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Moulting in Ordovician dalmanitoid and acastoid trilobites of the Prague Basin. Preliminary observation

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ABSTRACT

A review of the supposed moulting positions of the Bohemian Ordovician dalmanitoid and acastoid trilobites is presented. Five main moulting positions are described, but some combinations of these are also widespread. The variability of the supposed moulting mechanisms is surprisingly high, especially in Middle Ordovician taxa. All and/or almost all moulting positions may occur together even within a single species. In advanced representatives, only a few of the described mechanisms prevail. Nevertheless, the occurrence of the moulting positions in the Bohemian Ordovician dalmanitoid and acastoid trilobites is considered to be constrained by the overall body morphology, rather than the result of phylogenetical relations. Functionality of the facial suture in these groups during the ontogeny and phylogeny is discussed.

KEYWORDS **Dalmanitoidea. Acastoidea. Moulting. Ordovician. Barrandian.**

INTRODUCTION

Dalmanitoid and acastoid trilobites are amongst the most common Bohemian Ordovician trilobites. The systematic concept of Edgecombe (1993) is followed in the Bohemian Ordovician "acastid" and/or "calmonid" trilobites that share features of both families. Similarly some of Ordovician "dalmanitids" as *Duftonia* DEAN have problematical systematic position because of possible affinities to the pterygometopids). In the Prague Basin (Fig. 1), these trilobites range from the Lower Ordovician (middle to upper, but not uppermost Arenigian) Klabava Fm to the Upper Ordovician Kosov Fm (Fig. 2) where they are amongst the most important elements of the so called "Hirnantia fauna". The aim of this contribution is to evaluate and summarize possible dalmanitoid and acastoid exuviae and to distinguish the main types of moulting positions of these trilobites, on the basis of the available material from the Prague Basin. The occurrence of these moulting positions with respect to the phylogenetical rank and overall body morphology is reviewed as well. A short preliminary discussion of this problem was published by Budil and Bruthansová (2003). This contribution discusses this topic in detail.

GEOLOGICAL SETTING

The Prague Basin (Figs. 1 and 2) is situated in the Czech Republic. It originated in the lower Tremadocian and marine sedimentation persisted here up to the Middle Devonian (see Havlícek in Chlupác et al., 1998). During the Ordovician, the Prague Basin was filled mostly with siliciclastics (shales, claystones, siltstones, sandstones, greywackes), which usually formed continuous sequences ranging from fine-grained conglomerates or coarse-grained sandstones probably of shallow water origin to deeper basinal, mostly clayey and bituminous shales. Impure carbonates are rather an exception and form only small lenticular bodies, calcareous nodules and/or irregularly beds especially in the Upper Ordovician Zahorany and Bohdalec Fms. Volcanics and volcaniclastics with oolithic ferrolites of marine origin are frequent especially in the NW part of the basin. The uppermost Ordovician is represented by the siliciclastic Kosov Fm (greywackes, sandstones, siltststones, dropstones), which probably represents a glacio-eustatic sea level drop and major cooling of the climate.

MATERIAL AND METHODS

Only specimens that show particular and common types of exoskeletal configurations are considered to be the results of moulting. These include the occurrence of inverted and/or isolated sclerites together with the articulated or slightly disarticulated remains of the body, missing exoskeletal elements; or showing well-known moulting configurations such as “Salterian mode”, “axial shield” and configurations described by Speyer (1985) in phacopid trilobites. The moulting configurations described herein mostly represent its variations. Only such configurations as those that occur frequently and regularly were included in the study. Moreover, we selected only the common taxa of Bohemian dalmanitoid and acastoid trilobites, which are abundantly represented in the collections by sufficient, stratigraphically well-constrained material.

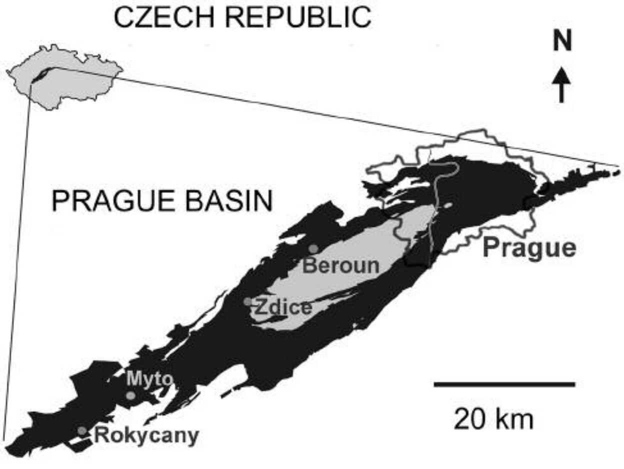


FIGURE 1 **Geographical position of the Prague Basin, Czech Republic, where the occurrence of the Ordovician (black) and Silurian + Devonian (grey) marine rocks is marked. Modified after Fatka (unpublished).**

These studies, based especially on material stored in the collections, were supplemented (in many cases) by field investigations and include *Ormathops* (*O.*) *atavus* (BARRANDE), *Dalmanitina proaeva proaeva* (EMMRICH), *Eudolatites dubius* (BARRANDE), *Baniaspis* ? *quadrata* (HAWLE et CORDA), etc. Nevertheless, this present work should still be considered only as a general review of the problem; more detailed studies based on well documented, newly gathered field material should follow. All analyses published in this contribution, therefore, should be considered as preliminary.

TYPES OF MOULTING CONFIGURATIONS

Budil and Bruthansová (2003) pointed out a surprisingly great variability in the moulting mechanisms, which were probably used by Bohemian dalmanitoid and acastoid trilobites. This variability is especially remarkable in comparison with their distant relatives – phacopid trilobites (see Chlupác, 1977).

Five main observed types of the supposed moulting configurations are described and discussed in detail on the basis of the available Bohemian Ordovician material shown in Fig. 3.

1. In almost all species, the commonest mode of moulting was the simple separation of the cephalon from the complete thorax (Fig. 3B$_1$), but without the inversion typical for the “Salter’s position” (Speyer, 1985). The ecdysial “gape suture” thus lies between the cephalon and the thoracopygon. In some cases the thoracopygon can be slightly overlapped by the cephalon (see Busch and Schwartz, 1985 a.o.). Often (Fig. 3B$_2$), the thorax is partially enrolled - see also Speyer (1985) at *Greenops boothi* (GREEN).

2. Moulting configurations similar to the true “Salter’s position” (see Richter, 1937; Chlupác, 1977; Speyer, 1985) are rare but they have been observed in many species (Fig. 3C). In some specimens of *Ormathops* (*O.*) *atavus* (BARRANDE) preserved in this and/or in similar positions, the librigenae are clearly separated from the cranidium (Figs. 4E and 5C).

