

Malformed agnostids from the Middle Cambrian Jince Formation of the Příbram-Jince Basin, Czech Republic

OLDŘICH FATKA, MICHAL SZABAD & PETR BUDIL



Two agnostids from Cambrian of the Barrandian area bear different types of skeletal malformations. The tiny pathological exoskeleton of *Hypagnostus parvifrons* (Linnarsson, 1869) has asymmetrically developed pygidial axis, while the posterior pygidial rim in the larger *Phalagnostus prantli* Šnajdr, 1957 has an irregular outline. • Key words: agnostids, Middle Cambrian, Jince Formation, Příbram-Jince Basin, Barrandian area, Czech Republic.

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Numerous examples of exoskeletal abnormalities have been described in various polymerid trilobites (*e.g.*, Owen 1985, Babcock 1993, Whittington 1997), including paradoxid trilobites from the Cambrian Příbram-Jince Basin of the Barrandian area (Šnajdr 1978). However, anomalous agnostid skeletons are very rare; there are only four Cambrian and one Ordovician malformed agnostid specimens recorded.

Babcock (1993, 2003, 2007) documented and briefly described scars on the posterolateral pygidial margin in two isolated pygidia of *Peronopsis interstricta* White, 1874, both collected from the Middle Cambrian Marjum Formation (House Range, Utah, U.S.A.). These scars were interpreted as healed injuries of uncertain origin by Babcock (1993, 2003, 2007). Also, Buchholz (2000) interpreted one pathologic pygidium of the “Upper” Cambrian *Agnostus procerus* Buchholz, 1999 as result of a failed durophagous predation which he considered happened shortly after exuviation.

Another type of healed injury is recorded from Cambrian and Ordovician agnostids. Babcock (1993, 2003, 2007) figured dorsal and ventral views of a cephalon of *Arthrorhachis elspethi* Raymond, 1925 from the Middle Ordovician Edinburgh Limestone of Virginia, U.S.A. with a small boring along its right posterior pygidial axis. A similar, anteromedially inclined pit in the right posterolateral corner of the cephalic axis in a specimen of *Ptychagnostus atavus* (Tullberg, 1880) from the Middle Cambrian Huaqiao Formation in northwestern Hunan, China was

discussed by Babcock and Peng (2001). Öpik (1967) described and figured one pathological pygidium of *Glyptagnostus stolidotus* Öpik, 1961 with hypertrophic development of the left side of the pygidium.

Partly broken and slightly scattered pygidial fragments of two complete specimens of *Ptychagnostus stenorrhachis* (Grönwall, 1902) and *Ptychagnostus (Goniagnostus)* sp. recorded by Jago (1974) from the Middle Cambrian Que River Beds of Tasmania were interpreted as the result of the activities of an unknown benthic scavenger.

This paper describes two new articulated agnostid specimens with malformed pygidia collected from different stratigraphical levels of the Jince Formation (Drumian, Příbram-Jince Basin).

Agnostids in the Jince Formation

Agnostids have been known for more than 160 years from the Jince Formation of the Příbram-Jince Basin (Beyrich 1845, Barrande 1846). Since these pioneer works, several thousand intact agnostid exoskeletons and/or disarticulated parts of the eleven valid species have been collected at several tens of outcrops (Šnajdr 1958, Fatka *et al.* 2004, Fatka 2006). Such extensive material has allowed the recognition of three major agnostid assemblages: 1. *Peronopsis-Phalagnostus* Assemblage; 2. *Phalacroma-Condylomyge* Assemblage and 3. *Onymagnostus-Hypagnostus* Assemblage (Fatka *et al.* 2007). Stratigraphical and spatial

