

Evolutionary implications of a new transitional blastozoan echinoderm from the middle Cambrian of the Czech Republic

Elise Nardin,¹ Bertrand Lefebvre,² Oldřich Fatka,³ Martina Nohejlová,³ Libor Kašička,⁴ Miroslav Šinágl,⁵ and Michal Szabad⁶

¹Géosciences Environnement Toulouse (GET), Observatoire Midi-Pyrénées, CNRS/UPS/IRD/CNES, 14 avenue Édouard Belin, F-31400 Toulouse, France (elise.nardin@get.omp.eu)

²UMR CNRS 5276 Laboratoire de Géologie, Université Lyon 1, Géode, 2 rue Raphaël Dubois, F-69622 Villeurbanne Cedex, France (bertrand.lefebvre@univ-lyon1.fr)

³Charles University, Institute of Geology and Palaeontology, Albertov 6, 128 43 Praha 2, Czech Republic (fatka@natur.cuni.cz) (martina.nohejlova@natur.cuni.cz)

⁴Koněprusy 45, 266 01 Beroun, Czech Republic (libor.kasicka@email.cz)

⁵Osvobození 390, 26101 Příbram VII, Czech Republic (mira.sinagl@seznam.cz)

⁶Tisová 29, Bohutín 261 42, Czech Republic (geosz.pb@seznam.cz)

Abstract.—The primitive blastozoan *Felbabkacystis luckae* n. gen. n. sp. is described from the Drumian Jince Formation, Barrandian area (Czech Republic) from eleven fairly well-preserved specimens. Its unique body plan organization is composed of a relatively long, stalk-like imbricate structure directly connected to the aboral imbricate cup of the test and of an adoral vaulted tessellate test supporting the ambulacral and brachiolar systems. Its bipartite test, called prototheca, highlights the evolution of the body wall among blastozoans. *Felbabkacystis* n. gen. shows the combination of plesiomorphic (imbricate stalk-like appendage) and derived features (highly domed peristome, elongate epispires). The new genus is interpreted as a transitional form between calyx-bearing and theca-bearing blastozoans, and is attributed to the new family Felbabkacystidae. The lithology, the associated fauna, and the possession of a long stalk suggest that *Felbabkacystis* was probably a low-level suspension feeder living in relatively deep settings.

Introduction

The Cambrian succession of the Příbram-Jince Basin is famous for being abundantly fossiliferous. Numerous fairly well-preserved fossils from a large number of distinct fossil groups have been collected in the Cambrian Series 3 (latest Drumian) Jince Formation of the Příbram-Jince Basin (Barrandian area) for more than 230 years. During that time, those fossils have been intensively studied and include the primary producers (e.g., acritarchs and prasinophytes), different primary and higher consumers (like agnostids, brachiopods, echinoderms, foraminiferans, hyoliths, trilobites), and traces of their life activities (see Fatka et al., 2004 and references therein). Echinoderms are highly diverse in the Jince Formation (Fig. 1), being represented by numerous species including at least one lepidocystoid (*Vyscystis ubaghsi* Fatka and Kordule, 1990), five eocrinoids (*Acanthocystites briareus* Barrande, 1887; *Akadocrinus jani* Prokop, 1962; *A. knizeki* Fatka and Kordule, 1991; *Lichenoides priscus* Barrande, 1846, and *L. vadosus* Parsley and Prokop, 2004), two (?) rhombiferans (Dibrachiacystidae gen. indet. sp. indet., *Vizcainoia* sp.), one cinctan (*Asturicystis havliceki* Fatka and Kordule, 2001), three ctenocystoids (*Etoctenocystis bohémica* Fatka and Kordule, 1985; Ctenocystoidea gen. indet. sp. indet.), and one edrioasteroid

(*Stromatocystites pentangularis* Pompeckj, 1896 and *S. flexibilis* Parsley and Prokop, 2004), in addition to one stylophoran (*Ceratocystis perneri* Jaekel, 1901) and the problematic *Cigara dusli* Barrande, 1887. This assemblage is mainly endemic from this basin; only a few of these genera allow comparison with fauna elsewhere (see Lefebvre and Fatka, 2003; Zamora et al., 2013). Here, we document a remarkable new blastozoan, *Felbabkacystis* n. gen., from the Jince Formation of Czech Republic interpreted to represent the oldest record of a unique morphology showing a mixture of plesiomorphic and more derived features.

Geological setting

The Jince Formation, with a thickness of about 450 m, is predominantly composed of greywacke interbedded with mudstone to clayshale beds and locally contains subordinate sandy layers in the Příbram-Jince Basin. Fossiliferous layers are composed of relatively massive dark shales grading into fine-grained shales (Fatka and Szabad, 2014). Paleoenvironmental conditions might be interpreted as relatively deep, quiet water below storm base (mid offshore) on a siliciclastic platform. Fossil content is mostly represented by fragments and isolated elements spread over large surfaces. Well-preserved specimens

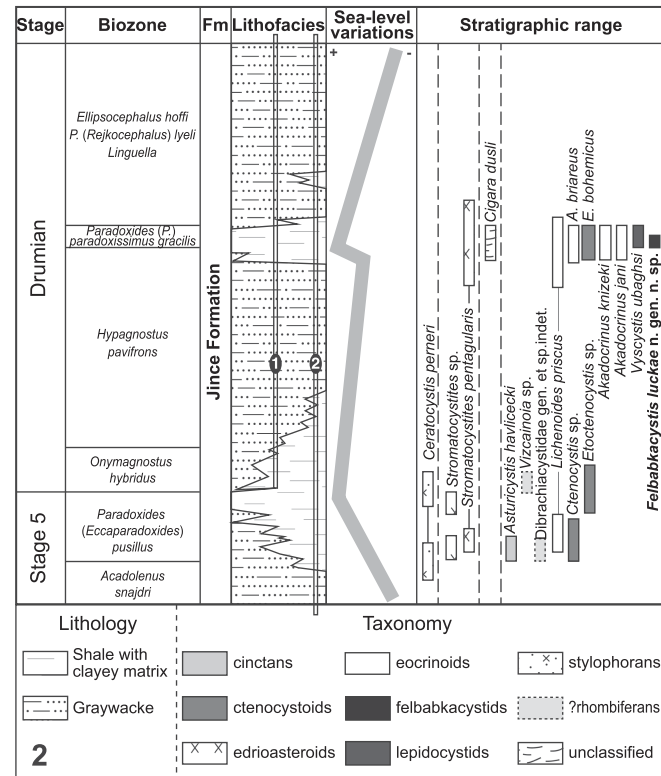
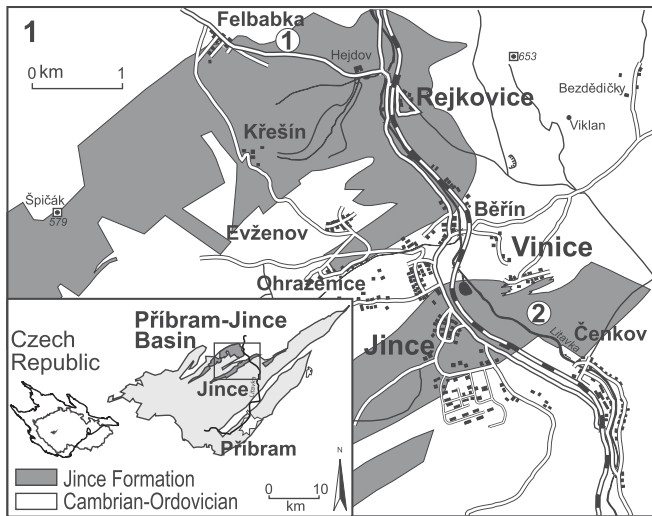


Figure 1. (1) Geographical location of fossiliferous sites in the Příbram-Jince Basin. 1 = Rejkovice-Ostrý Hill; 2 = Hill slope of Vinice near Jince. (2) Synthetic stratigraphic column of the Jince Formation (Stage 5–Drumian) in the Příbram-Jince Basin with the stratigraphic range of the echinoderm species. Modified from Fatka and Szabad (2014) and Fatka et al. (2015).

can occur abundantly but in restricted areas. Better-preserved echinoderm material is composed of fully articulated specimens either isolated or clustered.