3. Frequently, especially in *Ormathops* DELO, but also in some other genera as *Zeliszkella* DELO, *Dalmanitina* REED, and *Kloucekia* DELO, at least two, but usually three

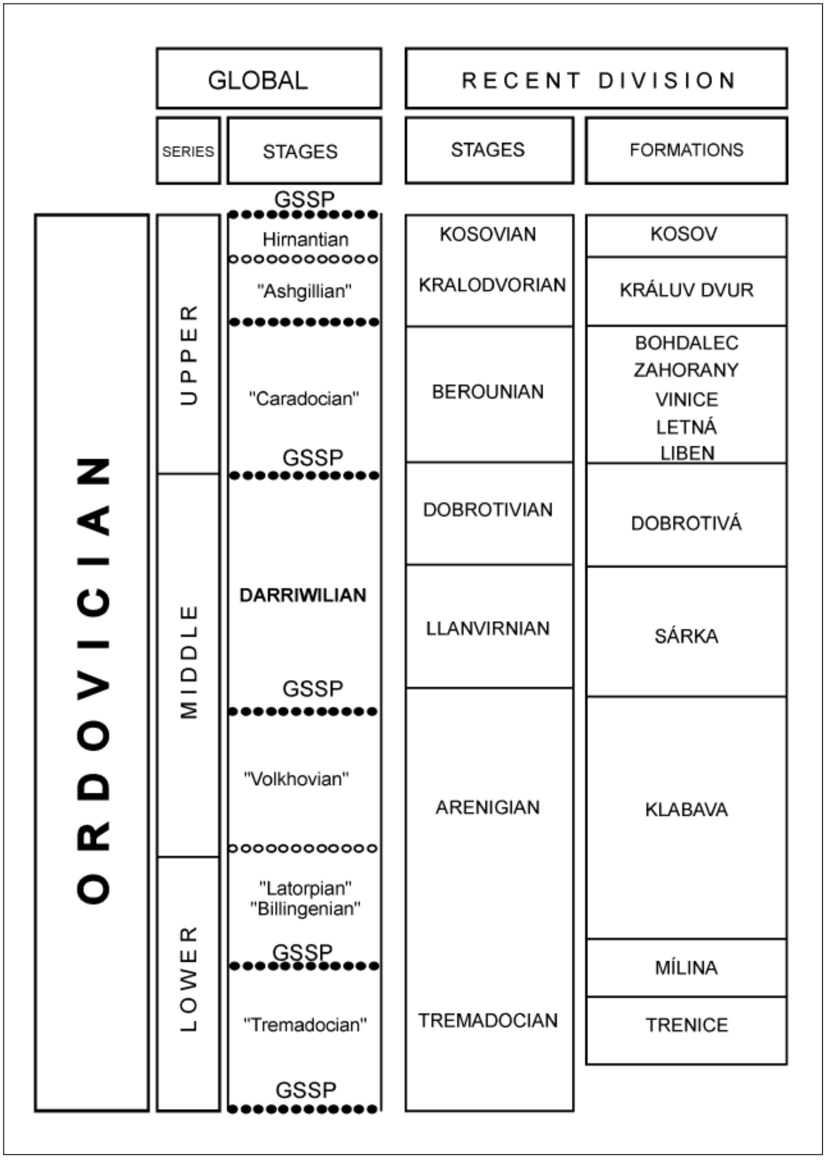


FIGURE 2 **Ordovician stratigraphy review in the Prague Basin. After Fatka and Pek (1999).**

segments are still articulated with the cephalon and this part of the exoskeleton is separated from the articulated rest of the thorax + pygidium (Fig. 3D). The ecdysial "gape suture" is not placed between the thorax and cephalon (cf. Speyer, 1985; Wenndorf, 1990), but lies between the thoracic segments. In *Ormathops* (*O.*) *atavus* (BARRANDE), incomplete cephalothoraxes with preserved hypostoma in situ have rarely been found (Fig. 6A).

4. A thorax broken into two or more independent parts (Fig. 3E) is also a very common supposed moulting position in Bohemian dalmanitaceans (especially in subfamily Zeliszkellinae). Two or more ecdysial "gape sutures" are present in this type of moulting configuration. A similar moulting strategy was interpreted by Fortey and Owens (1991) in *Shumardia* (*Conoprys*) *salopiensis* as escapist (i.e. when the efforts of the animal to remove old exoskeleton were not successful). A mode of moulting resembling the above described was also discussed by Snajdr (1990) in Bohemian paradoxiid trilobites.

5. In only a few complete large specimens of *Ormathops*. (*O.*) *atavus* (BARRANDE), but comparatively more frequently in young individuals of many dalmanitoids - *Ormathops* (*O.*) *atavus* (BARRANDE), *Dalmanitina proaeva elfrida* SNAJDR, *Dalmanitina proaeva proaeva* (EMMRICH) a.o. (Figs. 7B and 7C), configurations resembling (by cranidium articulated with the thorax) the "axial shield" of Henningsmoen (1973) have been observed. In this type of supposed moulting position, the librigenae are completely separated from the cranidium (Fig. 3A), which implies the full functionality of the facial suture

during moulting. This type of moulting is considered as "primitive", and was replaced very early during the phylogeny of the groups studied by more advanced modes. Nevertheless, it is still preserved in young individuals. Since this configuration appears only occasionally in some adult specimens (see below), the most probable explanation is that the loss of the functionality of the facial suture was not entirely genetically fixed.

The issue of functionality and/or loss of functionality of the facial suture during ontogeny and phylogenetical development in Bohemian Ordovician dal-

