Morphology, ontogeny and phenotypic plasticity of the microcrinoid *Treocrinus* from the Třebotov Limestone (Devonian, Daleje–Třebotov Formation; Barrandian area, Czech Republic)

Michal Mergl & Iva Traxmandlová

New data on morphology, ontogeny, phenotypic plasticity and mode of life of the microcrinoid *Treocrinus ericius* from the Třebotov Limestone are discussed. The aboral cup shape variations from the barrel- to the bowl-shaped and the ontogenetic sequence of radial facets are presented. Some specimens were likely stemless to the adult stage, and their cup bases were directly fitted to a holdfast. The irregularity of cup shape is explained by different habitats. Individuals in the restricted, likely cryptic habitat lacked the stem. They had low barrel-like cups, whereby while those in more spaced microhabitat formed higher bowl-shaped cups. Examination of 160 specimens indicate that bowl-shaped cup represents a prevalent form of a theca. The aboral articular facet of bowl-shaped specimens keep a distinct lumen, a narrow crenularium and a shallow areola that confirm a development of a column in part of the population. The species achieved the maximum occurrence in the upper part of the Třebotov Limestone (Daleje–Třebotov Formation) near the Emsian–Eifelian boundary. Abundance of the *Treocrinus* and other microcrinoids, and abundance of associated invertebrates in the Třebotov Limestone clearly contrast with the invertebrate diversity after the Choteč Event near the base of the Choteč Formation. • Key words: microcrinoid, Devonian, Emsian–Eifelian boundary, ecology, *Polygnathus costatus partitus* Zone, Praha-Barrandov.

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The microcrinoids are micromorphous crinoids, defined arbitrarily as having an upper limit thecal height of 2 mm (Sevastopulo 2008). Their abundance may be surprising. Sevastopulo (2008) suggested that the number of microcrinoid individuals likely overpassed the number of larger crinoids in, but not only, the Carboniferous faunas. Ancestral microcrinoid faunas are less known (Sevastopulo & Lane 1981) but have been similarly diverse. This is evidenced by data from weathered limestone beds of the Gorstian to Eifelian age of Central Bohemia (Prokop & Petr 1991). The microcrinoid *Treocrinus ericius* Prokop & Petr, 1991, the type and the only known species of the genus *Treocrinus* Prokop & Petr, 1991, is a distinctive microcrinoid coming from several limestone beds near the top of the Třebotov Limestone (Daleje–Třebotov Formation) in the Barrandian area of the Central Bohemia. Its abundance peak occurs just near the Lower–Middle Devonian boundary, immediately before the environmental disturbance of the Choteč Event. Its diminutive cups, some keeping a tegmen are abundant in washings of deeply weathered soft limestones, so-called "white beds". Prokop & Petr (1991) mentioned considerable shape variation of the theca in an original description of this species. The new extensive material brings new observations on the morphology and the ontogeny of *Treocrinus ericius*. A remarkable phenotypic plasticity evokes some suggestions about its mode of life.

Geological setting

The localities carrying *Treocrinus ericius* specimens lie at the northeast limb of the Devonian infilling of the Prague Basin in Central Bohemia (Czechia) (Fig. 1). The

Lochkovian to Eifelian infill of the basin is characterised by shallow water, mostly perireefal crinoidal limestones. There are also small reef and mud-mound bioskeletal accumulations of Pragian to Eifelian age. These facies continued basinward into micritic limestones and calcareous shales (Chlupáč 1998) bearing principally a pelagic fauna.

The Třebotov Limestone is a perireefal member of the Daleje–Třebotov Formation that is considered of late Emsian to early Eifelian age. Its upper limestone beds are early Eifelian in age. This is proven by the appearance of the conodont *Polygnathus partitus* in the several highest meters of the Třebotov Limestone (Klapper *et al.* 1978; Chlupáč 1982, 1985; Berkyová 2009; Mergl & Vodrážková 2012; Klapper & Vodrážková 2013). The Třebotov Limestone is followed by the Choteč Limestone. The unit represents a relatively deep-water member of the Choteč Formation of Eifelian age. The extracted material from the washings of white beds of the topmost Třebotov Limestone and the lowest Choteč Limestones provided a remarkably diverse fossil assemblage of crinoids, brachiopods, gastropods, cephalopods, dacryconarids and other shelly fossils at the Praha-Holyně locality (Bouček 1931, 1964; Šulc 1932; Bouška 1948; Horný 1955, 1963, 1964, 1992; Přibyl 1955; Havlíček 1956, 1977; Prokop 1970, 1976, 1982, 1997, 2002, 2013; Lukeš 1977; Chlupáč

