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RESEARCH PAPER

Eckicrinidae: a new lineage of Triassic crinoids and the diversification of attachment strategies in the Early and Middle Triassic

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Abstract

The re-discovery of a distal pluricolumnal of the Middle Triassic *Eckicrinus radiatus* requires separation of *Eckicrinus* from Holocrinidae and to establish the new family Eckicrinidae of undetermined systematic position. The pluricolumnal with enlarged radicular cirri with multiradiate articulations acted as a rhizoid holdfast. In the Early and Middle Triassic, three attachment modes occurred among benthic crinoids: (1) discoid or incrusting holdfasts (Encrinida, Millericrinida), (2) rhizoid holdfasts with radicular cirri (Eckicrinidae, Qingyanocrinidae), (3) motile cirri with synarthrial articulations (Holocrinida, Isocrinida). Encrinida and Holocrinida representing the two well known major clades of Middle Triassic crinoids are rooted in different Permian Ampelocrinida rather than in one Early Triassic common ancestor. Eckicrinidae may represent a third lineage. This evidence contributes to challenging the prevalent opinion that just one lineage of each of the five extant echinoderm groups passed the end-Permian extinction event.

Keywords Crinoidea (Articulata) · New family · Attachment modes · Phylogeny · Triassic · Tethys · Europe

Introduction

The number of Triassic crinoid taxa has much increased during the last decades (Hagdorn 1995; Hess et al. 2011a, b, c). However, many species and genera are based on column material with no assignable cup or arm remains or even complete articulated specimens. This applies particularly to Early Triassic crinoids because conservation Lagerstätten prior to the early Anisian have not yet been discovered. As long as all column characters of such an incompletely known taxon conform with the diagnosis of a definite family, assignment is plausible. Otherwise, if the material combines characters diagnostic of different families, assignment proves to be debatable. Thereby convergent column morphologies must be taken in consideration. Earlier assignments have to be questioned when new material yields new evidence. This is the case in *Eckicrinus*, a common and well diagnosed columnal-based Middle Triassic crinoid that inhabited wide areas of the Palaeo-Tethys.

For low circular columnals with finely crenulated articulation facets and pyriform petals from the Middle Triassic Calcare à Brachiopodi of Recoaro (Recoaro Formation; Vicentinian Alps, Italy), Schauroth (1859) erected a new species that he tentatively assigned to *Encrinus*. This *Encrinus*? *radiatus* (Fig. 1) was synonymized by Eck (1865: 88) with *Entrochus silesiacus* (Beyrich, 1857), which, however, is much larger, has multiradiate articulation facets devoid of petals, no cirri, and a much wider axial canal. Quenstedt (1876: 479–482), who described additional material from Recoaro and columnals from the famous crinoid locality of St. Hyacinth´s well near Beuthen (Upper Silesia; now Bytom, Poland), clearly underlined these diagnostic characters. Obviously, he was not aware of Schauroth´s publication, otherwise he would certainly have assigned his specimens to Schauroth´s *Encrinus*? *radiatus*. Among his specimens, Quenstedt observed cirrus sockets of variable size and assigned them rather to the Pentacriniten' than to the 'Encriniten'. In the typical *Entrochus silesiacus,* he noticed similarities with the Jurassic Millericrinidae. Later on, *Encrinus*? *radiatus* was allocated with the Isocrinidae and assigned to *Balanocrinus* by Bather (1909: 15) and to *Laevigatocrinus* by Klikushin (1979: 89; 1986: 103; 1992: 90). Eventually it

