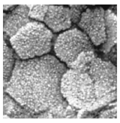
Ontogeny and morphology of Cambrian eocrinoid *Akadocrinus* (Barrandian area, Czech Republic)

MARTINA NOHEJLOVÁ & OLDŘICH FATKA



The gogiid eocrinoid *Akadocrinus jani* Prokop, 1962 is known from the mid-Cambrian (Drumian) Jince Formation of the Příbram-Jince Basin (Barrandian area, Czech Republic). Excellently preserved specimens of this species are described in detail. Our primary focus was on juvenile specimens, described here for the first time. Detailed comparison among juvenile specimens makes it possible to establish changes in morphology during ontogeny. Juvenile specimens differ considerably from adult specimens in (1) a lower number of thecal plates, (2) a complete absence of epispires, (3) comparatively shorter brachioles, comprising a small number of brachiolar plates, (4) a comparatively shorter stem, comprising a small number of columnals and (5) a relatively large attachment disc. Study of the Jince material makes it possible to establish two basic phases in the development of *Akadocrinus*: the pre-epispire bearing phase and the epispire bearing phase. • Key words: *Akadocrinus*, Eocrinoidea, mid-Cambrian (Cambrian Series 3), Příbram-Jince Basin, Barrandian area, Czech Republic.

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The Cambrian was an important period in the evolution of echinoderms as during that time they originated and underwent their initial diversification, which established many of their major clades. The record of Cambrian echinoderms includes nearly 200 species classified into eight major groups: helicoplacoids, eocrinoids, edrioasteroids, rhombiferans, cinctans, ctenocystoids, solutans and stylophorans (Zamora *et al.* 2013).

Eocrinoids represent one of the main echinoderm groups in Cambrian associations (Sprinkle 1973). It is a paraphyletic class of basal blastozoans (Sprinkle 1973, Smith 1984). The body of eocrinoids is usually composed of three major parts: (1) erect biserial brachioles, (2) polyplated theca, (3) stem used for attachment and to elevate the theca above see sea floor (see Fig. 1). The oldest occurrence of the class Eocrinoidea is from Cambrian Stage 4 in Laurentia (Durham 1978), and both East and West Gondwana (South China, see Zhao *et al.* 2007, Hu *et al.* 2007, Hu & Luo 2008; Spain and Morocco, see Ubaghs & Vizcaïno 1990, Nardin & Lefebvre 2005, summary in Zamora *et al.* 2013). During the mid-Cambrian, eocrinoids reached their maximum diversity (Sprinkle 1973, Sprinkle *et al.* 2011). Their numbers and diversity declined steadily from the late Cambrian until their extinction in the Silurian (Sprinkle 1973, Zhao *et al.* 2008).

Cambrian eocrinoids have been reported from North and Central America, Europe, North Africa, East Asia, Australia and Siberia (Yakovlev 1956, Sprinkle 1973, Jell *et al.* 1985, Parsley & Zhao 2006, Zamora *et al.* 2013).

Echinoderms show great diversity in the Cambrian of the Barrandian area. Disarticulated remains of eocrinoids are quite abundant in Cambrian sediments in this area, while remains of more complete specimens have been documented less often. From the Barrandian area, the following five eocrinoid genera have been described: *Lichenoides* Barrande, 1846; *Acanthocystites* Barrande, 1887; *Akadocrinus* Prokop, 1962; *Luhocrinus* Prokop & Fatka, 1985 and *Vyscystis* Fatka & Kordule, 1990 (see Nohejlová & Fatka 2015); a sixth genus, *Cigara* Barrande, 1887 is also found there, but its systematic position is still uncertain (see Lefebvre & Fatka 2003, Fatka & Szabad 2014b).

Our study is focused on a detailed morphological description of several tens of well- to excellently-preserved specimens of *Akadocrinus* Prokop, 1962 from Cambrian deposits in the Příbram-Jince Basin. Prokop (1962) established two species of the genus *Akadocrinus*: *A. jani* Prokop, 1962 and *A. nuntius* Prokop, 1962, both originating from the same stratigraphic level within the Jince Formation. However, Sprinkle (1973) concluded that these two

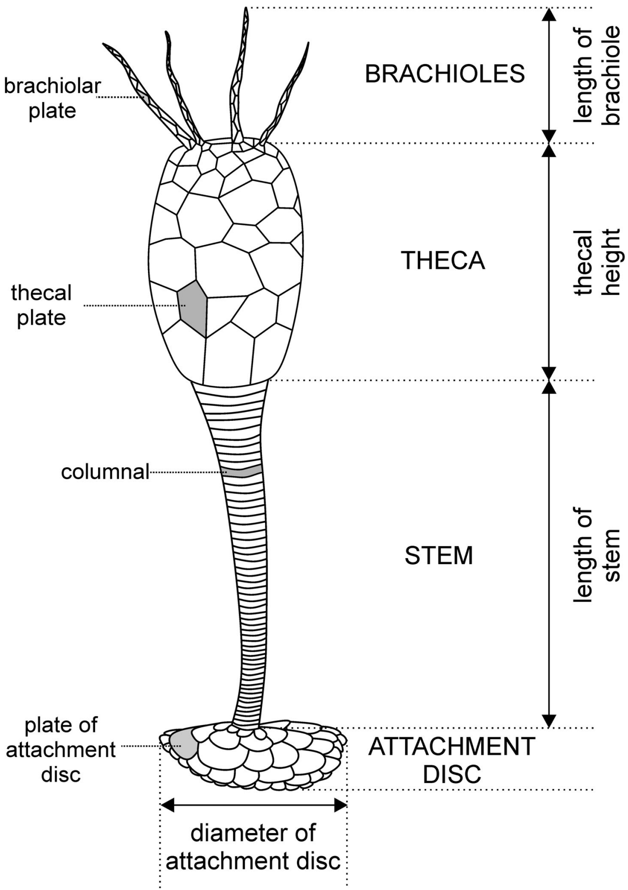


Figure 1. Reconstruction of morphology of a juvenile specimen of *Akadocrinus jani* Prokop, 1962 showing morphology of the body: brachioles, theca, stem and attachment disc. Lateral view.

species are very likely synonyms, and that the differences between *A. jani* and *A. nuntius* can be interpreted as the result of individual variation, ontogeny and taphonomic processes. We agree with the synonymy of these two species. The new material shows that the morphological differences between *A. jani* and *A. nuntius* are caused by different ontogenetic phases, and new data from this material has helped us to better understand the taxonomic position of the genus among eocrinoids. A third species, *A. knizeki* Fatka & Kordule, 1991 is not the topic of this contribution.

