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Healed injury in a nektobenthic trilobite: "Octopus-like" predatory style in Middle Ordovician?

Oldřich Fatka[1], Petr Budil[2] and Radek Mikuláš[3]

[1] Charles University, Institute of Geology and Palaeontology, Albertov 6, CZ–128 43, Prague 2, Czech Republic; (fatka@natur.cuni.cz)
[2] Czech Geological Survey, Klárov 3, 118 21 Prague 1, Czech Republic; (petr.budil@geology.cz)
[3] Academy of Sciences of the Czech Republic, Institute of Geology, v.v.i., Rozvojová 269, CZ–165 02 Praha 6 – Lysolaje, Czech Republic; (mikulas@gli.cas.cz)

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Abstract

The Lower Paleozoic sediments of the Barrandian area are globally renowned as a classical example of well-preserved skeletal marine fauna, including abundant remains of trilobites. Several tens of morphologically anomalous exoskeletons of trilobites have been collected and documented from Cambrian to Devonian clastic sediments and carbonates. One of them, an exceptionally well preserved, articulated and partly enrolled exoskeleton of the Ordovician nektobenthic trilobite *Parabarrandia bohemica* (NOVÁK, 1884) exhibits a prominent palaeopathological anomaly in its pygidium. We interpret this anomaly as a healed traumatic injury and attribute this damage to a failed predatory attack. The subsequently healed injury is classified as the ichnogenus *Oichnus* BROMLEY, 1981. The structure on the pygidium is strongly reminiscent of injuries caused by octopods and a large cephalopod is proposed as a potential durophagous predator responsible for the herein described trilobite injury. However, an attack from an unknown arthropod while the trilobite was in a soft-shelled stage cannot be excluded.

1. INTRODUCTION

Abnormalities and malformations provide a unique insight into the palaeobiology and regenerative abilities of animals, including trilobites (BABCOCK, 2003). The fossil record of trilobites in particular contains numerous examples of morphological abnormalities that have been variously interpreted. OWEN (1985) reviewed all earlier documented trilobitic abnormalities and suggested three types: injuries, pathologies, and teratologies. OWEN (1985), BABCOCK (1993, 2003, 2007), FATKA et al. (2015), BICKNELL & PATERSON (2018), BICKNELL & PATES (2020) concluded that the majority of trilobite abnormalities represent healed injury. The general rarity of repaired injuries in trilobites suggests that predatory attacks (particularly on soft-shelled individuals) were often successfully executed (BICKNELL & PATERSON, 2018).

In the Barrandian area, the study of anomalous trilobite exoskeletons has a long tradition. BARRANDE (1852, pl. 9, FIG. 19)

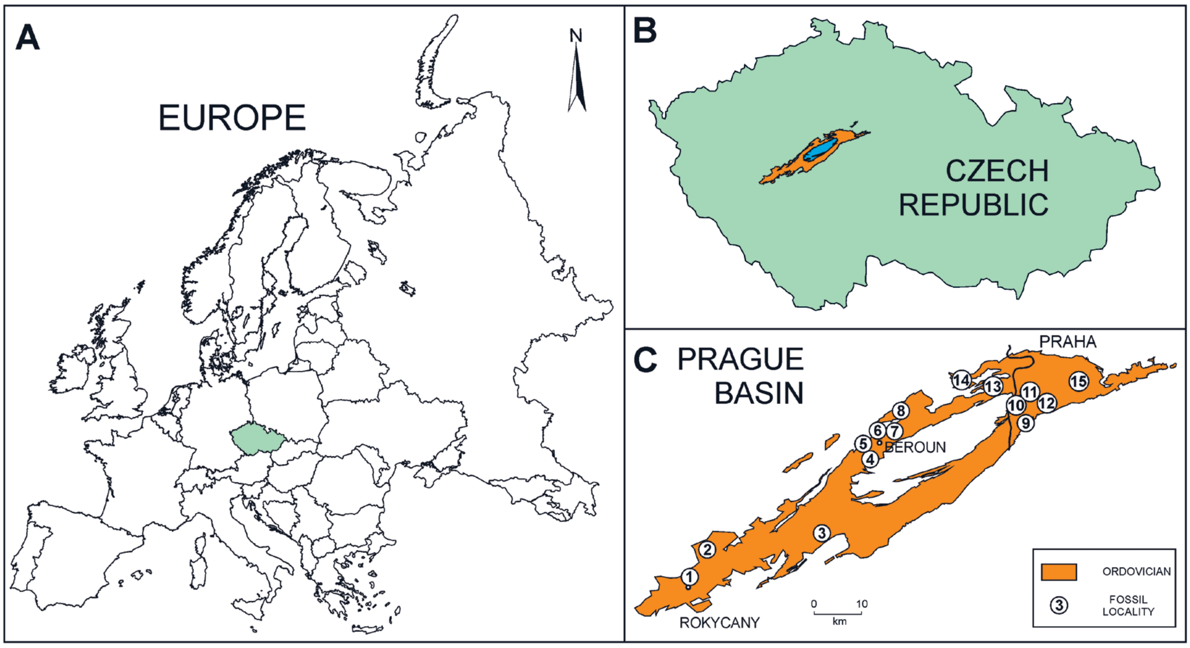

Figure 1. Location of the Prague Basin. **A.** Map of Europe showing the Czech Republic, **B.** Map of the Czech Republic with the location of the Prague Basin. The studied specimen comes from the Šárka locality, **C.** Detailed geographical position of the named localities within the Prague Basin. Localities: 1 – Osek, 2 – Čilina, 3 – Svatá Dobrotivá, 4 – Králův Dvůr, 5 – Drabov, 6 – Brdatka, 7 – Veselá, 8 – Malé Přílepy, 9 – Libuš, 10 – Hodkovičky, 11 – Michle, 12 – Spořilov, 13 – Jinonice, 14 – Šárka, 15 – Hloubětín and Štěrboholy.