All known specimens of *Felbakkacystis luckae* n. gen. n. sp. were collected in two fossil sites: (1) Rejkovice-Ostrý Hill locality (49.8207°N, 13.9593°E) (samples SZ343, SZ349, MI2, LK1-2); and (2) Jince-slope called Jince-Vinice locality (49.7844°N, 13.9930°E) (samples SZ344–347) (Fig. 1.1). Both are situated in the Jince Formation, within the lower third

of the *Paradoxides (P.) paradoxissimus gracilis* trilobite Zone. The holotype SZ349 was collected about 10 m above the base of the *Paradoxides (P.) paradoxissimus gracilis* Biozone at the Jince-Vinice locality. The *Paradoxides (P.) paradoxissimus gracilis* Biozone is correlated with the middle and higher levels of the Baltic *Paradoxides (P.) paradoxissimus* Biozone Biozone (Fatka et al., 2014). This level corresponds to the Drumian, Cambrian Series 3 in the new international global stratigraphic chart (Babcock et al., 2004; Geyer and Landing, 2004; Fatka, 2006; Zamora et al., 2009; Fatka et al., 2014).

Materials

Repositories and institutional abbreviations.—Specimens of *Felbakkacystis* n. gen. and comparative materials of *Vyscystis ubaghsi* Fatka and Kordule, 1990 are deposited in the collections of the Czech Geological Survey, Prague (SZ, LK, MI) and the National Museum, Prague (NML). Comparative materials of *Lepidocystis wanneri* Foerste, 1938 and *Kinzercystis durhami* Sprinkle, 1973 are deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ).

Systematic paleontology

Subphylum Blastozoa Sprinkle, 1973

Remarks.—The subphylum Blastozoa contains at present ten classes. Since Chauvel (1941), many authors considered that the class Eocrinoidea “includes a heterogeneous assemblage of species whose only similarity is that they lack the autapomorphic characteristics of the other, less ambiguously defined, cystoid [blastozoan] groups” (Smith, 1984, p. 439). Eocrinoids are mostly defined as basal blastozoans (brachiole-bearing echinoderms) having an irregular plated body wall (with imbricate or tessellate plating), with or without epispires, and an irregularly multiplicated stalk or a holomeric stem (Ubaghs, 1968; Sprinkle, 1973; Broadhead, 1982; Paul and Smith, 1984). “The diagnoses [of the class Eocrinoidea] are so broad that they essentially define those blastozoans that are not clearly assignable, by default, to a cystoid or blastoid group” (Parsley and Zhao, 2006, p. 1063). Therefore, the class Eocrinoidea, which corresponds to a paraphyletic assemblage, is not considered here as a valid taxonomic entity, and basal-most blastozoans are not assigned to any existing class.

Family Lepidocystoidae Durham, 1968
Figure 2

Diagnosis.—‘Calyx-bearing’ blastozoans. Oral disc made of numerous adjacent plates, with simple sutural pores along their sutures; anal pyramid, hydropore-gonopore located in the ‘CD’ interradius in the oral disc. Ambulacral system confined to oral disc, consisting of a central, covered mouth, several radially arranged ambulacral grooves embedded into the oral surface, and numerous straight or coiled biserial brachioles alternately arranged alongside each ambulacral groove. Aboral cup cone-shaped or elongated into a cylindrical stalk, and composed of numerous imbricate plates.

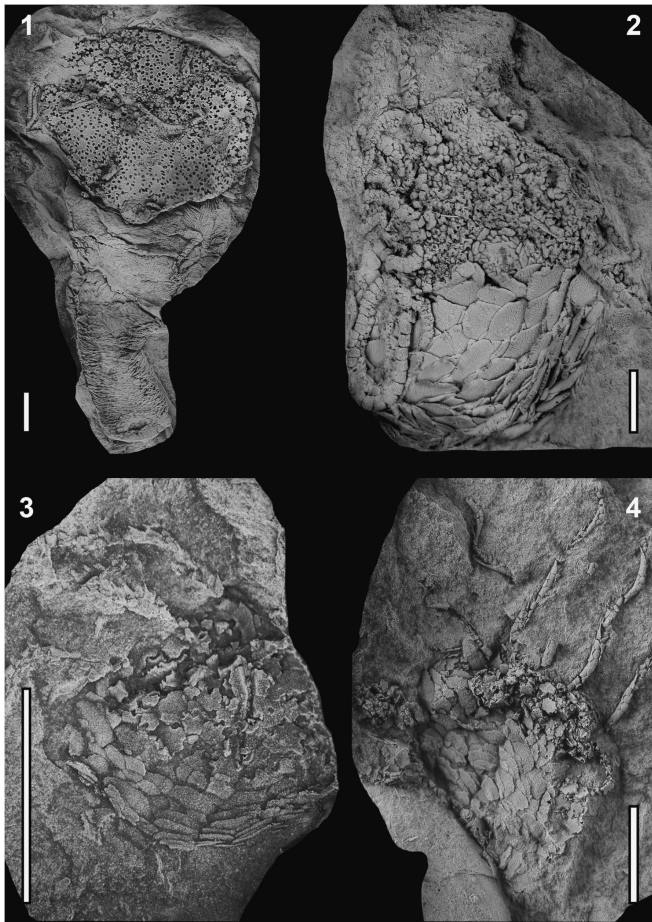


Figure 2. Photographs of selected specimens representing the Family Lepidocystoidea Durham, 1968. (1) Holotype MCZ 581 of *Kinzercystis durhami* Sprinkle, 1973 (Kinzers Formation, Pennsylvania) showing the circular oral disc, composed of large adjacent plates bearing roundish epispires and bearing the periproct laterally, overlapping the conical aboral cup; (2) plesiotype MCZ 588A of *Lepidocystis wanneri* Foerste, 1938 (Kinzers Formation, Pennsylvania) showing narrow oral surface composed of small platelets bearing small epispires and damaged periproct, few brachioles attached to the ambulacra; (3, 4) specimens of *Vyscystis ubaghshi* Fatka and Kordule, 1990 for comparison (Jince Formation, Pířbram-Jince Basin, Czech Republic); (3) partial small specimen NML28665 showing long imbricate plates and adjacent plates pierced by small roundish epispires, embedded ambulacral flooring plates bearing brachiole facets; (4) holotype NML 28664, showing disarticulated imbricate plates and epispire-bearing adjacent plates with five coiled brachioles. Latex casts have been whitened with ammonium chloride. Scale bars = 5 mm.

Remarks.—This family, based on the genus *Lepidocystis* Foerste, 1938, was initially assigned to an independent class (Lepidocystoidea Durham, 1968). Durham (1968) differentiated lepidocystoids from eocrinoids on three main features: (1) the restriction of the epispires-bearing surface to the oral surface, (2) the imbricate plating on the aboral region, and (3) the circlet of ‘free arms’ (brachioles) on the oral surface and their mode of attachment. With the description of a second genus (*Kinzercystis* Sprinkle, 1973), Sprinkle (1973) suggested that these differences were not supported by the new discoveries and not sufficiently grounded to maintain the class Lepidocystoidea. Accordingly, he decided to assign lepidocystoids to the new order Imbricata, within the class Eocrinoidea, and to synonymize the class Lepidocystoidea with the new order Imbricata. Sprinkle (1973) interpreted lepidocystoids as eocrinoids

because of the presence of both brachioles and sutural pores and the similar morphology of their attachment disc (holdfast). He diagnosed the order Imbricata on the basis of the well-marked differentiation between the tessellate plating of the oral surface and the imbricate plating of the aboral region (Sprinkle, 1973, p. 60). However, several other echinoderms exhibit a comparable combination of imbricate and tessellate platings (e.g., *Camptostroma* Ruedemann, 1933; several edrioasteroids, primitive solutans). The discovery of *Felbabkacystis* n. gen. confirms that the order Imbricata Sprinkle, 1973 was mostly described on plesiomorphic characters (e.g., imbricate plating, sutural pores). Therefore, the order Imbricata is not considered here as a valid taxonomic entity, and the family Lepidocystoidea, with a diagnosis emended from Durham (1968), is retained as a basal blastozoan family. Lepidocystoids possess one single apomorphy of the subphylum (presence of brachioles), but they lack all other apomorphies present in more advanced taxa (e.g., theca, spout-like oral area, holomeric stem). The particular morphology of the lepidocystoids recalls the bipartite body-wall organization (disc-like oral surface and elongate aboral cup; Fig. 2) also occurring in other primitive echinoderms (camptostromatoids, basal crinoids, edrioasteroids, etc.). The body wall of the lepidocystoids is therefore called here a ‘calyx’ by comparison to the structure observed in many other basal echinoderms (see Nardin et al., 2009 for further discussion).

