



## ENROLLMENT AND THORACIC MORPHOLOGY IN PARADOXIDID TRILOBITES FROM THE CAMBRIAN OF THE CZECH REPUBLIC

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**Abstract:** The discovery of the partially enrolled specimens of large, late holaspid specimens of paradoxidid trilobites *Paradoxides paradoxissimus gracilis*, *Hydrocephalus minor* and *Acadoparadoxides cf. sacheri*, together with the investigation of functional morphology of their thorax suggest that these arthropods were able to enclose their bodies. The different morphology of thoracic tergites and different outline of the trunk implies different enrollment styles in these species. Consequently, it is possible to distinguish four styles of enrollment within the family Paradoxididae. This variability of enrollment styles not only extends our knowledge about enrollment of paradoxidid trilobites, but also widens our view to diverse protective adaptations in closely related taxa of one family.

**Key words:** Trilobita, Paradoxididae, enrollment, Cambrian, Příbram-Jince Basin

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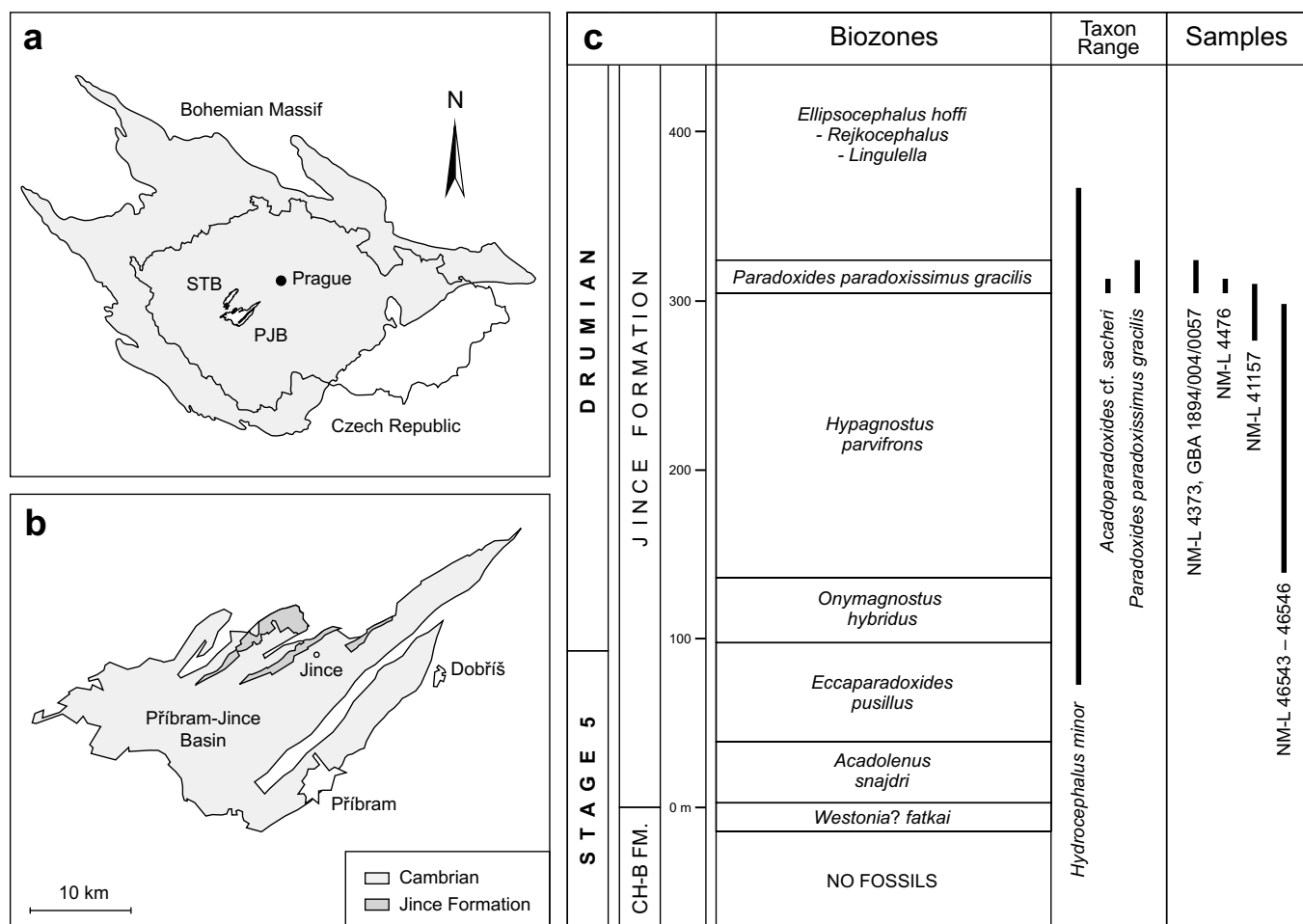
### Introduction

Enrollment likely represents the most iconic behavior in trilobites, mainly because enrolled trilobite exoskeletons are beautiful. They represent a complex life activity that improves our understanding of the evolution and behavior in early arthropods. The ability to enroll (enabling much more effective protection from predatory pressure and the surrounding environment generally) triggered, among other factors, the successful evolution of trilobites during more than 250 million years from the early Cambrian (Ortega-Hernández et al. 2013) through the entire Paleozoic (Clarkson and Henry 1973, Henry and Clarkson 1974, Babcock and Speyer 1987, Esteve et al. 2011) until the last Permian representatives (Lerosey-Aubril and Angiolini 2009). However, early development of enrollment in trilobites is poorly understood (see Ortega-Hernández et al. 2013).