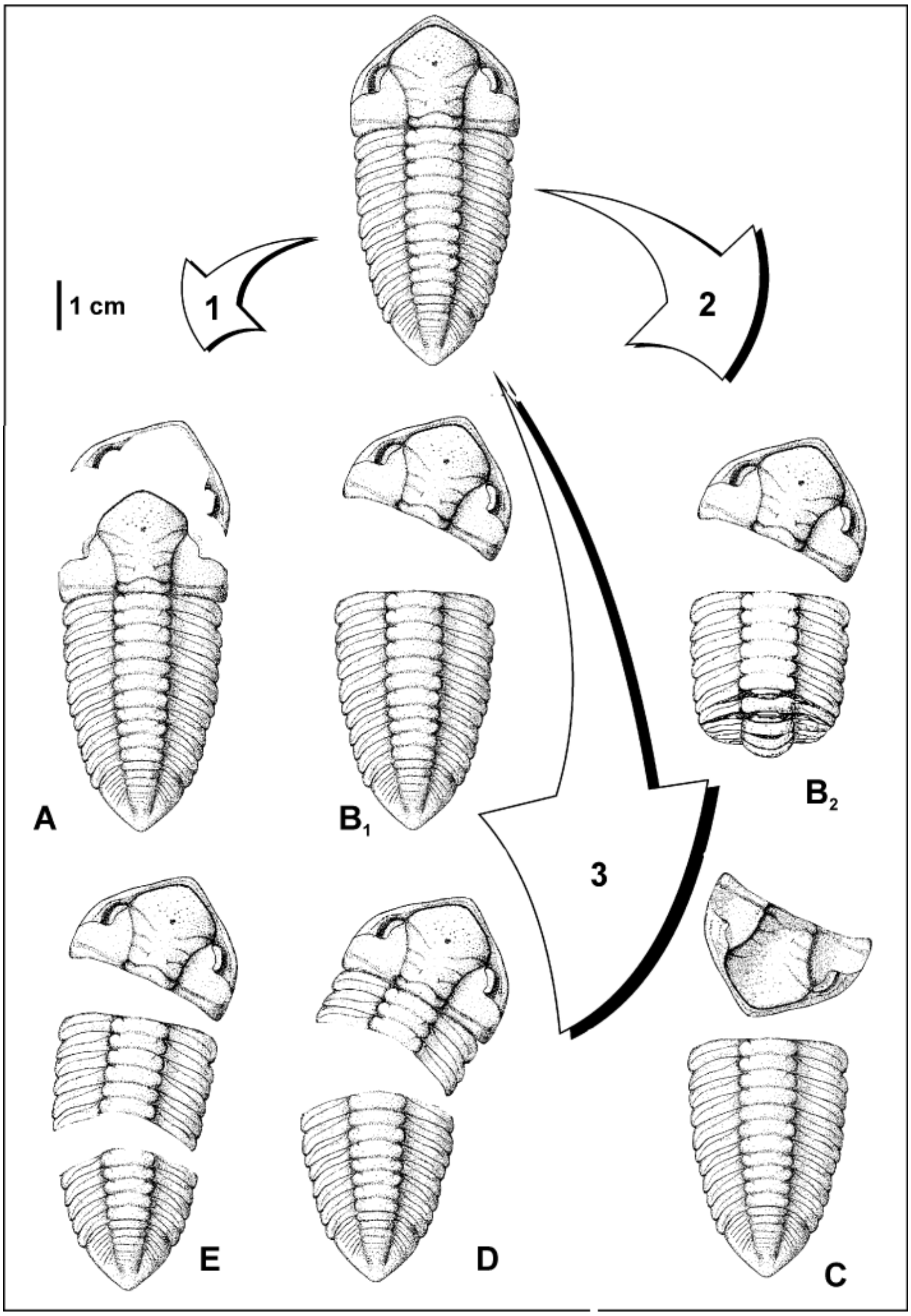


FIGURE 3| **Review of the main observed types of the moulting positions in Bohemian Ordovician dalmanitid and acastid trilobites at *Ormathops (Ormathops) atavus* (BARRANDE), Middle Ordovician Sárka Fm (Llanvirnian = Darriwillian). Modified after Budil and Bruthansova (2003). The arrows (1-3) mark the main supposed courses of the exuviation. A) The configurations resembling the "axial shield" of Henningsmoen (1973), where the librigenae are completely separated from the cranidium. B$_1$) Separation of the cephalon from the complete thorax but without the typical inversion for the "Salter's position" (Speyer, 1985). B$_2$) the thorax is partially enrolled - see also Speyer (1985) at *Greenops boothi* (GREEN). C) Configurations similar to the true "Salter's position" with inverted cephalon. D) At least two, but usually three segments are articulated with the cephalon and this part of the exoskeleton is separated from the articulated rest of the thorax + pygidium. E) A thorax is broken into two or more independent parts.**

manitoid and acastoid trilobites has not been discussed in detail, although many revisions of these trilobites have been published during the last 40 years (Snajdr, 1982a, 1982b, 1984, 1987), Pribyl and Vanek (1972, 1976, 1980).

On the basis of the study of the available material stored in the collections and gathered during field researches, a loss of functionality of the facial suture in moulting during the ontogenetic development both of dalmanitoid and of acastoid trilobites seems to be well docu-

