

Remarks on the palaeoecology of agnostid trilobites

Poznámky o paleoekologii agnostidních trilobitů

(3 figs)

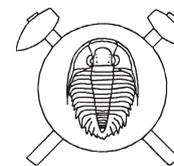
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Several enrolled specimens of agnostid trilobites, partly in an aligned row, from the Šárka Formation (Barrandian Ordovician), occur in a relationship with an enigmatic fossil. This fossil is a fragment of a branched axis resembling similar ones from the Klabava Formation interpreted before as possible octocorals. This association provides evidence for a partly epibenthic mode of life for some agnostids.

Key words: Palaeozoic, Ordovician, Trilobita, Agnostida, problematic octocorals, palaeoecology



Introduction

In general, agnostid trilobites are not very common in the Bohemian Ordovician. They usually occur incomplete as separate cephalons or pygidia, and either isolated or in accumulations with other fauna. The complete specimens occur predominantly enrolled.

Agnostid trilobites of the Šárka Formation (Middle Ordovician) were revised by Pek (1977) in the framework of the overall revision of the Bohemian agnostids and, recently, their stratigraphical occurrence was summarized by Fatka – Pek (1999). They mentioned 7 species from the Šárka Formation. For the species studied herein, we follow the systematic position proposed by Nielsen (1997).

Prantl (1948), Příbyl – Vaněk (1976) and Pek (1977) described agnostid trilobites arranged in clusters or aligned rows from the Bohemian Ordovician. They advocated the epifaunal mode of life for agnostids with attachment on algal strands.

A sample of several enrolled specimens from the Šárka Formation, partly arranged in an aligned row is described in this paper. It represents an extraordinary find on account of its apparent, at least spatial relationship to an enigmatic fossil occurring in close proximity. Such an arrangement of fossils is interpreted as not being an accidental case.

The studied sample is deposited in the National Museum in Prague, Czech Republic, No. L 36065.

Supposed mode of life of agnostid trilobites

Various modes of life have been suggested by many authors for agnostids: pelagic (Robison 1972, Jago 1973, Lochman-Balk – Wilson 1958, etc.), ectoparasitic (Bergström 1973), benthic (Jaekel 1909), infaunal (Lochman 1940), and epifaunal attached to algal strands (Příbyl – Vaněk 1976, Pek 1977). According to Robison's (1972) suggestion, agnostids spent most of their time enrolled, swimming by clapping of the cephalon and pygidium. Clarkson et al. (1998) found this mode of life not to be in contradiction with their observations but the question of agnostid life habits was kept open.

Bergström (1973) concluded that at least some agnostids were ectoparasitic and the ability of enrolling helped them to have a better attachment to their hosts. He also noted that some species were probably pelagic while others might be benthic.

Müller – Walossek (1987) found extremely well preserved phosphatised specimens of *Agnostus pisiformis* with appendages. Based on a functional morphological study of such material, they concluded that agnostids were completely enrolled in a resting or protective position. During locomotion and feeding, tests were slightly opened. These authors suggest a connection with the bottom environment which they stated to be not in conflict with morphological details indicating an ability to swim or float. This idea was recently adopted by Schovsbo (2000) for Cambrian agnostids.

Nielsen (1997) proposed the idea that agnostids originated as benthic trilobites adapted to dysoxic facies with a high production of spat, and, even more so by long-lived spat.

Fortey – Owens (1999) suggested planktic, benthic and probably epipelagic modes of life for various agnostid trilobites. For more specialized agnostids they also supposed a similar mode of life as interpreted for eodiscids. Based on the possession of a natant hypostome they are considered to be benthic feeders on minute organic particles such as algae, detritus, and animalcules. These same authors found the parasitic mode of life (Bergström 1973) improbable. They also criticised the mode of life suggested by Müller – Walossek (1987) while the epifaunal mode of life on free-floating algal strands they supposed to be secondary and developed after a putatively planktic larval phase. According to them, at least some agnostids could adopt this mode of life, which is common among living ostracods.

Geological setting and material

The studied sample of agnostids and the problematic fossil is preserved three-dimensionally in a siliceous nodule which was discovered by I. Chlupáč in the 1950's at Praha-Vokovice. The siliceous nodule was collected on the