This is the first study of eocrinoid material from the Czech Republic that deals with ontogenetic development. Worldwide, only two similar studies have been performed, so our knowledge about eocrinoids ontogeny is still scant. It is very rare to find echinoderm material that encompasses a wide range of developmental phases. This new *Akadocrinus* material provides critical information that helps us understand morphological changes during growth. Not only could ontogenetic questions be addressed, but the new data also helped to clarify some classification issues, as mentioned above, and describe newly observed morphological details. The primary aim of this paper is to show morphological changes during *Akadocrinus* ontogenetic development.

Geological setting

The Jince Formation is a siliciclastic unit dominated by greywacke, claystone and sandstone (Kukal 1971). The formation is less than 100 m thick in the western part of the basin, and reaches up to 450 m in the Litavka River Valley (Havlíček 1998, Fatka & Szabad 2014a). Trilobites and other skeletal fauna of agnostids, echinoderms, hyoliths and brachiopods are generally common throughout the Jince Formation (see Šnajdr 1958, Havlíček 1998, Geyer *et al.* 2008, Fatka & Szabad 2014a). Recently, exceptionally well-preserved specimens of Burgess Shale-type fauna have been recognized in the Jince Formation (*e.g.* Mikuláš & Kordule 1998, Chlupáč & Kordule 2002, Maletz *et al.* 2005, Mikuláš *et al.* 2012, Fatka *et al.* unpublished data).

A large part of the studied eocrinoid material comes from the collection of the late Vratislav Kordule. This collection was purchased in part by the Czech Geological Survey, Prague and the National Museum, Prague. This echinoderm material was collected from two outcrops in the Jince Formation in the vicinity of the town of Jince: the stratotype section of the Jince Formation above the Litavka River on the south-eastern slope named Vinice (outcrop 1 in Fig. 2C; 49° 47´ 12.898˝ N, 13° 59´ 8.673˝ E; see Šuf 1928, Fatka & Kordule 1992) and the north-eastern slope of the Vystrkov Hill near Jince (outcrop 2 in Fig. 2C; 49° 46´ 45.922˝ N, 13° 58´ 2.379˝ E). In both outcrops, a continuous succession in greywackes to shales of the *Paradoxides* (*P.*) *paradoxissimus gracilis* Trilobite Biozone contains moderately diverse fauna, which includes abundant conocoryphid, ptychoparidand paradoxidid trilobites, agnostids (*Peronopsis* and *Hypagnostus*) and hyolithids, all associated with rare bivalved arthropods (*Tuzoia*, *Forfexicaris*, *Konicekion* and *Liangshanella*), brachiopods, gastropod-like molluscs, diverse problematica, acritarchs and ichnofossils (for a list of taxa see Fatka *et al.* 2004, Geyer *et al.* 2008, Fatka & Szabad 2014a).

Abundant occurrence of the paradoxidid trilobite *Paradoxides* (*P.*) *paradoxissimus gracilis* and the agnostid *Hypagnostus parvifrons* indicates an age corresponding to middle and higher levels of the Baltic *Paradoxides* (*P.*) *paradoxissimus* Biozone (see Weidner & Nielsen 2013), which is equivalent to the Caesaraugustian Regional Stage in the West Gondwana chronostratigraphic sequence (see Geyer *et al.* 2008, Gozalo *et al.* 2011); these levels thus correspond to the Drumian Stage of Cambrian Series 3 (Fatka *et al.* 2014).

Material and methods

The studied specimens are preserved articulated, nearly complete to complete external molds in very fine-grained shale. Excellently preserved material allows detailed study of both external and internal surfaces of thecal walls, but only the external surfaces of brachioles, stems and attachment discs. One to four latex casts were made from all studied specimens. At first, one or two cleaning casts were produced, they cleaned the rock surface from dust and products of weathering (*e.g.* limonite). Subsequently, one or more new latex casts were made; one of them was coated with ammonium chloride and photographed using an Olympus SZX-12 optical microscope with an Olympus D digital camera. A number of different morphological measurements were made in order to analyse the studied specimens. The following parameters were measured using Quick PHOTO MICRO 3.0.: length of brachioles and brachiolar plate; thecal height, thecal width and thecal plate size; length and width of stem, height of columnal, width, height and diameter of attachment disc, and size of attachment disc plates. Drawings were produced from the photographs using Corel Draw X6 and Adobe Photoshop CS5. All specimens are deposited in collections of the National Museum, Prague (L42222, L42223, L42226, L42227a, L42227b and L42230) and in the Czech Geological Survey, Prague (YA1191, YA1193, YA1195, and YA1197).

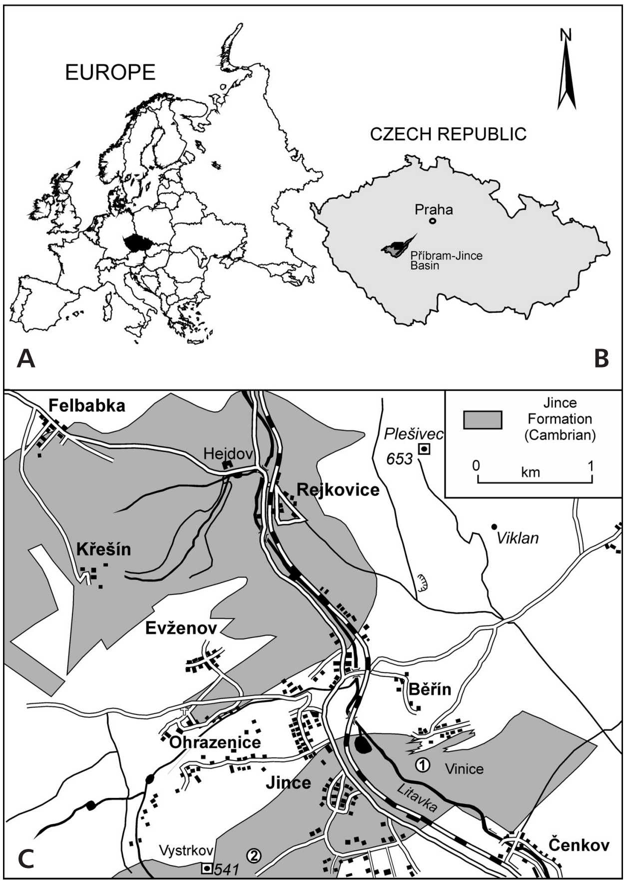


Figure 2. Geological setting. • A – location of the study area in Europe. • B – map of the Czech Republic and the Příbram-Jince Basin. • C – simplified sketch map showing the location of fossil sites in the mid-Cambrian Jince Formation within the Příbram-Jince Basin (geology modified from Havlíček 1971). 1 – hill slope of Vinice near Jince; 2 – Vystrkov Hill near Jince.