The family Lepidocystoidea contains the three closely related genera *Lepidocystis* and *Kinzercystis* (both from the Cambrian Stage 4 Kinzers Formation of Pennsylvania, USA) and *Vyscystis* Fatka and Kordule, 1990 (from the Drumian Jince Formation of Czech Republic).

Family Felbabkacystidae new family

Type genus.—*Felbabkacystis* new genus

Diagnosis.—As for type species by monotypy.

Remarks.—The presence of brachioles supports the assignment of felbabkacystids to the subphylum Blastozoa. The combination of plesiomorphic (e.g., imbricate plating, sutural pores) and derived characters (vaulted oral surface, tessellate region extended beyond the body wall edge, elongate epispires, lateral location of the periproct) is not present among members of the family Lepidocystoidea (Fig. 2). It therefore justifies the erection of a new family, which occupies a relatively basal position within blastozoans (see the following for an extended explanation). Felbabkacystids differ from lepidocystoids by: (1) the higher ratio between tessellate/imbricate regions of the body wall, associated with the overgrowth of the tessellate region not only restricted to the oral disc; and (2) the strongly indented shape of the plates, the length of the epispires, and the location of the periproct high in the lateral tessellate area (Figs. 3, 4). They share with lepidocystoids the presence of an elongate aboral region (cup and stalk) made of imbricate elements.

Genus *Felbabkacystis* new genus

Figures 3–5

Type species.—*Felbabkacystis luckae* n. gen. n. sp.

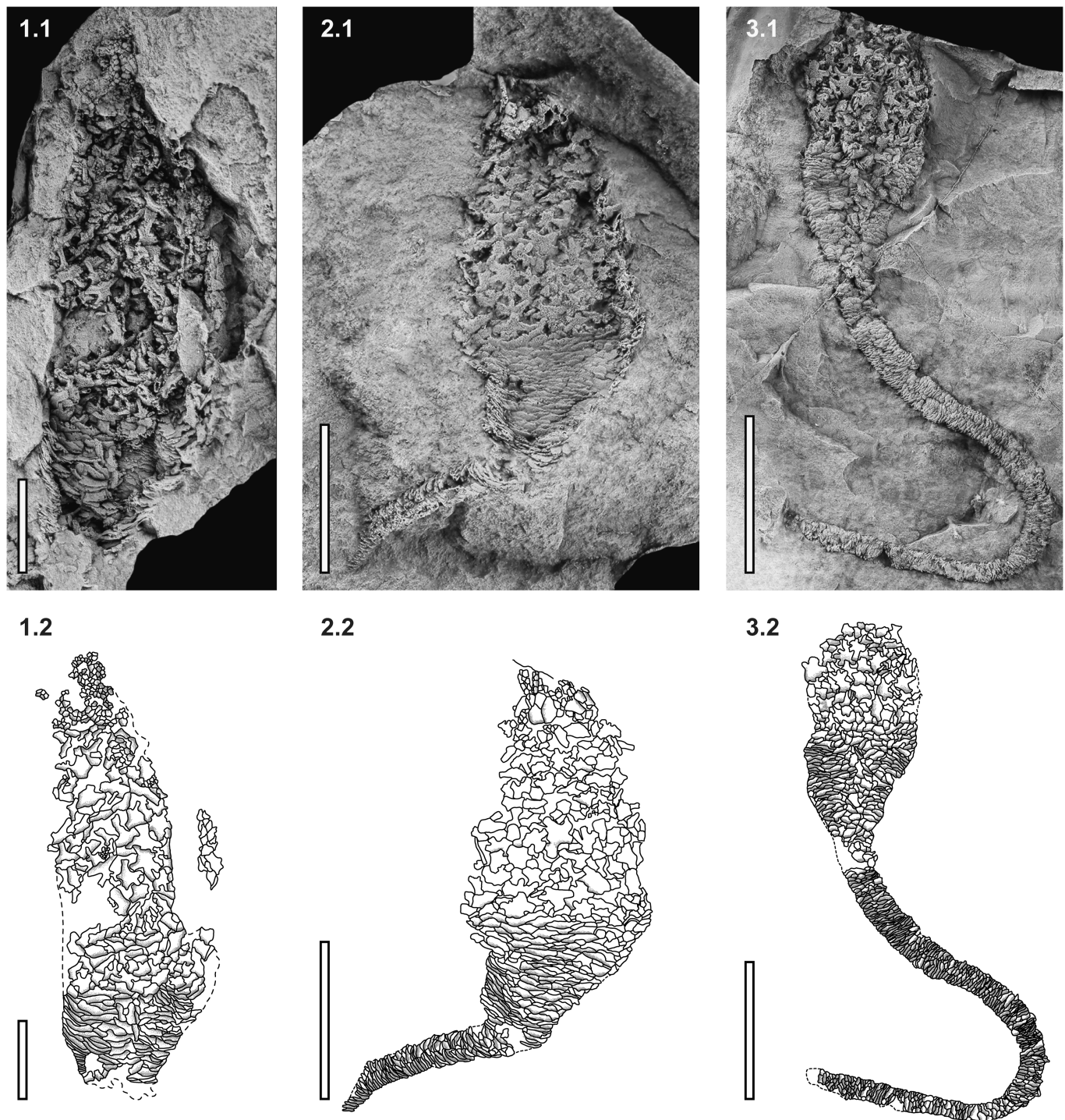


Figure 3. (1.1, 2.1, 3.1) Photographs of latex casts whitened with ammonium chloride and (1.2, 2.2, 3.2) the corresponding camera lucida drawings of selected specimens of *Felbakkacystis luckae* n. gen. n. sp. (Jince Formation, Pířbram-Jince Basin, Czech Republic). (1) Internal view of a selected paratype on the slab SZ343 showing slightly disarticulated brachioles at the top of the narrow vaulted tessellate region, and the anal structure; (2) internal view of the holotype SZ349 showing straight brachioles grouped on flooring plates in the narrow oral zone; (3) external view of the paratype MI2 showing the clear transition between the tessellate and imbricate parts of the body wall and the long aboral appendage with imbricate plating. Scale bars = 5 mm.

Diagnosis.—As for type species by monotypy.

Etymology.—From the village Felbabka in Czech Republic (type locality).

Felbakkacystis luckae new species
Figures 3–5

2004 n. gen. n. sp., Fatka et al., p. 379.

2015 Undescribed transitional form, n. gen., n. sp., Lefebvre et al., p. 89, fig. 1B.

2015 Imbricate eocrinoid, Noheřlová and Fatka, p. 119, fig. 2D

Holotype.—SZ349, complete body wall and articulated brachioles.



Figure 4. (1–5) Photographs of selected specimens of *Felbakkacystis luckae* n. gen. n. sp. (Jince Formation, Příbram-Jince Basin, Czech Republic). (1) Paratype slab SZ343 showing aggregated specimens showing articulated thecae bearing brachioles and/or proximal stalk; (2) partially preserved paratype SZ347 associated with one autochthonous ctenocystoid echinoderm; (3) badly preserved paratype SZ346 associated with one large specimen of *Lichenoides priscus* Barrande, 1846; (4) partial specimen LK1 showing the transition between the aboral imbricate and the adoral tessellate regions of the body wall, possible peristomial organization at the top with few disarticulated brachioles; (5) disarticulated specimen LK2, showing brachioles restricted to the top of the tessellate region, composed of large star-shaped granulated plates; co-occurring with partial specimen of *Vyscystis ubaghysi* Fatka and Kordule, 1990, showing small polygonal plates forming the oral surface and bearing small roundish epispires, crushed on the aboral imbricate body wall. Scale bars = 5 mm.

Diagnosis.—Blastozoans with a cylindrical to fusiform body wall. Part of the lateral body wall, made of numerous adjacent plates, with large elliptic simple sutural pores along their sutures. Ambulacral system confined to body-wall summit, consisting of a central mouth, several radially arranged ambulacral grooves embedded into the oral surface, and straight biserial brachioles, each mounted on two ambulacral flooring plates. Aboral region exclusively composed of numerous imbricate plates, overlapping adorally; proximal part (cup) forming the aboral part of the body wall; distal part (stalk-like extension of the cup) elongate and forming a relatively long and narrow, cylindrical attachment structure.