Table 1. Summary of trilobites with abnormalities documented from the Ordovician of the Barrandian area

Species	Anomaly / culprit of the attack	Contribution	**Stratigraphy / locality** (Figs 1 and 2)
Pricyclopyge binodosa binodosa (SALTER, 1859)	large anomalous eye / culprit unknown	MAREK (1961, pl. 2, fig. 8), KRAFT (1972, pl. 3, fig. 6), BRUTHANSOVÁ (2004, Text-fig. 8G)	middle-late Darriwilian (Šárka Formation) / Osek or Praha – Libuš locality
Asaphellus desideratus (BARRANDE, 1872)	extensive injury of pygidium / supposedly nautiloid cephalopod	ŠNAJDR (1980)	middle-late Darriwilian (Šárka Formation) / unknown
Areiaspis barrandei (NOVÁK in PERNER, 1918)	shortened and healed left pleura of the 9th thoracic segment / culprit unknown	BUDIL et al. (2010, p. 100-102, fig. 3A-C)	middle-late Darriwilian (Šárka Formation) / Osek locality
Parabarrandia bohemica (NOVÁK, 1884)	pygidium bearing two punctures surrounded by swelling / large cephalopod or unknown arthropod	This study	middle-late Darriwilian (Šárka Formation) / Praha – Šárka locality
Eoharpes benignensis (BARRANDE, 1872)	teratological right margin of brim / culprit unknown	PRANTL & PŘIBYL (1954, pl. 10, fig. 3)	late Darriwilian – early Sandbian (Dobrotivá Formation) / Svatá Dobrotivá locality
Placoparia zippei (BOECK, 1827)	anomalous third to fifth right pleurae of thorax / culprit unknown	ŠNAJDR (1979b, fig. 1)	late Darriwilian – early Sandbian (Dobrotivá Formation) / Malé Přílepy locality
Placoparia zippei (BOECK, 1827)	anomalous glabellar lobe L2 / culprit unknown	ŠNAJDR (1979b, figs 2, 3)	late Darriwilian – early Sandbian (Dobrotivá Formation) / Malé Přílepy locality
Placoparia zippei (BOECK, 1827)	anomalous glabellar lobe / culprit unknown	ŠNAJDR (1979b, fig. 4)	late Darriwilian – early Sandbian (Dobrotivá Formation) / Praha – Hodkovičky locality
Dalmanitina socialis (BARRANDE, 1846)	first to third pleurae at the right side of pygidium / culprit unknown	ŠNAJDR (1956, pl. 4, fig. 2)	middle Sandbian (Letná Formation) / Čilina at Rokycany locality
Dalmanitina socialis (BARRANDE, 1846)	anomalous right fixigena / durophagous predator	ŠNAJDR (1990, p. 58-59)	middle Sandbian (Letná Formation) / Beroun, exact locality unknown
Dalmanitina socialis (BARRANDE, 1846)	anomalous pygidial axis and of both right and left pleurae / durophagous predator	ŠNAJDR (1990, p. 60-61)	middle Sandbian (Letná Formation) / Beroun, exact locality unknown
Dalmanitina socialis (BARRANDE, 1846)	anomalous three anterior pleurae at the right side of pygidium / culprit unknown	VOKÁČ (1996, p. 20, fig. 5)	middle Sandbian (Letná Formation) / Drabov near Beroun locality
Dalmanitina socialis (BARRANDE, 1846)	anomalous three anterior pleurae at the left side of pygidium / culprit unknown	VOKÁČ (1996, p. 20, fig. 6)	middle Sandbian (Letná Formation) / Veselá near Beroun locality
Dalmanitina socialis (BARRANDE, 1846)	deformed right fixigena and librigena of cephalon / culprit unknown	VOKÁČ (1996, p. 20, fig. 7)	middle Sandbian (Letná Formation) / Veselá near Beroun locality
Dalmanitina socialis (BARRANDE, 1846)	regenerated visual surface of the left eye, the palpebral lobe, the librigena and the fixigena / supposedly large arthropod or nautiloid cephalopod	FATKA et al. (2021, figs 4-7)	middle Sandbian (Letná Formation) / Veselá near Beroun locality
Eccoptochile clavigera (BEYRICH, 1845)	anomalous morphology of the second and third pleural lobe of pygidium / supposedly large arthropod or nautiloid cephalopod	ŠNAJDR (1980, pl. 1, fig. 2),	middle Sandbian (Letná Formation) / Drabov near Beroun
Eccoptochile clavigera (BEYRICH, 1845)	anomalous morphology of the second and third pleural lobes / supposedly large arthropod or nautiloid cephalopod	MORAVEC (2006, figs 1-3)	middle Sandbian (Letná Formation) / Veselá locality
Deanaspis goldfussi (BARRANDE, 1846)	traumatic damage of the right anterolateral margin of cephalic fringe, callused distal end of the fifth and sixth right thoracic pleura and right posterolateral margin of pygidium / unknown	ŠNAJDR (1979a, p. 49, pl. 1, fig. 1)	middle Sandbian (Letná Formation) / Praha – Letná locality
Deanaspis goldfussi (BARRANDE, 1846)	irregular distribution of fringe pits / unknown	ŠNAJDR (1979a, p. 49, pl. 1, fig. 2)	middle Sandbian (Letná Formation) / Praha – Letná locality
Deanaspis senftenbergi (HAWLE & CORDA, 1847) as *Marrolithus senftenbergi*	callused rounded indentation at the left postero-lateral margin of pygidium / unknown	ŠNAJDR (1979a, p. 49, pl. 1, fig. 4)	late Sandbian to early Katian (Vinice Formation) / Praha

figured a pathological cephalon of the Devonian *Lioharpes venulosus* (HAWLE & CORDA, 1847). Other pathological specimens were studied by PRANTL (1948, 1954). In the last sixty years, numerous trilobite exoskeletons showing healed traumatic injuries and other kinds of anomalies have been documented from Cambrian to Devonian deposits (e.g., PRANTL & PŘIBYL, 1954; ŠNAJDR, 1978a, b, 1981, 1985, 1990a, b; BUDIL et al., 2010; FATKA et al., 2009, 2015; BICKNELL et al. 2021).