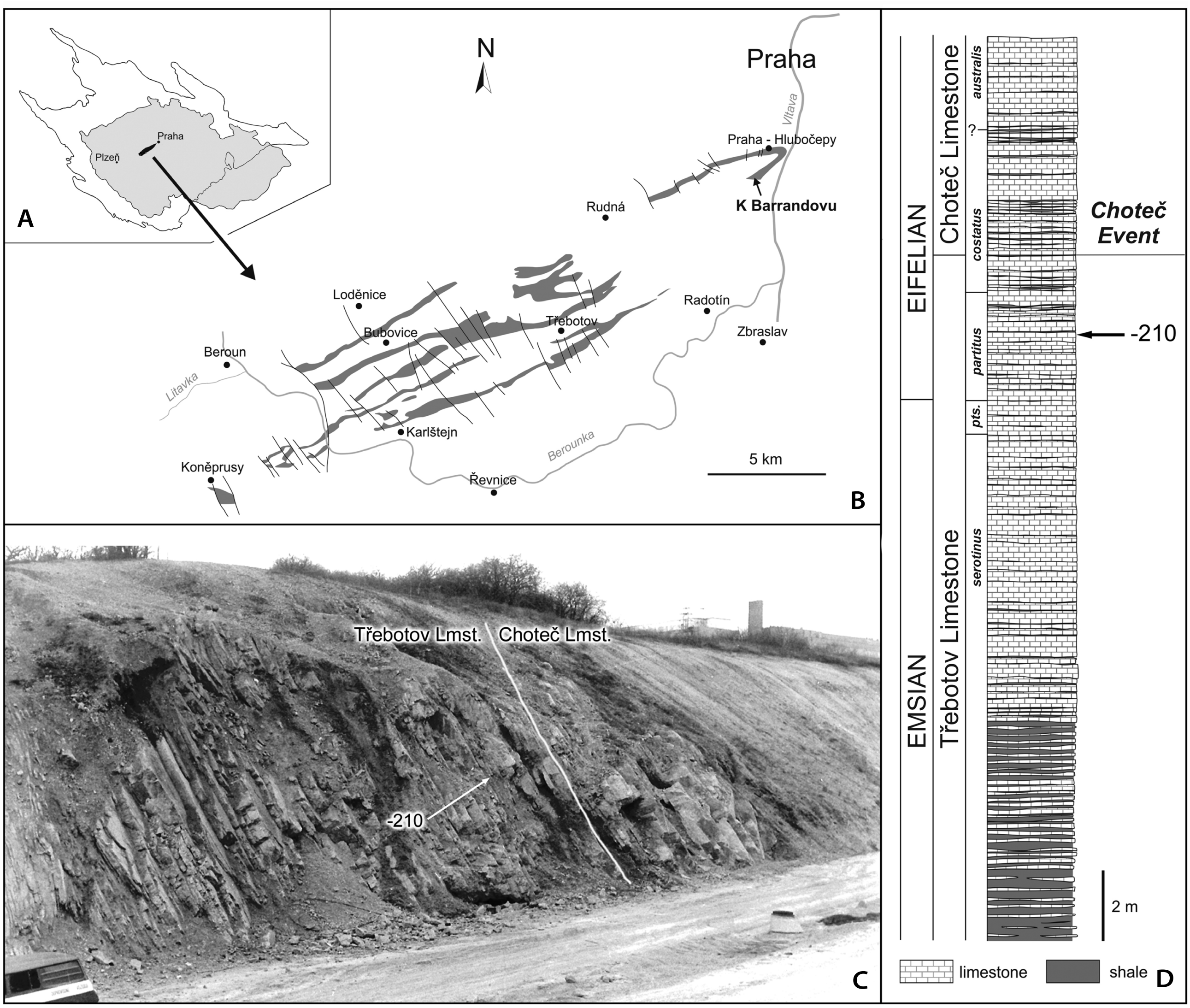


Figure 1. A – geographical setting of the Devonian (A) in the Bohemian Massif (white area) and the Czech Republic (grey area). • B – the Daleje–Třebotov and Choteč formations (Upper Emsian to Eifelian) in the Prague Basin. • C – the road cut in Praha-Barrandov with the Daleje Shale and the Třebotov Limestone (left to centre), the Choteč Limestone (right) followed with siltstone beds of the Srbsko Formation (Givetian) in the background; the sample Barr: −210 and the Třebotov/Choteč limestones boundary are marked. The photo came from the field work conducted in 1984. • D – the lithological section at the road cut in Praha-Barrandov with marked the stratigraphic level of the Barr: −210 sample.

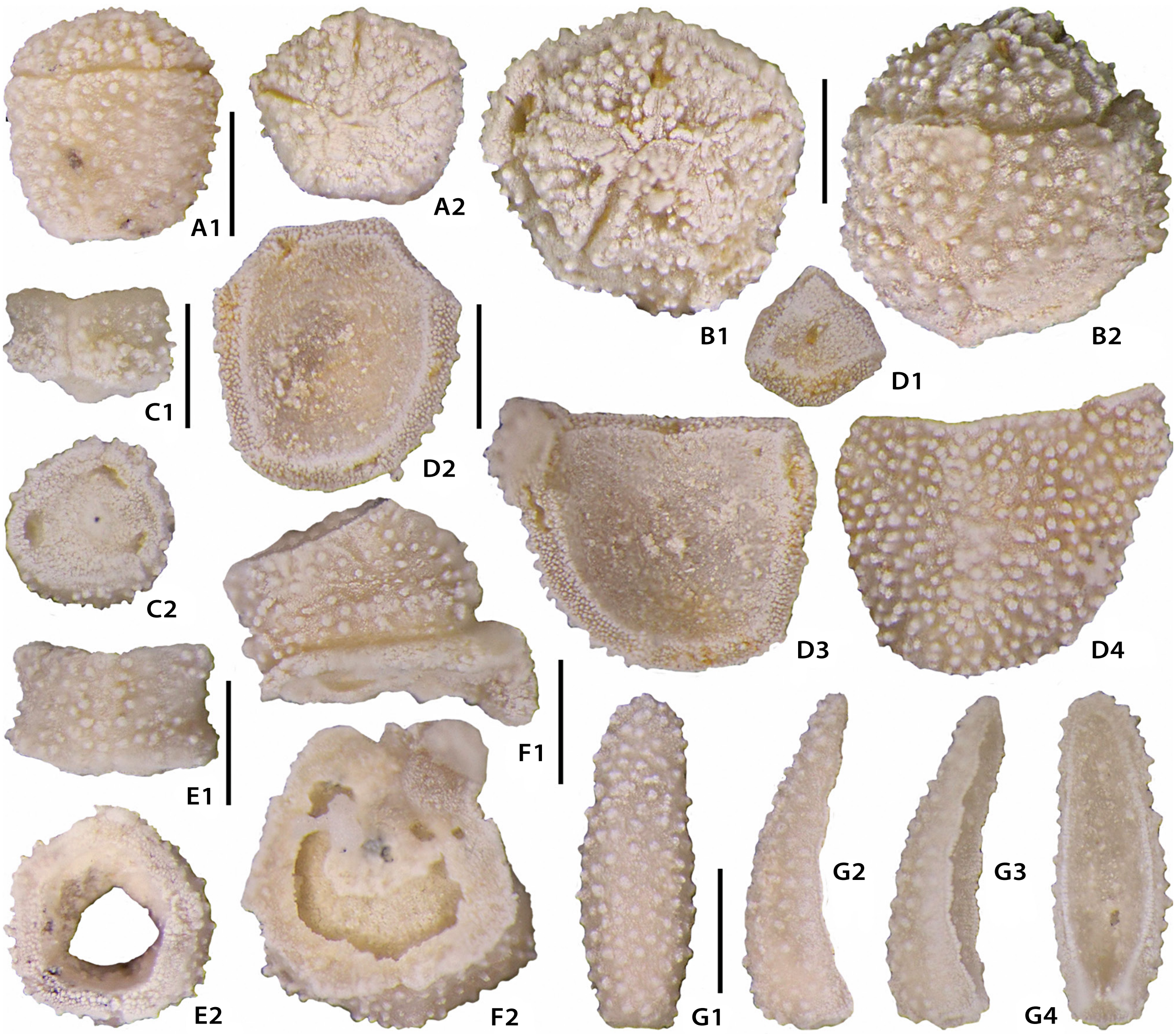


Figure 2. *Treocrinus ericius* Prokop & Petr, 1991. A – small theca without radial facets in side (A1) and oral (A2) views, PCZCU 2793. B – small theca with E and smaller C radial facets in oral (B1) and side (B2) views, PCZCU 2780. C – the smallest cup observed, in side (C1) and basal (C2) views, PCZCU 2776. D – disintegrated cup; interior of three fused infrabasal plates (D1), interior of CB basal plate (D2), interior (D3) and exterior (D4) of EB basal plate with attached E radial plate, PCZCU 2777. E – small theca, ring of basal plates with removed infrabasal plates in side (E1) and oral (E2) views, PCZCU 2565. F – small irregular theca with holdfast preserved in side (F1) and basal (F2) views, PCZCU 2779. G – primibrachial exterior (G1), side (G2) and oblique views (G3) and interior (G4), PCZCU 2564. Age and locality: Třebotov Limestone, sample Barr: −210; Praha-Barrandov. Bar lengths equal to 500 µm.