Occurrence.—Jince Formation, Drumian; slope called Jince-Vinice locality, Czech Republic.

Description.—Skeleton of *Felbakkacystis luckae* n. sp. consisting of large fusiform bipartite body wall with both tessellate

(upper) and imbricate (lower) plated regions, long cylindrical stalk forming its aboral end, and oral surface bearing both ambulacral system and brachioles (Figs. 3–5).

Stalk-like body-wall extension relatively long (>66 mm in length) and cylindrical (1.6 ± 0.2 mm in diameter); at least three times the length of the body capsule (Fig. 3.3). Plates being adorally imbricated, ~40% of their height exposed; not ornamented, as long as wide, but shorter than plates of the tessellate part. Transition between stalk and imbricate part of the body wall marked by diameter and plate size increase. No attachment disc or holdfast observed at the distal end of best-preserved stalk, as well as in other specimens.

Body capsule cylindrical to fusiform, height around three times width; its length varying from 14 mm to 32 mm, and its width from 4 mm to 10 mm; divided into two distinct aboral, imbricate, and adoral, tessellate regions. Aboral part of the test

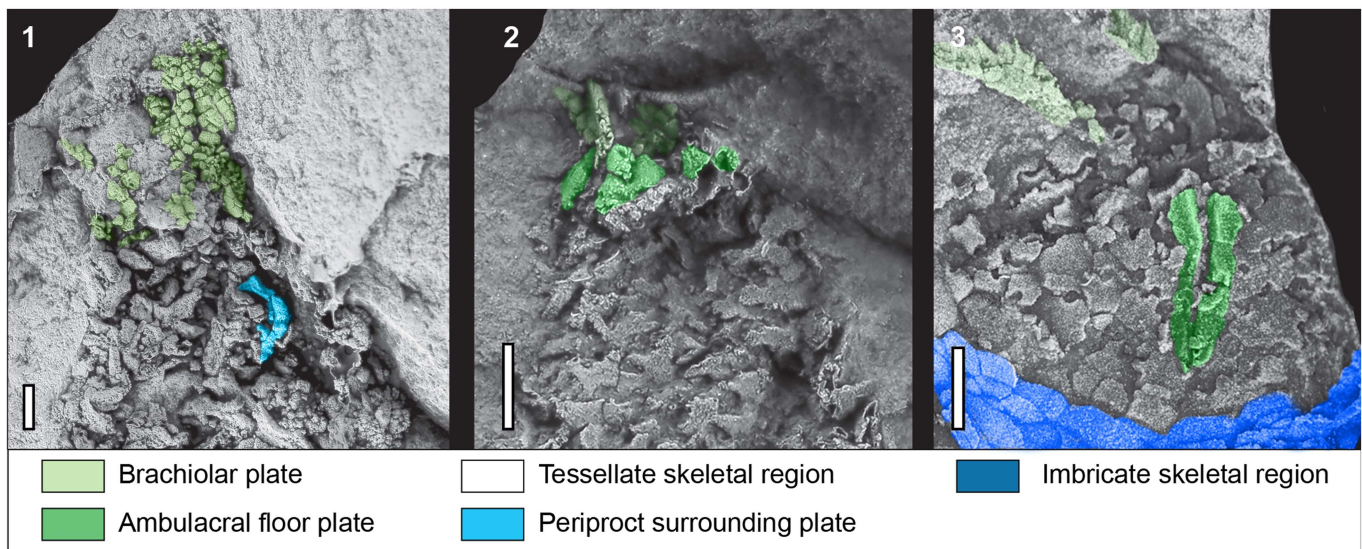


Figure 5. (1, 2) Photographs of two specimens of *Felbakkacystis luckae* n. gen. n. sp. (Jince Formation, Příbram-Jince Basin, Czech Republic). (1) Internal view showing the location of the periproct in the lateral body wall in the paratype SZ343; (2) details on the subvective system restricted in the narrow oral area of the holotype SZ349. (3) Enlargement on the oral surface of the small specimen NML28665 of *Vyscystis ubaghshi* Fatka and Kordule, 1990 (Jince Formation, Příbram-Jince Basin, Czech Republic) showing the periproct border laterally to the oral disc and the relatively long embedded ambulacrum bearing brachiolar facets. Colors indicate the different skeleton regions according to the extraxial-axial theory framework (Mooi and David, 1998; Nardin et al., 2009; Lefebvre et al., 2015). Latex casts have been whitened with ammonium chloride. Scale bars = 1 mm.

conical, expanding in diameter from the stalk to its lower part (Figs. 3.2, 3.3, 4.2); width regularly increasing from the base to the upper part of the test. Adoral tessellate part ($L = 8.2\text{--}22.2$ mm, $W = 5.8\text{--}8.1$ mm) ~ 1.8 times length and ~ 1.3 times width of imbricate one ($L = 5.8\text{--}10.0$ mm, $W = 4.5\text{--}6.7$ mm). All specimens showing approximately the same proportions for the two regions. Imbricate part of the test with length 1.5 times width, composed of numerous, scalar plates, slightly overlapping adorally (about 60% exposed), small and squamous, longer than high, thin (0.08 mm on average), constant in size from the base to the top of that part; organized in circlets (Fig. 3.3); slightly domed, without any respiratory structures, smooth on their exterior and interior surfaces. Connection between the two parts of the body wall consisting of one or two circlets of straightened-up imbricate-type plates without epispires (Figs. 3.2, 4.4). Tessellate part of the body wall region with length 1.5 to 2.1 times width, constituted by numerous large adjacent plates, polygonal in shape, possibly organized into poorly defined circlets aborally and with no apparent organization in the oral region (Figs. 4.3, 5.1, 5.2). Interior surface of the plates smooth; exterior surface slightly granular. Adjacent plates twice as thick as imbricate ones (0.15 mm), flat to slightly domed, depending on the number of epispires. One to three simple epispires occurring on each plate side; deeply excavated into adjacent plates, forming elongate peripores (Fig. 4.1); elliptical and large only at the suture margins, probably uncovered. Periporal edges thin and short. Periproct opening in the first adoral third of the tessellate part of the body wall (Fig. 3.1).

Oral surface relatively narrow, composed of few adjacent plates, each bearing only a few small epispires (Fig. 3.2). Plates irregularly pentagonal to hexagonal in shape. Oral area not sufficiently well preserved to show complete ambulacral system. Straight and thin (0.7 mm in diameter) brachioles

probably originating at the border of peristomial area, at least six in number, being mounted on two large, domed plates with no epispires, interpreted as ambulacral flooring plates (Fig. 5.1, 5.2). Brachiolar plates pentagonal, unornamented, domed, and alternating in a biserial pattern. Few plates covering brachiolar food grooves proximally observed; their presence over the entire length of the brachioles being highly probable, due to the presence of two slits occurring on interior edge of brachiolar plates. At present, no hydropore and gonopore observed in any specimen.

Etymology.—From Lucka, daughter of the third author.

Material.—Holotype, SZ349, complete body wall and articulated brachioles. Best paratype, MI2, complete body wall and long stalk. Other figured paratypes SZ343 (slab with several specimens), SZ346–347, SZ349, LK1, and LK2 (slab with one specimen of *Vyscystis*); five additional unfigured partial specimens, some with preserved stalk attached to the body wall and proximal parts of brachioles.

Remarks.—*Felbakkacystis* n. gen. differs from all lepidocystoids and gogiid eocrinoids described so far. The occurrence of the lepidocystoid *Vyscystis* in the same level and same locality as *Felbakkacystis* could question the validity of the new genus and suggest that putative differences in morphology may simply result from differences in ontogeny and/or in preservation: individuals assigned to these two taxa are sometimes found associated, on a same slab (Fig. 4.5). However, in recent years, the discovery of several new, well-preserved specimens of *Vyscystis* shows that their morphology is clearly distinct from that of *Felbakkacystis* (Table 1; Figs. 2.3, 2.4, 4.5, 5). Main differences between the two genera concern: (1) the morphology of the brachioles (straight in *F. luckae*, spiraled

Table 1. Comparison of the morphological characters of selected lepidocystoids and eocrinids genera with *Felbabkacystis* n. gen. Refer to the Supplementary Data S1 for the sources of the description.