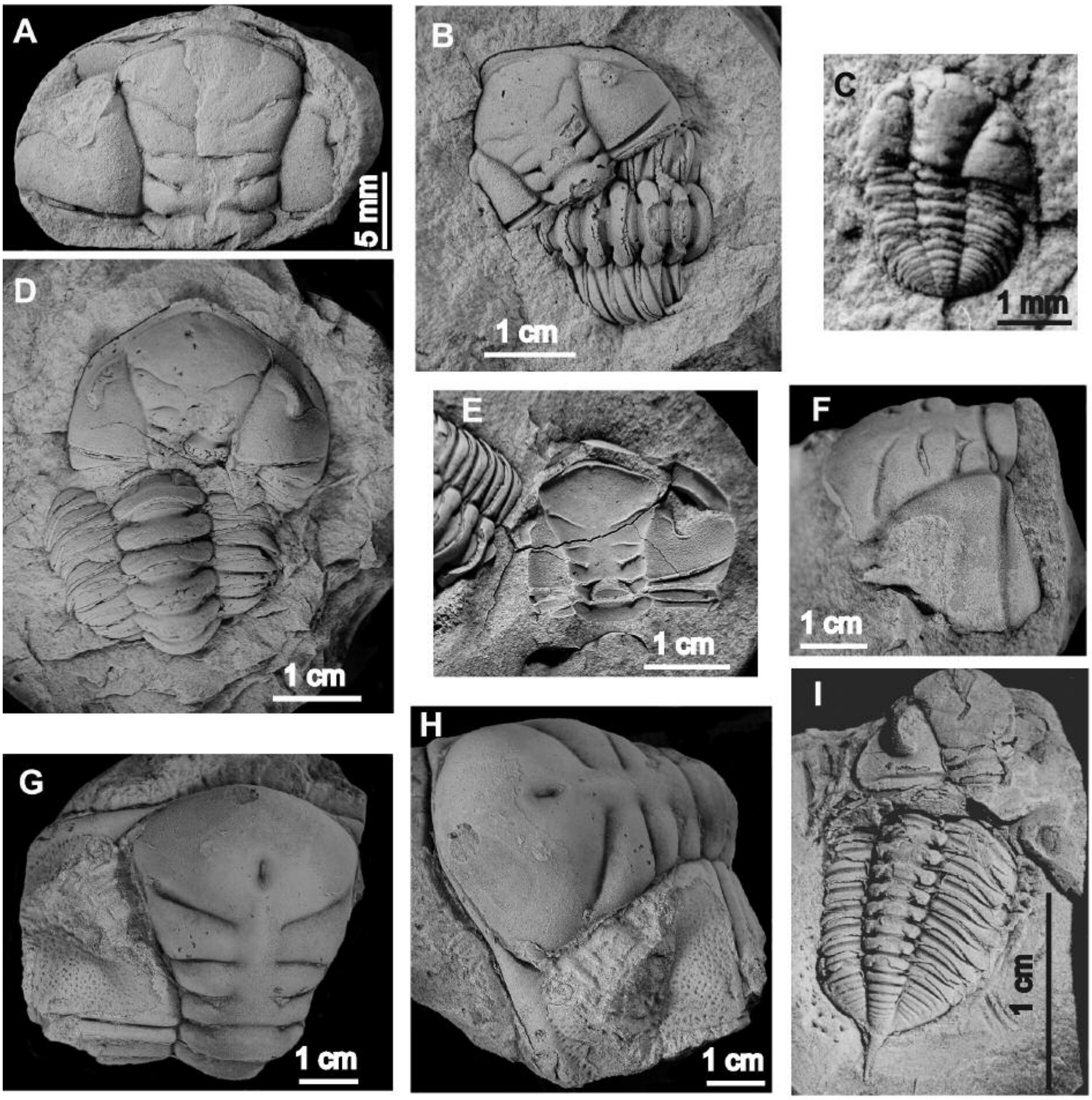


FIGURE 4 | **Examples of supposed moulting positions observed in the Bohemian Ordovician dalmanitoid and acastoid trilobites. All specimens have been coated with ammonium chloride before photographing. A) *Ormathops (O.) atavus* (BARRANDE). Cephalon with the slightly inverted and separated left side of the free cheeks. Ex CGS JV 1779, Volduchy, Sarka Fm. B) *Ormathops (O.) atavus* (BARRANDE). Cephalon and enrolled remain of the thorax, probably representing the moulting position B2. Ex CGS PP 470, Teskov, Sarka Fm. C) *Dalmanitina proaeva elfrida* SNAJDR. Young, meraspid specimen with displaced cephalon, perhaps representing the moulting position B1. Specimen was figured by Barrande (1852) at Pl. 26, fig. 10, NM L15053. Trubín, Vinice Fm. D) *Ormathops (O.) atavus* (BARRANDE). Cephalon and enrolled remain of the thorax, probably representing the moulting position B2. Ex CGS PP 435, Osek, Sarka Fm. E) *Ormathops (O.) atavus* (BARRANDE). A detail of an inverted cephalon + one thoracic segment separated from the slightly displaced remains of the thorax (the same individual is shown in Fig. 8C). Free cheeks are not attached to the cranidium, but a slight gap exists between these parts of the exoskeleton. CGS MS 6172, Rokycany-Osek, Sarka Fm. F) *Dalmanitina proaeva proaeva* (EMMRICH). Cephalon with clearly displaced free cheeks along the facial suture. CGS PB 130, Praha-Dubec, Zahorany Fm. G) *Eudolatites dubius* (BARRANDE). Cephalon with slightly inverted and separated left side of the free cheeks. CGS PB 131. H) Ditto, anterolateral view. I) *Sokhretia solitaria* (BARRANDE), lectotype NML 15119, individual representing the moulting position B1. Praha-Velka Chuchle, Bohdalec Fm.**

mented. In comparison with their distant relatives the phacopid trilobites (Chlupác, 1977; Crônier et al., 1998), in the Bohemian Ordovician dalmanitoids and probably also in acastoids, the onset of this change corresponds with a comparatively late stage of ontogeny – during the holaspid period (Fig 7C). In adult specimens more than 99% of the supposed moulting configurations have the complete cephalon (e.g. cranidium and attached librigenae) preserved. This implies that the facial suture was not ordinarily used as the "ecdysial gape" suture in these trilobites.