Systematic palaeontology

We used the terminology proposed by Sprinkle (1973) – brachioles, stem, attachment disc. However, we prefer to use the term theca instead of calyx (see Ubaghs 1967, Parsley 2012, Zamora *et al.* 2013).

Subphylum Blastozoa Sprinkle, 1973
Class Eocrinoidea Jaekel, 1918
Order Gogiida Broadhead, 1982
Family Eocrinidae Jaekel, 1918

Genus *Akadocrinus* Prokop, 1962

Diagnosis. – (after Sprinkle 1973, pp. 105–106) Eocrinoids having an elongate, flat-topped, irregularly multiplated calyx bearing epispires (sutural pores) medially, numerous biserail brachioles branching off the summit in groups, and a long, large-diameter stem having a few irregularly wedge-shaped columnals proximally, a large diameter lumen, and a rounded, irregularly plated attachment disk at the distal end.

Type species. – *Akadocrinus jani* Prokop, 1962. Jince Formation, *Hypagnostus parvifrons* Biozone, Drumian, Příbram-Jince Basin, Barrandian area, Czech Republic.

***Akadocrinus jani* Prokop, 1962**
Figures 3–6

1962 *Akadocrinus jani* (Prokop). – Prokop, pp. 2–4, pl. 1, figs 1, 2.
1967 *Akadocrinus jani* (Prokop). – Ubaghs, pp. S479–S480, fig. 307 2a, 2b, 2c.
1973 *Akadocrinus jani* (Prokop). – Sprinkle, pp. 105–106; 248, pl. 26, figs 1, 2.
1975 *Akadocrinus jani* (Prokop). – Ubaghs, p. 90, fig. 6D.
2002 *Akadocrinus jani* (Prokop). – Cid & Alonso, p. 27.
2002 *Akadocrinus jani* (Prokop). – Chlupáč & Kordule, p. 177.
2004 *Akadocrinus jani* (Prokop). – Parsley & Prokop, p. 148.
2004 *Akadocrinus jani* (Prokop). – Fatka *et al.*, p. 379.

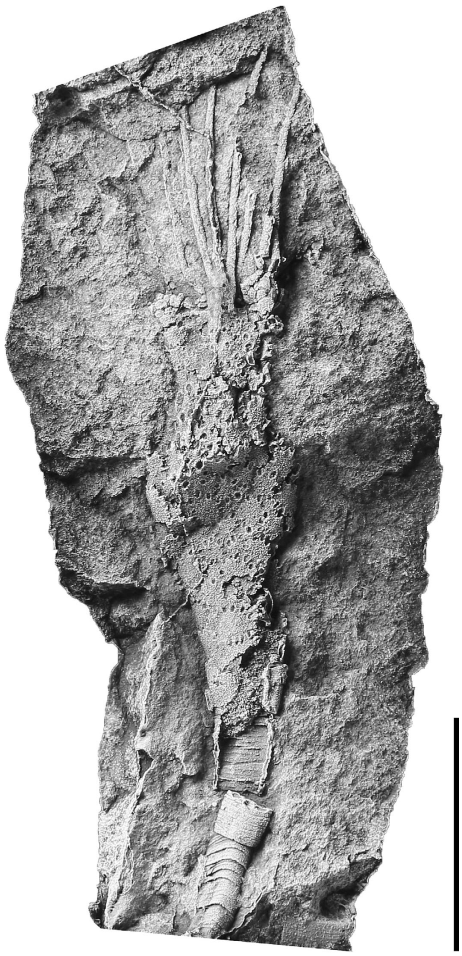


Figure 3. Latex cast of the holotype of *Akadocrinus jani* Prokop, 1962; mid-Cambrian, Jince Formation, *Paradoxides* (*Paradoxides*) *paradoxissimus gracilis* Zone. Housed in collections of the National Museum Prague under number BR-76/1960, L 8045. Scale bar = 1 cm.

2008 *Akadocrinus jani* (Prokop). – Clausen & Smith, p. 746.

Holotype. – Almost complete specimen housed in the collections of the National Museum Prague under number BR-76/1960, L 8045 (see Fig. 3).

Diagnosis (emended). – Theca elongate, barrel-shaped, composed of polygonal plates (often irregularly pentagonal and hexagonal plates). Theca narrowing to both aboral and adoral ends. Polygonal plates of varying size, on external surface fine granulation. Internal surface smooth. Smaller plates situated in oral part of theca, usually irregularly arranged. Minute plates intercalated between larger plates in all parts of theca. Between thecal plates, oval epispires with well-distinguishable raised rims. Numerous long and thin brachioles, with biserial structure, simple, never branched. Base of theca grades into stem composed of equally sized, low columnals. Stem long, distally narrowing. Stem with comparatively large ovoid disc, composed of varying number of polygonal plates.

Remarks. – The original diagnosis was established by Prokop (1962). Additional material of this species has been found since then, and shows previously unknown characters. Consequently an emended diagnosis is proposed.

General morphological description of studied material

Ten specimens were used for this study; eight nearly complete and two less so.

In this section that is focused on a detailed morphological description of the studied specimens we decided to divide the material into two main groups, based on differences in morphology. Our principal interest was in juvenile specimens, which have not yet been studied. This previously undescribed material yields new information about morphology of this group of early echinoderms. The connection with ontogenetic development is discussed below.