	<i>Akadocrinus</i>	<i>Felbabkacystis</i>	<i>Gogia</i>	<i>Lepidocystis</i>	<i>Lichenoides</i>	<i>Kinzercystis</i>	<i>Vyscystis</i>
Brachioles	straight	straight	straight	straight	straight	straight	coiled
Length of the ambulacra	short, restricted to the peristomial area	probably very short, restricted to the peristomial area	short, restricted to the peristomial area	relatively long extending over the oral disc	long, reaching the lateral circlet	relatively long extending over the oral disc	relatively long extending over the oral disc
Location of the ambulacral flooring plates	most likely embedded in the oral disc	most likely embedded in the oral disc	embedded in the oral disc	embedded in the oral disc	no flooring plates	embedded in the oral disc	embedded in the oral disc
Branching of the ambulacral ray	isotomy	isotomy	isotomy	holotomy	heterotomy	holotomy	exotomy
Shape of the oral zone	flat	strongly vaulted	flat to slightly domed	flat	flat	flat	flat
Extension of the tessellate region	forming the entire body wall	forming the oral zone and part of the lateral body wall	forming the entire body wall	restricted to the oral disc	forming the entire body wall	restricted to the oral disc	restricted to the oral disc
Shape of the adjacent plates	small, irregularly pentagonal to hexagonal	medium-sized to large, star-shaped	small, polygonal	small, polygonal	large, subhexagonal	medium-sized, subhexagonal	medium-sized and polygonal
Epispines	small, roundish to ellipsoidal	elongate and V-shaped	small and roundish	small and roundish	elongate and V-shaped	small, roundish to ellipsoidal	small and roundish
Location of the periproct	unknown	adoral third of the lateral body wall	aboral third to half of the lateral body wall	oral disc	unknown	oral disc	oral disc
Shape of the stalk-like appendage	sub- to holomeric column	homeomorphic long peduncle	heteromorphic relatively short stalk	homeomorphic long peduncle	atrophied basal disc of platelets	homeomorphic long peduncle	homeomorphic cup
Plating of the stalk-like appendage	tessellate	imbricate	tessellate	imbricate	tessellate	imbricate	imbricate

in *V. ubaghsi*); (2) the extension of ambulacra (short and restricted to the summit of the vaulted oral area in *F. luckae*); (3) the morphology of the oral surface (strongly vaulted in *Felbabkacystis*, almost flat in *Vyscystis*); (4) the extension of the tessellate part of the body wall (restricted to the apical part of the test in *V. ubaghsi*, more extensive and forming the upper two-thirds of the lateral walls in *F. luckae*); (5) the morphology of tessellate thecal plates (they are large, granulated, star-shaped, with incurved edges in *F. luckae*, but small, polygonal, smooth, and flat in *V. ubaghsi*); (6) the morphology of epispines (elongate and V-shaped in *F. luckae*, consistently small and roundish in *Vyscystis* at all growth stages); and (7) the extension of the imbricate, stalk-like appendage (long and cylindrical in *Felbabkacystis*, apparently short and wide in *Vyscystis*).

Felbabkacystis differs from *Lepidocystis* by having thinner brachioles, larger plates, and wider epispines in a more extended tessellate region and narrower ornamented plates in the imbricate region (Fig. 2.2; Table 1; Foerste, 1938; Sprinkle, 1973). Comparison with *Kinzercystis* shows that *Felbabkacystis* has larger epispines over a more contracted oral area, and a fusiform tessellate plating area (Fig. 2.1; Table 1; Sprinkle, 1973). *Felbabkacystis* contrasts with the coeval eocrinoids (*Akadocrinus* Prokop, 1962; *Lichenoides* Barrande, 1846) in its bipartite body wall and the imbricate plating of its aboral cup and the stalk-like appendage, and the possession of thin, large star-shaped adjacent plates (Table 1; Fig. 6). It resembles some co-occurring gogiid eocrinoids by possessing elongate elliptical epispines (as in *Lichenoides*) and short isotomous ambulacra (as in *Akadocrinus*).

The absence of identified gonopore in *Felbabkacystis* does not allow documenting the degree of maturity of observed specimens. All *Felbabkacystis* specimens are homogeneous in size and in the relative proportions of the tessellate and imbricate regions of the body wall. This suggests that all specimens were probably at similar ontogenetic stage.

Evolutionary implications

Phylogenetic results.—The peculiar morphology of *Felbabkacystis* n. gen. allows interpreting the relationships and the evolutionary history within the early blastozoan genera (lepidocystoids, coeval eocrinids, and later eocrinids), using *Stromatocystites* Pompeckj, 1896 as an outgroup (Appendix, Supplementary Data S1). Primary homologies have been identified independently among the three morphological modules (aboral region, body wall, and feeding system; Table 1, Appendix), whereas mechanistic homologies were used to describe the organization of each module, independently from any terminological influence (David et al., 2000; Nardin et al., 2009; Zamora et al., 2012; Zamora and Rahman, 2014).

Phylogenetic analysis of the 13 characters scored for 13 taxa found nine equally parsimonious cladograms (see Appendix for further details). The majority-rule consensus of these trees places *Felbabkacystis* n. gen. near the base of the blastozoans, more derived than the lepidocystoids and as a sister-group of the two crownward clades: the gogiids and the later eocrinids (Fig. 7). Among the blastozoans, the basal lepidocystoids are characterized by the plesiomorphic features

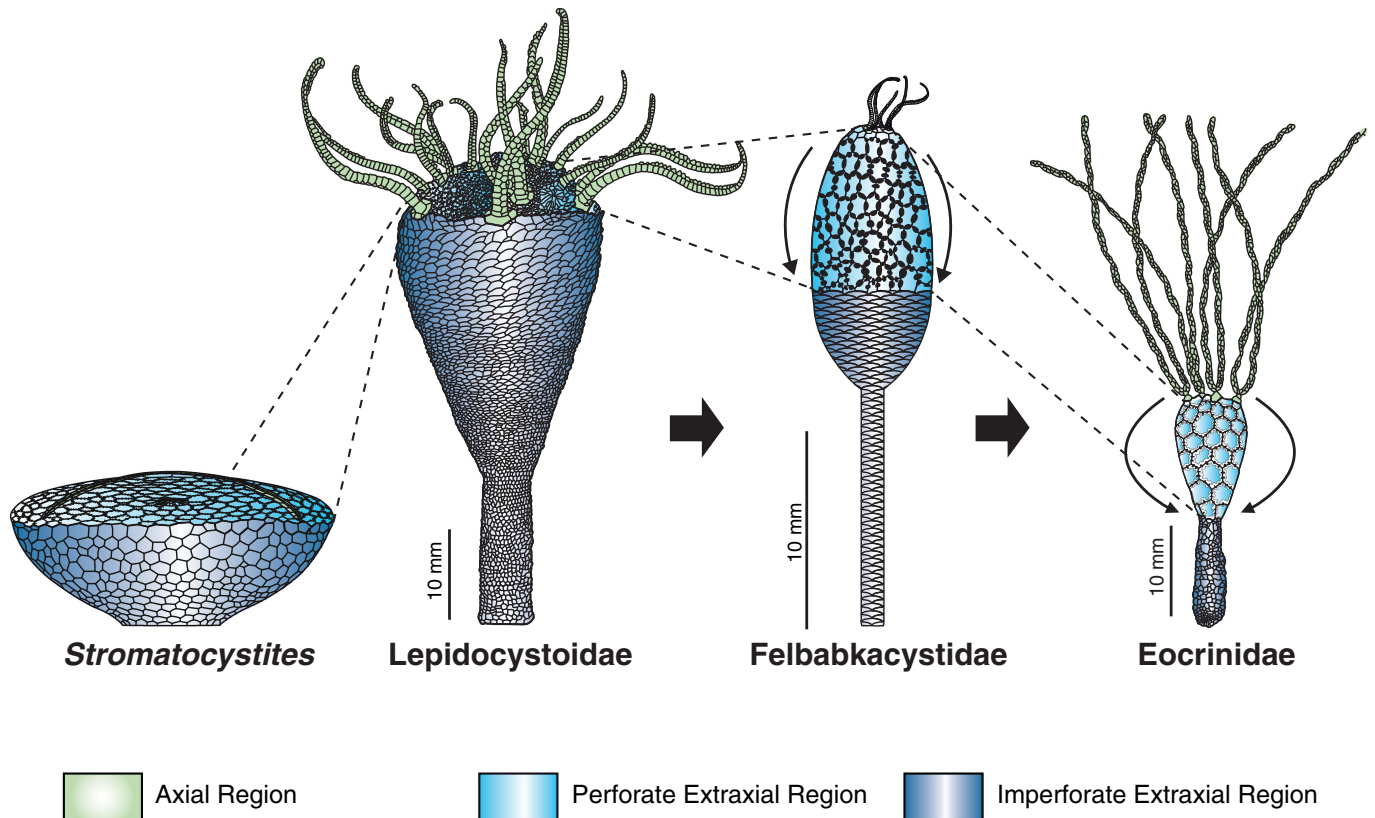


Figure 6. Sketch indicating the homology and relative body regions in selected Cambrian echinoderms, according to the extraxial-axial theory framework (Mooi and David, 1998; Nardin et al., 2009; Lefebvre et al., 2015).

of having both imbricate and tessellate platings on their test in addition to slender brachioles born by five embedded ambulacra and epispires at the plate margins in the tessellate region (Fig. 2, Table 1).