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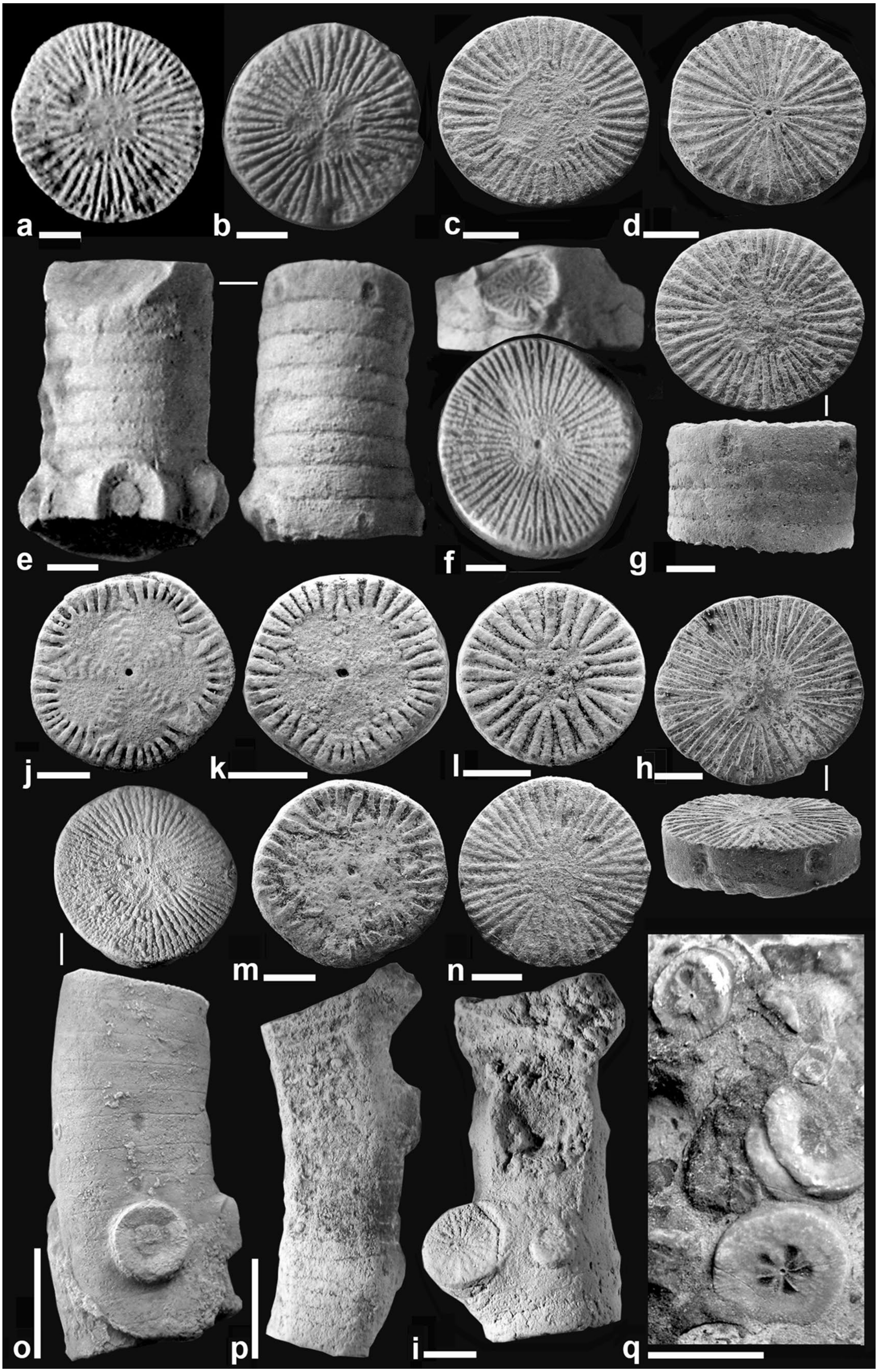
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◂**Fig. 1** *Eckicrinus radiatus* (Schauroth, 1859), columnals and pluricolumnals from the Tethyan and Germanic Middle Triassic. **a**–**i** Recoaro Formation (Anisian, Pelsonian), Recoaro (Vicentinian Prealps, Italy). **a** Internodal, Lectotype, NMC 2682_L; **b** proximal internodal, GPIT Quenstedt collection, Quenstedt (1876: pl. 107, fig. 83); **c** proximal internodal, GPIT Quenstedt collection, GPIT 1623/8; **d** distal internodal, GPIT Quenstedt collection 1623/11; **e** distal pluricolumnal, nodals with small and enlarged cirrus scars, GPIT Quenstedt collection, Quenstedt (1876: pl. 107, fig. 86); **f** distal pluricolumnal, nodal with small indistinct and two enlarged cirrus scars with multiradiate articulations, GPIT Quenstedt collection, Quenstedt (1876: pl. 107, fig. 84), see also Fig. 6d; **g** pluricolumnal, nodal with small circular cirrus scars, GPIT Quenstedt collection 1623/10; **h** nodal with small circular cirrus scars, GPIT Quenstedt collection 1623/7; **i** distal pluricolumnal, nodals with small circular cirrus scars and two strongly enlarged cirrus scars with multiradiate articulations, MHI 1266/1/1, see also Fig. 6c. **j**–**l** Middle Muschelkalk Jemielnica Formation (=Diplopora Dolomite) (Anisian, Illyrian), Piekary Śląskie (Upper Silesia, Poland). **j** Subcircular proximal internodal with large pyriform petals and short crenulae, GIUS-7–59/9b; **k** subcircular proximal internodal with large pyriform petals and short crenulae, GIUS-7–59/9a; **l** juvenile internodal with long crenulae, GIUS-7–59/13a. **m**–**n** Lower Muschelkalk Lima striata Beds (Anisian, Pelsonian), Wolica (Holy Cross Mountains, Poland). **m** Subcircular proximal internodal, MHI 1164/1/8; **n** distal internodal, MHI 1164/1/3. **o**–**p** Vászoly Formation (Avisianum subzone, late Anisian, Illyrian), Öskü (Veszprém-Plateau, Hungary). **o** Distal pluricolumnal, nodals with small indistinct and two enlarged cirrus scars callus-sheathed by neighbouring internodals, MHI 1799/1/1, see also Fig. 6a; **p** slightly corroded distal pluricolumnal, nodals with enlarged cirri pointing to one direction, MHI 1799/1/2, see also Fig. 6b. **q** Recoaro Formation (Anisian, Pelsonian), Monte Rite (Cadore, Italy), MHI 2185. *Scale bars* 1 mm (**a**–**n**), 5 mm (**o**–**q**)