Here we describe an internal mould of the nileid trilobite *Parabarrandia bohemica* (NOVÁK, 1884) housed in collections of the National Museum Prague. This partly enrolled specimen shows the below described palaeopathological anomaly on its pygidium.

2. GEOLOGICAL SETTING

Ordovician skeletal fossils, including trilobites, have been known for more than 200 years in the Barrandian area (e.g., SCHLOTHEIM, 1823; BARRANDE, 1846; for summary see BRUTHANSOVÁ et al., 2007). The late Middle-early Upper Ordovician Šárka and Dobrotivá formations of the Prague Basin (Fig. 1) are a classical source of diverse and well-preserved skeletal fauna (e.g., HAVLÍČEK & VANĚK, 1966), including abundant trilobites (BUDIL et al., 2007). A rich association of disarticulated and articulated trilobites, agnostids, echinoderms, brachiopods, hyoliths, organic-walled microfossils, and graptolites associated with remains of phyllocarid crustaceans, bivalves, cephalopods, ostracods, and trace fossils have been thoroughly examined from these two formations for nearly two hundred years (CHLUPÁČ, 1970; KRAFT, 1972; BUDIL et al., 2007; MANDA, 2008; POLECHOVÁ, 2013; LAJBLOVÁ & KRAFT, 2014; AUBRECHTOVÁ & TUREK, 2018; KRAFT et al., 2020). Since the 19th century studies, several tens of thousands articulated trilobite exoskeletons have been collected at several tens of outcrops of Middle Ordovician rocks (e.g., MAREK, 1961; BUDIL et al., 2007; MERGL et al., 2008). Such extensive material occasionally includes anomalous specimens.

2.1. Previously described cases of anomalous trilobites

From the Barrandian area, twenty anomalous trilobites showing healed traumatic injuries have been reported from late the Middle to early Late Ordovician strata; data about these earlier reports are summarized in Table 1 and Figures 1 and 2.

3. MATERIAL AND METHODS

The studied specimen of *Parabarrandia* is preserved as an internal mould in a siliceous nodule and is housed in the National Museum, Prague (inventory number NM L59869). The external mould is unknown. The specimen was collected by V. Schüs from an unknown locality within the Praha-Šárka area in 1943. Considering the lithology, it is likely to have been from the “U trianglu” site, which is within the higher levels of the Šárka Formation (see PERŠÍN & BUDIL, 2009). The specimen was coated with ammonium chloride to enhance contrast and photographed with a digital Canon EOS 70 D camera.

4. DESCRIPTION OF THE INJURED PARABARRANDIA (FIG. 3)

The dorsoventrally flattened, slightly damaged and partly enrolled exoskeleton is 42 mm wide and 90 mm long. The smooth