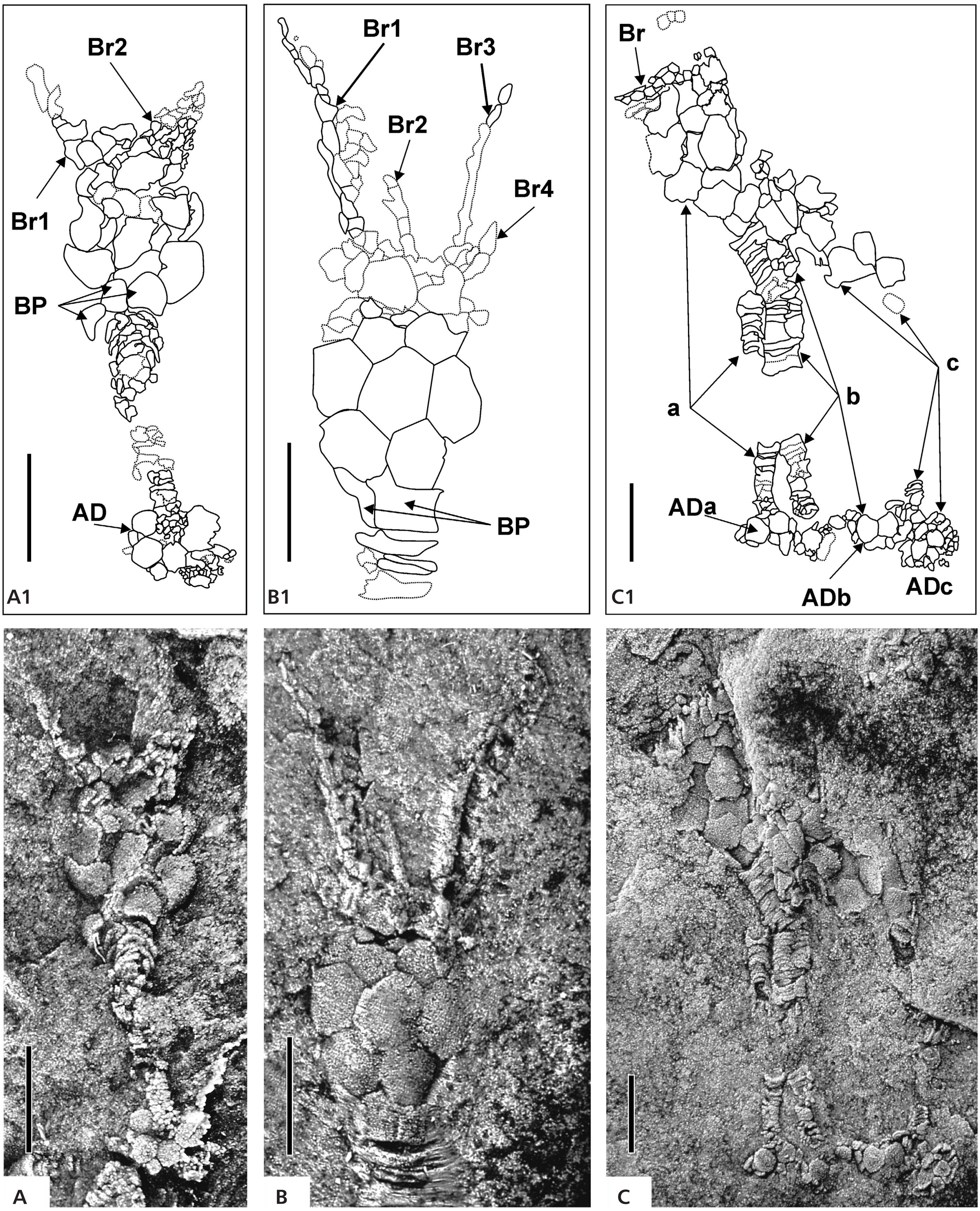
Juvenile specimens (Figs 4–6)

This material has been never studied before, and small specimens of *Akadocrinus* were not known. The excellent preservation of this material allowed observation of new morphological details, and comparison of juvenile against adult specimens. These data are important to properly understand the ontogeny of this eocrinoid species.

Brachioles. – All brachioles show a biserial structure. In juveniles specimens, quite short brachioles (maximal length of preserved brachioles is 2.09 mm) are composed of a variable number of brachiolar plates, which usually measure from 0.08 to 0.44 mm. Juvenile specimens of *Akadocrinus* generally have two to four brachioles.

Theca. – Juvenile specimens generally show a common outline of theca, elongated and barrel-shaped. In juvenile

Figure 4. Early ontogenetic specimens of *Akadocrinus jani* Prokop, 1962; mid-Cambrian, Jince Formation, *Paradoxides* (*Paradoxides*) *paradoxissimus gracilis* Zone. Three specimens with the smallest thecal dimension. Specimens YA1191 and YA1193 housed in the Czech Geological Survey, Prague, specimen L42227b stored in the collection of the National Museum in Prague. • A – slightly damaged complete specimen. Latex cast of



YA1191, Vystrkov Hill near Jince near Jince, TH = 1.74 mm. • B – theca with proximal part of stem and partly preserved brachioles. Latex cast of YA1193, Vystrkov Hill near Jince, TH = 1.84 mm. • C – three slightly damaged specimens (designated as a, b and c). Latex cast of L42227b, hill slope of Vinice near Jince, TH = 2.01 mm. A1, B1, C1 – drawing of specimens made in CorelDrawX6. AD – attachment disc. Br1 to Br4 – brachioles. All scale bars represent 1 mm. All latex casts of natural external molds are coated with ammonium chloride.

Table 1. Table showing important morphological parameters, which were measured on studied material. All measured parameters are in mm.

specimen	TH	number of thecal plates	size of thecal plates		number of brachioles	max length of brachioles	length of stem	diametre of attachment disc
			min	max				
YA1191	1.74	40	0.17	0.60	2	1.04	2.18	1.07 × 0.41
YA1193	1.84	30	0.08	0.69	4	2.09	1.30	–
L42227b	2.01	25	0.10	0.55	–	–	3.53	1.00 × 0.46
YA1195	2.02	10	0.22	0.57	2	1.41	2.89	1.09 × 0.68
YA1197	2.14	7	0.28	0.97	3	0.90	2.24	–
L42230	2.19	30	0.11	0.70	3	2.00	4.18	1.42 × 0.7
L42227a	2.70	36	0.20	0.60	3	1.60	3.75	1.37 × 0.50

specimens, thecal height varies from 1.74 to 2.7 mm. The number of thecal plates is usually less than 50. It can be supposed that thecal plates were arranged in several more or less regular circlets. However, some of the studied specimens show more or less apparent distortions of this arrangement. The lowest number of preserved thecal plates is seven, in specimen YA1197 (Fig. 5B). Thecal plates of different size are roughly tetragonal to hexagonal in outline. The average size of thecal plates ranges around 0.40 mm in juvenile specimens. Plates situated in the radial part of the theca are larger than in the oral part. Their external surface bears fine granulation.

Epispires. – Juvenile specimens have no epispires; this was in fact the criterion we used to separate the specimens into juvenile and adult groups.

Stem. – The stem is composed of columnals of quite uniform height, about 0.06 mm, wider proximally, narrower distally. The length of the stem is variable, ranging from 1.30 (incomplete stem, Fig. 4B1) to 4.18 mm (Fig. 5C). In complete specimens, the stem is terminated by a distal attachment disc (Fig. 6).

Attachment disc. – The attachment disc quite large, ovoid in outline, composed of plates of various sizes.

Mature specimens (Fig. 7)

Here we present three excellently preserved specimen of *Akadocrinus jani*. The exceptional quality of preservation shows rare details, which have never before been observed in this eocrinoid echinoderm. For the first time, we were able to observe internal surfaces of thecal plates and ambulacral furrows in specimens from the Barrandian area.