& Turek 1983; Hotchkiss *et al.* 1999, 2007; Prokop & Petr 1991, 1998, 2004; Frýda 1999a, b, d; Manda & Turek 2011; Prokop & Nohejlová 2015).

This now well-collected exploited locality has been called Holyně or Praha-Holyně (*i.e.* Prokop & Petr 1991), but also other names have appeared ("U Nového mlýna National Nature Monument" by Kříž 1999 or "V Rokli" by Prokop & Nohejlová 2015). The coeval succession of the Třebotov and Choteč limestones, only 2600 m east from the Praha-Holyně locality was temporarily accessible in the excavation of a roadcut at Praha-Barrandov (begun in 1984 year) (Fig. 1). Unlike the Prastav Quarry parastratotype section but just as at the Praha-Holyně locality, the limestone beds in the uppermost Třebotov Limestone and the lowermost Choteč Limestone have been deeply weathered into the yellowish white beds in the road cut of Praha-Barrandov. These beds provided exceptionally rich and excellently preserved fossils, mostly of dacryoconarids, conodonts, ostracods, echinoderms, gastropods, brachiopods and other skeletal invertebrates. The dacryoconarids (Lukeš 1989), ostracods (Šlechta 1996), conodonts (Zusková 1991, Berkyová 2009, Berkyová *et al.* 2009), gastropods (Frýda & Bandel 1997; Frýda 1998, 1999b, c), selected groups of echinoderms (Prokop & Petr 1991, 1993, 1994, 2004; Prokop 1997; Prokop & Nohejlová 2015; Mergl & Šmídtová 2022a), and dendritic borings on brachiopod shells (Mergl & Šmídtová 2022b) have been described to date. The *Polygnathus serotinus* to *P. australis* zones (Berkyová 2009) have been described in the Praha-Barrandov section. The studied material of *Treocrinus ericius* has been sampled almost exclusively from the bed labelled Barr: −210 which is in the *P. partitus* Zone (Berkyová 2009), and *Nowakia holynensis* Zone (Lukeš 1989) respectively.

Material and methods

All examined specimens of *Treocrinus ericius* came from the white beds sampled 2.00 to 2.20 m below the base of the Choteč Limestone (sample labelled Barr: −210) (Fig. 1). In total, 160 loose complete or almost complete thecae were picked out under a binocular microscope from a largely crinoidal detritus of the washing. Thecae are principally undeformed and untectonized, excellently preserve both external and internal features. Some thecae have attached peristomal cover plates, whereas others without them exhibit the interior of a cup. All preserved thecae lack arms. Arm length and shape has been deduced from troughs along sutures between peristomal cover plates (see Prokop & Petr 1991, fig. 2). Three loose primibrachials that most probably belong to the species were picked out from the finest fraction of the washing.

The cleaned specimens were weakly whitened by ammonium chloride before taking photos by a Canon camera mounted on an Olympus SZX7 binocular microscope. The pictures were processed by Deep Focus QuickPhoto Micro 3.2. software. Selected specimens were examined in Scanning Electron Microscope JEOL 7001.

All specimens are stored in the palaeontological collections of the West Bohemia University at Plzeň (PCZCU 2550 to 2565; PCZCU 2776 to 2793).

Terminology generally follows that of Prokop & Petr (1991), Ausich & Donovan (2023) and Kammer *et al.* (2013).

Systematic palaeontology

Subclass Inadunata Wachsmuth & Springer, 1885
Order Cladida Moore & Laudon, 1943
Family uncertain

Genus *Treocrinus* Prokop & Petr, 1991

Type species. – *Treocrinus ericius* Prokop & Petr, 1991; Daleje–Třebotov Formation, Upper Emsian; Bohemia, Czech Republic.

***Treocrinus ericius* Prokop & Petr, 1991**
Figures 2–8

1991 *Treocrinus ericius* n. sp.; Prokop & Petr, p. 135, text-fig. 2; pl. 4, figs 1–5.

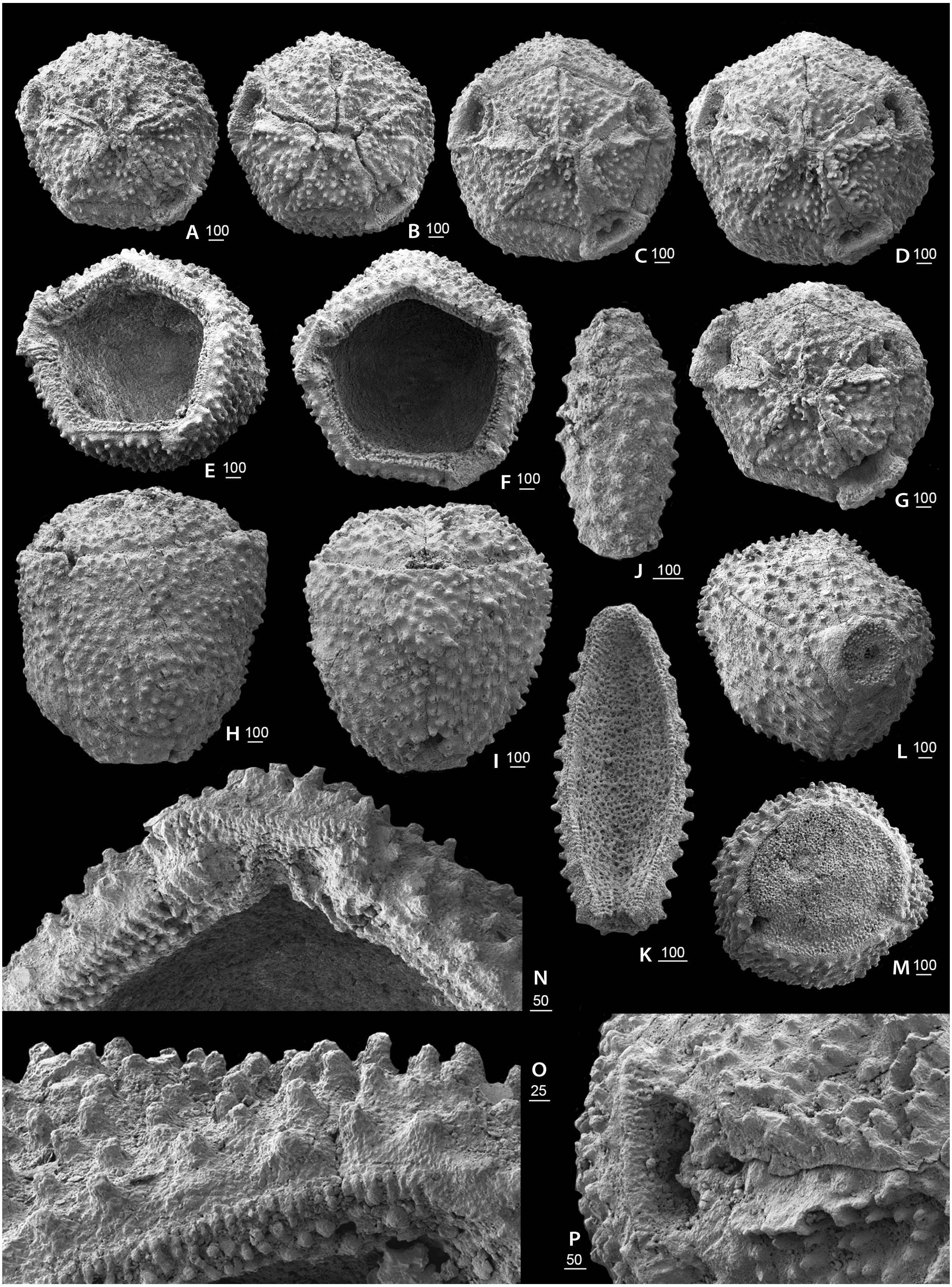
Material. – One hundred and sixty thecae.