Felbakkacystis n. gen. is considered as a sister-taxon of the second clade (Fig. 7). It shares similarities with that of various eocrinoids (Table 1), such as: (1) the presence of an overgrown tessellate vaulted region, forming the theca in all eocrinid genera and further derived blastozoans; (2) larger adjacent plates (e.g., *Sinoeocrinus* Zhao et al., 1994, *Trachelocrinus* Ulrich, 1929); (3) shorter ambulacra embedded into the apical area (e.g., *Gogia* Walcott, 1917); (4) isotomous ambulacral pattern leading to the clustering of the brachioles at the edge of the oral surface (e.g., *Gogia*, *Sinoeocrinus*); and (5) elongate epispires (e.g., *Lichenoides*) (Sprinkle, 1973). It still retains some plesiomorphies, shared with *Lepidocystis* (e.g., presence of a long imbricate stalk and a relatively narrow tessellate oral surface), and with *Kinzerocystis* and *Vyscystis*, (e.g., comparable size and organization of imbricate cup plates; Table 1). Felbakkacystids differ from lepidocystoids by: (1) the relative proportions of the tessellate and imbricate regions of the body wall, (2) the length and shape of the epispires and the resulting plate shape, and (3) the location of the periproct in the lateral tessellate area.

The first crownward cluster is composed of the eocrinids, except *Lyracystis*, which are only united on the heteromorphous polyplating of the aboral stalk-like appendage and the possession of a relatively organized theca (Fig. 7). The presence of numerous plesiomorphies (e.g., heteromorphous polyplated

stalk, holotomous biserial long ambulacra, periproct located in the oral disc, etc.) might explain the basal position of *Lyracystis* regarding the other eocrinids. Their paraphyly is sustained by the location of the periproct and the organization of the ambulacral system, showing various degrees of derivation (e.g., convergent recumbency or erection of the ambulacra, symmetry). The association of *Ubagsicystis* Gil Cid and Domínguez-Alonso, 2002 to this cluster is supported by the plesiomorphies of the theca. The second crownward cluster is composed of the most derived genera (*Ridersia* Jell et al., 1985, *Trachelocrinus*), in addition to the lichenoid *Lichenoides*. This clade prefigures the typical morphology of later blastozoans, with a holomeric or atrophied stem, a more regularly plated theca, heterogeneous oral surface organization, and a strong variability in the ambulacral system (Fig. 7).

Evolutionary trends.—The globular, elongate test of *Felbakkacystis luckae* n. gen. n. sp. shows a clear differentiation into two well-separated regions (Fig. 3). The lower (aboral) region of the test without any body opening and its stalk-like extension, which contain no main body orifice or any ambulacral (axial) element, are both probably made of imperforate extraxial plates (cf. Nardin et al., 2009; Lefebvre et al., 2015). Consequently, it is very likely that these two regions, which display the same imbricate pavement and are in physical continuity with each other, are all together equivalent to the aboral cup of *Stromatocystites* and of the lepidocystoids, and to the stalk or the (developed to atrophied) column of the other blastozoans, even

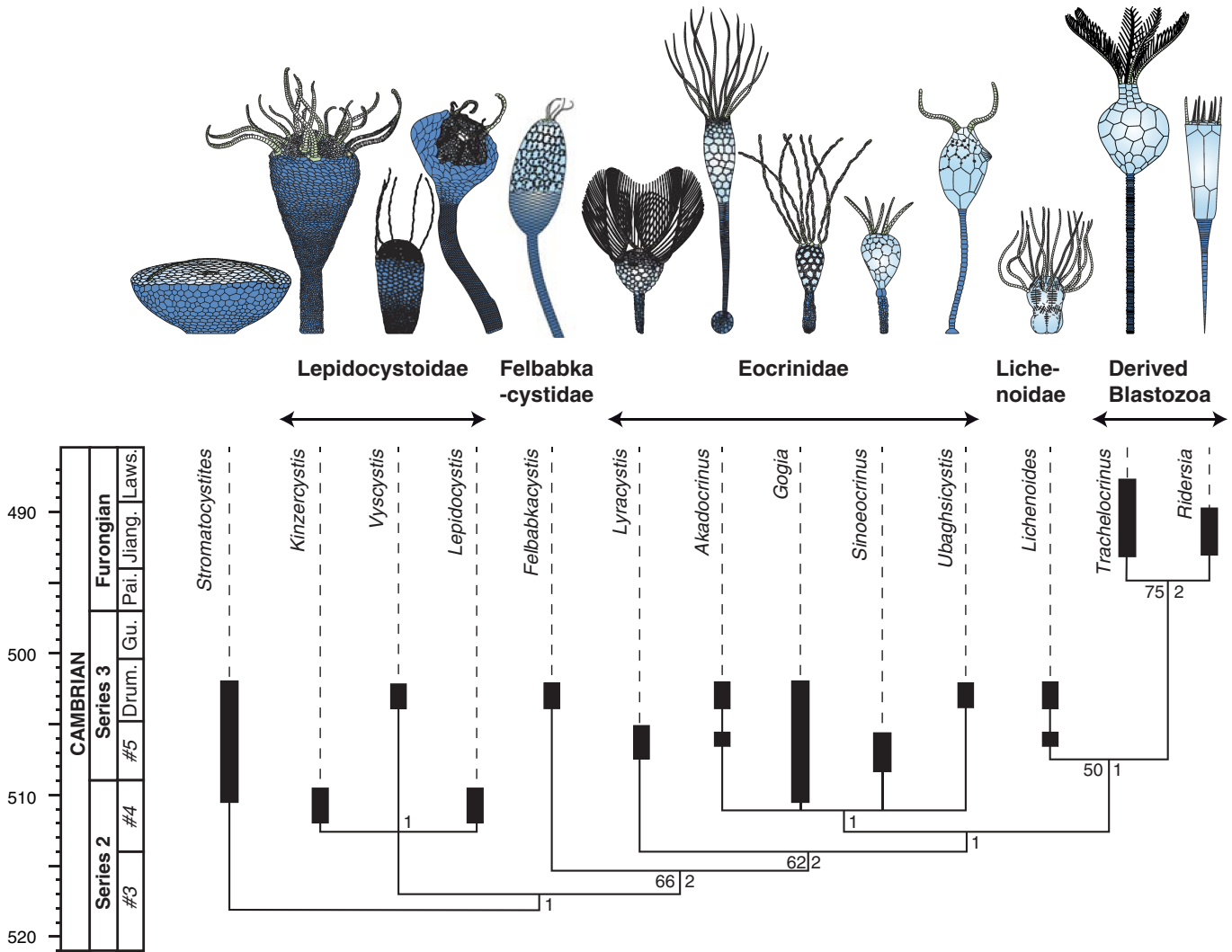


Figure 7. Geographical time framework of the majority-rule consensus of nine equally parsimonious trees (L = 27 steps, CI = 0.741, RI = 0.800, RC = 0.593), showing the idealized morphology of the genera included in the analysis. Bootstrap and Bremer support values are to the left and to the right side of each node, respectively. Drawings to scale. Abbreviations: Drum. = Drumian; Gu. = Guzhangian; Pai. = Paibian; Jiang. = Jiangshanian; Laws. = Lawsonian.

if some do not show an imbricate plating (Figs. 5–7). The upper two-thirds of the test of *Felbakkacystis* is entirely made of adjacent plates bearing respiratory structures and pierced by the main body openings (anus, mouth) (Fig. 5.1, 5.2). The oral surface of *Stomatocystites* and lepidocystoids, the aboral tessellate part of the felbakkacystid test, and the entire theca of the later blastozoans are interpreted as made of perforate extraxial skeleton (Figs. 5, 7) because of the presence of the primary openings (David et al., 2000; Nardin et al., 2009; Lefebvre et al., 2015). Therefore, the degree of stretching of the tessellate region in the felbakkacystids is unique within blastozoans. The test, called prototheca sensu Lefebvre et al. (2015), is interpreted as representing a transitional form between calyx-bearing primitive blastozoans (lepidocystoids) and more advanced, theca-bearing blastozoans (Fig. 6). The recently described bipartite test of the Cambrian *Helicocystis* Smith and Zamora, 2013 has been similarly interpreted as transitional between the helicoplacoids and the more derived pentaradial forms (Smith and Zamora, 2013).