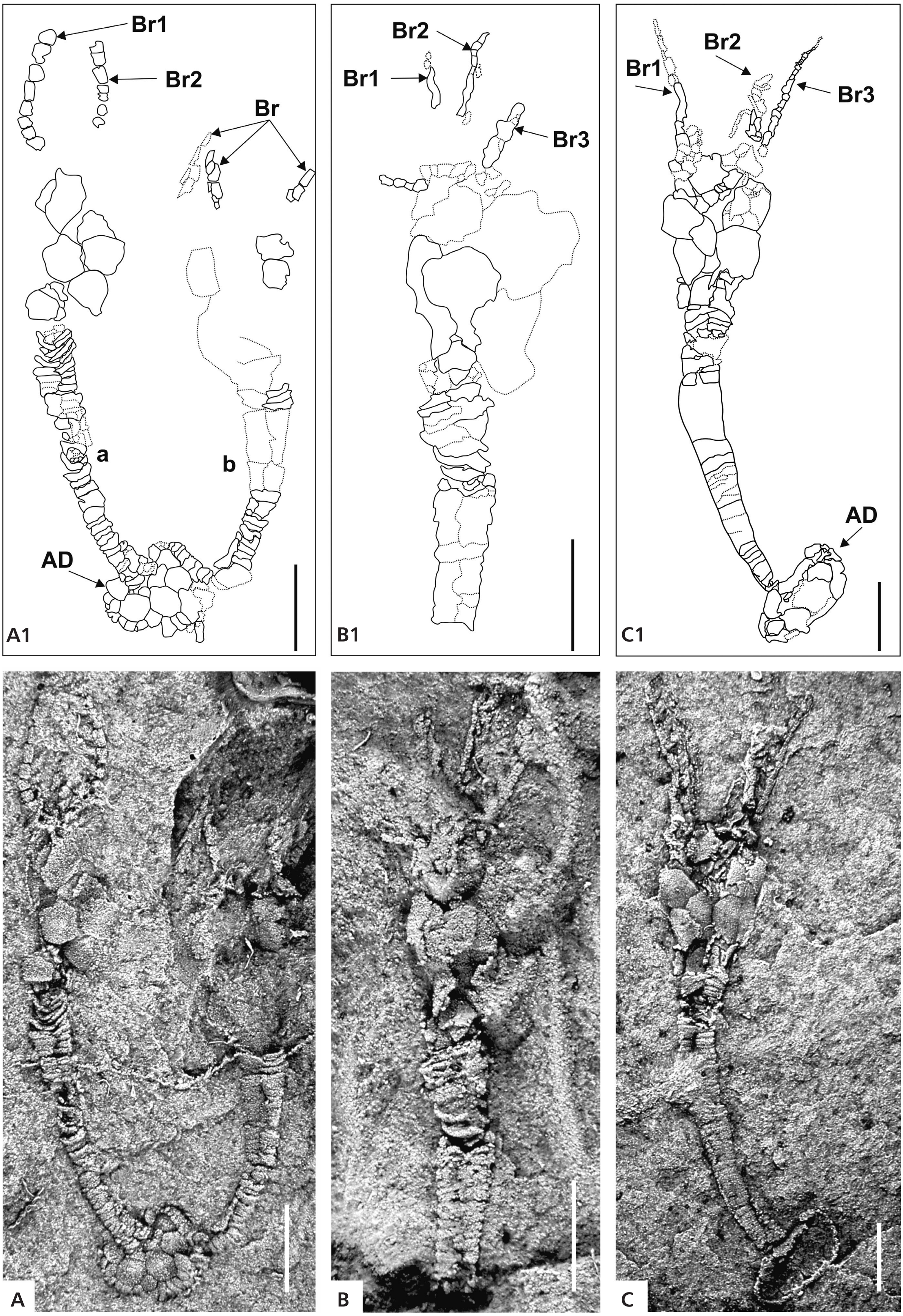
Brachioles. – Biserial brachioles quite long (maximum length of preserved brachioles is 20.00 mm), composed of variable number of brachiolar plates, usually from 0.17 to 0.82 mm. Number of brachiolar plates is several times higher than in juveniles. Number of preserved brachioles varies, usually from 7 to 14. Specimen L42226 (Fig.7C) has preserved ambulacral furrow.

Theca. – Elongate, barrel-shape, distally narrowing. Adult specimens always have more than 50 plates in theca, often around 100. Adults also usually have more irregularly shaped thecal plates. Average size of thecal plates around 0.99 mm in adults. Smallest plates are 0.21 mm high, largest around 1.69 mm. Thecal height more than 10 mm.

Minimally three generations of plates in theca, of differing sizes. In most cases, developmentally older plates are larger than younger one. New plates are intercalated between older plates. Sometimes new small plates make a ring, called rosette, around older plates. Intercalation of new plates disrupts the circlet plate order observed in juvenile stages. External surface of thecal plates bears fine granulation, internal surface smooth (Fig. 7B).

Epispires. – Adult specimens (thecal height greater than 10 mm) bear ellipsoidal epispires with clearly visible rim (Fig. 8B). Number of epispires corresponds with size of thecal plates. Small plates show a low number of epispires, larger plates more than ten.

Figure 5. Early ontogenetic specimens of *Akadocrinus jani* Prokop, 1962; mid-Cambrian, Jince Formation, *Paradoxides* (*Paradoxides*) *paradoxissimus gracilis* Zone. Specimens YA1195 and YA1197 housed in the Czech Geological Survey, Prague, specimen L42230 stored in the collection of the National Museum in Prague. • A – two nearly complete severely damaged specimens (designated as a and b). Latex cast of YA1195, Vystrkov Hill near Jince, TH = 2.02 mm. • B – partly preserved specimen with four poorly-preserved brachioles. Latex cast of YA1197, Vystrkov Hill near Jince, TH = 2.14 mm. • C – complete specimen with three brachioles. Latex cast of L42230, locality unknown, TH = 2.19 mm. A1, B1, C1– drawing of specimens made in CorelDrawX6. Br1 to Br4 – brachioles. BrPl – brachiolar plates. All scale bars represent 1 mm. All latex casts of natural external molds are coated with ammonium chloride.