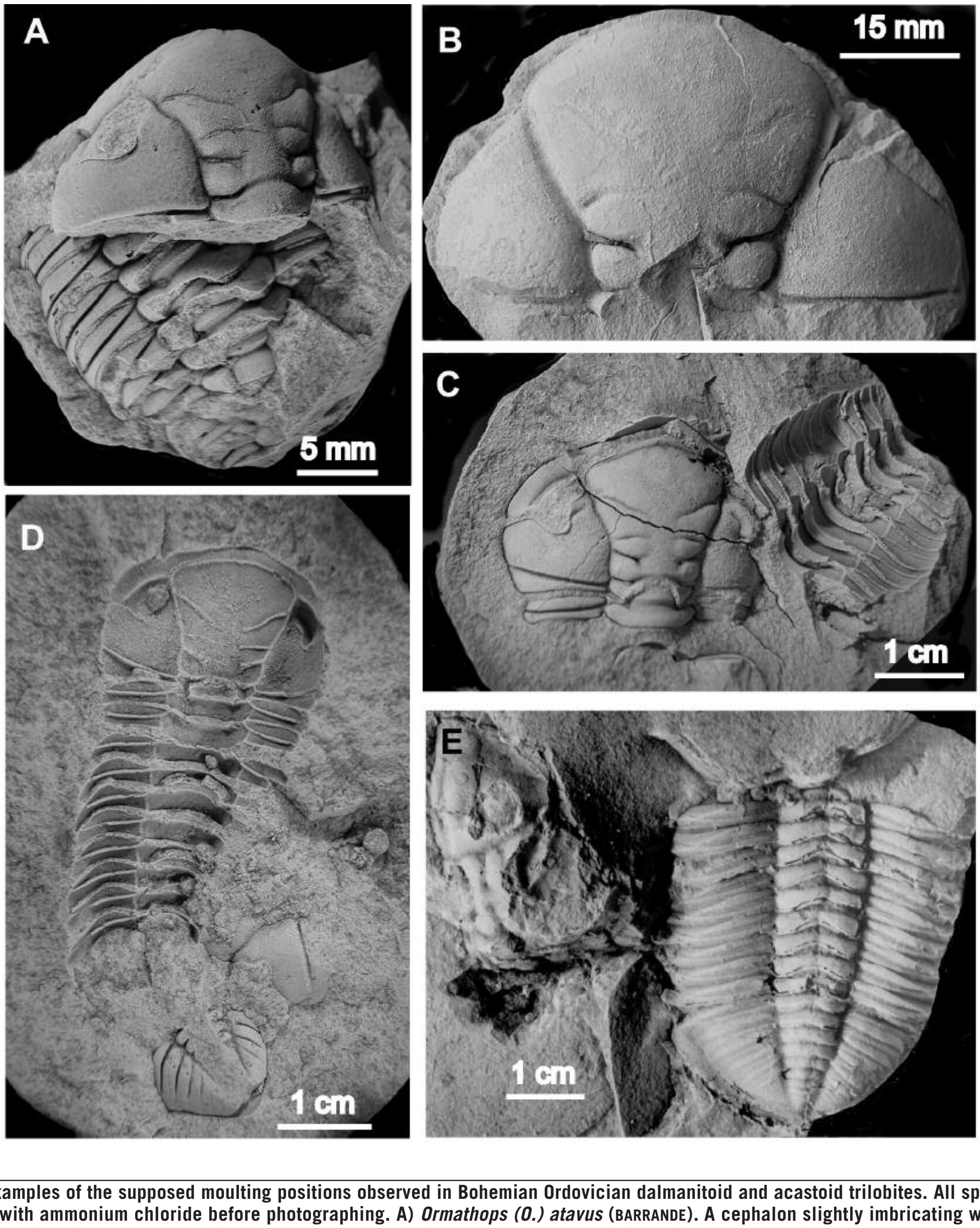


FIGURE 5 **Examples of the supposed moulting positions observed in Bohemian Ordovician dalmanitoid and acastoid trilobites. All specimens have been coated with ammonium chloride before photographing. A) *Ormathops (O.) atavus* (BARRANDE). A cephalon slightly imbricating with the thorax remains slightly disarticulated. Left eye is broken, but free cheek is attached to the cranidium without any disarticulation; probably representative of the moulting position B1. CGS PP 441, Rokycany-Dily, Sarka Fm. B) *Ormathops (O.) nicholsoni (=barroisi)* (SALTER). A cephalon of a large specimen with displaced free cheeks. NM L 32421, Praha-Vokovice, Sarka Fm. C) *Ormathops (O.) atavus* (BARRANDE). An inverted cephalon + one thoracic segment separated from the slightly displaced remains of the thorax. Left eye is broken, but free cheeks are not attached to the cranidium, though there is a slight gap between these parts of the exoskeleton. This gap is also clearly visible at the counterpart (see Fig 4E). Representative of the moulting position C. CGS MS 6172, Rokycany-Osek, Sarka Fm. D) *Ormathops (O.) atavus* (BARRANDE). A cephalon with the thorax remains slightly disarticulated. Pygidium, questionably assigned to the same specimen is displaced and inverted. Problematical specimen, perhaps this may also be an exuvia. CGS PP 473, Cekov, Sarka Fm. E) *Dreyfussina ? simaki* (PRIBYL AND VANEK). A specimen typically representative of the moulting position B1. CGS PB 121, Praha – Radotin, Kraluv Dvur Fm.**

This presumption is also supported by the very widespread finding of piled cephala and pygidia of some species (*Dalmanitina socialis*, *D. proaeva*), which are interpreted by many authors (Pribyl and Vanek, 1976; Snajdr, 1990) as accumulated exuviae. Nevertheless, separated free cheeks have been observed in isolated adult cephala (about 1%) in *Dalmanitina cilinensis* SNAJDR, *D. proaeva proaeva* (BARRANDE), *D. proaeva elfrida* SNAJDR, *Eudolatites dubius* (BARRANDE) and *Duftonia morrisiana* (BARRANDE). A similar observation has been made during the first author's investigations of the Silurian dalmanitoid material (*Dalmanites* BARRANDE) from the classical British localities stored in the collections of the Natural History Museum and Charles Lapworth Museum, University of Birmingham. In many cases, the free cheeks seem to be slightly displaced in isolated cephala but this feature probably originated during sediment compaction, because these cephala are damaged and broken along the cracks intersecting the cranidium and/or free cheeks. Nevertheless, out of 200-250 specimens studied, a few show displacement of the free cheeks along the facial suture, without any other marks of brittle deformation. In these samples, the functionality of the facial suture may be considered as authenticated.