The family Paradoxididae HAWLE et CORDA, 1847 represents a diverse group of Cambrian Series 3 trilobites. Though enrolled paradoxidids are rare in the fossil record, enrolled specimens were already reported more than a hundred years ago (Pompeckj 1896: pl. 16, fig. 1; Text-fig. 2b herein). The rare occurrence and the absence of advanced articulation devices suggests that members of this family were considered to be unable to enclose their bodies (Bergström 1973, Whittington 1990, 1992). However, the

lack of fully enrolled specimens of paradoxidids in the fossil record, as well as other Cambrian trilobites, is likely related to poor development of the interlocking devices that enhance preservation, rather than their inability to enroll (cf. Esteve et al. 2011, Esteve and Yuan in press). Moreover, the recent description of the enrollment procedure in *Eccaparadoxides pradoanus* (VERNEUIL et BARRANDE in PRADO et al., 1860) suggests that some members of this family were capable of encapsulated enrollment, i.e. enrollment without lateral or ventral gaps (Esteve et al. 2013). Some other Cambrian trilobites, on the other hand, had gaps during their enrollment (Ortega-Hernández et al. 2013, Esteve and Yuan in press). Unfortunately, detailed information about enrollment in members of Paradoxididae, other than in *E. pradoanus* is very scarce. Given the high diversity of body patterns within this family, the ways in which individual paradoxidid species enrolled could be highly variable, but still open.

In this contribution, we describe partially enrolled individuals of three paradoxidid species from the Příbram-Jince Basin of the Czech Republic: *Paradoxides paradoxissimus gracilis* (BOECK, 1827), *Hydrocephalus minor* (BOECK, 1827) and *Acadoparadoxides cf. sacheri* (BARRANDE, 1852), including a description of their thoracic structure, articulation and coaptative devices. Subsequently, we discuss how functional morphology of the thorax was linked with different enrollment styles in paradoxidid trilobites to show



Text-fig. 1. Geology and stratigraphy: a – Czech Republic with position of the Skryje-Týřovice Basin (STB) and Příbram-Jince Basin (PJB); b – distribution of Jince Formation in Příbram-Jince Basin, c – biostratigraphy of Jince Formation with taxon ranges of studied taxa and supposed stratigraphic position of studied specimens. Geology according to Havlíček (1971), biozones according to Fatka and Szabad (2014). Abbreviations: CH-B FM. – Chumava-Baština Formation.

the unexpectedly high variability of this behavior in Paradoxididae.

## Geology, material and terminology

### Geological setting

In the Bohemian Massif, unmetamorphosed and fossiliferous Cambrian rocks are known in two separate areas: in the larger Příbram-Jince Basin and the smaller Skryje-Týřovice Basin (PJB and STB in Text-fig. 1a). In Příbram-Jince Basin (Text-fig. 1b), a more than 2500 m thick siliciclastic sequence of Cambrian conglomerates and sandstones with interlayers of greywackes and shales is divided into thirteen lithostratigraphical units of eight formations. The Cambrian Series 3 Jince Formation (Havlíček 1971, Geyer et al. 2008) is up to 450 m thick and contains a rich marine skeletal fauna (Fatka and Mergl 2009). The diverse associations usually include common brachiopods, trilobites, agnostids, echinoderms, hyoliths, palynomorphs and ichnofossils associated with sponge spicules, bivalved arthropods, molluscs and foraminifers (for summary see Fatka et al. 2004). The enrolled and partly enrolled paradoxid trilobites studied herein were collected

from diverse stratigraphic levels of the Jince Formation in the Litavka River Valley (Text-fig. 1c).

### Material

All studied specimens are preserved as internal and/or external molds in fine lithic arenites and shales. The specimens were coated with ammonium chloride and photographed using Canon EOS 6D and Nikon D300 digital cameras. Details of exoskeleton were taken by a Keyence VHX-2000 digital microscope. The studied material is deposited in the collections of the National Museum, Cirkusová 1740, Prague, Czech Republic (samples no. NM-L 4373, NM-L 4776, NM-L 41157, NM-L 41167, NM-L 46543, NM-L 46544, NM-L 46545, NM-L 46546, NM-L 46547, NM-L 46548, NM-L 46549, NM-L 46550, NM-L 46551, NM-L 46552) and in the collections of the Geologische Bundesanstalt, Rasumofskygasse 23, Wien, Austria (sample no. GBA 1896/004/0057).

### Terminology and classification

The morphological terminology follows Whittington and Kelly (1997) and Esteve et al. (2011) for coaptative devices. The term pseudo-isopygous condition refers to the general shape of the trunk, and was introduced by Esteve et al. (2013).

Apparent inconsistencies in the use of morphological characters of the four paradoxiid genera separated by Šnajdr (1957, 1958) resulted in a quite intensive and long-lasting discussion on classification of paradoxiids. Some authors prefer a pragmatic treatment, in which Šnajdr's taxa are considered to be subgenera of *Paradoxides* s.l. in a more or less modified classification (e.g. Sdzuy 1967, 1970, Repina 1969, Solov'ev 1969, Liñan and Gozalo 1986, Geyer and Landing 2001, Fletcher et al. 2005, Fletcher 2007), while others accept the Šnajdr's proposal with smaller or larger modification (e.g. Bergström and Levi-Setti 1978, Dean and Rushton 1997, Dean 2005, Dies Álvarez et al. 2010, Ebbestad et al. 2013, Esteve 2014, Weidner and Nielsen 2014, Geyer and Vincent 2015, Rushton et al. in press). The classification of paradoxiid trilobites used herein follows the generic concept proposed by Dean and Rushton (1997) in the Treatise on Invertebrate Paleontology, and the species concept of Bergström and Levi-Setti (1978). We are aware that this approach needs a careful revision, but that is beyond the scope of this contribution.

## Description of enrolled individuals

### *Paradoxides paradoxissimus gracilis* (BOECK, 1827)

Text-fig. 2

Two partially enrolled specimens are discussed. The first specimen (Text-fig. 2a, NM-L 4373) is 115 mm long and strongly flexed in the middle part of the thorax, so the cephalon and anterior-most part of the thorax are sub-parallel with the posterior-most part of the thorax and the pygidium. The cephalon is not in contact with pygidium and the specimen shows large lateral gaps filled by sediment. The maximal bending of the thorax is achieved from the 7<sup>th</sup> to the 16<sup>th</sup> tergite. From the dorsal view, the axial part of the anterior half of the body does not accurately overlap the posterior part; the posterior part is slightly inclined to the left. This specimen shows both left librigena and rostral-hypostomal plate preserved in situ. All pleurae are horizontally oriented in relation to the particular axial ring, and their distal parts and pleural spines do not overlap.