Br1
Br2
Br
a
b
AD
A1
Br2
Br1
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B1
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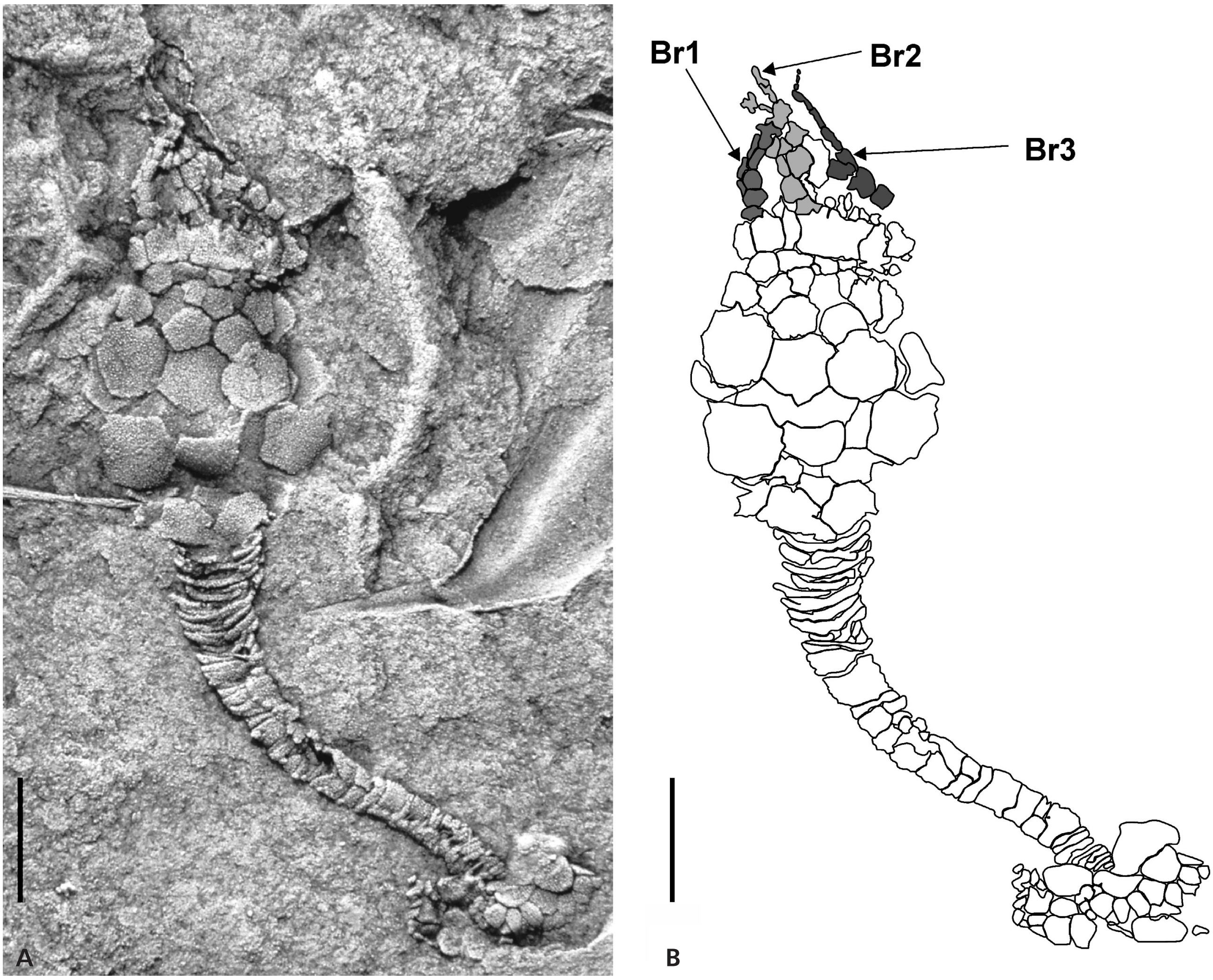

Figure 6. Early ontogenetic specimen of *Akadocrinus jani* Prokop, 1962; mid-Cambrian, Jince Formation, *Paradoxides* (*Paradoxides*) *paradoxissimus gracilis* Zone. The specimen is stored in the collection of the National Museum in Prague. • A – complete specimen with three brachioles. Latex cast of L42227a, hill slope of Vinice near Jince, TH = 2.7 mm. • B – drawing of specimen L42227a made in CorelDrawX6. Br1 to Br3 – brachioles. Scale bar represents 1 mm. Latex cast of natural external molds is coated with ammonium chloride.

Stem. – Stem composed of columnals, quite uniform height. Normal size of columnal about 0.06 mm. Stem wider proximally, narrower distally. Length of stem variable, usually more than 20 mm long on studied specimens. We do not have a complete preserved stem.

Attachment disc. – Not preserved in studied specimens.

Discussion

Ontogeny of eocrinoids

It is generally rare to describe complete ontogenetic development in fossil echinoderms. Currently, the ontogeny of eocrinoids echinoderms is poorly understood, since well-preserved material is extremely rare. Only a few studies have been done with gogiids echinoderms; Parsley & Zhao (2006) and Parsley (2012) described specimens originating from the early and mid-Cambrian of South China, and Zamora *et al.* (2013) discussed North American materials. In the first two papers, an informal classification of ontogenetic development of *Gogia* was proposed. Parsley (2012) distinguished several ontogenetic stages using thecal height (TH = the distance from the summit of the theca to the top of the stalk) as a scale, complemented by five identifying characters that are important for ontogeny. Based on three Chinese species, *Guizhocrinus yui*, *Sinoeocrinus lui* and *Globoeocrinus globulus*, a complete ontogenetic sequence was established with three different stages: (a) juvenile stage (with early, middle and late substages); (b) mature stage (early, middle and late substa-