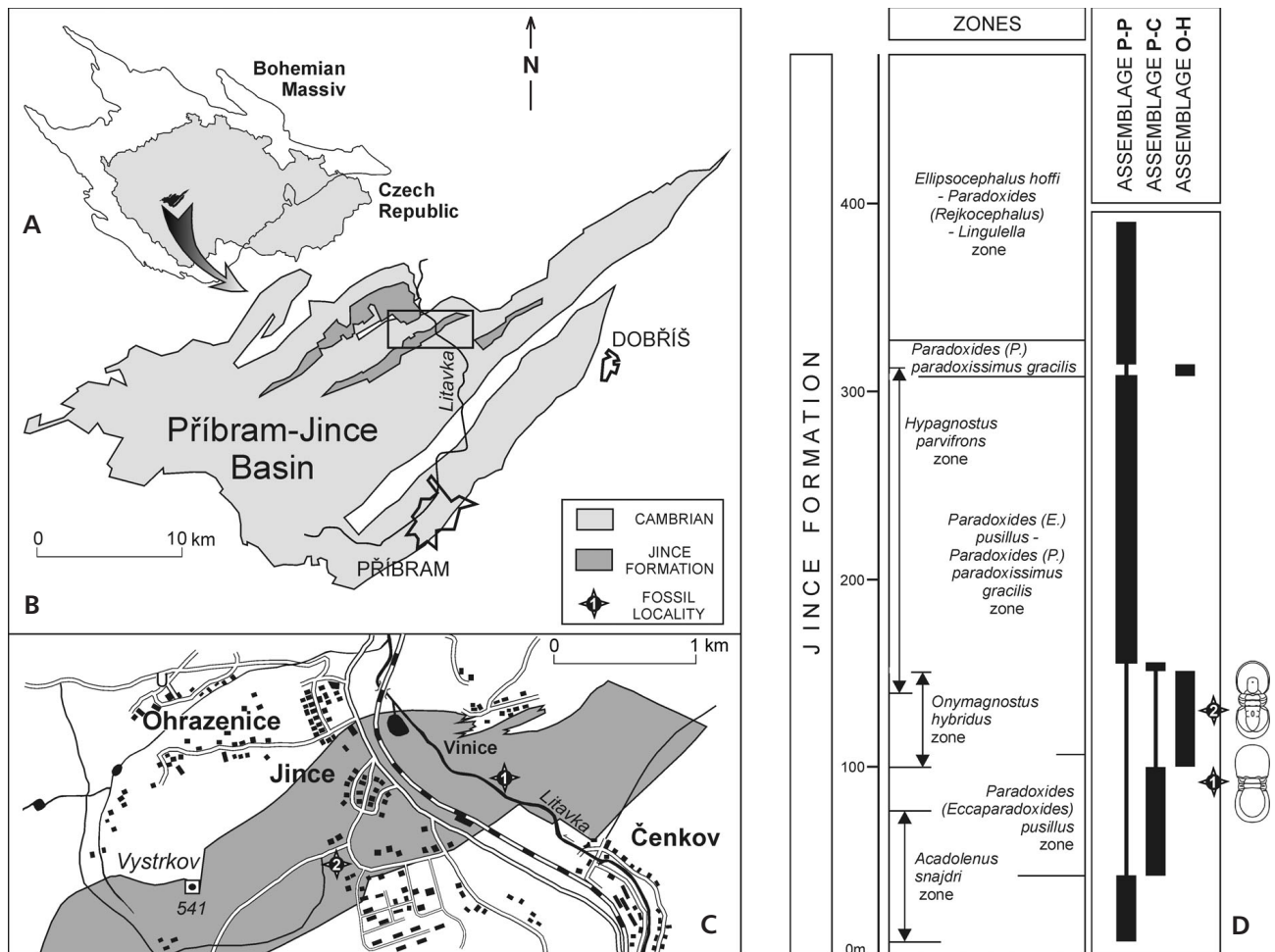


Figure 1. A – map of the Bohemian Massif showing the Czech Republic and the Přebíram-Jince Basin. • B – sketch map of the Přebíram-Jince Basin. • C – map of the Jince area showing location of outcrops at which the described materials have been found: ① Vinice Hill locality near Jince, ② Obalovna locality at Vyrkov Hill. Geology modified after Havlíček (1971). • D – biostratigraphy of Jince Formation in the Přebíram-Jince Basin with marked levels at which the malformed specimens of *Phalagnostus prantli* Šnajdr, 1957 and *Hypagnostus parvifrons* (Linnarsson, 1869) were collected. Also shown are the vertical distribution of agnostid assemblages (P–P = *Peronopsis–Phalagnostus*; P–C = *Phalacroma–Condylopyge*; O–H = *Onymagnostus–Hypagnostus*). Modified after Fatka *et al.* (2004, 2007) and Fatka & Szabad (in press).

distribution of these three assemblages reflect transgressive-regressive pulses during sedimentation of the Jince Formation and agree with the Cambrian biofacies model established by Bordonaro *et al.* (2008).

All the assemblages and the majority of agnostid species show an apparent relation to palaeobathymetrical and sedimentological gradients.

Recently two anomalous agnostid specimens have been collected at two different outcrops of the Jince Formation in the Litavka river Valley (Fig. 1). The first of the malformed specimens, an articulated exoskeleton of *Phalagnostus prantli* Šnajdr, 1957 was collected from higher levels of the *Paradoxides (Eccaparadoxides) pusillus* Biozone on the slopes of Vinice Hill near Jince (Fig. 1C, D). The second example is represented by an internal mould of a small articulated specimen of *Hypagnostus parvifrons* (Linnarsson, 1869) and comes from the stratigraphically

higher *Onymagnostus hybridus* Biozone at the Obalovna locality at the Vyrkov Hill (Fig. 1C, D).

Phalagnostus prantli Šnajdr, 1957

Figure 2A, B

Description. – Complete exoskeleton with slightly displaced and rotated cephalon; pygidium and both thoracic segments associated, preserved as internal and external moulds in mudstone. Both moulds show atypically developed posteral pygidial margin as well as flattened pygidial furrow in its right postero-lateral sector (Fig. 2A). The pygidial margin bears five (?six) irregular bite (?) marks of different dimensions and shape. Three of them are interconnected (arrows a, b, c in Fig. 2B), two other a little smaller ‘bites’ are seen on the right postero-lateral part of