The second specimen (Text-fig. 2b, GBA 1896/004/0057) was described and figured by Pompeckj (1896: pl. 16, fig. 1). This specimen is 160 mm long and has the posterior part of the trunk (behind the 10<sup>th</sup> thoracic tergite) flexed antero-ventrally. The dorsal part of its internal mold consists of cranidium and the anterior part of thorax; the 10<sup>th</sup> posterior tergite is slightly inclined backwards. The antero-ventrally flexed posterior part of the thorax is partly seen under the exfoliated pleurae on the left side, and is also slightly imprinted on the right side of the body. From the position of the ventral part, it can be inferred that the pygidium, when preserved, is located approximately under the occipital ring, and that the posterior part of the thorax does not cover the entire ventral surface of the exoskeleton. The librigenae of this specimen are not preserved, nor is the rostral-hypostomal plate.

### *Hydrocephalus minor* (BOECK, 1827)

Text-fig. 3

Five partially enrolled specimens of *H. minor* were studied. The first specimen (NM-L 46543, Text-fig. 3a) is

a nearly complete, dorsally strongly arched exoskeleton, 135 mm long. The cephalon and the pygidium are inclined at an angle around of 80–90 degrees to each other. The left librigena is preserved in situ, the right librigena and part of the right fixigena are missing, due to splitting off of the rock. The facial suture is not opened. The exoskeleton is slightly compressed obliquely and laterally, suggesting that the specimen is preserved rather obliquely to perpendicularly to the lamination and main compaction vector. From the dorsal view, the flexed rear part of the trunk is slightly bent to the left. The articulating half-rings seem to be nearly completely exposed in the middle part of the thorax. The distal parts of pleurae in the posterior half of the thorax overlap each other. The three other specimens (NM-L 46544, NM-L 46545 and NM-L 46546, Text-fig. 3b–d) are represented by incomplete dorsally arched exoskeletons (with 14, 16 and 16 preserved thoracic tergites, respectively). Sagittal lengths of preserved parts of these specimens range from 110 mm in NM-L 46545 to 130 mm in both NM-L 46544 and NM-L 46546. The main flexure of the thorax is located from the 10<sup>th</sup> to the 14<sup>th</sup> tergite, and in two specimens, NM-L 46545 and NM-L 46546, the thorax is upturned antero-ventrally. All three specimens have both librigenae preserved in situ, unopened facial sutures and in one specimen the hypostome is preserved in situ (NM-L 46545). Specimen NM-L 46545 shows distally overlapping pleurae. No posterior part of the trunk of any specimen is preserved, due to splitting of the rock samples.

The last specimen (NM-L 41157, Text-fig. 3e) is represented by both internal and external molds of a large exoskeleton of a late holaspid stage, 145 mm long. This specimen has the last nine thoracic tergites and the pygidium flexed ventrally. The posterior part of trunk reaches the second thoracic tergite. Both librigenae are attached to the cranidium. The axis of the ventrally flexed posterior part of the trunk is not parallel to the axis of the anterior part of the trunk, but is slightly inclined (ca. 5 degrees) to the right.