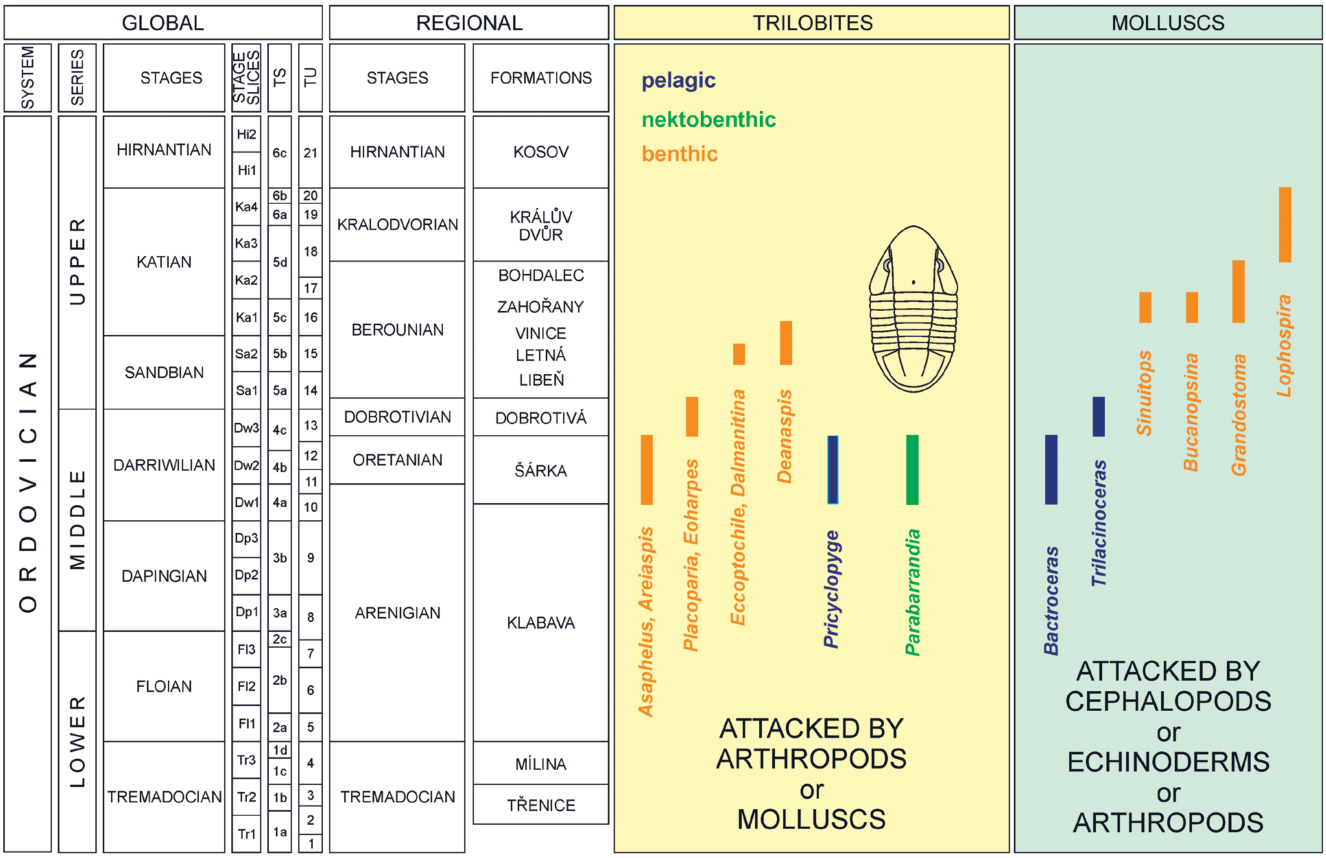

Figure 2. Stratigraphic ranges of injured trilobites and molluscs from the Ordovician of the Prague Basin (Barrandian area, Czech Republic). Correlation modified from FATKA et al. (2013), GUTIÉRREZ-MARCO et al. (2017) and COLMENAR et al. (2017).

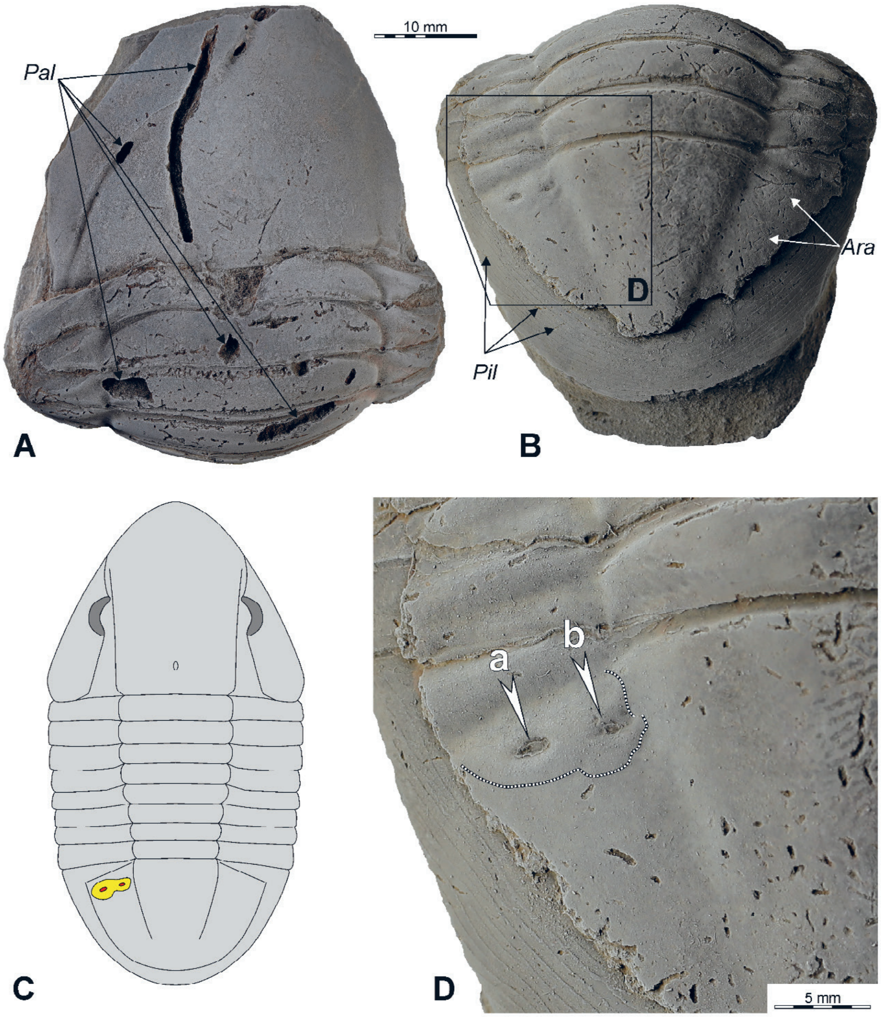

Figure 3. *Parabarrandia bohemica* (NOVÁK, 1884), Šárka Formation (Middle Ordovician, middle-late Darriwilian), Prague Basin, Praha-Šárka locality. Internal mould of the partly enrolled exoskeleton housed in the National Museum Prague under the inventory number NM L59869.

A. View of the cephalon with four anterior thoracic segments, **B.** View of the pygidium with exposed doublure and the three posterior-most thoracic segments, **C.** Reconstruction of the unrolled exoskeleton (adopted after FORTEY, 1985, fig. 5C), **D.** Detail of the left side of the pygidium showing the position of the two punctures (a and b) and the surrounding swelling (marked by dotted line). *Ara* - *Arachnostega* isp., *Pal* - *Palaeophycus* isp., *Pil* - *Pilichnus* isp. A, B, D – coated with ammonium chloride.

surface of the internal mould has slender unbranched to irregularly branched burrows assigned herein, following KRAFT et al. (2020), to the ichnogenera *Palaeophycus* HALL, 1847, *Arachnostega* BERTLING, 1992 and *Pilichnus* UCHMAN, 1999. Unbranched cylindrical tunnels in the cephalon and the thoracic axis (reaching ~ 2 mm in diameter) are classified as *Palaeophycus* isp. (*Pal* in Fig. 3A). Narrow straight to slightly curved tunnels are common at the axial surface of the thorax and are observed in the axial and pleural pygidial surface; several intricate tunnels are noted in thoracic pleurae. Such fine homogeneously distributed tunnels along the internal surface of the exoskeleton are classified as *Pilichnus* isp.