was designated as type species of the new genus *Eckicrinus* by Hagdorn and Głuchowski (1993). Hagdorn et al. (1996) added a full description and synonymy list of the available material including Schauroth´s type material from Recoaro and Quenstedt´s specimens from Recoaro and Beuthen, and designated NMC 2682-L as Lectotype. They also revised Beyrich´s *Entrochus silesiacus* assigning it to the new genus *Silesiacrinus* and specified the diagnostic characters of this taxon. Their material comprised several hundreds of columnals from different localities in Italy and Poland. However, apart from some pluricolumnals this material contained no articulated specimens or assignable cup or brachial ossicles.

Because of the limited fossil record and the incomplete morphological data, assignment of *Eckicrinus* to a higher taxonomic rank proved to be contentious. In the petaloid columnal articulation pattern with symplectial lower nodal facets Hagdorn et al. (1996) recognized holocrinid affinity, although the low columnal height and the circular cirri with indistinct or multiradiate articulation facets are not observed among Holocrinidae. They also pointed at similarities in articulation facet pattern and size and morphology of the cirrus sockets with the (?) Carnian *Entrochus insignis* Toula, 1890, which was assigned to *Laevigatocrinus* (Isocrinidae, Balanocrininae) by Klikushin (1979), and the Late Cretaceous *Austinocrinus* (Isocrinidae, Isselicrininae). Hagdorn et al. (1996) explained these similarities as convergencies and recommended to include *Eckicrinus* provisionally into family Holocrinidae as long as the cup and the arms remained unknown. This decision was shared by Hess (2011a) in the Revised Crinoid Treatise. Among columnal material of a new but still undescribed crinoid from Smithian Hallstatt Limestones of Timor mentioned by Hagdorn (2018) is a taxon with a column terminating in a discoid holdfast of encrinid-type (Fig. 2). This material also comprises a single nodal with large multiradiate cirri reminiscent of *Eckicrinus* and *Tollmannicrinus* specimens (e.g., Hagdorn et al. 1996: fig. 6a, b; Kristan-Tollmann 1975: figs. 13,1, 3a–c; 14, 1a–b). The cirrinodal in Fig. 2e induced Hagdorn (2018) to allocate this Early Triassic crinoid as well as *Eckicrinus* closer to the Order Encrinida than to Holocrinida. Most recently, Stiller (2019) suggested for *Eckicrinus* a family incertae sedis assigned with question mark to Order Holocrinida, which, however, was not formally established.