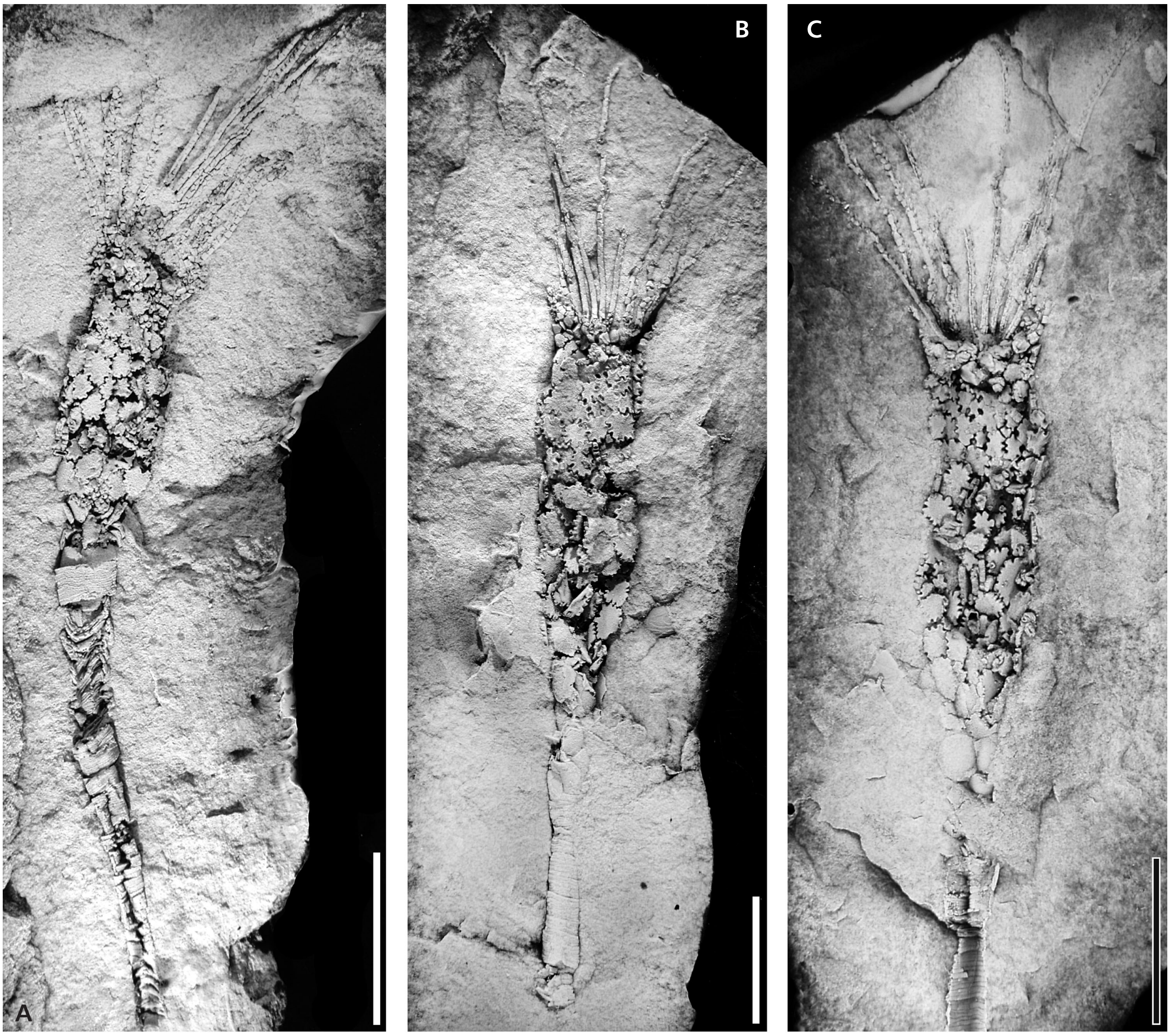

Figure 7. Late ontogenetic specimens of *Akadocrinus jani* Prokop, 1962; mid-Cambrian, Jince Formation, *Paradoxides* (*Paradoxides*) *paradoxissimus gracilis* Zone. The specimens are deposited in the collections of the National Museum in Prague. • A – almost complete specimen without attachment disc, latex cast of L42222, hill slope of Vinice near Jince, TH = 18.39 mm. • B – almost complete specimen, without attachment disc, latex cast of L42223, TH = 33.93 mm, locality unknown. • C – almost complete specimen, without attachment disc, latex cast of L42226, hill slope of Vinice near Jince, TH = 34.21 mm. Scale bar 1 cm. Latex cast of natural external molds is coated with ammonium chloride.

ges), and (c) gerontic stage. The five important characters are: (1) number and morphology of brachioles; (2) the number of thecal plates and their arrangement; (3) the number, order, and morphology of epispires; (4) development of the stalk (= stem), and (5) morphology of the distal attachment structure.

Zamora *et al.* (2013) showed that all studied specimens of *Gogia* sp. have TH spanning a size interval that encompasses all the stages that Parsley (2012) distinguished in the Chinese material. This important study of *Gogia* sp., in which Zamora *et al.* (2013) statistically analyzed a large amount of material, showed that post-metamorphic development most probably represents a continuous process. There are no statistical support for any of the size groupings separated previously by Parsley & Zhao (2006) and Parsley (2012) .We agree with the opinion that a separation of distinct ontogenetic stages based only on TH represents an artificial classification (Zamora *et al.* 2013). On the basis of additional, newly analyzed material, we suspect that TH is insufficient to completely distinguish the three stages, although the limited number of specimens and partial knowledge of the complete population of the Jince material somewhat restricts our analyses.

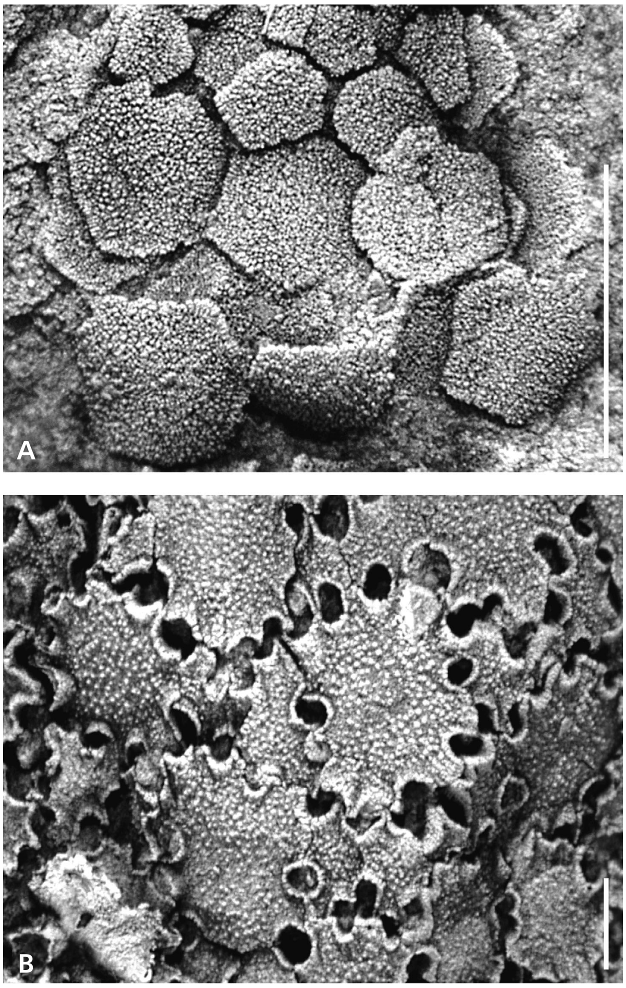

Figure 8. Detail of thecal plates. There are clearly visible differences between plates of pre-epispire bearing phase specimen and epispire bearing phase specimen. • A – *Akadocrinus jani* Prokop, 1962; latex cast of specimen L42227a, hill slope of Vinice near Jince. Juvenile specimen with quite regular thecal plates and no evidence of epispires. • B – *Akadocrinus jani* Prokop, 1962; latex cast of specimen L42228, locality unknown. Mature specimen has irregular shape of thecal plates with epispires boundered by clearly visible rims. Scale bar represents 1 mm. Both latex casts of natural external molds are coated with ammonium chloride.