Description. – See Prokop & Petr (1991). We describe and illustrate some new details of the thecal morphology and formerly unknown primibrachials.

The plates of the cup are thick relative to their size. The basal plate between E and B radials (Fig. 2D3, D4) is highly convex, symmetrically hexagonal, with long adoral margin and weak mound-like elevation in the centre. The fine indentation at the adoral edge (Fig. 2D3) marks the A ray suture of peristomal cover plates (PPCP). The CDE basal plate has the same morphology. The BC basal plate (Fig. 2D2) is symmetrical, narrowly hexagonal, having the adoral margin shorter than the aboral margin. The internal surface of all plates is smooth. The external surface of basal, radial and peristomal cover plates bear high evenly spaced pustules of uniform size (Fig. 2B2, D4). Their height is about one-third of cup wall thickness (Fig. 3N, O). All pustules have the truncated tops. Tiny pits of the top of pustules noted by Prokop & Petr (1991) are present but not in all pustules (Fig. 3I).

The surface of sutures between basal as well as infrabasal plates are smooth, with only uniform structure of the stereom (Fig. 2D2, D3). The thickness of the infrabasal, basal, and radial plates is similar in all directions.

Figure 3. *Treocrinus ericius* Prokop & Petr, 1991. A – theca with C and E radial facets, oral view with posterior down, PCZCU 2778. B – theca with C and E radial facets, oral view with posterior down, PCZCU 2781. C – theca with C and E radial facets, oral view with posterior down, PCZCU 2784. D, P – theca with B, C and E radial facets in oral view with posterior down, and enlarged detail of the B radial facet, the suture between oral plates and the nerve foramen, PCZCU 2785. E, O – cup with E radial facet, small C arm facet in oral view with posterior down, and enlarged detail of pustules and the radial facet with fine dentition of basal plate (left) and radial (right) plate; note suture between basal and radial plates, PCZCU 2782. F, N – cup with B, C, and E radial facets in oral view with posterior down, and enlarged detail of E radial facet showing fossae and groove, PCZCU 2783. G – theca with B, C, and E radial facets, oral view with posterior down, PCZCU 2790. H – theca facing BB plate in side (A-ray) view, PCZCU 2787. I – theca facing RR plate in side (E-ray) view, PCZCU 2786. J – small primibrachial, exterior, PCZCU 2789. K – large primibrachial, interior, PCZCU 2788. L – cup with small articular facet and distinct lumen in laterobasal view, PCZCU 2791. M – cup with large articular facet in basal view, PCZCU 2792. Age and locality: Třebotov Limestone, sample Barr: −210; Praha-Barrandov. Bar scale in μm.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The aboral edge of basal plates is finely denticulate by two types of denticles. Larger randomly space nodose denticles form the internal row (Fig. 3O). Smaller parallel-aligned elongate denticles form the outer row (Fig. 3O). The outer row obviously forms the articulation surface for adjoining peristomal cover plates. The similar transverse ridge of parallel sharp-crested small denticles develops on the extended adoral surface of a radial facet (Fig. 3N). Two shallow concave fossae that likely represent the ligament area are present on the internal face of radial facet (Fig. 3N). A narrow groove separated the fossae each another (Fig. 3N).

The primibrachial has a shape of broad, elongate-elliptical weakly tapering rod, which as about three-times higher than wide (Figs 2G1–G4; 3J, K). It is gently arched having the adorally decreasing convexity. The small triangular articular facet is present at the proximal end (Fig. 3K). The distal tip lacks the articular facet. Indeed, the whole arm is presumably formed by a single plate. The deep and wide food groove almost completely occupies the adoral surface of the primibrachial (Figs 2G3, G4; 3K). Truncated pustules of similar shape and size to those on the cup tegmen cover the external surface of primibrachials (Figs 2G1, 3J).

Remarks. – In the original description, Prokop & Petr (1991) stated that the species is morphologically very variable. They noted difference in height and width of theca, uneven arch of peristomal cover plates, various number and length of spine-like pustules on the external surface of the theca and uneven shape, diameter and deflection of radial facets. However, the authors did not provide the discussion on the asymmetry of the theca, a shape infrabasal circlet, and presence or absence of a column.

Prokop & Petr (1991) located three radial facets and adjacent hollowed sutures in B, D, and E rays (Prokop & Petr 1991, fig. 2), but the real locations of these sutures are in the B, C, and E rays. Correspondingly, their diagram of theca needs a correction because their radials actually are in E, C, and B positions (Fig. 4). The position of A ray is clearly defined by the bilateral symmetry of ambulacral grooves in the adoral surface of the peristomal region (Fig. 3B).

Occurrence. – According to Prokop & Petr (1991) and Prokop & Nohejlová (1995) the species is significant for the uppermost layers of the Třebotov Limestone at Praha-Holyně, Praha-Hlubočepy, and Praha-Barrandov, with the majority of individuals coming from the layers 2.2 to 1.4 m below the boundary with the Choteč Limestone. New data from the Praha-Barrandov locality indicate that the species is most abundant in beds 2.1 to 2.5 m below the first limestone bed referred to the Choteč Formation.

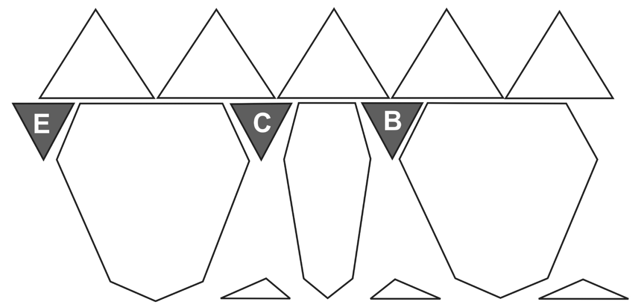


Figure 4. *Treocrinus ericius* Prokop & Petr, 1991. Diagram of the theca. Radial plates in black (modified after Prokop & Petr 1991).