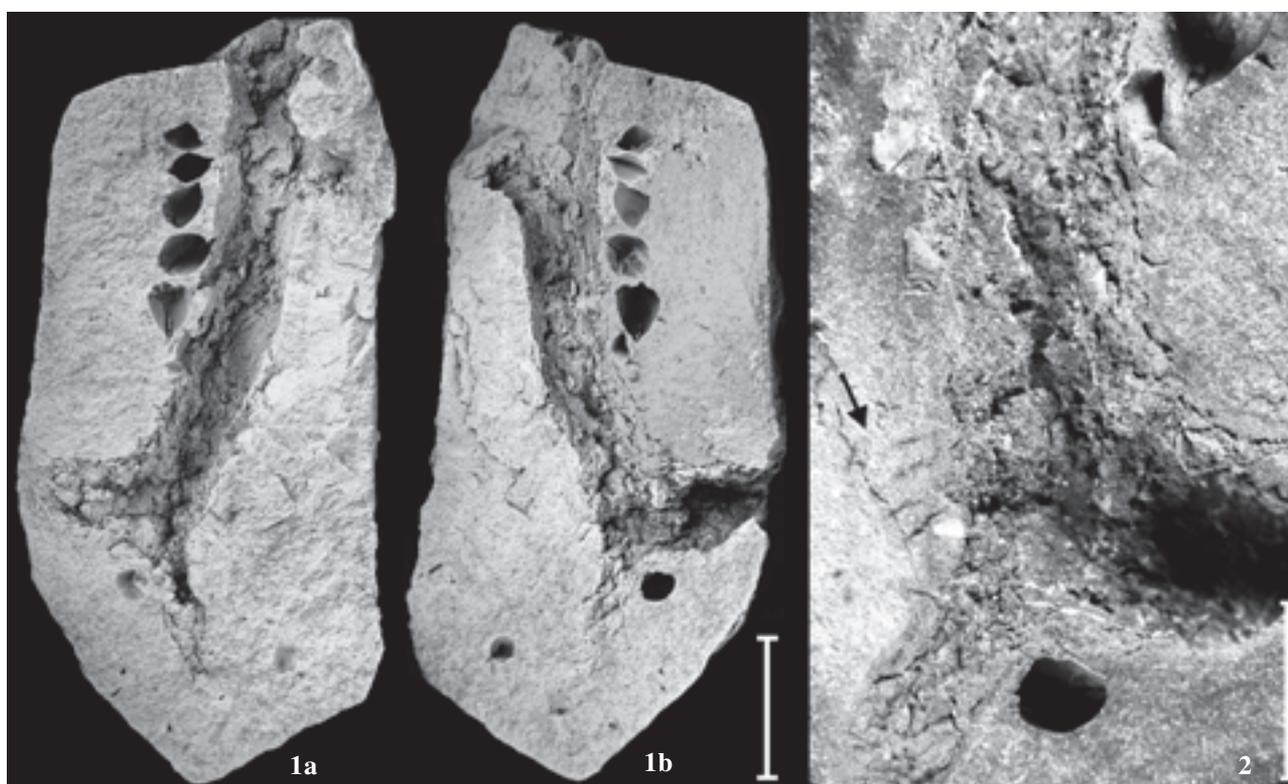


Fig. 1 1a, 1b – Counterparts of the nodule with enrolled *Geragnostus* (*Geragnostella*) *tullbergi* in relationship with the axis-fossil, Praha-Vokovice – field near Bořislavka, L 36056, coated with ammonium chloride, scale bar = 10 mm; 2 – Detail of spine-like processes, portion with four ones indicated by arrow, scale bar = 5 mm.

field between Bořislavka and Červený vrch. At this locality, which does not exist anymore, there occurred nodules mixed from various stratigraphic levels. However, those from the *Didymograptus clavulus* Biozone prevailed. The investigated nodule most probably comes from that biozone. Based on the location, attributes of nodules from the locality and their fossil content, and the shape, size and lithology of the studied nodule it seems that it comes from layers corresponding to the lowermost part of layer 9a (Bouček 1926) which was exposed in the former Vokovice brickfield (Chlupáč pers. com.).

The nodule weathered out from shales of the Šárka Formation (Middle Ordovician, Darriwilian, Llanvirnian). This formation consists of dark shales with horizons of siliceous nodules of early diagenetic origin. In contrast to the fossils from the shales, those from the nodules are 3-D preserved and their spatial orientation can be studied well. However, the investigated fossils are preserved just as external moulds, which is one of the typical modes of preservation in the Šárka Formation nodules. Thus only outer surfaces of fossils can be studied.

Description

The fossils are preserved in a broad spindle-like siliceous nodule which is 56 mm long and max. 26 mm in diameter. Its longitudinal shape is determined by the contained remain of the axis-fossil. This fragment is 48 mm long and is of circular outline, maximum 7.5 mm in diameter. The main axis is two or possibly three times laterally branched.

The interval between two apparent secondary branches alternating to opposite sides is 27 mm. The surface of this fossil, by contrast with the agnostids, is heavily limonitized. The limonite forms a thin layer (“crust”), in some portions extended up to the infilling of the space of the external mould. The outline of this fossil is diffused rather than sharp in some portions because of the limonitization. Its visible surface is coarse and tuberos with some irregular longitudinal linear structures indicated. The axes bear on their surface spine-like processes. These hair-like processes are some 2 mm long and not straight but slightly wavy. They are also limonitized and thus well marked as brown lines in the dark grey material of the split nodule. The spiny processes were observed only sporadically, but in one portion four in a row indicate their quite dense distribution. These 4 processes occur within 2.5 mm.