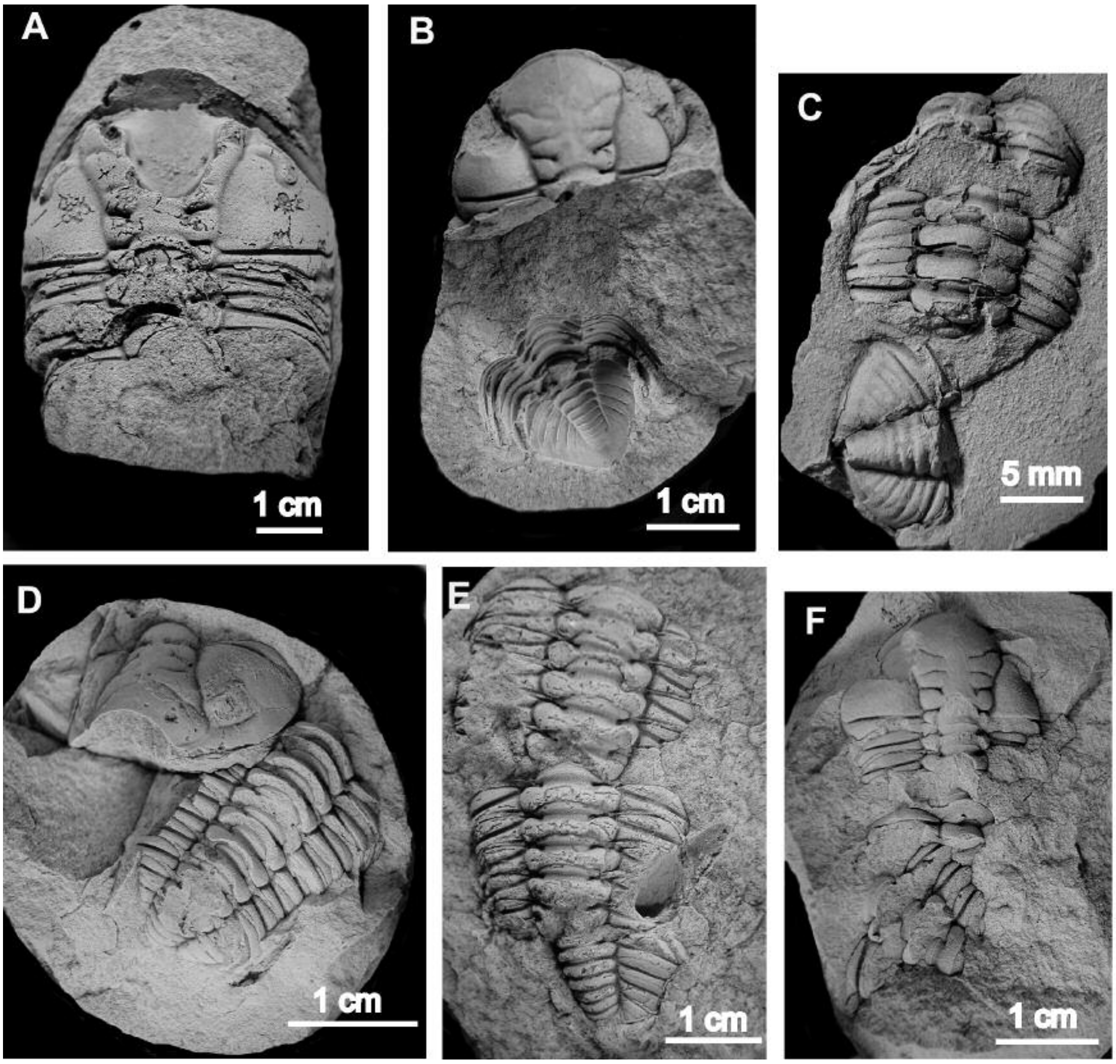


FIGURE 6 **Examples of the supposed moulting positions observed at the Bohemian Ordovician dalmanitoid and acastoid trilobites. All specimens have been coated with ammonium chloride before photographing. A) *Ormathops (O.) atavus* (BARRANDE). Cephalon and part of the thorax with the hypostoma in situ. Probable exuvia (remain of the moulting position D?). CGS MS 14073, Teskov, Sarka Fm. B) *Ormathops (O.) atavus* (BARRANDE). Cephalon and inverted enrolled part of the thorax with pygidium, probably representing subtype of moulting position C. Ex CGS PP 471, Teskov, Sarka Fm. C) *Baniaspis ? quadrata* (HAWLE ET CORDA). A thorax broken into three parts, cephalon is damaged; probably representative of moulting position E. CGS MS 11597, Praha-Velka Chuchle, Bohdalec Fm. D) *Ormathops (O.) atavus* (BARRANDE). Cephalon and isolated, slightly disarticulated thorax with pygidium, representative of moulting position B1. Ex CGS PP 442, Rokycany-Dily, Sarka Fm. E) *Ormathops (O.) atavus* (BARRANDE). A thorax broken into three parts, cephalon is missing; probably representative of moulting position E. CGS JH 927, Cekov, Sarka Fm. F) *Ormathops (O.) atavus* (BARRANDE). A cephalon with the disarticulated thorax broken into several parts, pygidium is missing; probably representative of the moulting position E. CGS PP 437, Teskov, Sarka Fm.**

In *Dalmanitina cilinensis* SNAJDR, isolated and often broken free cheeks are locally relatively common in the organic detritus of the lower Berounian Revnice quartzite (=sandstone). In such cases, without any other supplementary features suggesting that separation of librigenae occurred as a result of moulting, post-ecdysial and/or post-mortal disintegration of the exoskeleton and subsequent transport of the organic remains by currents should be also considered. Despite these doubts, the presence of this part of the exoskeleton suggests the facial suture to be at least a line of mechanical weakness of the exoskeleton in this species.

PROBLEMATIC AND INSUFFICIENTLY UNDERSTOOD CONFIGURATIONS

The lack of a pygidium in complete cephalothoraxes (in some cases with the pygidium lying close) has often been observed in Bohemian Ordovician dalmanitoid and acastoid trilobites (*Dalmanitina socialis* (BARRANDE), *Kloucekia*? *ruderalis* (HAWLE et CORDA = *pachypa* PRIBYL and VANEK) but it is not clear if this configuration really represents a moulting position, and the same can be said for enrolled samples without a pygidium. In these cases,