Ontogeny of *Treocrinus*

One small specimen with attached peristomal cover plates possesses only a 0.85 mm high theca (Fig. 2A1) and lacks traces of the holdfast. It has a low barrel-shaped cup, and its large articular facet for the column almost equals to the diameter of the cup. Its basal plates are subrectangular, low. The infrabasal plates make up a subplanar bottom of the cup, and generate a gentle convex surface of the articular facet. Radial plates are not developed in the specimen yet. Other even smaller but incomplete specimen (Fig. 2C1, C2) exhibits the circlet of low subrectangular basals, surrounding a triangular infrabasal plate circlet. The pustulous exterior is clearly developed in both small specimens. A somewhat larger specimen (Fig. 2B1, B2) having 1.35 mm high theca possesses small triangular radial plates wedged between larger basal plates. The small E radial facet is already developed on the convex edge of the radial plate. The trough between adjacent peristomal cover plates in the E ray is not developed yet.

The sequence of development of the radial facets in *Treocrinus* is orderly and in agreement with a sequence reported by earlier authors examining the microcrinoids (Peck 1935, 1936; Strimple & Koenig 1956; Koenig 1965; Gutschick 1968; Lane & Sevastopulo 1981, 1982, 1986). The smallest examined specimen with preserved peristomal cover plates (Fig. 2A1) lacks all radial facets (Fig. 2A2). The radial facet in the E ray appears to be the first (Figs 2B1, 3E). Thecae with just one facet are very rare, being represented only by two specimens in our sample. The E ray is followed by development of C radial facet, but the C facet is somewhat smaller than the E facet (Fig. 3A, B). The development of the B facet followed subsequently. The specimens having three radial facets (radials B, C, E) occur most abundantly in our sample (Fig. 3C, D, G). Even the largest examined specimens have only three facets. None specimens with four or five radial facets have been observed. The size of radial facets is uneven: The E facet is the largest, followed by a similarly sized or smaller C facet (Fig. 3C, D, G). The B facet is

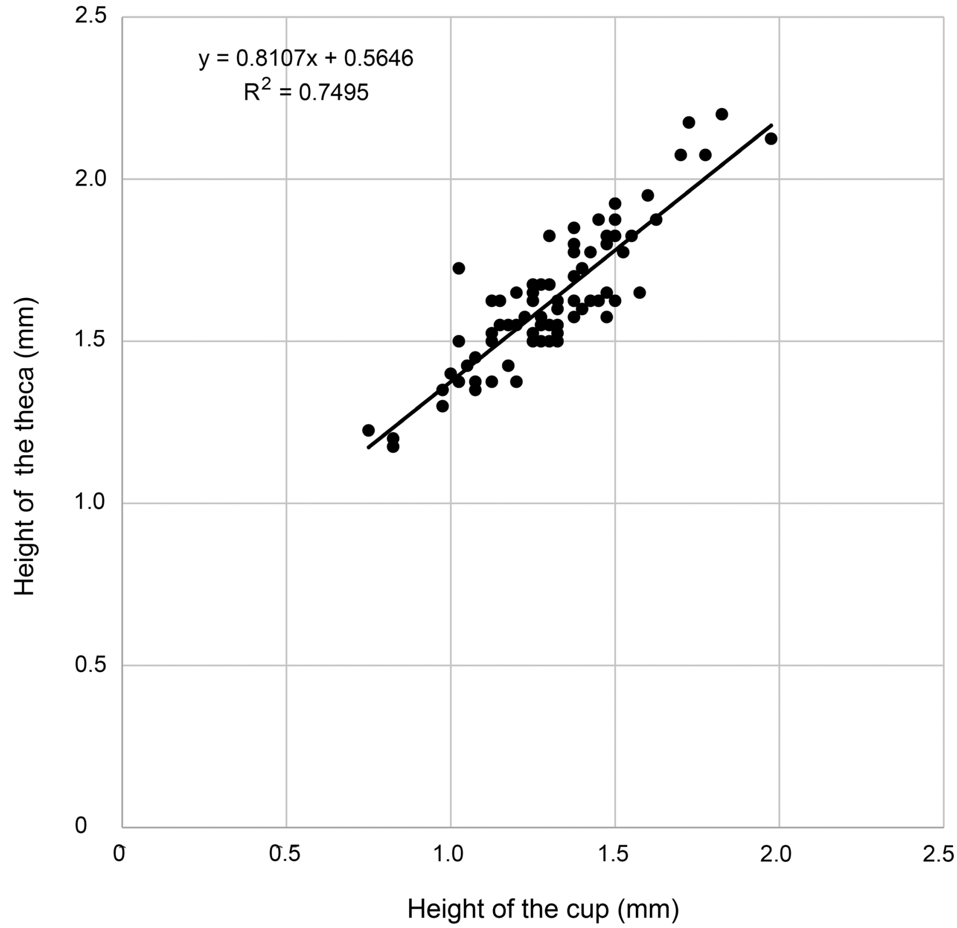


Figure 5. *Treocrinus ericius* Prokop & Petr, 1991. Scatter diagram of height of the cup versus height of the whole theca.

always the smallest. Among 87 examined specimens with preserved radials, two specimens developed only the E facet (= 2%), 21 specimens have E and C facets (= 24%), and 64 specimens have E, C and B facets (= 74% of specimens).

The size and depth of troughs bordering the sutures between peristomal cover plates depend on the development of arm facets. The negligible trough is developed along the suture between peristomal cover plates adjoining to small arm facet (Figs 2B1, 3A). The surface of peristomal cover plates adjoining to large arm facets is deeply hollowed along their suture (Fig. 3B–D, G). The surface of the trough near shared sutures is smooth (Fig. 3G, P). This smooth surface of the peristomal cover plates is bordered by a distinct ridge of fused pustules from the adjoined external surface, which is covered by prominent pustules (Fig. 3G). As the radial facets are of different sizes, the corresponding depth of the trough follows the ontogenetic stage. The troughs accommodated primibrachials in the resting stage. The pustules aligned along the sides of primibrachials (Fig. 3J, K) likely fit in between pustules on ridges bordering the trough (Fig. 3P).

Phenotypic plasticity

The stable feature of *Treocrinus ericius* is principally a small bilaterally symmetrical theca in the oral view, almost regularly shaped and remarkably thick infrabasal, basal, radial and peristomal cover plates, and a pustulose exterior of the cup, peristomal cover plates and primibrachials. Apart from early juvenile individuals, there are always three small radial plates with conspicuously projecting arm facets. A strict size limit of the theca (Fig. 5) is another characteristic feature. This indicates that the largest examined specimens are not the juveniles, but really represent the adult individuals.