### *Acadoparadoxides cf. sacheri* (BARRANDE, 1852)

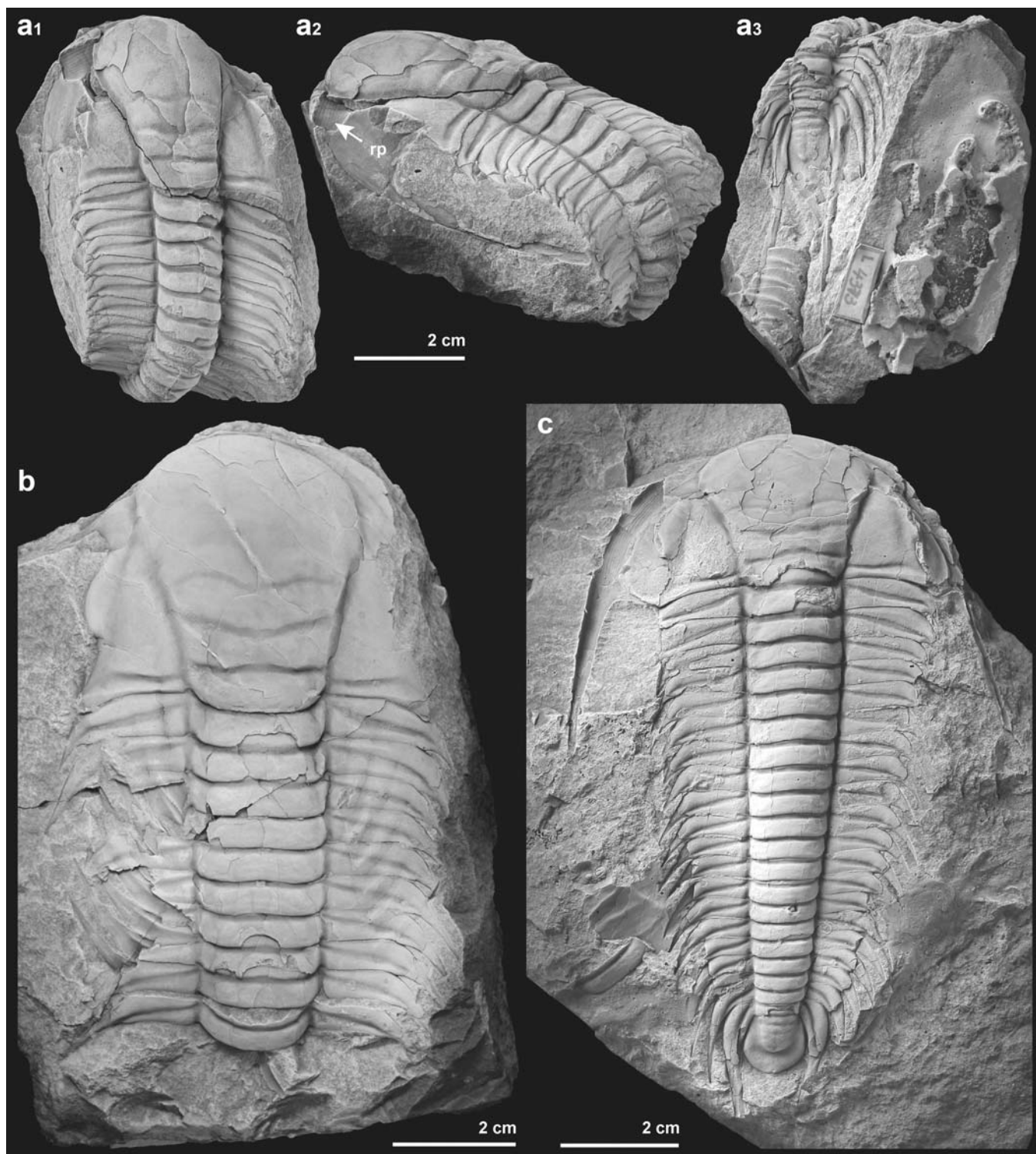
Text-fig. 4

Only one, incomplete, partially enrolled specimen (NM-L 4776, Text-fig. 4a) has been at our disposal. The preserved part of the exoskeleton is 155 mm long; the length of complete specimen is supposed to reach about 180 mm. The posterior part of the thorax is strongly flexed ventrally. The maximal bending of the thorax is between the 10<sup>th</sup> and 15<sup>th</sup> tergite. The right librigena is preserved in situ; the left librigena together with a part of fixigena and the anterior-most part of glabella are split off. The posterior-most part of the exoskeleton behind 15<sup>th</sup> tergite is not preserved. The flexed posterior part of the trunk is slightly inclined to the right. The pleural spines overlap in the flexed part of the thorax. A small rounded tumor-like neoplasm is developed at the right side of occipital ring (see Šnajdr 1978 and Babcock 2007).

