Earth Science Reviews 154*, 301–335. DOI 10.1016/j.earscirev.2016.01.004

Orlov, A. 1942. Sedimentární proplástky radnické uhelné sloje v Břaské pánvi. *Zprávy geologického ústavu pro Čechy a Moravu 18*, 1–21.

Pešek, J. 1994. *Carboniferous of Central and Western Bohemia (Czech Republic)*. 61 pp. Czech Geological Survey, Prague.

Petrunkevitch, A.I. 1945. Palaeozoic Arachnida. An inquiry into their evolutionary trends. *Scientific Papers, Illinois State Museum 3(2)*, 1–76.

Petrunkevitch, A.I. 1949. A study of Palaeozoic Arachnida. *Transactions of the Connecticut Academy of Arts and Sciences 37*, 69–315.

Petrunkevitch, A.I. 1953. Paleozoic and Mesozoic Arachnida of Europe. *Geological Society of America: Memorials 53*, 1–128. DOI 10.1130/MEM53-p1

Pocock, R.I. 1911. A monograph of the terrestrial Carboniferous Arachnida of Great Britain. *Monographs of the Palaeontographical Society 64*, 1–84.

Přibyl, A. 1958. Some new Carboniferous arachnids from the Ostrava-Karviná coal district. Časopis *pro Mineralogii a Geologii 3*, 425–434.

Pšenička, J. & Opluštil, S. 2013. The epiphytic plants in the fossil record and its example from in situ tuff from Pennsylvanian of Radnice Basin (Czech Republic). *Bulletin of Geosciences 88*, 401–416. DOI 10.3140/bull.geosci.1376

Pšenička, J. & Schultka, S. 2009. Revision of the Carboniferous genus *Rhodeites* Němejc from European and American localities. *Bulletin of Geosciences 84*, 241–256. DOI 10.3140/bull.geosci.1105

Pšenička, J., Bek, J., Cleal, C.J., Wittry, J. & Zodrow, E.L. 2009. Description of synangia and spores of the holotype of the Carboniferous fern *Lobatopteris miltoni*, with taxonomic comments. *Review of Palaeobotany and Palynology 155*, 133–144. DOI 10.1016/j.revpalbo.2007.12.005

Roemer, F. 1866. *Protolycosa anthracophyla* eine fossille Spinne aus dem Steinkohlengebirge Oberschlesiens. *Neues Jahrbuch für Mineralogie 3*, 136–143.

Rößler, R. 1998. Arachniden-Neufunde im mitteleuropaischen Unterkarbon bis Perm: Beitrag zur Revision der Familie Aphantomartidae Petrunkevitch 1945 (Arachnida, Trigonotarbida). *Paläontolgische Zeitschrift 72*, 67–88. DOI 10.1007/BF02987817

Rößler, R. & Brauckmann, C. 2000. Der erste Arachnidenfund im Paläozoikum der Alpen: *Aphantomartus pustulatus* (Scudder 1884) aus dem ältesten Ober-Karbon (mittleres bis oberes Namurium A) von Nötsch (Österreich). *Jahrbuch der Geologischen Bundesanstalt 142*, 227–234.

Selden, P.A. 2021. New spiders (Araneae: Mesothelae), from the Carboniferous of New Mexico and England and a review of Paleozoic Araneae, 317–358. *In* Lucas, S.G., DiMichele, W.A. & Allen, B.D. (eds) *Kinney Brick Quarry Lagerstätte. New Mexico Museum of Natural History and Science Bulletin 84*.

Šimůnek, Z., Opluštil, S. & Drábková, J. 2009. *Cordaites borassifolius* (Sternberg) Unger (Cordaitales) from the Radnice Basin (Bolsovian, Czech Republic). *Bulletin of Geosciences 84*, 301–336. DOI 10.3140/bull.geosci.1130

Štamberg, S. & Zajíc, J. 2008. *Carboniferous and Permian faunas and their occurrence in the limnic basins of the Czech Republic*. 224 pp. Muzeum východních Čech v Hradci Králové.

Størmer, L. 1970. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 1: Arachnida. *Senckenbergiana lethaea 51*, 335–369.

Stur, D. 1877. Die Culm-Flora der Ostrauer und Waldenburger Schichten. *Abhandlung der königliche geologische Reichanstalt 4*, 5.

Tomek, F., Opluštil, S., Svojtka, M., Špillar, V., Rapprich, V. & Míková, J. 2021. Altenberg–Teplice Caldera sourced Westphalian fall tuffs in the central and western Bohemian Carboniferous basins (eastern Variscan Belt). *International Geology Review*. DOI 10.1080/00206814.2020.1858357