Columnals of *Eckicrinus radiatus* are diagnostic, easily determinable, and commonly found in the Middle Triassic of the western Palaeo-Tethys and the palaeo-northeastern part of the Central Europaean Basin, which was connected to the open Tethys shelf via marine straits (East Carpathian and Silesian-Moravian gates). During this time interval, the Muschelkalk fauna in southern Poland was strongly influenced by Tethyan elements (e.g.,Eck 1865; Assmann 1937; Hagdorn and Głuchowski 1993; Hagdorn 2020). The genus was also described from the Anisian of Southwest China and thus from the eastern Palaeo-Tethys (Stiller 2019, *Eckicrinus* cf. *radiatus*).

In search of a historical specimen of *Encrinus aculeatus* in the vast collections of the Bundesanstalt für Geowissenschaften und Rohstoffe (BGR), Dienstbereich Berlin (Hagdorn et al. 2018: fig. 8a), another historical crinoid find was detected. This specimen was collected by Heinrich Eck in 1864, labeled by himself, and later inventoried as *Entrochus silesiacus* Beyr. with an institutional label of the Geologischer Dienst, Berlin (Geological Survey Berlin) under number X 13379 from sheet Broslawitz (3257) of the Geological Map of Prussia (Fig. 3). Eck was certainly aware of the rarity and importance of the cirriferous stem fragment and described it in meticulous clarity and detail (Eck 1865: 88) but he omitted to include a picture and it was never mentioned subsequently. As ascertained above, he synonymized Schauroth´s *Encrinus*? *radiatus* with Beyrich´s *Entrochus silesiacus* and assigned it to this taxon. The specimen was collected in the early Illyrian 'Mikultschützer Kalk' (now Karchowice Formation) of a mining shaft near Repten south of Tarnowitz (now Repty Śląskie, a suburb of Tarnowskie Góry) in Upper Silesia, Poland (Fig. 4).