## Body pattern, articulation and morphology of coaptative devices

### *Paradoxides paradoxissimus gracilis* (BOECK, 1827)

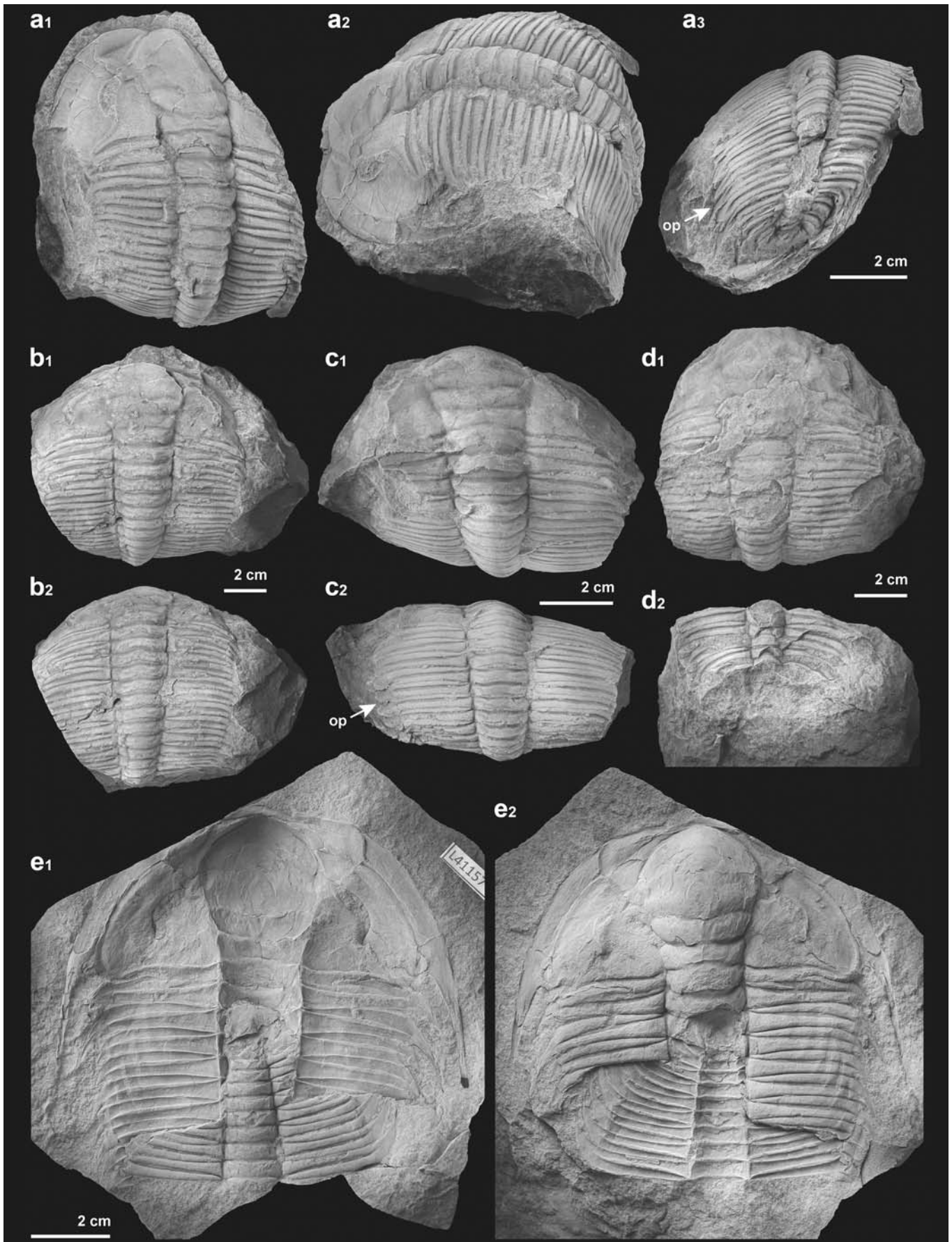
Text-figs 2a, c, 5c, e, h–j



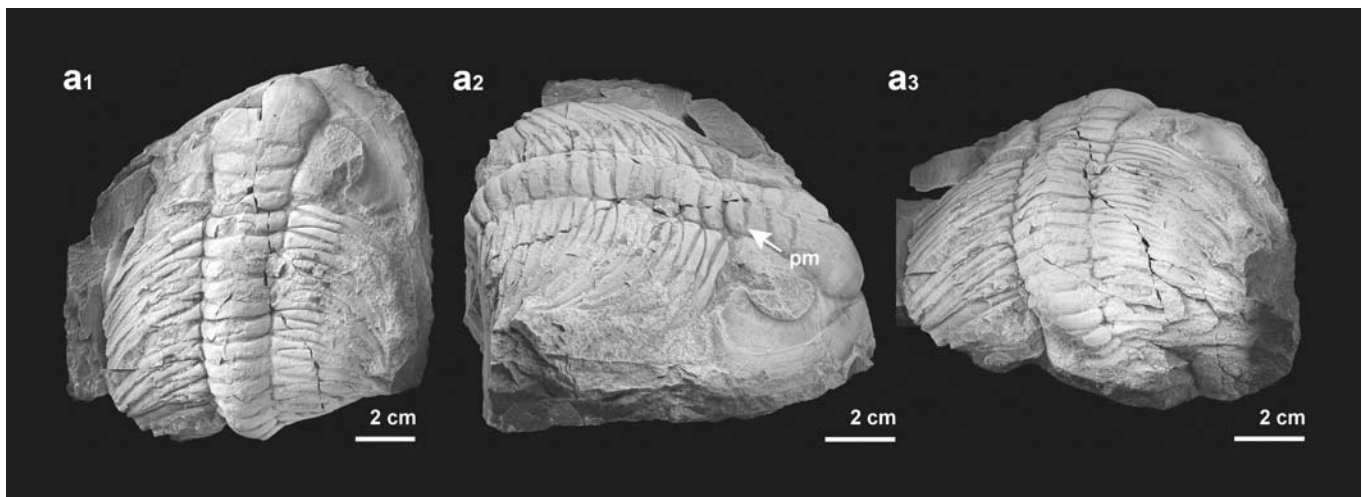
Text-fig. 2. *Paradoxides paradoxissimus gracilis* (BOECK, 1827); Jince Formation, *Paradoxides paradoxissimus gracilis* Biozone, Píbram-Jince Basin: a – specimen no. NM-L 4373, from dorsal (a1), oblique lateral (a2) and ventral (a3) view; b – specimen no. GBA 1896/004/0057, dorsal view; c – outstretched specimen no. NM-L 41167, dorsal view. Abbreviations: rp – rostral-hypostomal plate.

In overall morphology, the exoskeleton of *P. paradoxissimus gracilis* is conspicuously micropygous, with thorax slightly narrowing posteriorly (the posterior width of the thorax reaches about 60% of its anterior width, Text-fig. 2c). The structure of the thorax consists of comparatively narrow (tr.) pleural parts, which are roughly the same width as the axial lobe of the same tergite (Text-fig. 2c). The pleurae are flat, non-fulcrate and horizontally oriented, as is clearly

visible in the tergites that are perpendicular to the main compression pressure (Text-fig. 2a); they therefore are not flattened dorso-ventrally. This is in contrast with Whittington's assumption that pleurae sloped downward abaxially, being gently curved distally (Whittington 1990). Only the slightly wider (tr.) pleurae in first two thoracic tergites seem to be slightly curved ventrally in their distal parts (Text-fig. 2a). The posterior margin of all pleurae bears



Text-fig. 3. *Hydrocephalus minor* (BOECK, 1827); Jince Formation, *Hypagnostus parvifrons* to *Paradoxides paradoxissimus gracilis* Biozones, Příbram-Jince Basin: a – specimen no. NM-L 46543, from dorsal (a1), oblique lateral (a2) and posterior (a3) view; b – specimen no. NM-L 46544, from dorsal (b1), and posterior (b2) view; c – specimen no. NM-L 46545, from dorsal (c1) and posterior (c2) view; d – specimen no. NM-L 46546, from dorsal (d1) and ventral (d2) view; e – specimen no. NM-L 41157, external (e1) and internal (e2) mold. Abbreviations: op – overlapping pleurae.



**Text-fig. 4.** *Acadoparadoxides* cf. *sacheri* (BARRANDE, 1852); Jince Formation, *Paradoxides paradoxissimus gracilis* Biozones, Příbram-Jince Basin: a – specimen no. NM-L 4776, from dorsal (a1), oblique lateral (a2) and posterior (a3) view. Abbreviations: pm – pathological malformation.

an inconspicuous backward oriented projection at the base of pleural spine (Text-fig. 5c). In the anterior edge of each pleura, a wide (exsag.) but shallow flange with a small projection at the antero-lateral corner (Text-fig. 5c) is developed. This structure is inserted below the posterior part of the previous pleura. The articulating half-rings are comparatively short, reaching about 40% of length (sag.) of the axial rings (Text-fig. 5e). The pleural spines are slender, comparatively long (sag.), directed postero-laterally in the anterior part of the thorax and more posteriorly toward its rear part. Dorsal surface of pleural spines is smooth, without any surface sculpture, with the exception of a few terrace lines sub-parallel to the antero-lateral margin of spine in the first two thoracic tergites (Text-fig. 5h–i). The pleural spine doublure bears a furrow running from the tip of the spine, sub-parallel with the posterior margin of the spine (Text-fig. 5j). Terrace lines on the doublure are apparently restricted only to the area anterior from this furrow (Text-fig. 5j), and are sub-parallel to the main axis of the exoskeleton.

#### *Hydrocephalus minor* (BOECK, 1827)

Text-figs 3e, 5a, d, f–g

The exoskeleton is micropygous and the overall outline of the trunk is parabolic (posterior width of the thorax ca. 50–55% of the anterior width). The pleural parts are wider (tr.) than in *P. paradoxissimus gracilis*, being ca. 1.6 times wider than the width of the corresponding axial ring (Text-fig. 3e). Several posterior-most pleurae are inclined backward. In the cross-section, the pleurae are considerably vaulted, without any prominent fulcrum, as was described by Whittington (1990) for the other Barrandian species, *H. carens* BARRANDE, 1846. The flange in the anterior part of each pleura is wide, concave (sag.) and more distinct than in *P. paradoxissimus gracilis*, with a prominent projection at the antero-lateral corner (Text-fig. 5a). Articulating half-rings are short (sag.), reaching ca. 40% of the length of axial rings (Text-fig. 5d), with the exception of the first one, which is slightly longer, similarly to *H. carens* (see Whittington 1990). Pleural spines are flat and claw-like, with a backward

projection at their posterior bases (Text-fig. 5f). The dorsal surface of the pleural spines bears terrace lines, which are inclined in an angle of around 45 degrees to the sagittal axis of the exoskeleton (Text-fig. 5g). On the doublure of the pleural spines, the terrace lines are sub-parallel to the body axis, slightly turned adaxially in the posterior half of the spine (Text-fig. 5f). The mutual orientation of the dorsal and ventral terrace lines forms a criss-cross pattern when the pleurae overlap.