Eight specimens of agnostid trilobites, all enrolled, are situated close to the axis-fossil. All determinable specimens belong to the species *Geragnostus* (*Geragnostella*) *tullbergi* (Novák, 1883). One specimen is further away (5 mm) from the fragment of the axis fossil. The other specimens were found in close proximity to its main branch. Two of them occur individually, one situated just below the first preserved second order branch of the axis-fossil, the other isolated on the opposite side, some 5 mm above the row of the four spine-like processes (see above). The remaining five agnostids are aligned in a row along the main axis in the upper portion of the axis-fossil fragment. This row is placed on the opposite side to the latter isolated trilobite. The upper limit of the row is on the same

level as the second apparent branching of the axis-fossil. These specimens in a row are situated close to each other, at distances less than 1 mm. In some cases they are almost in contact.

The spatial orientation of each of the trilobites is slightly different, but all are oriented with the free margins of the cephalon and pygidia (tests) facing the axis-fossil.

There are also other fossils close to the axis-fossil. The latter isolated trilobite is placed near a flat fragment of impossible determination. Near the lower limit of the aligned row there are visible two transverse cross sections of hyolithids. The axes of shells are oriented perpendicular to the plane of the split nodule and perpendicular to slightly oblique to the axis of the agnostid row. One hyolithid can be determined as *Elegantilites elegans* (Barande, 1847).

Discussion

The described axis-fossil could represent the robust part of an algal strand. However, its branching pattern does not resemble that of an alga (Kvaček pers. com.).

Some fragments of ichnofossils, which occur in nodules of the Šárka Formation, resemble it in some respects as well. However, in contrast to the ichnofossils, it maintains no constant diameter and it shows no wall linings as typical for the ichnogenus *Thalassinoides*; the branching is different from that of *Planolites* or *Palaeophycus* especially because the second order branches are of smaller diameter than the main branch (Mikuláš pers. com.).

It looks most similar to the fossils described recently by Kenrick et al. (1999) from the Barrandian Klabava Formation which were interpreted as octocorals. Both specimens from the Klabava Formation and our axis-fossil possess the spine-like processes. The main difference consists in the different mode of branching (in triades versus lateral in the specimens from the Klabava and Šárka formations, respectively). Their robustness (slender vs. robust) and intervals of branching (relatively long vs. short) are also not in correspondence.

The octocoral *Nonnegorgonides ziegleri* Lindström, 1978 described from the basal Volkhovian (Arenigian) of Sweden (Lindström 1978) is much more slender and smooth, i.e. bearing no processes but with a similar branching pattern in comparison with the specimen from the Bohemian Šárka Formation.

No other similar axis-fossil from the Šárka Formation has been recorded in any public collection in the Czech Republic. This problem could arise because such objects have not been collected in the past. It is only during the

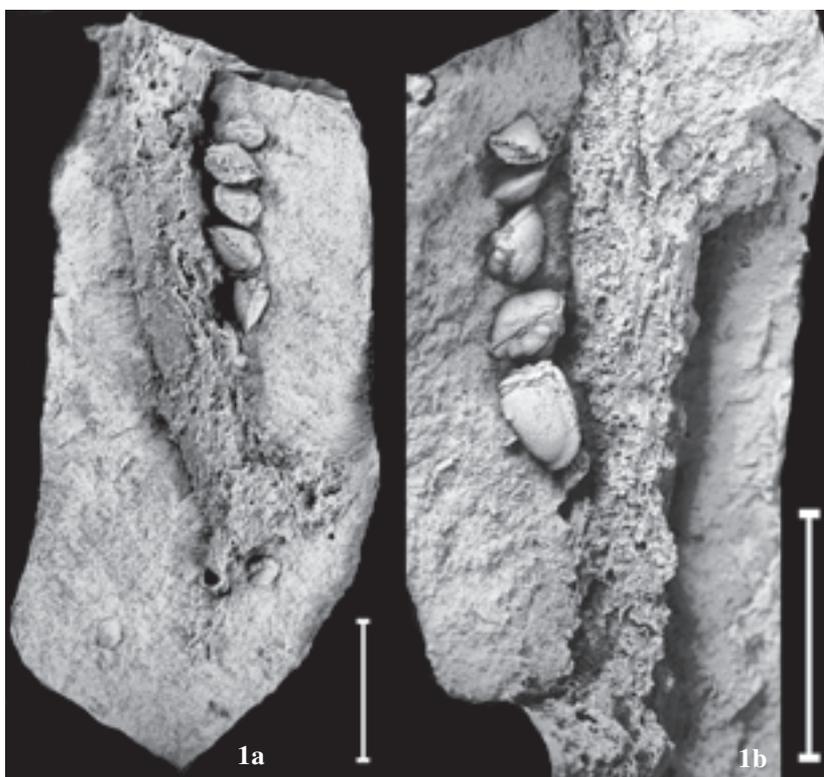


Fig. 2 1 – Latex cast of the half of nodule figured on Fig. 1-1a; 2 – Latex cast of the counterpart figured on Fig. 1-1b, detail of aligned row of five agnostids in oblique view. Both casts coated with ammonium chloride, scale bars = 10 mm.