The shape of dicyclic adoral cup varies from a low tubular or a sac-like to a high bowl. The prevalent shape is a high to medium bowl (Figs 3H, I; 6). However, there is a minor proportion of cups that have strikingly different shapes, principally make up by a low circlet of rectangular to trapezoidal basal plates (Figs 6; 7; 8D1, E1). In a biological sense this means that it was not advantageous for the theca of *Triacrinus* to be too narrow or too wide. The most advantageous is to have a width of thecae somewhere between these two extremes. The evolution

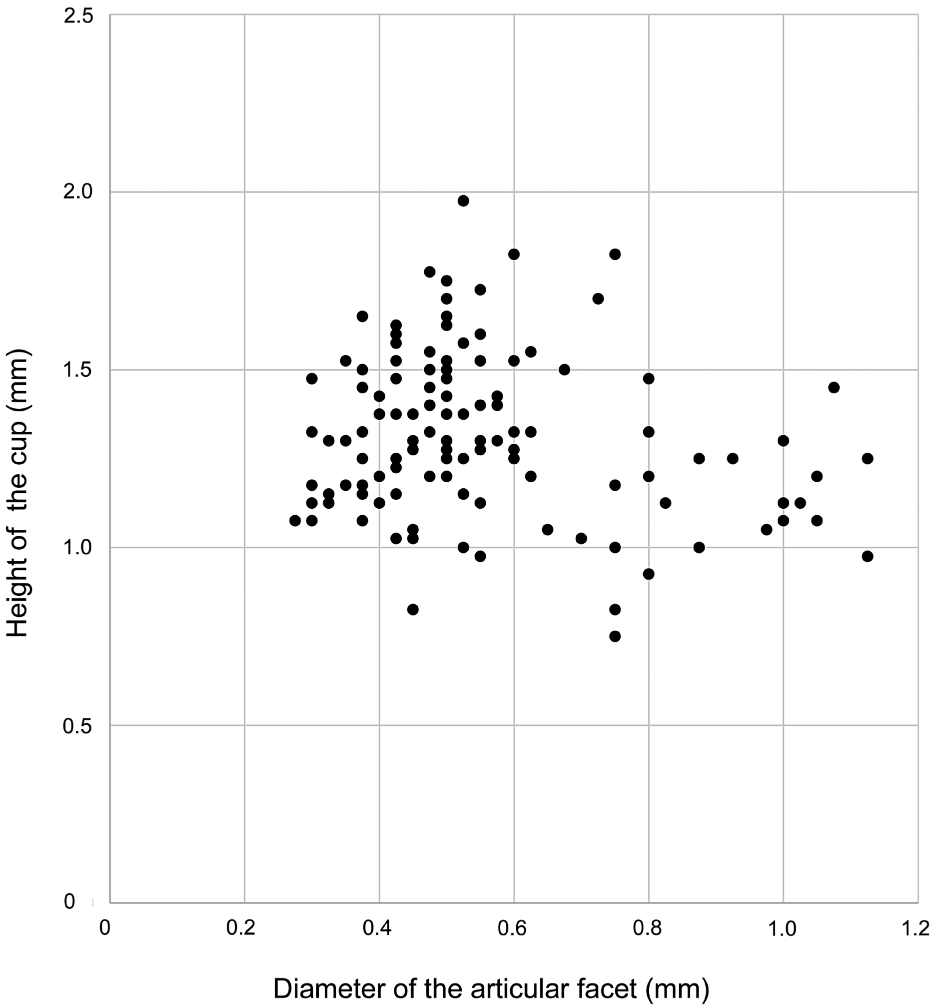


Figure 6. *Treocrinus ericius* Prokop & Petr, 1991. Scatter diagram of height of the cup versus the diameter of the articular facet.

should result in the individuals with the most advantageous width of thecae. The non-modal shape of theca can be related with unusual habitat of the minor part of the population, but also other stressing factors cannot be eliminated. This non-modal part of population likely differs from the modal shape also by absence of the stem.

This deviation from the modal shape is typically associated with an increase of asymmetry of the theca. The base of the cup is convex to weakly depressed. The basals are evenly convex or have more or less prominent mound-like elevation at the centre. The planes enclosed by the articular facet of the infrabasal circle and the adoral cup top vary from parallel (Fig. 8A1–A3) to almost 45° angle (Fig. 8D1, D2). In an appropriate manner, the size and outline of the basal plates differ depending on the location in the cup. The size of infrabasal plates varies considerably depending on the size of the articulation facets (Figs 3L, M; 8F–N).

The base of the adoral cup displays a variably sized articular facet. In the majority of individuals, the articular facet attains less than 25% of a cup diameter (Figs 6, 8F–J). However, there are specimens in which the diameter of the articular facet exceeds 50% of a cup diameter (Figs 6; 8L, M) and exceptionally, the facet diameter is almost equal to the width of the theca (Figs 3M, 8N). The articular facet is generally planar in side view, but some large facets possess a moderate convex surface. Some small facets are very weakly concave, slightly depressed below the adjacent surface of infrabasal plates (Fig. 8H). The surface of facet is smooth with small lumen which may be asymmetrically situated (Fig. 8L–N). A small circular lumen is always present (Fig. 8F–N). The crenula bordering a smooth surface may be present in small facets (Fig. 8F, J). The sutures between the infrabasal plates and inferbasal sutures are quite distinct in large facets (Figs 3M, 8N).

Holdfast

The holdfast attached to basal circlet has been observed in six specimens (Figs 2F, 8A–E). The holdfast width is equally sized (Fig. 6A–C) to distinctly larger than the width of the cup (Fig. 8D, E). The margins of holdfasts are uneven, scalloped but never extended into rhizoid or digitate protrusions. The height of the examined holdfasts is low, approximately less than 20% of the cup height. The basal side of the holdfasts may be smooth (Fig. 6B–D) or having the imprint of an uneven surface of the substrate (Fig. 6E). The base of the largest holdfast (Fig. 6E) has a set of ten parallel ridges arranged in regular intervals. This wrinkled surface indicates fixation of a larva to any ribbed objects. The same wrinkled surface was observed on the underside of one rhizoid crinoid holdfast at the same locality (Mergl & Šmídtová 2022a, pl. 2, fig. 16b). Unfortunately, the restricted area of the holdfast does not have a distinct convergence (suggested on a brachiopod shell) or strict parallelism (suggested on a cephalopod shell) of ribs. However, a ribbed surface is faintly concave (Fig. 8E1) that likely copies a finely convex and ribbed surface of a cephalopod shell. The large articulation facets with weakly convex surface (Fig. 8N) indicate that some holdfasts were attached to the concave surface, most likely the internal surface of cephalopod shells or similar objects.