#### *Acadoparadoxides* cf. *sacheri* (BARRANDE, 1852)

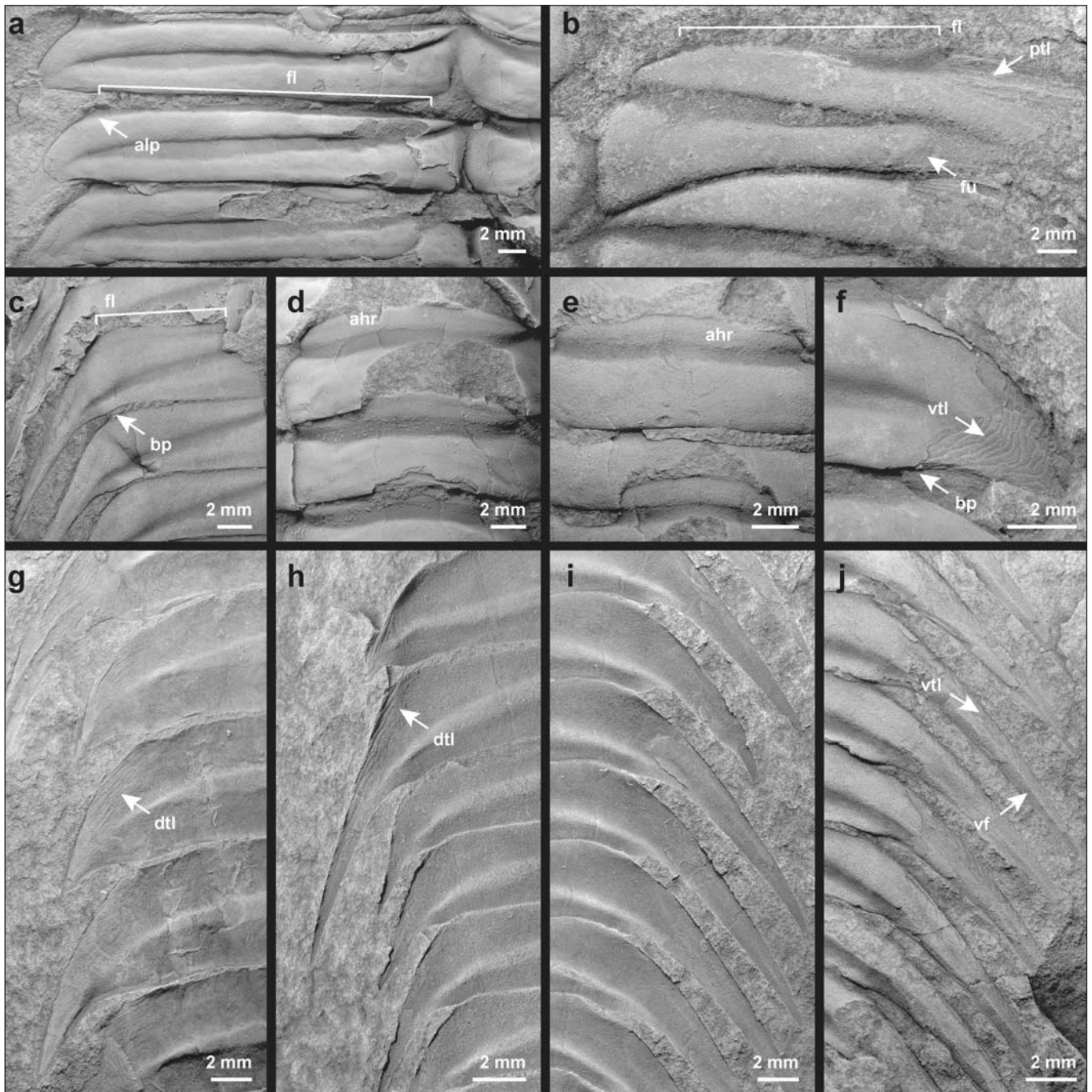
Text-fig. 5b

Well preserved complete specimens of this species are very rare, and detailed information about the thoracic structure and pleural morphology is thus limited. The exoskeleton is micropygous, with rather sub-rectangular thorax. The posterior-most pleurae of *A. cf. sacheri* seem to be separated by comparatively wide gaps (cf. Barrande 1852: pl. 9, fig. 30, Šnajdr 1958: pl. 17, fig. 1). Articulating half-rings length (sag.) varies between 50–45% of the axial ring length. Pleurae in the anterior part of the thorax are fulcrate (Text-fig. 5b). At their anterior margin, they bear a narrow (sag.) flange that widens abaxially, and ends with a small projection near the fulcrum (Text-fig. 5b). Pleural spines are comparatively long and saber-like in shape. The petaloid-like terrace lines are sub-parallel to anterior margin of the pleural spines, and are developed on their dorsal surfaces (Text-fig. 5b). The ventral doublure of pleural spines is poorly preserved.