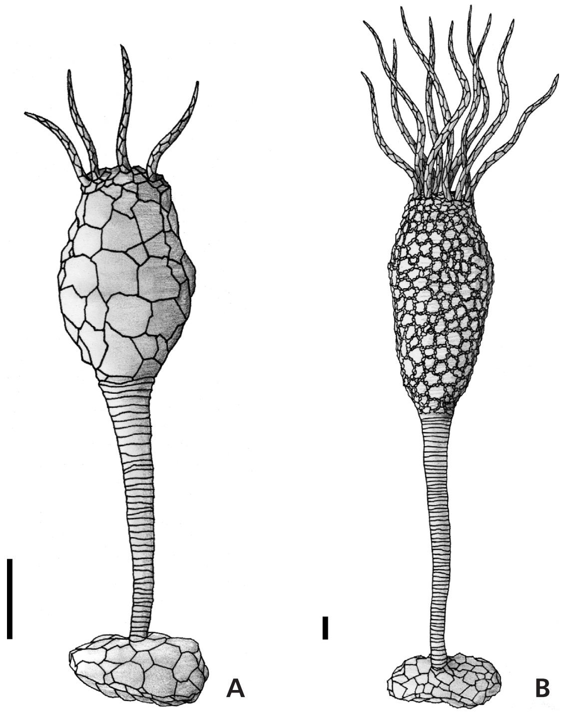

Figure 9. A – pre-epispire bearing phase – *Akadocrinus*. • B – epispire bearing phase – *Akadocrinus*. Both scale bars represent 1 mm.

Ontogenetic development of *Akadocrinus jani*

Morphological characterization of the studied material was described in an earlier part of this paper and we are confident that data from our material shows differences in morphology during the ontogenetic development. The juvenile specimens of *Akadocrinus jani* have different morphology from adult specimens. It is possible to document the following changes during ontogeny:

(i) increasing number and prolongation of brachioles,
(ii) increasing thecal height,
(iii) increasing number of enlarging thecal plates,
(iv) prolongation of stem.

When we compare the number of brachioles in juvenile and adult specimens, we see a clear difference in the number. Smaller specimens usually have 2–4 brachioles, older ones 7–14. Also, the length of brachioles and thecal height both increase during ontogeny. The smallest specimen has TH = 1.74 mm (specimen YA1191, Fig. 4A), the largest 34.21 mm (specimen L 42226, see Fig. 7C). The number of thecal plates increases, as well as their size. Juvenile *Akadocrinus* have less than 50 thecal plates, with average size around 0.40 mm, as opposed to adult specimens, which have more than 100 thecal plates, with average size around 0.99 mm. During ontogenetic development, the theca grows by two basic mechanisms: (1) increasing size of primary plates, and (2) intercalation of new small secondary plates between the older plates. This mechanism is known also from other eocrinoids. It is usually possible to distinguish three generations of thecal plates in adult specimens. No epispire has been observed in studied juvenile specimens. In comparison, adult specimens bear ellipsoidal epispires, with a clearly visible rim (Fig. 8). The number of epispires correlates with the size of thecal plates. Small plates show a low number of epispires, while larger plates bear more than ten epispires. The length of stem increases with age; juveniles have maximal stem length 4.18 mm. Adults present a small problem, in that we do not have a single preserved complete stem. Even so, we know from fragments that we do have, that the length of stem is markedly longer, usually more than 20 mm. Most juvenile

Table 2. Table showing comparison of thecal heights of Czech and Chinese material typical for each ontogenetic stage. For measurement were used nineteen specimens of *Akadocrinus jani* Prokop, 1962 deposited in collection of the Czech Geological Survey and the National Museum in Prague. Used Chinese data after Parsley (2012). All thecal heights were measured in millimeters.

	Czech material	Chinese material
juvenile stage	TH ≥ 1,74	TH ≥ 1,4
mature stage	TH > 10	TH > 8
gerontic stage	TH > 25	TH > 22

specimens have a preserved attachment disc, but in our material, there is no adult specimen with an attachment disc.

Ontogenetic development is a continual process, with no strict boundaries separating different stages. Based on the above-mentioned morphological changes, we suggest distinguishing only two major phases in ontogenetic development of *Akadocrinus*. The main difference between these two ontogenetic phases is in the presence/absence of epispires (Fig. 8), although other, less significant morphological changes also occur during the transition between phases. We propose the following dividing into:

I. Pre-epispire bearing phase. – Specimens belonging to this phase show no evidence of epispires, between thecal plates or on the external surface of thecal plates. All described juvenile specimens are included in this phase of the ontogeny.

II. Epispire bearing phase. – Specimens show well developed epispires, both with and without a visible rim. All adult specimens described here belong to this phase.

We prefer to distinguish these two phases, rather than division into juvenile, adult and gerontic stage. Epispires are for us the most significant developmental character, because they indicate a marked change in the respiratory mechanism. Epispires are the most primitive respiratory structures in echinoderms (Parsley 2013). During the first phase of ontogeny, specimens were able to respire without epispires.

It is not yet possible to determine a thecal height above which *Akadocrinus* starts to have epispires. All small specimens are without epispires, and all large ones already have epispires. There is no specimen corresponding to the transitional stage between the pre-epispire bearing and epispire bearing phase. We consider it likely that epispires started to appear at the oral part of theca, then later in the other parts of theca, as has been described in other eocrinoids (Parsley 2013, Parsley & Prokop 2014). Juvenile specimens – the pre-epispire bearing specimens – have maximum thecal height not more than 3 mm. Adult specimens – of the epispire bearing phase – have thecal height more than 10 mm. Epispires begin to appear somewhere in the interval of TH = 3–10 mm.

Based on thecal height in *Akadocrinus* it could be possible to follow the approach of Parsley (2012) in separation of three informal ontogenetic stages in the studied material from the Barrandian area.

As shown in Table 2, specimens from the Barrandian area reach larger dimension in each stage when compared with Chinese material. However, we have not observed any difference in development between the mature and gerontic stages.

Conclusions

Akadocrinus is the first Cambrian eocrinoid from West Gondwana in which ontogenetic development is documented. The excellently preserved juvenile specimens show clear morphological differences from adult specimens. The juvenile specimens are characterized by the following morphology: (1) a lower number of thecal plates, (2) a complete absence of epispires, (3) comparatively shorter brachioles, composed of a lower number of brachiolar plates, (4) comparatively shorter stem, comprising lower number of columnals, and (5) relatively large attachment disc. The main ontogenetic changes are seen in thecal morphology. It is possible to distinguish two basic phases of development; (A) the pre-epispire bearing phase (thecal plates without epispires) and (B) epispire bearing phase (thecal plates with epispires).

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