Within early blastozoans, the progressive replacement of imbricate aboral stalk-like appendages (plesiomorphic condition)

by tessellate ones has often been considered as a major evolutionary trend (Sprinkle, 1973, 1981; Ubahgs, 1968, 1975; Broadhead, 1982). The morphology of *Felbakkacystis* n. gen. not only confirms this trend, but also illustrates the transition between lepidocystoids and eocrinids (Figs. 6, 7). Those and/or further observations may support the phylogenetic significance of the nature of aboral plating (imbricate vs. tessellate) in blastozoans or even within the early echinoderms. This trend is associated with the progressive increase (Fig. 7) in regularity of the multiplied eocrinid stalks (e.g., *Gogia*, *Sinoeocrinus*) and with the convergent transition toward holomeric columns in several blastozoans (e.g., *Akadocrinus* vs. *Ridersia*, *Trachelocrinus*), as suggested by Sprinkle (1973).

The presence of a narrow, vaulted oral region leading to the restriction of the ambulacral system at the summit of the body wall in *Felbakkacystis* n. gen. is a derived but probably convergent feature (Figs. 5–7). Similar domed or spout-like organizations occur in several Cambrian eocrinoids (e.g., *Trachelocrinus*), as well as in many younger and more derived blastozoans (e.g., *Bockia* Hecker, 1938, *Helicocrinites*

Eichwald, 1840). The grouped arrangement of exothecal feeding appendages (brachioles) at the end of the ambulacral ray or as lateral branches of the ambulacral ray reflects convergences among blastozoans (e.g., *Aristocystites* Barrande, 1887, *Felbabkacystis* n. gen., *Gogia*, *Palaeosphaeronites* Prokop, 1964 vs. *Eumorphocystis* Branson and Peck, 1940, *Kinzercystis*, *Macrocystella* Callaway, 1877, *Trachelocrinus*).

The trait set of *Felbabkacystis* n. gen. appears as fundamentally transitional between the lepidocystoids and the eocrinids, combining both apomorphies (e.g., partially overgrown tessellate region, large epispires, vaulted oral area, roundish lateral periproct) and plesiomorphic features (e.g., imbricate stalk-like appendage) of the blastozoans (Fig. 7). Such atypical morphology reinforces the unity of the blastozoans on the possession of brachioles as appendages disconnected from the body wall cavity, clearly contrasting from arms as outgrowth of the body wall (Ubaghs, 1968, 1975; Sprinkle, 1973; David et al., 2000; but see Zamora and Smith, 2012 for an alternative interpretation). It emphasizes the strong but natural variability affecting the ambulacra-oral surface plate patterns (embedded, recumbent, erect, or nonmineralized ambulacral flooring plates, see Nardin et al., 2009) and the ambulacral grooves branching and their associated structures plating (Nardin et al., 2010).

The stratigraphic scaling of the phylogenetic hypothesis supports the concept of a rapid early blastozoan diversification (Guensburg and Sprinkle, 1992; Smith et al., 2013). Major homologies defining the derived blastozoans as well as the more basal blastozoan clades seem to appear in the fossil record before the Drumian (Fig. 7). However, the morphological characters defining the clades suggest an asynchronous development of various versions of plesiomorphic and apomorphic trait sets, as well as strong convergences in the evolution of the plating of the aboral region (as suggested by Sprinkle, 1973) and of the ambulacral architecture (as proposed by Zamora and Smith, 2012).

Paleoecological implications

On some slabs, *Felbabkacystis* n. gen. co-occurs with a well-preserved individual of the eocrinoid *Lichenoides priscus* and two individuals of an undescribed ctenocystoid, in addition to small fragments of trilobites (Fig. 4). The relatively large (10 mm) specimen of *Lichenoides priscus* (slab SZ346) shows well-developed epispires and an unusual prominent ornamentation as large vermicular and branched ridges on the thecal plates and large granules sometimes fused in ridges in the brachiolar plates (Fig. 4.3). Two strongly disarticulated ctenocystoid specimens are preserved on the same slab as specimen SZ347 (Fig. 4.2). Both are ovoid in shape (8 mm in diameter), made of numerous rectangular plates surrounded by 10 triangular plates on the periphery. Ornamentation is relatively dense, being composed of long sinuous ridges over the rectangular plates of the surface and of small granules aligned in fine straight centripetal lines on the frame plates. The good state of preservation (slight disarticulation to full articulation) and the high fragility of the Czech echinoderm material (type 1 echinoderms sensu Brett et al., 1997) would suggest that specimens were probably quickly buried or transported a short

distance (parautochthonous to autochthonous material; Ausich, 2001; Gorzelak and Salamon, 2013).

Felbabkacystids can be interpreted as epifaunal suspension feeders, filtering with a small brachiole fan and exploiting the relatively high tier class +5–10 cm above the seafloor, in comparison to other Cambrian echinoderms (Bottjer and Ausich, 1986; Bottjer et al., 2000). The absence of a fully preserved stalk with holdfast in any collected specimen of *Felbabkacystis* prevents a definitive interpretation of their motility level. However, lepidocystoids, possessing similar stalk, have been interpreted as suspension feeders living attached on hard substrate (pebble, skeletal fragments) (Sprinkle, 1973; Fatka and Kordule, 1990) or sticking (bioglue as ligament fibers of collagen) to firm sediment (Parsley and Prokop, 2004; Dornbos, 2006; Parsley and Zhao, 2010; Kloss et al., 2015). Felbabkacystids may have had a similar mode of attachment (Supplementary Data S2).

Felbabkacystids and coeval fauna exhibit an unusual well-developed ornamentation and/or respiratory structures (epispires). Low-level bottom-dweller and shallow sediment sticker taxa (e.g., ctenocystoids, *Lichenoides*) show thicker thecal plates bearing stronger ornamentation than the higher (5–10 cm) tierers (e.g., *Akadocrinus*, *Felbabkacystis*). If felbabkacystids are interpreted as hard-substrate attachers, then the high flexibility of their imbricate skeleton might suggest a strong resistance to moderate lateral bottom current, which is also consistent with the strength of the skeleton of *Lichenoides* (swollen and strongly ornamented thecal plates). This interpretation is in good accordance with the model of latitudinal distribution of Ordovician blastozoans (Paul, 1976), suggesting a higher efficiency of the respiratory structures when slightly lower oxygen settings are reached (e.g., in the colder and deeper environment of the Příbram-Jince Basin). By contrast, taxa with rather small epispires and thin body wall plates tend to occur in the better-oxygenated depositional environments, such as the Impure Carbonate Facies of the Kinzers Formation, which have yielded species with rather small epispires and thin body wall plates (Skinner, 2005; Powel, 2009).