Column

It is not clear, whether *Treocrinus ericius* was a stemless microcrinoid or had any form of a column. The size of the cup of a few specimens with preserved holdfast are almost equal to the maximum size of the loose specimens. This implies that the former was stemless over their entire life. Their articular facet at the base of the cup directly adhered to the holdfast (Fig. 8C2, E1). Unlike these specimens, the small size of articular facets (250–300 µm) observed in the majority of loose specimens suggest presence of a column. This suggestion is supported by the presence of fine crenula developed on the surface of some articular facets (Fig. 8F, J). In some specimens, the surface of the articular facet is gently submerged below a neighbour surface of infrabasals (Fig. 8F, H). This observation demonstrates the existence of a column, at least in part of the population. Whether the cup of *Treocrinus* maintained a short or long column is unknown, as is the diameter of a column. Loose, small, and almost featureless columnals of corresponding size are present in fine crinoidal debris of washings. However, whether these small columnals

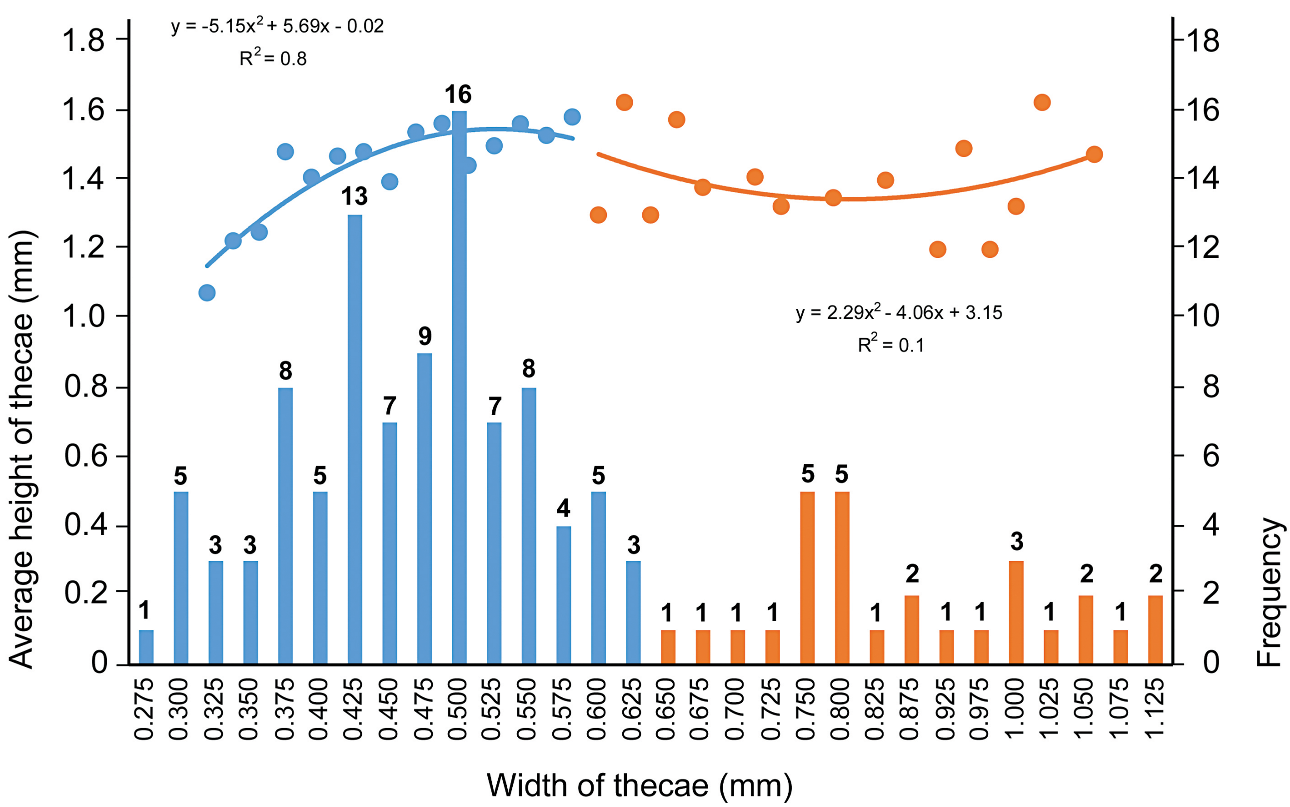


Figure 7. Phenotypic plasticity of *Treocrinus ericius* Prokop & Petr, 1991. The dependence of average height of thecae on average width of thecae forms a concave parabolic curve. We used a data set with higher frequency of individuals with specific width of thecae (= blue part of the figure, coefficient of determination – $R^2 = 0.8$). Low number of individuals measured in the right half of the figure revealed a convex parabola (red part of the figure, $R^2 = 0.1$).

belong to *Treocrinus* or to another microcrinoid is unclear because washings contain more species of similarly sized microcrinoids (Prokop & Nohejlová 2015).

Mode of life

The relation of microcrinoids to substrate is not well known, because examples with columns attached and holdfasts preserved are extremely rare (Sevastopulo 2008). There are some examples of Carboniferous allagecrinids (Lane & Sevastopulo 1981, 1982; Mapes *et al*. 1986) that indicate that these microcrinoids had a rather long column. Unlike the allagecrinids, the codiocrinaceans had short and rigid columns. Sevastopulo (2008) illustrated an immature specimen of the Carboniferous *Monobrachiocrinus* with short straight column and holdfast. A similar short column has been observed in the Visean genera *Neolageniocrinus* and *Hemistreptacron* (Arendt 1970). Sevastopulo (2008) illustrated an undescribed codiacrinacean microcrinoid cemented to the substrate at its lower end. In summary, the data suggests that codiacrinaceans could have very reduced short column cemented to firm substrate (Sevastopulo 2008).

As clarified above, the majority of the specimens of *Treocrinus ericius* likely has any form of a column. The part of the population having a modal shape of a high- to medium bowl-like cup were elevated by a short column above the sea floor. The sea floor was greatly covered by crinoid-dacryoconarid ooze. The elevation of crinoid theca above the substrate of fine bioclasts was likely no more than tens of millimetres or a few centimetres. A minute size of the microcrinoids suggests that they occupied of sheltered microhabitats between shells, crinoid columns, and cirri snarl. However, a higher secondary tier on elevated columns of other crinoids, elevated surface of larger shells, or an external surface or internal surface of floating objects (*e.g*. empty cephalopod shells) cannot not be dismissed. However, a smaller part of the population likely remained without the column throughout life. The individuals without a column have a large articular facet and a low, barrel-like commonly asymmetric cup. These specimens with a large articular facet represent a smaller portion of the population (Fig. 7). These deviant specimens likely occupied unusual, maybe cryptic habitats, *e.g*. sheltered spaces under a more convex brachiopod or bivalve shell and empty chambers of cephalopod shells. A high proportion of bioeroded shells (Mergl & Šmídtová 2022b) in the same bed confirmed the exposure of shells on a sea floor for a longer time. However, the microcrinoid individuals in a cryptic habitat might be restricted in a space and their growth and development of column was limited. The attachment by the aboral side of the cup directly to the substrate was more advantageous than achievement of the modal shape of theca with the column. The enlargement of a greater body volume was accomplished by a lateral growth of the cup and not by elongation of the theca. Unlike the individuals in more spacious habitats, the development of the column was senseless inside a restricted space of a cryptic habitat.