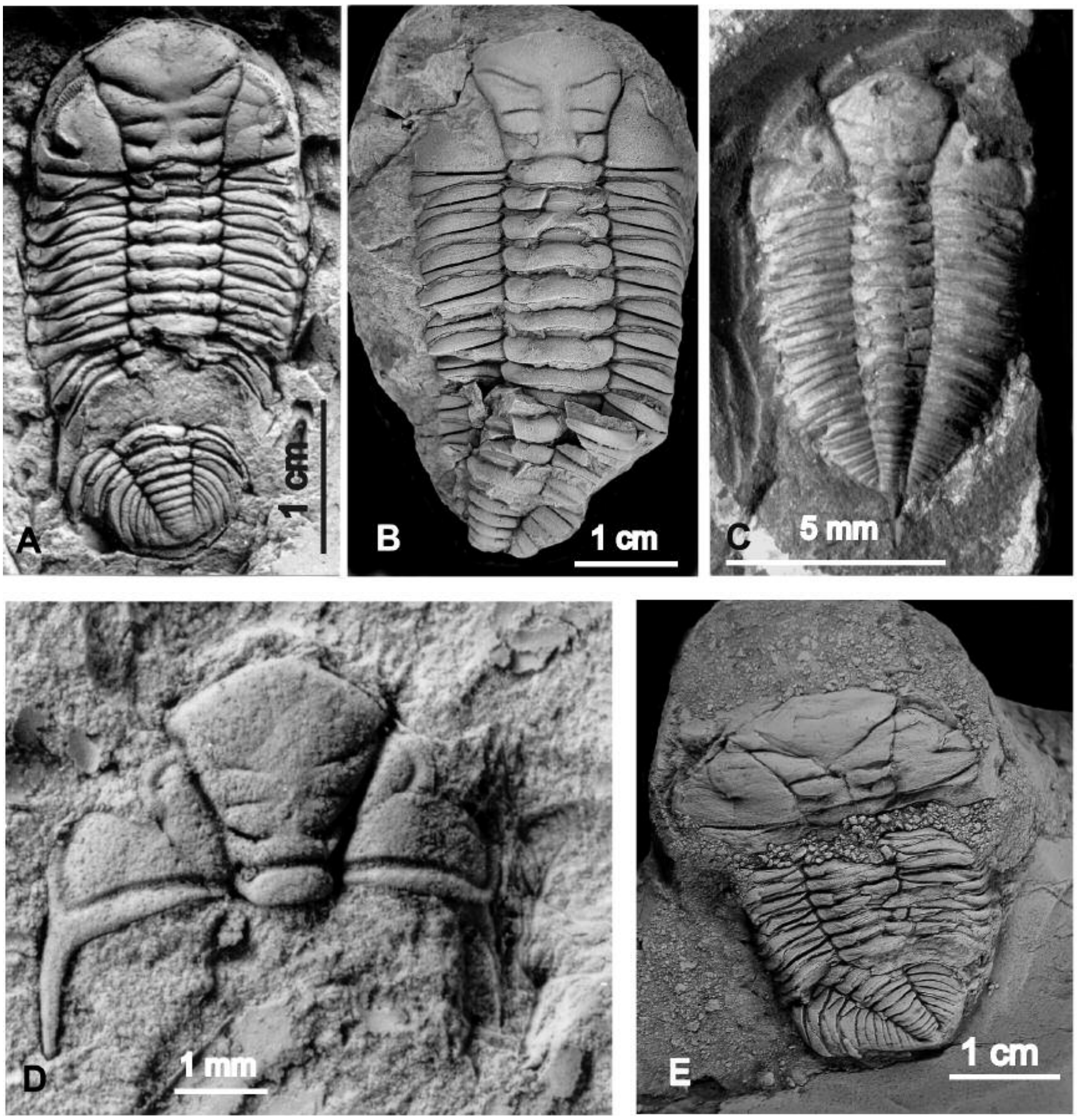


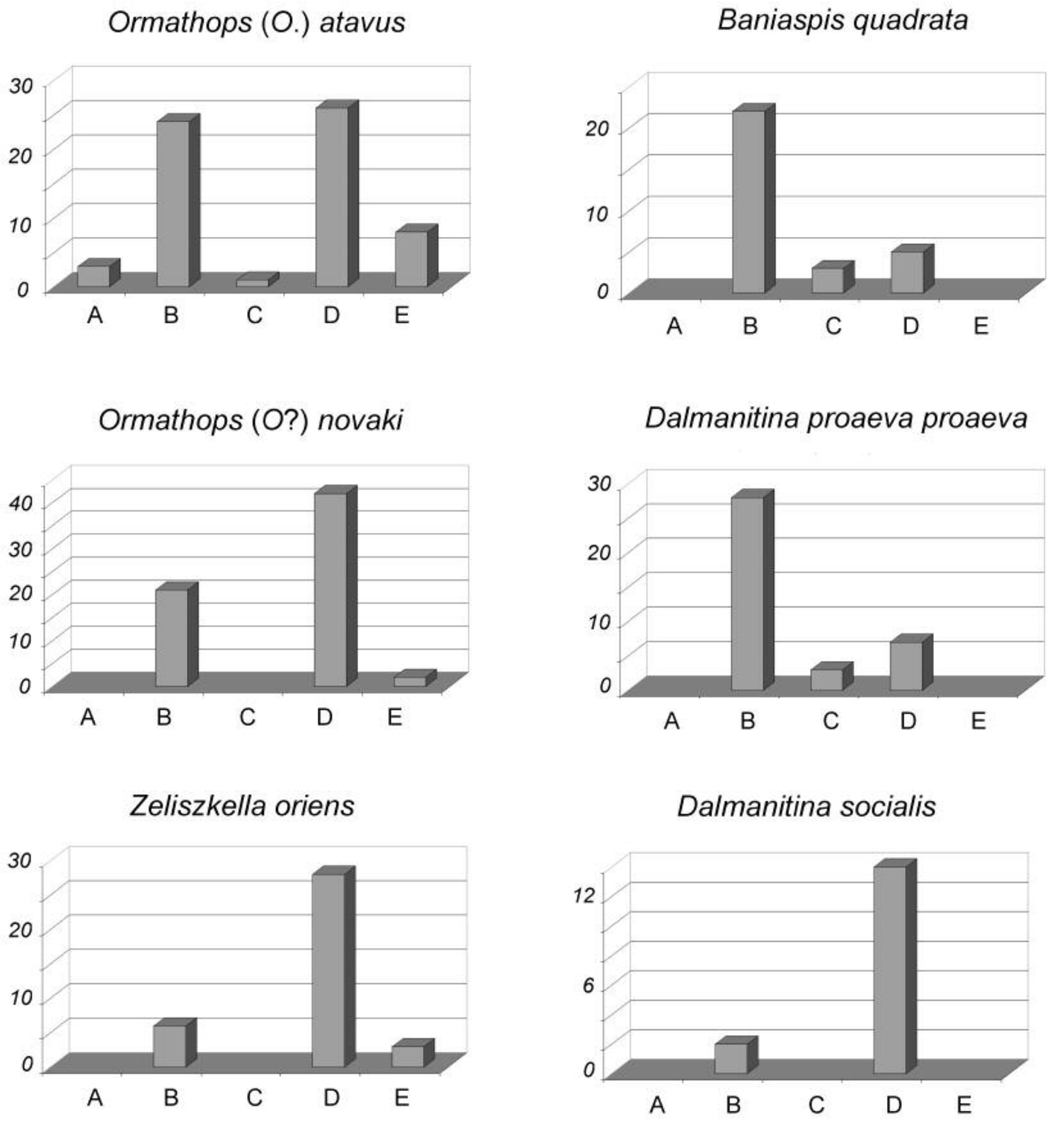
FIGURE 7 **Examples of the supposed moulting positions observed in the Bohemian Ordovician dalmanitoid and acastoid trilobites. All samples have been coated with ammonium chloride before photographing (except 7C). Specimens illustrated herein are housed in the palaeontological collections of the National Museum, Prague (NM L) and Czech Geological Survey, Prague (CGS). A) *Zeliszkella oriens* (BARRANDE), lectotype NM L 16946, AD Barrande (1872), Pl. 14, figs. 22-23, Sat· Dobrotiv·, Dobrotiva Fm. B) *Ormathops (O.) atavus* (BARRANDE). Incomplete individual with separated free cheeks. CGS JH 896, Volduchy, Sarka Fm. C) *Dalmanitina proaeva elfrida* SNAJDR. Young, early holaspid with displaced free cheeks. This specimen was figured (with the free cheeks in idealized reconstruction) by Barrande (1852) at Pl. 26, figs. 14-15, NM L15055, TrubÌn, Vinice Fm. D) *Dalmanitina proaeva elfrida* SNAJDR. Late meraspid cephalon with displaced free cheeks. Specimen was figured by Snajdr (1990) at p 43, fig. 9, NM L15066. E) *Zeliszkella* cf. *oriens* (BARRANDE), the specimen represents the moulting position E. CGS XB 512, Praha - Florenc, Dobrotiva Fm.**

it is to envisage how the soft-shelled trilobite could have left the old exoskeleton because the supposed "ecdysial gape" suture would be very narrow tot allow the animal to escape.

It is also surprising that the configurations described by McNamara and Rudkin (1984) in the related pterygometopid trilobite *Toxochasmops extensus* (BOECK) - isolated cephala and pygidia lying close each other, often with slight imbrication, without or with few thoracic segments only – have not been observed in the Bohemian material, although some of the configurations share some features described by the above mentioned authors.

DISCUSSION AND CONCLUDING REMARKS

A surprisingly high variability of moulting positions was observed in Bohemian Ordovician dalmanitoid and acastoid trilobites (for discussion of this subject see also Brandt, 2002). Especially in the phylogenetically early representatives (*Ormathops* DELO, *Zeliszkella* DELO) all and/or almost all the main moulting positions described and their combinations were observed. In advanced dalmanitoids and in most of the acastoids, only a few types of moulting positions (especially B, C and D) prevail and the diversity decreased markedly during the Upper Ordovician. No significant differences in the prevailing types of moulting were observed in late dalmanitoids


Ormathops (O.) atavus

Baniaspis quadrata

Ormathops (O?) novaki

Dalmanitina proaeva proaeva

Zeliszkella oriens

Dalmanitina socialis

FIGURE 8 **Histograms of the occurrence of the main moulting positions in adult specimens of selected Bohemian Ordovician dalmanitoids and acastoids. A-E = main moulting positions (see Fig. 3); y = number of the specimens.**

(*Dalmanitina* REED, *Sokhretia* HUPÉ, *Eudolatites* DELO a.o.) and early acastoids (especially in *Baniaspis* DESTOMBES =*Phacopidina* BANCROFT sensu Snajdr, 1987 and *Kloucekia* DELO), which occur together in the Prague Basin.