Felbabkacystid specimens and their associated fauna (e.g., the lepidocystoid *Vyscystis*, the eocrinid *Akadocrinus*, the lichenoid *Lichenoides*, and the enigmatic *Cigara*; Fig. 1.2) have been collected in transgressive medium- to fine-grained shales in the upper third of the Jince Formation (upper *Hypagnostus parvifrons-Paradoxides (P.) paradoxissimus gracilis* biozones) at the transition from the trilobite to the agnostid biofacies, sensu Fatka and Szabad (2014). The other highly fossiliferous level of the Jince Formation (not revealing any imbricate blastozoans) occurs in a similar configuration in the *Paradoxides (E.) pusillus*-lower *Onymagnostus hybridus* biozones (Fig. 1.2). The richly fossiliferous siliciclastic levels have been interpreted as deposited in a relatively deep (below storm-wave base) and quiet environment of a mixed platform (Fatka and Mergl, 2009). Blastozoan faunas from these two levels are either endemic species or close to typical taxa of Mediterranean peri-Gondwanan margin (e.g., undetermined lichenoid from the Tarhoucht Member of the Jbel Warwast Formation [global Cambrian Series 3, Stage 5], eastern Anti-Atlas [southern Morocco], Smith et al. (2013); unidentified lichenoid from the Murero Formation [global Cambrian Series 3, Stage 5], Iberian

Chains, Zamora (2010); the rhombiferan *Vizcainoia* Zamora and Smith, 2012 from the Coulouma Formation [global Cambrian Series 3, lower Drumian], Montagne Noire [France], Zamora and Smith (2012)). The Jbel Warwast Formation, the Murero Formation, and the Coulouma Formation consist of upper offshore fine siliciclastic sediments (siltstone to claystone) deposited under low or moderately low energy conditions in a temperate mixed platform (Liñan and Mergl, 2001; Landing et al., 2006; Álvaro et al., 2008). The closely related and contemporaneous lepidocystoids occur in obrution deposits in the Impure Carbonate Facies in the Emigsville Member of the Kinzers Formation (global Cambrian Series 2, Stage 4) in the Conestoga Valley (southern Pennsylvania), interpreted as an offshore environment with active bottom currents in a mixed platform (Skinner, 2005). An undetermined lepidocystoid was mentioned in the transgressive claystone-dominated Issafen Formation [global Cambrian Series 2, Stage 4] in the Central Anti-Atlas (Morocco) (Smith et al., 2013). The (par)autochthonous occurrences of the felbakcystids and lepidocystoids in the deeper facies in the *Paradoxides* (*P.*) *paradoxissimus gracilis* Zone [global Cambrian Series 3, mid-Drumian] suggest that the morphological innovation of the overgrown vaulted oral area might have occurred in an offshore and quiet environment. All occurrences of lepidocystoids, felbakcystids, and Mediterranean eocrinids-lichenoids are related to relatively deep (up to mid offshore) lithofacies in transgressive and/or drowning platform contexts (Skinner, 2005; Landing et al., 2006; Fatka and Szabad, 2014). The echinoderm plasticity and geographic distribution, even at low taxonomic levels, might be controlled by environmental changes such as the water energy, the water depth, and the substrate consistency (Guensburg and Sprinkle, 1992; Sprinkle and Guensburg, 1995; Álvaro et al., 2013; Smith et al., 2013). The morphological innovation and the high diversity in offshore environments during the early mid-Cambrian times seem to dispute the onshore-offshore pattern for the early echinoderm diversification (Jablonski et al., 1983; Sepkoski, 1991; Smith et al., 2013).

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Accessibility of supplemental data

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.sg931>

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Appendix. Rationale of the phylogenetic analysis

Method

Phylogenetic analysis was conducted in PAUP 4.0a150 (Swofford, 2016) using the criterion of maximum parsimony. All characters are treated as unordered, except for the fifth (David et al., 2000), and equally weighted. Analysis was a heuristic search with random addition (repeated 1,000 times) with a branch-swapping using the tree-bisection reconnection algorithm. The majority-rule consensus of nine equally parsimonious trees has been retained (L = 27 steps, CI = 0.741, RI = 0.800, RC = 0.593). Bootstrap and Bremer support have been calculated in PAUP 4.0a150. Analysis was performed on genera represented by exemplar species (see Supplementary Data S1). The taxon *Stromatocystites* Pompeckj, 1896 has been considered as outgroup according to previous phylogenetic analyses (Zamora and Smith, 2012; Zamora et al., 2012; Smith et al., 2013).

List of characters

Our phylogenetic analysis is based on a list of 13 characters, partly emended from Paul and Smith (1984), Nardin et al. (2009), Smith et al. (2013), and Zamora and Smith (2012). Coding has been based on new observations of specimens of the 13 considered taxa and on a reinterpretation according to the extraxial-axial theory framework (Mooi and David, 1998; David et al., 2000; Nardin et al., 2009; Zamora et al., 2012; Lefebvre et al., 2015).

Ambulacral system

1. Exothecal appendages: (0) absence, (1) presence
2. Ambulacral floor: (0) specialized flooring plates forming an integral part of the oral surface, (1) specialized flooring plates embedded in and then recumbent/erect on the body wall, (2) specialized flooring plates strictly erect or recumbent on the body wall, (3) ambulacral rays lying directly on perioral and thecal plates (no calcified flooring plates).

This character concerns the topology of the axial plates bearing the brachioles and the rest of the oral surface (perforate extraxial skeleton). Specific ambulacral plates have been detected in most of the genera (except in *Lichenoides* and *Ubaghsicystis*).

3. Ambulacral symmetry: (0) 2-1-2 pattern, (1) reduced
4. Ambulacral ray branching: (0) absence, (1) on lateral side(s) of the ray, (2) grouped at the end of the ray

This character focuses on the branching patterns of the ambulacral rays, with or without any specific ambulacral floor plates. Brachioles appear to be grouped at the end of the ambulacral rays in the eocrinid genera and *Ubaghsicystis*, whereas they rise alternately from both sides of the ray in the other genera of the ingroup.

Body capsule

5. Extension of the tessellate perforate extraxial region: (0) restricted to a plateau-like oral surface, above the body

capsule edge, (1) extended over the body capsule edge and forming part of the lateral vertical body capsule, (2) forming the entire body capsule enclosing viscera.

6. Body wall capsule: (0) antero-posteriorly flattened, (1) globular
7. Oral surface plating: (0) numerous, small elements, (1) few large plates
8. Organization of the perforate extraxial skeleton: (0) none (irregular plating), (1) in circlets
9. Respiratory structures as epispines: (0) presence, (1) absence
10. Location of the periproct: (0) within the oral disc, (1) within the lateral wall

Periproct has been detected in *Felbabkacystis* n. gen. relatively high in the lateral body wall. A similar location has been observed in *Gogia* (Zamora et al., 2009), *Sinoecrinus* (Parsley and Zhao, 2006), *Ubaghsicystis* (Gil Cid and Domínguez-Alonso, 2002), whereas it pierced within the oral disc in *Lepidocystis* and *Kinzercystis* (Sprinkle, 1973), *Vyscystis* (Figs. 2.4, 2.5, 4.3), *Lyracystis* (Sprinkle and Collins, 2006) and *Ridersia* (Jell et al., 1985). It remains unknown in *Trachelocrinus* (Sprinkle, 1973), *Akadocrinus* and *Lichenoides* (our observations).

Aboral region

11. Extension of the aboral part of the body wall (imperforate extraxial region): (0) extensive and forming lateral walls of the test, (1) elongate and contributing to lower part of body capsule, (2) elongate and not contributing to body capsule, (3) atrophied and reduced to few plates.

Lichenoides has no column but few platelets forming its attachment disc, considered as homologous of stalk (coding 3).

12. Plating of the aboral region: (0) tessellate, (1) imbricate
13. Plating of the aboral region: (0) homeomorphic elements, (1) polymorphic elements, (2) holomeric cylindrical elements

Character codification for each taxon

Thirteen genera, represented by the species listed in the Supplementary Data S1, have been selected on the basis of previous phylogenetic analyses.

<i>Stromatocystites</i>	00000 00000 000
<i>Lepidocystis</i>	10010 10000 010
<i>Felbabkacystis</i>	10121 10001 110
<i>Kinzercystis</i>	10010 10000 010
<i>Vyscystis</i>	10010 10000 010
<i>Lyracystis</i>	11012 10000 201
<i>Trachelocrinus</i>	12012 11?1? 202
<i>Ubaghsicystis</i>	13122 11101 202
<i>Ridersia</i>	10012 11110 202
<i>Lichenoides</i>	13012 1110? 301
<i>Akadocrinus</i>	10022 10?0? 201
<i>Gogia</i>	10022 10?01 201
<i>Sinoecrinus</i>	10022 10101 201