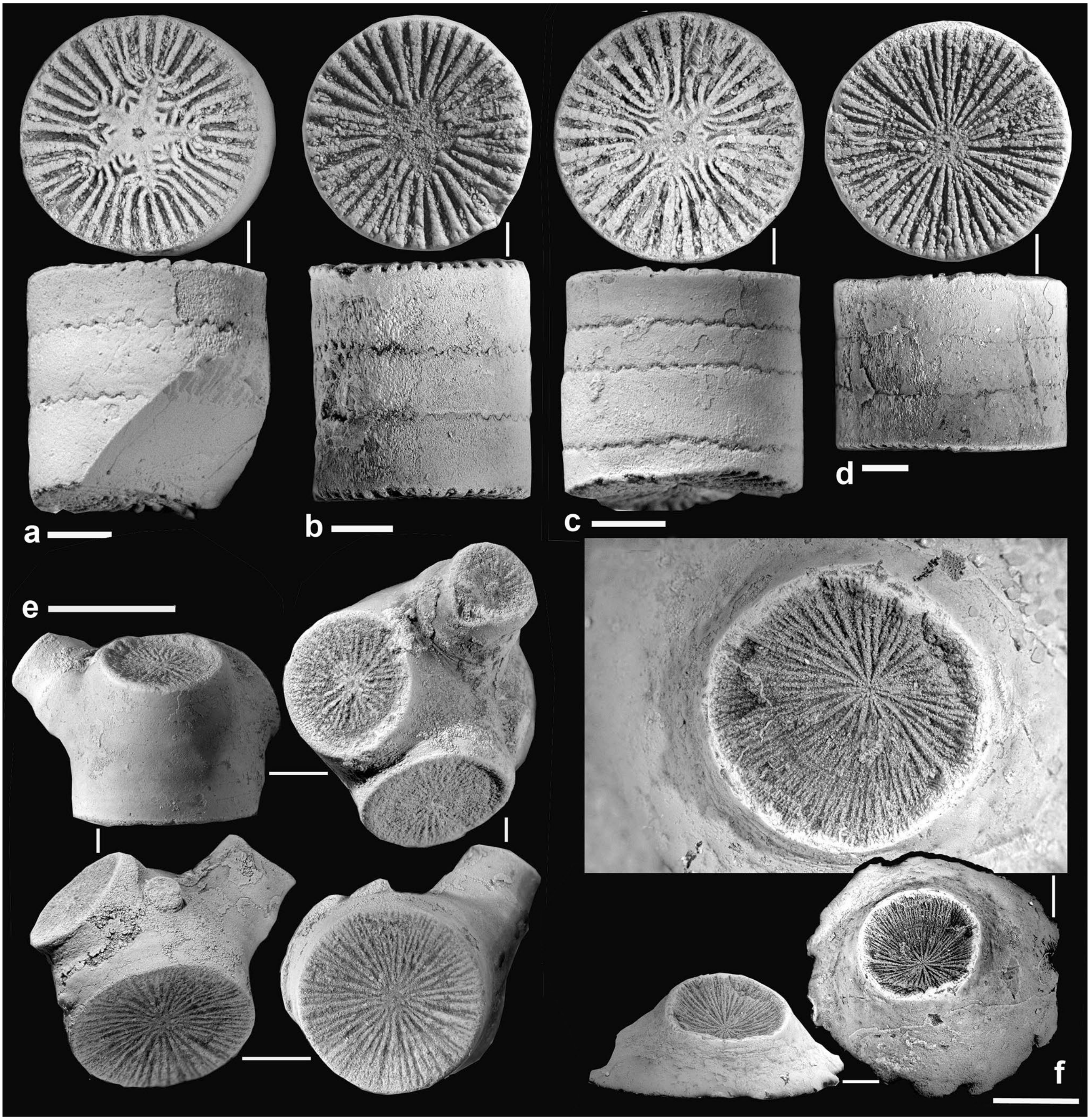

Fig. 2 Crinoidea indet., Hallstatt Limestones, Olenekian, (early?) Spathian, West Timor; the SNY numbers refer to individual limestone blocks from the "John Snyder collection" housed in the collection of the Paläontologisches Institut und Museum of the University of Zürich. **a** Pluricolumnal of three proximal internodals, articulation facet with star-shaped petaloid areole, PIMUZ 51923, from SNY 17. **b** Pluricolumnal of three internodals, areole indistinctly petaloid, latus, PIMUZ 51924, from SNY 13B. **c** Proximal pluricolumnal of three internodals and a higher nodal devoid of cirri, articulation facet with indistinctly petaloid areole, PIMUZ 51925, from SNY 17. **d** Pluricolumnal of three distal internodals, facet with no areole, PIMUZ 51926, from SNY 13B. **e** Distal nodal with two large cirrus sockets with multiradiate facets, upper and lower facet symplectial, PIMUZ 51927, from SNY 9A. **f** Discoid holdfast with even attachment area and crater-like depressed articulation area with column. Proximal, oblique lateral, enlarged articulation facet, PIMUZ 51928, from SNY 11B. *Scale bars* 1 mm (**a**), 2 mm (**b**, **c**, **d**, **e**), 5 mm (**f**)