## Discussion

### Remarks on the preservation

All specimens, with the exception of one specimen of *P. paradoxissimus gracilis* (specimen no. GBA 1896/004/0057), show in situ preserved librigenae still in direct contact with the cranidium (i.e. the facial sutures are not opened). In specimens NM-L 4373 and NM-L 46545, even the



**Text-fig. 5.** Thoracic structure, articulating and coaptative devices of *H. minor* (a, d, f–g), *P. paradoxissimus gracilis* (c, e, h–j) and *A. cf. sacheri* (b): a – specimen no. NM-L 46550, internal mold of pleurae; b – specimen no. NM-L 4776, internal mold of pleura; c – specimen no. NM-L 46551, internal mold of pleurae; d – specimen no. NM-L 46550, internal mold of axial rings and articulating half-rings; e – specimen no. NM-L 46552, internal mold of axial rings and articulating half-rings; f – specimen no. NM-L 46550, detail of pleural spine; g – specimen no. NM-L 41157, external mold of pleural spines; h – specimen no. NM-L 46547, external mold of pleural spines; i – specimen no. NM-L 46548, external mold of pleural spines; j – specimen no. NM-L 46549, pleural spines. Abbreviations: ahr – articulating half ring; alp – antero-lateral projection of flange; bp – backward projection at base of pleural spine; dtl – dorsal terrace lines; fl – flange; fu – fulcrum; pti – petaloid-like terrace lines; vf – ventral furrow of pleural spine; vtl – ventral terrace lines.

rostral-hypostomal plate or hypostome, respectively, are preserved in situ. Some specimens, however, lack the posterior-most part of the trunk (usually broken off between the last 2 and 4 thoracic tergites). This incompleteness, however, seems to be in all cases likely the result of splitting of the rock sample across the trilobite specimen.

The molting behavior of paradoxid trilobites suggests that the herein described specimens with librigenae in situ, undisturbed facial sutures and non-collapsed glabella are carcasses enrolled to various degrees, and do not represent exuviae (cf. Ebbestad et al. 2013, Daley and Drage 2016). The “enrolled” specimen figured by Šnajdr (1958: pl. 46,

fig. 2), seems to have opened facial sutures (personal observation), and therefore we regard it as a possible exuvia. An alternative explanation is that these specimens represent carcasses that became partially enrolled due to muscle contraction after death. This explanation seems to be, however, unlikely, since majority of the Cambrian trilobite carcasses are found outstretched. The flexion of the body and general configuration strongly resemble the initial phases of molting, as proposed by Whittington (1990). Alternatively, the partially enrolled individuals can therefore represent specimens which were suddenly buried in this initial phase of molting.

### Enrollment styles in paradoxidids

The specimens described herein suggest that *P. paradoxissimus gracilis*, *H. carens* and *A. cf. sacheri* were able to enclose their bodies. Although we have no fully enrolled specimen at our disposal, the functional morphology of the thorax implies that they were able to achieve a full enrollment (encapsulated or not, see below). The thoracic morphology of each aforementioned taxon varied (Text-fig. 6), and therefore it is likely they used slightly different enrollment procedures. Consequently, it is possible to distinguish four diverse styles of enrollment within the family Paradoxididae, which significantly extend our knowledge of the evolution of behavior in this trilobite group.

The most effective enrollment among paradoxidids was achieved by *E. pradoanus*, and possibly also by other species of *Eccaparadoxides* ŠNAJDR, 1957 (Esteve et al. 2013, personal observation). These species share several morphological advantages through which they were able to attain a fully encapsulated enrollment (see Esteve et al. 2013 for details): (1) their articulating half-rings were comparatively long, to enable sufficient flexure of the thorax; (2) the pleurae were fulcrate, and were articulated by a flange in the inner portion of the pleura only; (3) the overlapping of pleural spines was facilitated by petaloid-like terrace lines; (4) the so called pseudo-isopygous condition of the trunk and long pleural spines provided full encapsulation of the enrollment; (5) the terrace lines in the rostral plate and in pygidium worked as simple interlocking devices of the enrolled body.

A slightly different style of enrollment among paradoxidids can be suggested for *A. cf. sacheri*. Although fully enrolled specimens are not yet known, the thoracic morphology is similar to that of *E. pradoanus* (well developed fulcrum in the anterior part of the thorax, comparatively long articulating half-rings, well developed flange in the inner portion of the pleurae, the presence of the petaloid-like terrace lines, and rather sub-rectangular thorax, cf. Esteve et al. 2013), and most probably allowed complete enrollment. Comparable morphology of the trunk was also described by Geyer and Vincent (2014) for some other representatives of the genus *Acadoparadoxides* ŠNAJDR, 1957 from Morocco. However, opening gaps between pleural spines in the posterior part of the thorax of *A. cf. sacheri* would prevent full encapsulation in this species.

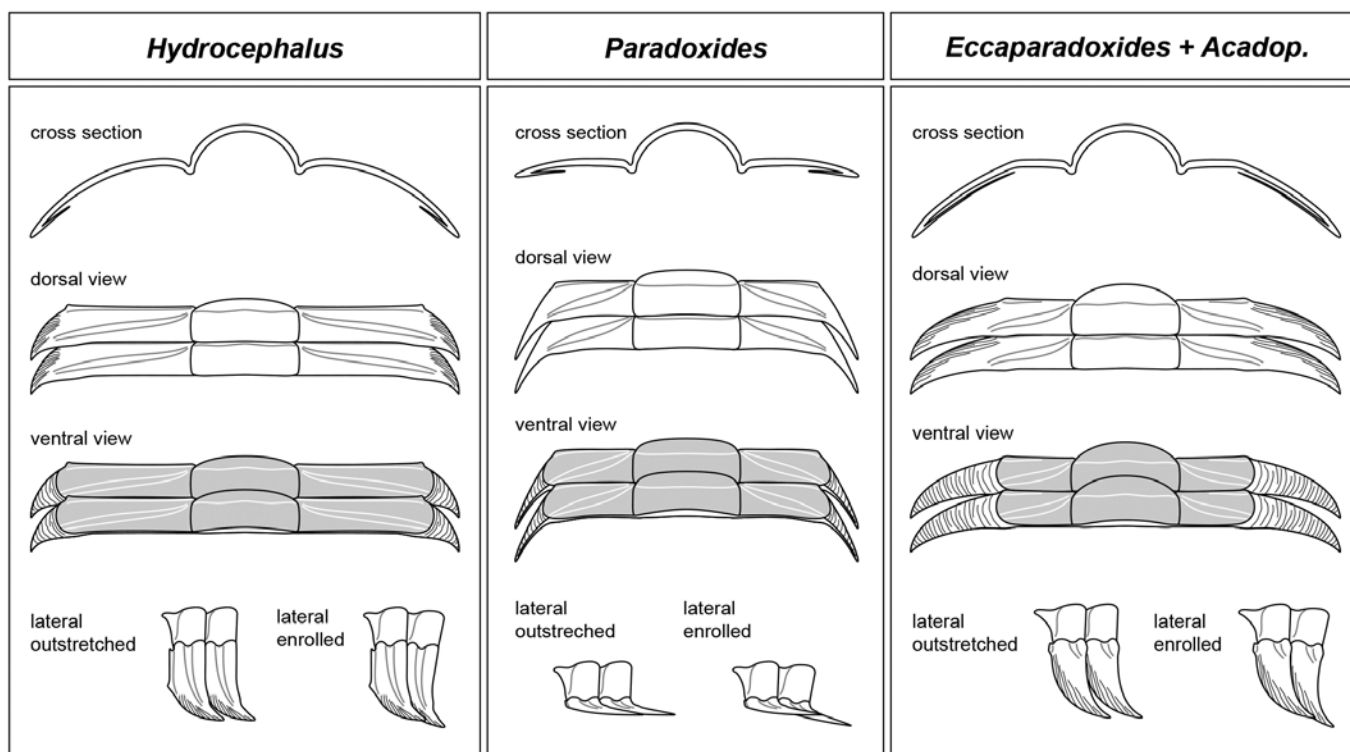
Bergström (1973) suggested for species of *Hydrocephalus* BARRANDE, 1846 a cylindrical enrollment, since the pleurae did not cover lateral gaps when the body was enrolled. In *H. minor*, the articulating half-rings are shorter than in *Eccaparadoxides* or *Acadoparadoxides*. Conse-