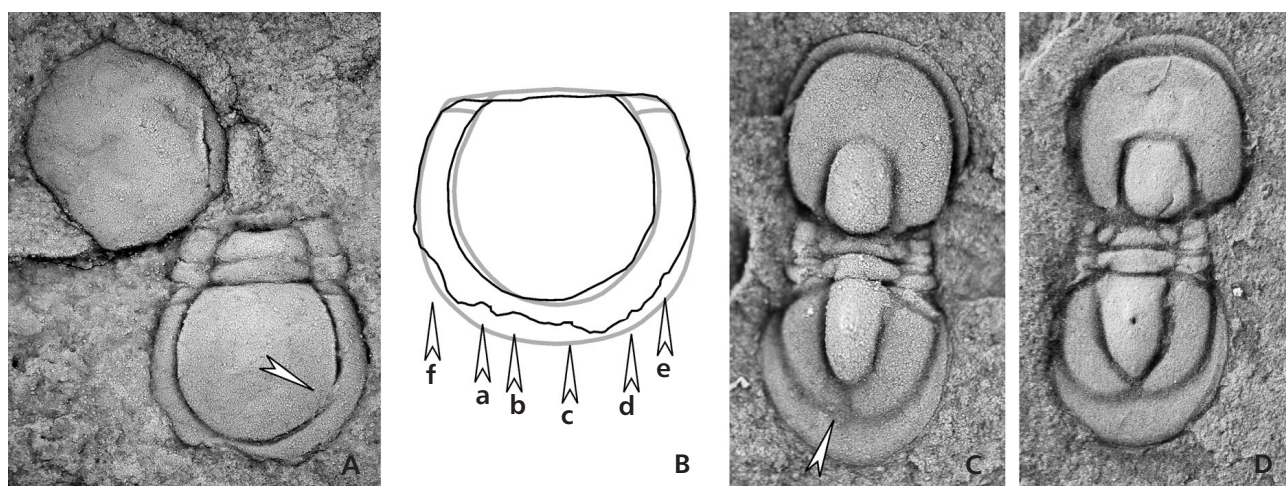


Figure 2. A – *Phalagnostus prantli* Šnajdr, 1957; internal mould with repaired injury on the posterior pygidial margin. CGS VL 176. • B – schematic drawing of the same pygidium (thin black line) with the six possible bites (arrows a–f) compared with normal pygidial morphology (grey line). • C – *Hypagnostus parvifrons* (Linnarsson, 1869); internal mould of pygidium with asymmetrically developed axial region. CGS SZ 227. • D – *Hypagnostus parvifrons* (Linnarsson, 1869); internal mould. CGS SZ 228. All specimens are stored in the Czech Geological Survey, Prague.

the pygidial margin (arrows d and e in Fig. 2B). The larger of the ‘bites’ is on the left postero-lateral sector of the pygidial margin (arrow f in Fig. 2B). Also, the right postero-lateral pygidial furrow is shallower and interrupted (arrow in Fig. 2A). All these morphological changes can be explained as resulting from a failed predatory attack.

Associated fauna. – At this outcrop the fossil association includes the common agnostids *Phalagnostus prantli* Šnajdr, 1957, *Peronopsis integra* (Beyrich 1845), *Phalacroma bibullatum* (Barrande, 1846), associated with complete specimens as well as disarticulated exoskeletal parts of the polymerid trilobites, e.g., *Paradoxides (Eccaparadoxides) pusillus* (Barrande, 1846), *Paradoxides (Acadoparadoxides) sacheri* (Barrande, 1852), *Paradoxides (Hydrocephalus) minor* (Boeck 1827), *Conocoryphe* spp., rare linguliformean and acrotretacean brachiopods, molluscs, edrioasteroid, eocrinoid and ctenocystid echinoderms and simple trace fossils (see Fatka et al. 2004). At this stratigraphical interval, agnostids of the shallow-water *Peronopsis-Phalagnostus* Assemblage occur together with taxa of the relatively deeper-water *Phalacroma-Condylopyge* Assemblage (Fig. 1D).

***Hypagnostus parvifrons* (Linnarsson, 1869)**

Figure 2C, D

Description. – Internal and external moulds of the tiny intact specimen show asymmetrically developed left postero-lateral margin of the pygidial axis and the left lateral pleural lobe. This results in the pygidium showing an apparent asymmetry when compared with normal specimens (cf. Fig. 2C, D).

Morphological changes on this pygidium recall the pathological specimen of *Glyptagnostus stolidotus* Öpik, 1961 in which the left side of the pygidium is also hypertrophic (see Öpik, 1967, p. 168, pl. 67, fig. 2).

Associated fauna. – At this stratigraphical level the fossil association is dominated by commonly articulated agnostids, *Doryagnostus vinicensis* (Šnajdr, 1957), *Hypagnostus parvifrons* (Linnarsson, 1869), *Onymagnostus hybridus* (Brøgger, 1878), *Peronopsis integra* (Beyrich, 1845), *Phalacroma bibullatum* (Barrande, 1846), *Phalagnostus prantli* Šnajdr, 1957 and *Tomagnostus perrugatus* (Grönwall, 1902) associated with the common polymerid trilobite *Paradoxides (Hydrocephalus) minor minor* (Boeck, 1827) and the rare *Luhops expectans* (Barrande, 1852), as well as rare representatives of the bivalved arthropod *Tuzoia* Walcott, 1912 (see Fatka et al. 2004).