A wide pygidial doublure with fine terrace lines is exposed due to breaks of pleurae and lateral, posteriolateral and posterior pygidial margin. Several minute *Pilichnus* isp. are also seen in the doublure (*Pil* in Fig. 3B). Fine, ramified burrows on the surface of internal moulds with an oval cross-section are classified as *Arachnostega* isp. (*Ar* in Fig. 3B). *Pilichnus* has primarily been described from fine-grained soft substrates (UCHMAN, 1999). In accordance with the limited acceptance of the substrate as an ichnotaxobase (BERTLING et al., 2006), we can also classify as *Pilichnus* thin branched tunnels made in direct contact with the trilobite shell. *Pilichnus* built in this way can be transferred to more complex systems corresponding to *Arachnostega*. We suggest that transitional forms between *Pilichnus* isp. (= thin branch tunnels in contact with the shell) and *Arachnostega* isp. (= open or almost closed networks in contact with the shell) can exist and are observed on the studied specimen.

Two prominent punctures are observed on the left anterior surface of the pygidial pleural field (arrows in Figs. 3B, D). The larger puncture is elliptical with its longer axis oriented parallel with the pleural furrow (a in Fig. 3D). The longer axis of this puncture reaches ~ 1.8 mm. The smaller puncture is rounded and measures 0.9 mm in diameter (b in Fig. 3D). Both punctures represent small craters surrounded by an elliptical swelling, which is ~ 9.5 mm wide and 4 mm long (dotted line in Fig. 3D).

Remarks. Morphologically comparable pit developed on upper and lower lamellae of the bilaminar cephalic fringe of the Silurian trilobite *Bohemoharpes ungula* was described and figured by ŠNAJDR (1978b, pl. 1, figs. 1-5; 1990, p. 62-63), who interpreted this anomaly as resulting from an activity of an endoparasitic organism. Recently, this interpretation was also accepted by DE BAETS et al. (2022, Table 1).

5. DISCUSSION

The Ordovician record of injured skeletal invertebrates in the Barrandian area includes gastropods, cephalopods, and trilobites. Up to now, only two injured brachiopods are known (BUDIL & FATKA, unpublished observation).

5.1. Injured gastropods

Failed predation and shell repair in Ordovician bellerophontoidean gastropods were studied by HORNÝ (1996, 1997a, b, c) who reported examples of repaired shell breakage in *Sinuitops neglecta* BARRANDE in PERNER, 1903, *Bucanopsina calypso* (PERNER, 1903), *Grandostoma bohemicum* (PERNER, 1903), and *Lophospira infausta* (BARRANDE in PERNER, 1903) from the Zahořany, Bohdalec and Králův Dvůr formations (Fig. 3). These specimens were collected from different districts of Prague, for example Spořilov, Michle, Hloubětín, Štěrboholy, Jinonice, and the Králův Dvůr locality (Fig. 1C). HORNÝ (1997a, p. 168-169) distinguished three types of shell injuries in bellerophontoidean gastropods: (1) scaloped U-shaped marginal breakages, (2) a scalloped crescentic marginal breakage, and (3) a deep local injury without a shell breakage and not representing the *Oichnus*-trace fossil. The first type was interpreted as injuries caused by predatory molluscs, likely small cephalopods; the second type was ascribed to non-biological causes or attacks by a small chelicerate arthropod or predatory echinoderms (e.g., ophiuroids). The third type of injury was explained as an injury made possibly by an ophiuroid or trilobite by HORNÝ (1997a, p. 167).

5.2. Injured cephalopods

AUBRECHTOVÁ (2015, p. 196, fig. 9C, J) described and figured two specimens of *Bactroceras sandbergeri* BARRANDE, 1867 with sub-lethally damaged shells from the middle-late Darriwilian Šárka Formation from the Osek and Šárka localities. Recently, AUBRECHTOVÁ & TUREK (2018, p. 408, figs. 5D, E, G) figured and briefly described *Trilacinoceras* cf. *discors* (HOLM, 1891) with sublethal shell damage associated with anomalous growth (Figs. 1C, 2) from the Dobrotivá Formation from the Šárka locality.

5.3. Injured trilobites

OWEN (1985), BABCOCK (1993, 2003, 2007), BICKNELL & PATERSON (2018), BICKNELL & SMITH (2021) and BICKNELL et al. (2022) published comprehensive reviews of trilobite abnormalities and discussed their possible causes. Injuries observed in diverse parts of the exoskeleton were ascribed to damage due to predation or during ecdysis (BABCOCK, 1993, p. 220). RUDKIN (1979, 1984), BICKNELL & PATERSON (2018, p. 5) and PATES & BICKNELL (2019) considered sub-lethal injuries of trilobites during a moulting event showing signs of regeneration including an over-thickened (calloused) cuticle along the scar. Conversely, injuries without callouses are attributed to attacks on fully calcified individuals (JAGO & HAINES, 2002).

In the Barrandian area, injured trilobites have been classified to nine genera (Table 1). The oldest recorded are the few trilobites from the Šárka Formation; similarly, there are rare specimens showing healed injuries in the overlying Dobrotivá Formation (Table 1, Fig. 2). The most abundant injured trilobite specimens are observed in the late Sandbian Letná Formation, and the youngest malformed specimen was described from the late Sandbian - early Katian Vinice Formation (Table 1, Fig. 2).

In following sections 5.3.1 – 5.3.3, the current knowledge on the supposed lifestyle of trilobite specimens is summarised. This summary reviews the potential predators. Some trilobites were able to eliminate the predation pressure by cryptic behaviour (see FATKA & BUDIL, 2014), while other heavily skeletonised species or good swimmers effectively used passive defensive strategies.