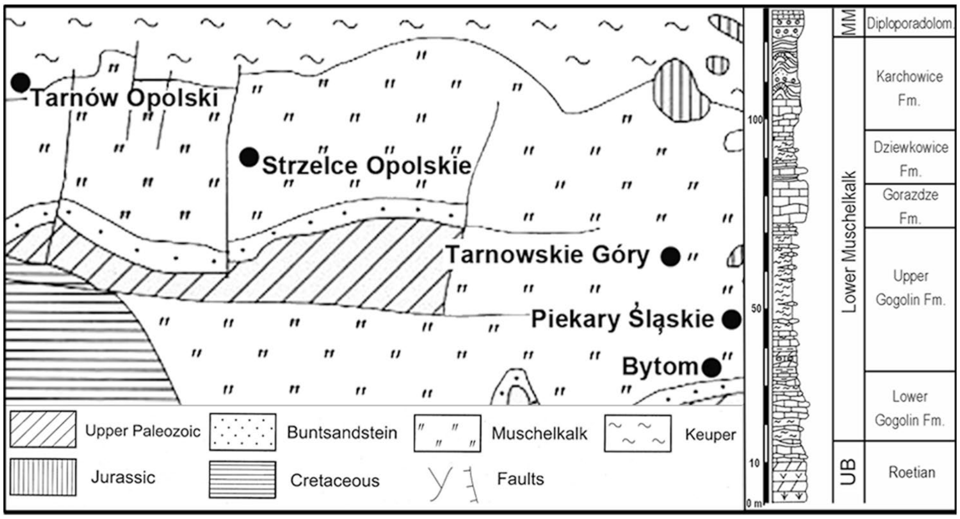

Fig. 3 Geological sketch map with *Eckicrinus* localities in Upper Silesia and simplified stratigraphic column of the Lower Muschelkalk in Upper Silesia. *UB* Upper Buntsandstein, *MM* Middle Muschelkalk. Modified from Szulc et al. (2009)

Material and methods

BGR X 13379 was photographed in various views of its natural surface (Fig. 4) and coated with ammonium chloride to visualize the otherwise faint or obscure suture lines (Fig. 5). Drawings of some of these views accentuate identified suture lines and surface characters (Fig. 6). On one side of the specimen, remains of the yellowish matrix indicative of the karstified Karchowice Formation limestone are preserved. The colour of the pluricolumnal is also yellow-orange and appears finely marbled as a result of partial silification, a common diagenetic feature among brachiopod and echinoderm remains in the Karchowice Formation. The pluricolumnal was incrusted by a few vermiform siliceous foraminifers assigned to Ammodiscidae. The columnals in Figs. 1a–h and i–n are repeated from Hagdorn et al. (1996); Figs. 1i and o–q were taken from whitened specimens. The columnals and holdfasts in Fig. 2 were photographed by A. Nützel, SNSB—Bayerische Staatssammlung für Paläontologie und Geologie, Munich.

Depository of specimens. BGR—Bundesanstalt für Geowissenschaften und Rohstoffe, Dienstbereich Berlin, Germany; GIUS—Laboratory of Paleontology and Stratigraphy, Silesian University Sosnowiec, Poland; GPIT—Institut für Geologie und Paläontologie, Universität Tübingen, Germany; MHI—Muschelkalkmuseum Hagdorn Ingelfingen, Germany; NMC—Naturkundemuseum Coburg, Germany; PIMUZ—Paläontologisches Institut und Museum, Universität Zürich, Switzerland.

Systematic palaeontology

Class **Crinoidea** Miller, 1821
Subclass **Articulata** Zittel, 1879
Order uncertain
Family **Eckicrinidae** fam. nov.

Diagnosis. Columnals low, discoidal; articulation facets with granulated radial bands, long marginal crenulae, and pyriform petals. Nodals only slightly higher than internodals, lower nodal facets symplectial. Nodals with small circular cirrus sockets. Column terminating in a rhizoid holdfast with individual enlarged cirri with multiradiate articulations. Noditaxis short. Crown unknown.

Type genus. *Eckicrinus* Hagdorn and Głuchowski, 1993.

Genus ***Eckicrinus*** Hagdorn and Głuchowski, 1993

Diagnosis (Hagdorn et al. 1996, emended herein). Columnals low, discoidal. Proximal columnals subcircular, with granulated radial bands and moderately long marginal crenulae; petal floors pyriform. Distal columnals circular, with long marginal crenulae; petal floors small; bifurcation and intercalation of additional culmina towards the periphery. Nodals not wider and only slightly higher than internodals; lower nodal facets symplectial. Nodals with up to five small circular cirrus scars with indistinct facets; cirri may be reduced to small bud-like extensions. Terminal column with individual modified and strongly enlarged cirri that may proximally be sheathed by callus of adjacent internodals; enlarged cirrals with multiradiate articulation facets; other cirri small, bud-like. Noditaxis short, comprising three to six columnals. Crown unknown.