last 25 years, that some paleontologists and collectors have focused on complete collecting of all faunal elements. Even still, such “not interesting” objects (fragments of ichnofossils etc.) have usually been avoided even by them. They were considered to provide almost no possibility to be determined or do not offer any relevant information.

As mentioned above the studied agnostid association seems to be monospecific. All determinable specimens belong to the species *Geragnostus (Geragnostella) tullbergi*. It is the most common agnostid of the Šárka Formation.

The agnostid trilobites in close proximity to the axis-fossil are supposed to have originally been attached to it. Even though it was not directly observed, it seems that they were attached to the spine-like processes. As the form of these processes indicates that they were flexible. The observed orientation of trilobites could be slightly different from the natural state. However, all enrolled trilobites remain facing the axis-fossil with their free margins of cephalon and pygidia. Their sagittal orientation to the axis-fossil has not been observed but the prevailing one is lateral to almost lateral. These circumstances suggest that the studied agnostids were attached to the spine-like processes by thoracic appendages rather than cephalic and/or pygidial ones, which could then remain free for feeding or other activities.

Stemming from an octocoral affinity for the axis-fossil, not only an epiplanktic mode of life, but also an

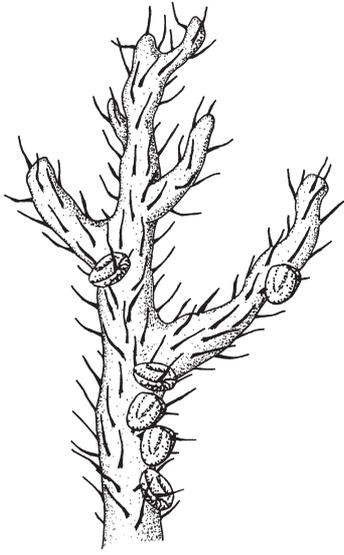


Fig. 3 Idealized reconstruction of the axis-fossils interpreted as octocoral and attached agnostid trilobites. (Drawn by M. Košťák)

epibenthic one comes into consideration for agnostids. They could be at least part of their life (e.g. resting, feeding) attached to this sessile benthic organism which possessed hair-like processes suitable for attachment. The relationship of enrolled agnostids with the robust axis-fossil also illustrates that these trilobites could search for such objects if they offered structures fine enough for attachment.

The agnostids attached to the axis-fossil most likely died and were buried suddenly together and thus found in a natural position.

Similar rows (without any axis-fossil) of agnostids have been described by several authors from the Bohemian Ordovician. Agnostids in such accumulations were mentioned by Prantl (1948), Příbyl – Vaněk (1976), Pek (1977) and described as tubes formed by the agglutinated shields, as a part of the benthic fauna on algal strands and as suggested epibionts on floating algae, respectively.

Based on our study, the accumulations of agnostids are usually small in size. They consist only of agnostids or of these trilobites associated with other fossils. All purely agnostid rows investigated are monospecific, consisting of solely enrolled specimens which are small in size. The rows with *Leiagnostus bohemicus* (Novák in Perner, 1918) or *Geragnostus (Geragnostella) tullbergi* (Novák, 1883) prevail.

Only rows with some common character of arrangement (orientation, no fragments etc.) can be considered as primary ones. However, their relationship to any organism, such as described above, cannot be proved. Unarranged rows might represent secondary accumulations or primary ones disordered by taphonomic processes.

In the course of our investigation it was recognized that almost all studied rows with agnostid trilobites (approx. 30) come from the eastern part of the Prague Basin, from the vicinity of Praha. The only exception is one row found in the western part of the basin in the Rokycany area. This may be the result of stratigraphical differences. In the Rokycany area, there occur only the nodules coming from the *Corymbograptus retroflexus* Biozone. On the contrary, the nodules from the *Corymbograptus retroflexus* Biozone

as well as the overlying *Didymograptus clavulus* Biozone have been collected in the Prague area. The rows seem to come predominantly from the upper biozone but palaeoecologic differences during the Llanvirnian (or Darriwilian) age in the Prague Basin cannot be excluded.

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