Agnostid palaeoecology

Mode of life of agnostids has been repeatedly discussed. Lochman-Balk & Wilson (1958), Öpik (1961), Robison (1972, 1975) and Jago (1973) provided arguments for their planktic life habit. However, a benthic life habit was first proposed by Jaekel (1909), it has been considered also by Robison (1972) and Müller & Walossek (1987) for several species of *Peronopsis* and for *Agnostus pisiformis*. More recently Babcock (1994), Nielsen (1997) and Chatterton et al. (2003) put forward various arguments for a benthic mode of life for agnostids. Also, Elicki & Pillola (2004) classified the genera *Condylopyge* and *Peronopsis* as benthic detritus suspension- or deposit-feeders. Clusters of complete specimens of several Ordovician agnostid

species were used as an argument for an epifaunal life habit by Pek (1977), Příbyl & Vaněk (1976), Havlíček *et al.* (1993) and Slavíčková & Kraft (2001). Öpik (1979) supported a microfiltration mode of life for agnostids on drifting algae, while Lochman-Balk (1940) supported an infaunal mode of life. Bergström (1973) considered that agnostids were ectoparasites. In several detailed analyses by Clarkson *et al.* (1998), Eklöf *et al.* (1999), Turvey & Zhou (2004) and Bruton & Nakrem (2005) the agnostid life habit was left open. Recently Lin & Yuan (2008) interpreted the eodiscid trilobite genus *Pagetia* as having benthic mode of life.

Lochman-Balk & Wilson (1958, p. 322) wrote that “The Agnostidae also are essentially adapted to the extracratonic biofacies. Only the ubiquitous *Peronopsis* is common in cratonic sites, but more genera appear in the intermediate realm.” Later, Robison (1975) elaborated a model of inferred depth stratification of agnostids. He supposed that the species *Peronopsis fallax* (Linnarsson, 1869) (= *Peronopsis acadica* Hartt (*in* Dawson, 1868) after Robison 1995) preferred to live in shallower water compared to some other agnostoids [*e.g.*, *Peronopsis interstricta* (White, 1874) or species of the genus *Ptychagnostus* Jaekel, 1909].

Discussion

Documentation of ancient predation is difficult. However, in rare cases, direct evidence of predator attack is observable in the skeletons of prey organisms (see Vermeij 1987).

The host sediment of the studied agnostids; the fine greywackes and mudstones of the Jince Formation contain well-preserved, often articulated specimens of agnostids and polymerid trilobites (*cf.* Fatka & Szabad *in press*). The high proportion of articulated specimens suggests minimal transportation of the assemblage and rules out a mechanical (non-biological) origin as the cause of the damage to *Phalagnostus*. By analogy with repaired skeletal injuries in Cambrian and other trilobites, the marginal scars in *Phalagnostus prantli* are interpreted here as a repaired sublethal injury following failed predation.

Phalagnostus prantli may have been the prey of contemporaneous paradoxid trilobites, whose functional morphology suggests a predatory lifestyle (Fortey & Owens 1999, Babcock 2003). The other potential predator is the arthropod *Tuzoia* sp. which occurs only rarely in the given stratigraphical level of the Jince Formation.

The apparently asymmetrical left posterolateral margin of the pygidial axis and the left lateral pleural lobe developed in both external and internal mould of *Hypagnostus parvifrons* is interpreted here as a possible teratology *s. s.*, *e.g.*, caused probably due to genetical malformation.

Conclusion

Within several thousand agnostids collected from the Jince Formation, only one exoskeleton shows a healed injury developed on the posterior pygidial margin, most probably representing sublethal predation. This low frequency of repaired injuries in the Cambrian Jince agnostids could reflect the inefficiency of Palaeozoic predators in breaking minute but robust CaCO₃ exoskeletons, as supposed by Vermeij (1987).

The producer of the injury is unknown. It is likely that the potential predators known from the Jince Formation (paradoxid trilobites with only weakly mineralized gnathobases and/or specimens of the genus *Tuzoia*) were most probably not able to crush the robust, minute and sphaeroidal but heavily mineralized agnostid exoskeleton.

The repaired injury is suggested to have been caused by an attack during the “paper shell” stage, *i.e.* soon after exuviation of the agnostid.

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