Mikultschützer
Kalk
= Schaumkalk.

aus einem Schachte
am östlichen Ende
von Repten.
Eck leg. 1864.

Geologischer Dienst, Berlin
Entrochus silesiacus Beyr.
Mikultsch. Kalk, aus einem
Schacht am östl. Ende v. Repten
Bl. Broslawitz Nr. 3257
Slg. Eck

Fig. 4 **a** Rhizoid root of *Eckicrinus radiatus* (Schauroth, 1859), BGR X 13379. Mikultschützer Kalk (= Karchowice Formation), from a mining shaft at the eastern margin of Repten (now: Repty Śląskie near Tarnowskie Góry, Upper Silesia, Poland), Geological Map of Prussia 1:25.000, Sheet 3257 Broslawitz, collected 1864 by Heinrich Eck and described in Eck (1865). *Scale bar* 10 mm. **b** Handwritten label by H. Eck. **c** Label of the Geologischer Dienst, Berlin (Geological Survey Berlin)

Fig. 5 Rhizoid root of *Eckicrinus radiatus* (Schauroth, 1859), BGR X 13379. Lower Muschelkalk, Karchowice Formation (Anisian), Repty Śląskie near Tarnowskie Góry (former Repten near Tarnowitz), Upper Silesia, Poland. Specimen in different views, whitened with ammonium chloride; matrix not completely removed. **a**–**c** Lateral views showing four rows of enlarged cirri uniformly directed towards the substrate (not preserved). **d**–**e** Lateral views showing the side directed away from substrate with very small or no cirri at all. **f** Proximal end with faint crenulation of most proximal columnal partly preserved, partly lacking due to abrasive preparation. **g** Distal end with typical petaloid articulation pattern facet of most distal columnal; enlarged cirri bending towards former substrate. *Scale bar* 10 mm

