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), Fríč (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 Doubra, 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). The last volcaniclastic bed intercalated in the Upper Palaeozoic continental basins in the western and central lithostratigraphic unit of the Pilsen Basin and other Late Old, which corresponds to the late Duckmantian regional Radnice Seam (Opluštil and in another volcaniclastic bed intercalated in the Upper Palaeozoic continental basins in the western and central part of the wider Radnice Member. This in turn makes the substage or the middle Moscovian stage of the global in situ (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, Lepidodendroides 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 havlenaæ Drábková, Bek & Opluštil (Drábková et al. 2004), the medulosan pteridosperm Laveineopteris loshi (Brongniart) Cleal, Shute & Zodrow, several lyginodendrid pteridosperm species comprising Sphenopteris mixta Shimper, Euopheopteris nummularia (Gutbier) Novik, Palmopteris 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 Rhodites guthieri (Ettingshausen) 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, b, 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 = 5 mm.
**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 trigonotarbid arachnids 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 trigonotarbits (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
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. Coxo-sternal 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: Trigonotarbid: Aphantomartidae). Abbreviations: L – left leg; R – right leg.

| Leg segment | (L)  | (R)  | (L)  | (R)  | (L)  | (R)  |
|-------------|------|------|------|------|------|------|
|             | I    | I    | II   | II   | III  | III  |
| Coxa        | ?    | 1    | ?    | ?    | ?    | ?    |
| Trochanter  | ?    | 2    | 2    | 2    | 2    | 2    |
| Femur       | 5    | 6    | 5    | 5    | 10   | 10   |
| Patella     | ?    | 5    | 5    | 5    | 3    | 3    |
| Tibia       | 5    | 9    | 7    | 9    | 9    | 9    |
| Metatarsus   | 3    | 4    | 2    | 4    | 4    | 4    |
| Tarsus      | ?    | ?    | ?    | ?    | ?    | ?    |
| Total       | 13   | 10   | 27   | 12   | 14   | 3    | 28   |

**Discussion**

Several trigonotarbids have been reported previously from Nyřany. 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). Ephryrididae is represented by *Nyranymartus hofmanni* (Frič, 1901) and *N. longipes* (Frič, 1901). As noted above, ephryrids 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. *Tyneotarbus 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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