quently, the possible extent of telescoping of the half-rings and the angle of mutual rotation between the adjacent tergites were quite limited. Moreover, the simple abaxially curved pleurae were obviously less effective than fulcrate pleurae with horizontal inner portion. In *Hydrocephalus*, the flange at the anterior part of the pleura has had to be necessarily curved abaxially compared to the rest of the pleura, and was not horizontal, as in *Eccaparadoxides* or *Acadoparadoxides*. This was already noted by Whittington (1990). In *H. minor*, during the rotation of adjacent tergites along the flange, the distal-most part of the flange with antero-lateral projection was thus slightly dislocated anteriorly, from its original position under the posterior part of the preceding pleura. The petaloid-like terrace lines on the dorsal surface of pleural spines in combination with approximately perpendicular terrace lines on their ventral doublure likely served in *H. minor* as a device reducing the friction of overlapping pleurae (similarly to *E. pradoanus*, see Esteve et al. 2013 and Hughes 1993 for details). The parabolic outline of the trunk probably did not allow encapsulated enrollment, since the posterior part was narrower than the cephalon. Hence, enrollment of *H. minor* was rather comparable to enrollment seen in some olenellids (Ortega-Hernández et al. 2013).

The last style of enrollment is observable in *P. paradoxissimus gracilis*. The thorax of this species is significantly different, compared with that of *E. pradoanus*, *A. cf. sacheri* or *H. minor*, both in overall appearance and in the structure of each tergite. In *P. paradoxissimus gracilis*, the rotation of the adjacent tergites was probably comparable with that of *H. minor*, because the articulating half-ring lengths were of a comparable proportion with respect to the axial rings. The pleurae and pleural spines were likely horizontally directed, and therefore the pleural spines would generally not overlap during enrollment. This can explain the absence of petaloid-like terrace lines in almost all pleural spines. However, the rather horizontal direction of the pleurae and pleural spines certainly could not cover the large lateral gaps when the animal was enrolled, and the enrollment of this species was non-encapsulated.

Esteve et al. (2011) and Esteve and Yuan (in press) demonstrated that presence of interlocking and articulation devices enhances preservation of enrolled specimens. On the other hand, some early developmental stages of current arthropods, such as giant mole crabs or mantis shrimp larvae also present interlocking devices in certain morphotypes (Haug and Haug 2014, Rudolf et al. 2016). Haug and Haug (2014) suggested that morphotypes with coaptative devices and other morphological features such as telson edges equipped with spines and denticles, and the tergopleurae of the pleomeres postero-distally projected into spine-like extensions were highly adapted to spend more time in this posture. In comparison, the absence of coaptative devices is present in forms that were less capable of enrollment. The almost complete lack of any interlocking devices, and shallow pleural flanges points towards a sporadic enrollment specialist. Such interpretation agrees with Haug and Haug (2014) statements, and suggests that enrolled specimens of *P. paradoxissimus gracilis* are extremely rare not only because the lack of interlocking devices that enhance the preservation, but also because this trilobite did not enroll efficiently.





Text-fig. 6. Simplified morphology of thoracic tergites of *Hydrocephalus*, *Paradoxides*, *Eccaparadoxides* and *Acadoparadoxides*. Morphology of *Hydrocephalus* based on *H. carens* (according to Whittington 1990) and *H. minor*; morphology of *Paradoxides* based on *P. paradoxissimus gracilis*; morphology of *Eccaparadoxides* and *Acadoparadoxides* based on *E. pradoanus* (according to Esteve et al. 2013) and *A. cf. sacheri*.

## Conclusions

Trilobites of the family Paradoxididae show encapsulated (*E. pradoanus*) and likely non-encapsulated (*P. paradoxissimus gracilis*, *H. minor* and *A. cf. sacheri*) enrollment. The question of whether *P. paradoxissimus gracilis*, *H. minor* and *A. cf. sacheri* could or could not achieve full enrollment is still open. Further work (e.g. 3D modeling) needs to be performed, or fully enrolled specimens found, in order to make a more definite assessment. In any case, the remarkable variability of enrollment styles in paradoxidids shows how different evolutionary processes and selective pressures can lead to diverse adaptations in closely related taxa of one family. This is even more striking, considering that these morphological and behavioral adaptations apparently evolved very quickly, within several million years, around the beginning of the Cambrian Epoch 3. The presence of several enrollment styles in this trilobite group also suggests that some of these styles could have evolved independently among Paradoxididae. Different environments or rapid changes in the abiotic factors could have been responsible for the appearance of new morphological devices among the representatives of Paradoxididae.

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