5.3.1. Benthic trilobites

In the Barrandian area, most Ordovician trilobites with healed traumatic injury after failed predatory attacks have been classified as benthic and nektobenthic forms.

Placoparia zippei

Placoparia is one of the most common Ordovician trilobites in the Barrandian area (BRUTHANSOVÁ & BUDIL, 2003). Because of the thick exoskeleton and the unattached (natant) hypostome condition, this blind pliomerid genus has been usually considered as a benthic, partly buried, particle feeder by PŘIBYL & VANĚK (1976, p. 11), HAVLÍČEK & VANĚK (1990, p. 228; 1996, p. 227, 228, 236, 237), VOKÁČ & GRIGAR (2010, p. 162), BRUTHANSOVÁ & BUDIL (2003, p. 217), BUDIL et al. (2007, p. 68), and RÁBANO et al. (2010). FORTEY (1985, p. 228) classified this genus tentatively as an atheloptic trilobite. Also, HENRY (1989, p. 148) included *Placoparia* to taxa typical for the atheloptic assemblage of FORTEY & OWENS (1987).

Because of the wide palaeogeographical distribution of the Darriwillian species *Placoparia cambriensis*, OWENS & SERVAIS (2007, p. 282) expressed the opinion, that this species might have been epipelagic. However, they did not definitely exclude the possibility that *Placoparia* belongs to atheloptic taxa.

Eoharpes and Deanaspis

Deanaspis belongs to the most common trilobites in the Letná Formation (PŘIBYL & VANĚK, 1969). In comparison, remains of *Eoharpes* are always rare in the Šárka and Dobrotivá formations (FATKA & BUDIL, 2014). Species of both *Eoharpes* and *Deanaspis* have been interpreted as benthic filter feeders (e.g., HAVLÍČEK & VANĚK 1990, p. 230; 1996, p. 228, 236; MERGL et al., 2008, p. 277). MIKULÁŠ & BUDIL (2013) supposed that in *Deanaspis*, the thorax was held above the water-sediment interface, while the flat cephalic rim and long spines surrounded the filter-chamber beneath the cephalon and thorax, similarly as in *Cryptolithus tesselatus* (see FORTEY & OWENS, 1999, p. 449, Fig. 16). A comparable strategy is also supposed in the morphologically similar harpetids (see FORTEY & OWENS, 1999, p. 448, Fig. 14), including *Eoharpes*. HENRY (1989, p. 148) listed *Eoharpes* as a typical member of the atheloptic assemblage of FORTEY & OWENS (1987).

A cluster of six articulated specimens of *E. benignensis* entombed under a large asaphid pygidium described by FATKA & BUDIL (2014) documents the cryptic behaviour of these benthic trilobites. This gregarious cluster of small trilobites, incapable of a group defence, was explained by the ‘‘guide effect’’ reducing their risk of predation through attack abatement, both through dilution and avoidance effects (see CHILDRESS & HERRNKIND, 1997).

Eccoptochile

Articulated exoskeletons of this large cheirurid trilobite are very rare, while disarticulated remains are quite abundant. HAVLÍČEK & VANĚK (1996, p. 236, 237), MERGL et al. (2008, p. 277) and VOKÁČ & GRIGAR (2010, p. 162) classified *Eccoptochile* as a benthic trilobite.

Dalmanitina

Both disarticulated parts and articulated exoskeletons and *Dalmanitina* are very common in the Letná Formation (FATKA et al., 2021). PŘIBYL & VANĚK (1976, p. 9) classified *Dalmanitina* as a good swimmer occasionally burrowing in the top layer of a shallow water bottom.

Asaphellus

BUDIL et al. (2007, p. 68) and MERGL et al. (2008, p. 277) assigned this genus to large benthic predators. GIBB et al. (2010), and more recently also NETO DE CARVALHO & BAUCON (2016) documented co-occurrence of the trace fossil genera *Rusophycus* and *Cruziana* and articulated exoskeletons of the asaphid trilobite *Asaphellus*. Such close association of the putative tracemarker and its trace documents a benthic life of these large and heavily skeletonised trilobites.

5.3.2. Nektobenthic trilobites

Most pelagic trilobites were poorly streamlined (see FORTEY 1985), and it is supposed that they swam quite slowly. Some larger trilobites like *Parabarrandia* show a hydrofoil shape, with the head end prolonged into an elongate "nose," comparable to extant sharks (FORTEY, 1985) and are hypothesized to have swum much faster.

Areiaspis

BUDIL et al. (2007, p. 68) and MERGL et al. (2008, p. 277) classified rare specimens of this genus as deeper-water nektonic or benthic trilobites. The narrow axis and shape of its exoskeleton precluded good swimming ability.

Parabarrandia

Remains of this large nileid trilobite occur infrequently in the north-eastern part of the Prague Basin. FORTEY (1985, p. 223-224; 2004, p. 450) assigned the large, nileid genus *Parabarrandia* with its very streamlined exoskeleton and long anterior snout (or 'nose') to actively swimming pelagic inhabitants of the mesopelagic cyclopygid biofacies (Fig. 4). In agreement with FORTEY (1985), HENRY (1989, p. 148) reported the occurrence of *Parabarrandia* classified as a mesopelagic predator. In comparison, HAVLÍČEK & VANĚK (1990, p. 228; 1996, p. 228, 236) preferred a benthic life, while BUDIL et al. (2007, p. 68), MERGL et al. (2008, p. 277), PERŠÍN & BUDIL (2009, p. 34), RABANO et al. (2010, p. 420) and DAVID & BUDIL (2015, p. 4) classified it as a nektobenthic trilobite.

5.3.3. Nektonic trilobites

Pricyclopyge binodosa binodosa

This is the most common cyclopygid trilobite in the Šárka Formation (MAREK, 1961; BRUTHANSOVÁ, 2004, p. 304). FORTEY (1985, p. 223) as well as BUDIL et al. (2007, p. 68) and MERGL et al. (2008, fig. 277) classified the poorly streamlined cyclopygid *Pricyclopyge* as a sluggish mesopelagic trilobite.