Nevertheless, it is necessary to call attention to the important lithological difference between the Middle and Upper Ordovician formations in the Prague Basin. In the Middle Ordovician Sarka and Dobrotiva Fms, dark, clayey and bituminous shales with rich fossil remains were probably deposited in the deeper basin zones under low-energy conditions. Accordingly, most of the abandoned trilobite moults may be preserved in-situ, although different interpretations of the sedimentary conditions also exist (P. Kraft, pers. comm.). On the contrary, in the Upper Ordovician, coarser-grained siliciclastic material was dominant. Therefore, some reworking of the supposed moults could not be entirely excluded; in fact, it is very probable and may be a determining factor in the preservation of the disarticulated arthropod exoskeletons. In addition, undoubted moulting configurations are comparatively rare in Upper Ordovician species (Fig. 8). Pygidia with attached remains of the thorax are the commonest kind of articulated remains in the dalmanitoid and acastoid trilobites (Fig. 9) in the Letná and Zahorany Fms - in *Dalmanitina socialis* (BARRANDE), *D. proaeva proaeva* (EMMRICH), *Kloucekia phillipsi* (BARRANDE), are rarely present also in *Zeliszkella deshayesi* (BARRANDE) and *Dalmanitina proaeva elfrida* SNAJDR from the Vinice Fm. These problematic remains are considered to be transported exuviae, but the determination of the moulting position is impossible. Nevertheless, the supposed moulting remains that we have studied from the clayey Vinice Fm and clayey facies of the Bohdalec Fm show no significant difference in the percentage occurrence of the main sup-

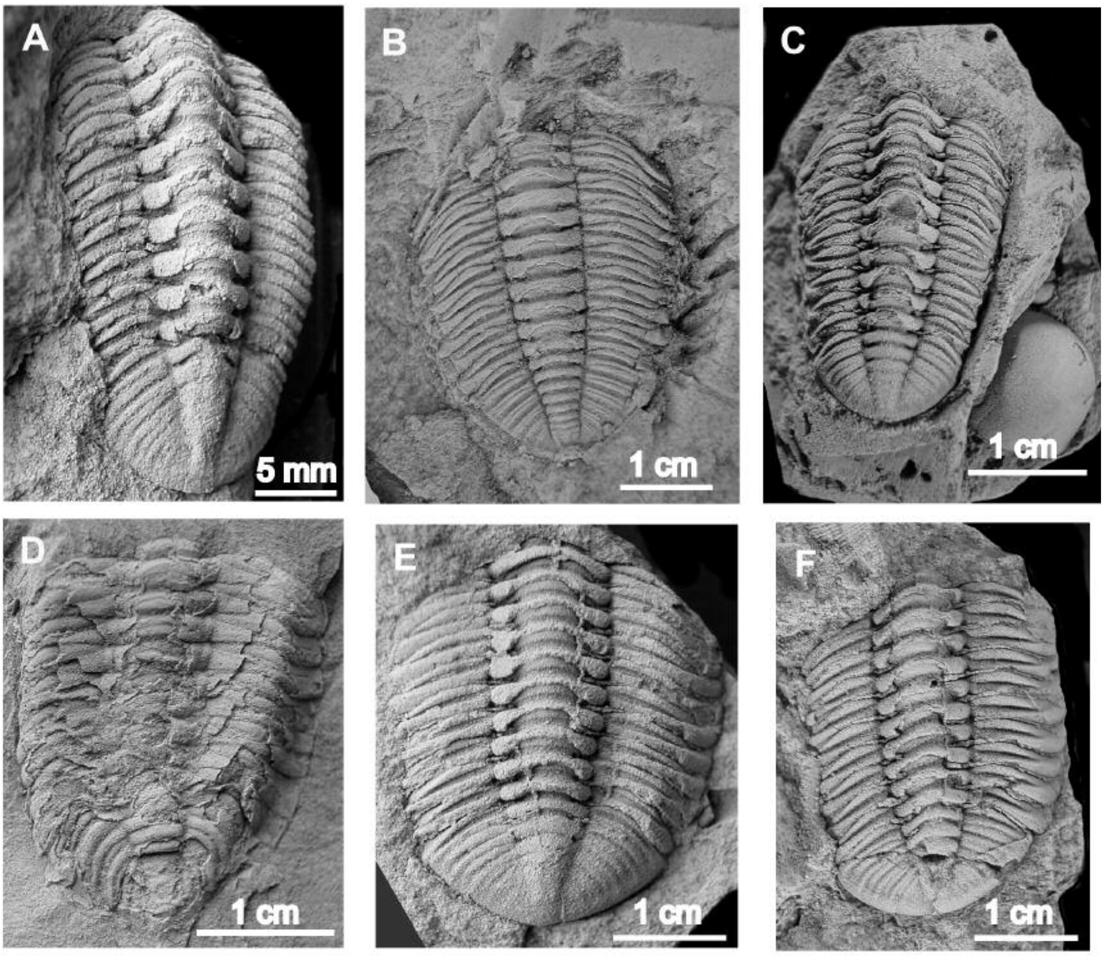


FIGURE 9 **Problematic remains of articulated complete and/or incomplete thoraxes with attached pygidia are surprisingly common, especially in the Bohemian Upper Ordovician dalmanitoid and acastoid trilobites. With some reserve, these remains may be considered as transported exuviae (probably remains of the moulting positions B, C, D, or E?) All samples have been coated with ammonium chloride before photographing. A) *Kloucekia phillipsi* (BARRANDE). NM L 37606, Zahorany, Zahorany Fm. B) *Dalmanitina proaeva elfrida* SNAJDR, CGS JV 1891, Trubín, Vinice Fm. C) *Kloucekia* cf. *phillipsi* (BARRANDE), NM 37607, Zahorany, Zahorany Fm. D) *Zeliszkella deshayesi* (BARRANDE), NM 37608, Trubín, Vinice Fm. E) *Kloucekia phillipsi* (BARRANDE). NM 37609, Zahorany, Zahorany Fm. F) *Kloucekia phillipsi* (BARRANDE). NM 37610, Lodenice, Zahorany Fm.**

posed moulting configurations observed in the Letná and Zahorany Fms.

We suggest that the diversity and prevailing types of the moulting mode seem to be rather a function of the overall body morphology (presence and absence of the genal spines, vaulting and thickness of the exoskeleton, dimensions of the animal, size and position of the eyes) than the actual phylogenetical relations of the species. For example, the morphologically similar, but probably unrelated *Ormathops* (*O.*) *atavus* (BARRANDE) and *Baniaspis* ? *quadrata* (HAWLE et CORDA) have a very similar percentage occurrence of the main moulting types, although the variability is comparatively grater in *Ormathops* (*O.*) *atavus* (BARRANDE). On the contrary, even in very closely related species of the same genus (*Ormathops* DELO, *Zeliszkella* DELO), differences in the variability of moulting were observed (Fig. 8). A body-upright moulting procedure (sensu Speyer, 1985), probably prevailed in the Bohemian Ordovician dalmanitoid and acastoid trilobites.

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