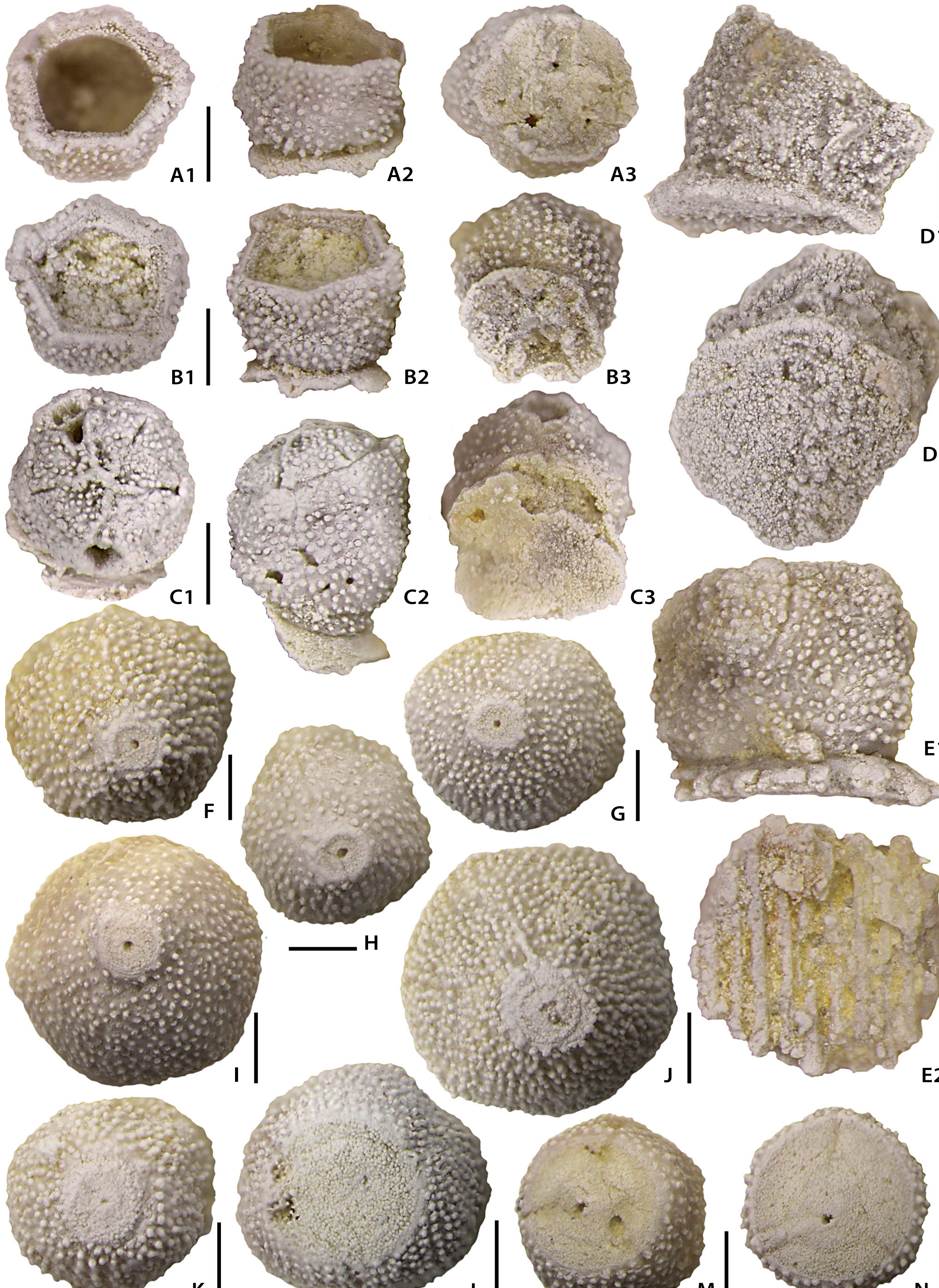
Conclusion

The growth stages of *Treocrinus ericius* confirm the gradual development of the radials, in E, C, and B rays. No specimens with radial plates in A and D rays have been observed. This is in agreement with previous observations on microcrinoid ontogeny (Peck 1935, 1936; Strimple & Koenig 1956; Koenig 1965; Gutschick 1968; Lane & Sevastopulo 1981, 1982, 1986).

The primibrachials of *Treocrinus ericius* are described for the first time. They bear the same pustulose surface of the cup and indicate development of very short arms.

The microcrinoid *Treocrinus ericius* has a remarkable phenotypic plasticity. It is apparent from different shape of the aboral cup, the size of articular facet and, likely some stemless individuals in its population. The holdfasts with complete cups of *Treocrinus* confirm that at least part of the adult population lacked a column, and individuals rested directly on subplanar firm surfaces by the entire surface of infrabasal plates and aboral parts of basal plates. Differences of thecal shapes could be explained by diverse microhabitats. The sheltered and cryptic sites offered only a restricted space for a growth. This restriction preferred the barrel-shaped cup morphology, and development of the column was ineffective. The individuals living in more spacious habitats developed the modal shape of a theca with a bowl-like cup, likely with the column (of unknown

Figure 8. *Treocrinus ericius* Prokop & Petr, 1991. A – small cup with holdfast, in oral (A1), side (A2), and basal views (A3), PCZCU 2550. B – small cup with holdfast, in oral (B1), side (B2), and basal views (B3), PCZCU 2551. C – small theca with holdfast, in oral (C1), side (C2), and basal views (C3), PCZCU 2552. D – cup with holdfast, in side (D1), and basal views (D2), PCZCU 2553. E – cup with holdfast, in side (E1), basal views (E2), PCZCU 2554. F–I – cups on basal views, all with small articular facets, showing central lumen, areola and crenularium, PCZCU 2562, PCZCU 2563, PCZCU 2560, PCZCU 2561. J – cup with extended articular facet in basal view, PCZCU 2559. K – cup with extended articular facet in basal view, PCZCU 2555. L – cup with large articular facet in basal view, PCZCU 2556. M – cup with large articular facet in basal view, PCZCU 2557. N – cup with extreme articular facet in basal view, PCZCU 2558. Age and locality: Třebotov Limestone, sample Barr: −210; Praha-Barrandov. Bar lengths equal to 500 μm.


A1
A2
A3
D1
B1
B2
B3
D2
C1
C2
C3
E1
F
G
H
I
J
E2
K
L
M
N

length) that maintained the crown at some height above the substrate. The utilization of a cryptic habitat of the barrel-shaped and stemless individuals is suggested by size and convexity of the holdfast facet. This gives indirect evidence that hard sheltered substrates on empty shells of brachiopods, bivalves, and cephalopods offered advantageous substrate for a settlement of the crinoid larva. Common bioclasts associated with *Treocrinus ericius*, mainly columnals, pluricolumnals and shells of brachiopods offered greatly convex or subplanar but exposed surfaces. No corresponding evidence, *e.g.* lobate holdfasts with articulation facet for the base of the column, was observed among bioclasts of the white beds' washings.

The cups and isolated plates of *Treocrinus ericius* are associated by other microcrinoids, crinoids and other, often diminutive invertebrates. The fossil assemblage represents the remarkably diverse benthic community, likely below the photic zone. The fossil diversity decreased dramatically with the propagation of the Choteč Event in the Praha-Barrandov section. That is apparent from the disappearance of the majority of the microcrinoids including also easily recognizable thecal remains of *Treocrinus ericius* in the washings of the white beds from the overlying Choteč Limestone. Its disappearance is also marked by changes in composition of other invertebrate fauna.

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