5.4. Potential predators

In the Ordovician of the Barrandian area, injured gastropods are ascribed to cephalopods, echinoderms and arthropods (HORNÝ, 1996, 1997a, b, c). Injuries to cephalopods were likely interpreted to be made by other cephalopods (AUBRECHTOVÁ, 2015; AUBRECHTOVÁ & TUREK, 2018). The malformed *Parabarrandia bohemica* described and considered here also requires an expla-

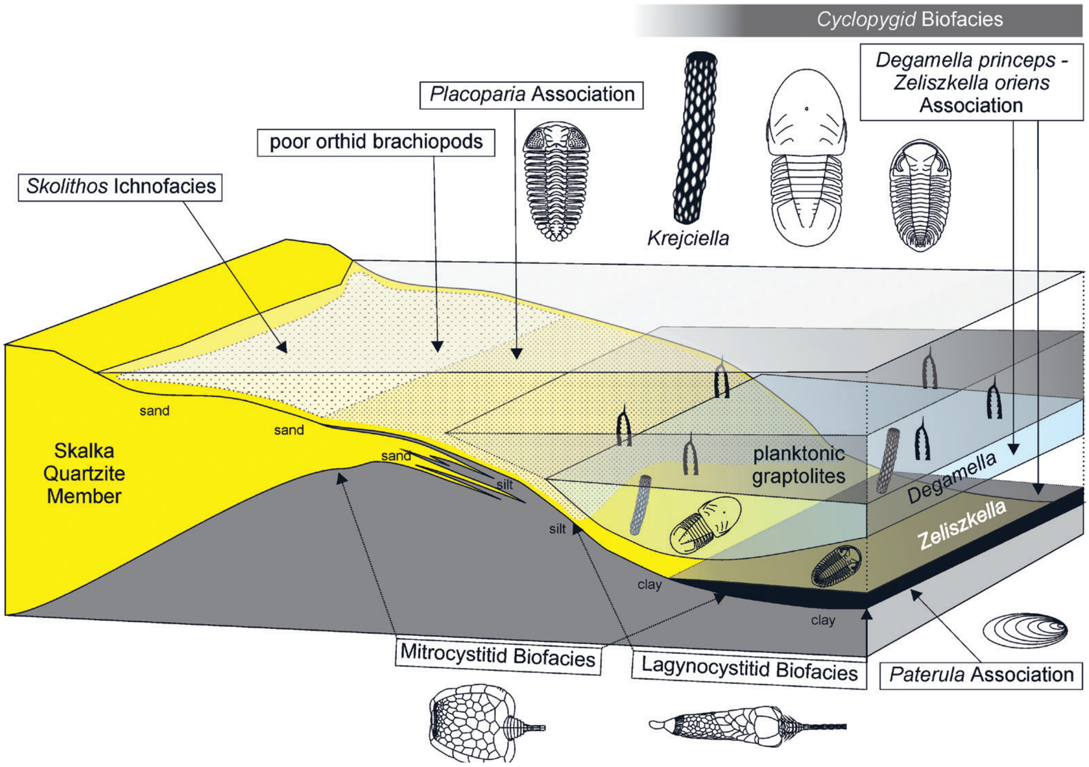

Figure 4. Middle-late Darriwilian Šárka Formation. Sketch representing the distribution of major biofacies associated with the Šárka Formation. The shallowest part of the basin was inhabited by the poor orthid brachiopod association, further basinward, the *Placoparia* Association with rich trilobites, brachiopods and other skeletal fauna prevails; in the offshore slope settings it continuously passed into the poor atheloptic trilobite association which also included the poor benthic dendroid 'gardens'. The water column was inhabited by sparse? planktonic graptolites and taxa of the poorly diverse caryocarids and *Cyclopygid* Biofacies. Poorly oxygenated black shales in the central parts of the basin were dominated by the *Paterula* Association. Modified after FATKA & MERGL (2009) with data published by LEFEBVRE (2007) and FATKA & VODIČKA (in press).

nation. ALPERT & MOORE (1975), WHITTINGTON & BRIGGS (1985), ŠNAJDR (1980, 1981) and RÁBANO & ARBIZU (1999) proposed that sea anemones, anomalocarids and cephalopods caused the injuries of Cambrian and Ordovician trilobites. BICKNELL et al. (2018, 2021 and 2022) suppose that trilobites could damage other trilobites. BRETT & WALKER (2002, p. 94) suggested that priapulids, nautiloid cephalopods, phyllocarid crustaceans and other arthropods (e.g., eurypterids) were likely Ordovician durophagous predators. The recently described specimen of *Dalmanitina* with a malformed and regenerated eye is interpreted as an unsuccessful attack by a cephalopod or a large arthropod (FATKA et al., 2021). From the morphology of the malformed *Parabarrandia*, combined with the large size of the taxon, we exclude predators including sea anemones, anomalocarids, echinoderms, and priapulids as the injury makers. Consequently, cephalopods and arthropods are the potential culprits.

5.4.1. Cephalopods

Recent cephalopods are commonly active carnivorous predators (FERNÁNDEZ-ÁLVAREZ et al., 2018). Similarly, fossil cephalopods are considered carnivorous (NIXON, 1988 but see MIRONENKO, 2020). Large cephalopods were abundant in marine assemblages from the Early Ordovician (e.g., BRETT & WALKER, 2002; KRÖGER, 2011), including the Barrandian area (MANDA, 2008; AUBRECHTOVÁ, 2015 and AUBRECHTOVÁ & TUREK, 2018).

5.4.2. Arthropods

The length of the carapace of planktic phyllocarids does not exceed 50 mm in the Ordovician (RACHEBOEUF & CRASQUIN, 2010). Consequently, phyllocarids are excluded as a potential culprit of the herein studied trilobite. Presuming a benthonic mode of life for Paleozoic marine chelicerates (for eurypterids see BRADY, 2001), sublethal predator–prey interactions between chelicerates and nektobenthic trilobites like *Parabarrandia* might be possible.

5.5. Ichnological aspect

5.5.1. Feeding *post-mortem*

After KRAFT et al. (2020) and other authors, producers of *Palaeophycus* apparently preferred an easily accessible and nourishing food that was easily consumed, e.g., their trace makers selectively oriented on decaying soft tissues. The *Arachnostega* and *Pilichnus* traces are oriented in a manner suggesting systematic feeding. These trace makers spent more time in a carcass. The occurrence of *Palaeophycus*, *Arachnostega* and *Pilichnus* in the internal mould of the *Parabarrandia* attests to a *post-mortem* feeding activity on the trilobite carcass. Also, the perfect articulation of the trilobite exoskeleton suggests a carcass, not an exuvium (see VALLON et al., 2015).

5.5.2. Attack on living specimen of *Parabarrandia*

Two prominent punctures penetrate the trilobite exoskeleton and are surrounded by swelling. The morphology in NM L59868 illustrates, that this exoskeletal anomaly occurred in life of the *Parabarrandia*, likely during the “paper-shelled” stage of HENNINGSMOEN (1975) or “soft-shelled” stage of SPEYER & BRETT (1985). The other possibility is *in vivo* attack by a culprit capable of boring.

Trace fossils representing morphologically recurring, lethal, sub-lethal (not completely successful) or “mistaken” (to empty shell) attacks are called *praedichnia* (see EKDALE, 1985; VALLON et al., 2016). Most documentation of these trace fossils ascribe the record to holes drilled in mollusc and brachiopods. MIKULÁŠ et al. (2006) and JACOBSEN & BROMLEY (2009) introduced ichnotaxonomical names for biting traces, subsequently attributed to *praedichnia* (compare PIRRONE et al., 2014 and VALLON et al., 2016).

Confirmed living marine perpetrators drilling their prey are mainly gastropods and octopod cephalopods (VERMEIJ, 2002, p. 385). Most drill holes are interpreted to be caused by predatory gastropods such as naticids and muricids. BROMLEY (1981) proposed that the ichnofossils that are made by naticid drilling were *Oichnus paraboloides* BROMLEY, 1981 and muricids made *Oichnus simplex* BROMLEY, 1981.

The holes in the pygidium of *Parabarrandia* are morphologically comparable to drill holes found in modern molluscs and crustaceans (e.g., ARNOLD & ARNOLD, 1969; BOYLE & KNOBLOCH, 1981; NIXON & MACONNACHIE, 1988; HARPER, 2002). The elliptical outline and dimensions of our drill holes are in accordance with the morphology of the ichnospecies *Oichnus ovalis* BROMLEY, 1993, an ichnofossil interpreted to be the result of boring by octopod cephalopods (see BROMLEY, 1993; WISSHAK et al., 2015). Further, the drilling of two or even three holes in one shell is a strategy known to be deployed in some species of recent octopods (NIXON & MACONNACHIE, 1988).

NIXON (1979, 1980) reported that in recent *Octopus vulgaris*, the drilling activities are carried out by a salivary papilla lying just below the radula. The role of saliva produced by salivary glands was later shown to be important for a successful attack, as it contains a wide spectrum of paralysing and proteolytic substances (NIXON, 1988, p. 709). Some of them are responsible for the breakdown of the musculo-skeletal attachment mechanism in crabs within 20 min of capture (NIXON, 1984). Similar breakdown of the musculo-skeletal attachment mechanism would probably mean the same for trilobites.

The key ichnogenus *Oichnus* BROMLEY, 1981 and other morphologically similar ichnotaxa have been recently revised (WISSHAK et al., 2015). For the creation of our trace, drilling behaviour seems to be the most plausible because of the absence of sharp edges typical for biting, combined with the diminutive, protected space.

In terms of systematic ichnology, the herein described structures from *Parabarrandia* are attributable to the ichnospecies *Oichnus ovalis* BROMLEY, 1993. Ancient, fossilised structures were interpreted as octopus borings, based on observations from studies of the recent octopods (BROMLEY, 1993; NIXON, 1979, 1980; NIXON & MACONNAICHE 1988). Based on these observations, we interpret the structures observed in the specimen of *Parabarrandia* studied here as resulting from an “Octopus-like” predatory attack.

Origination of the swelling on the internal mould. We suppose that the trilobite was attacked during the “soft-shelled” stage. The thin exoskeleton was probably drilled (= “Octopus-like” predatory style). Consequently, in the injured area, the soft tissue under the unbiomineralised exoskeleton overdeveloped. This swelling would have been recorded during exoskeletal hardening with swelling expressed both on the external and internal surfaces of the exoskeleton.

6. CONCLUSION

(1) The exoskeletal anomaly seen at the left pygidial side of *Parabarrandia* represents a partly healed injury after a failed predatory attack during life.

(2) Two scenarios explain this anomaly:

a – The healed injury classified as the ichnospecies *Oichnus ovalis* BROMLEY, 1993 can be interpreted as an exoskeletal anomaly which originated after a failed "octopus-like" strategy of the predatory attack. This preferred interpretation reflects the nektobenthic lifestyle of *Parabarrandia* and the nektonic lifestyle of the suspected predator.

b – The morphology and the extent of the swelling surrounding both punctures combined with the noticeable absence of any crack of the surrounding exoskeleton indicates the high flexibility of the cuticle during the attack. The attack resulted in two restricted perforations (punctures) followed by plastic deformation of the exoskeleton copying the swelling. In such cases, the injury could result from attack of an unknown predatory arthropod.

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