Eckicrinus radiatus (Schauroth, 1859)
Figures 1, 4, 5, 6

? 1846 *Pentacrinites*? *subteres* Münster—Catullo: p. 243, pl. 3, figs. 4a, b

v* 1859 *Encrinus*? *radiatus* n.sp.—Schauroth: p. 288, pl. 1, figs. 4a–c

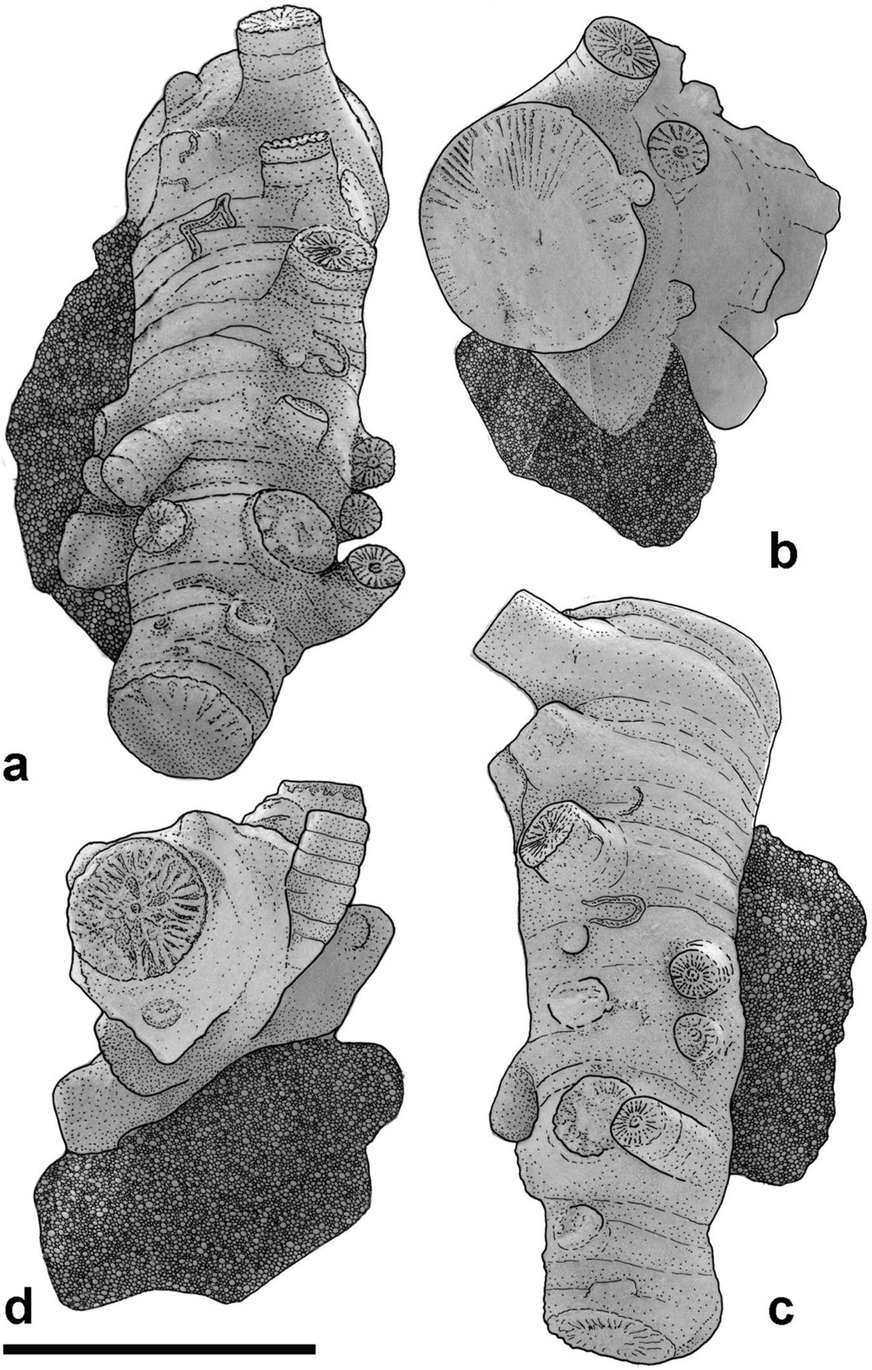

Fig. 6 Rhizoid root of *Eckicrinus radiatus* (Schauroth 1859), BGR X 13379. Lower Muschelkalk, Karchowice Formation (Anisian), Repty Śląskie near Tarnowskie Góry (former Repten near Tarnowitz), Upper Silesia, Poland. Specimen in four views highlighted with Indian ink to accentuate identified suture lines and surface characters. **a** Lateral view corresponding to Fig. 3b; note incrusting foraminifera. **b** Proximal end corresponding to Fig. 3f. **c** Lateral view corresponding to Fig. 3c. **d** Distal end corresponding to Fig. 3g. *Scale bar* 10 mm

non 1861 *Encrinus radiatus* Schauroth var. *verrucosus* Gümbel.—Gümbel: p. 220 [according to Bather 1909: 243 = *Encrinus cancellistriatus*]
1864 *Encrinus radiatus* v. Schauroth—Alberti: p. 58, 263, 304
v 1865 *Encrinus radiatus* Schauroth—Schauroth: p. 53
v 1865 *Entrochus silesiacus* Beyr. [pars]—Eck: p. 88
1868 *Entrochus silesiacus* Beyr.—Benecke: p. 41, pl. 4, figs. 12a–c
v 1876 bei den Pentacrinen—Quenstedt: p. 480, pl. 107, fig. 67
v 1876 dünne *Silesiacus*-ähnliche Glieder—Quenstedt: p. 481
v 1876 *Encrinus* cf. *silesiacus*—Quenstedt: pl. 107, figs. 83–87
? 1877 *Encrinus*? *radiatus* Schauroth—Toula: p. 502
1883 *Encrinus radiatus* Schauroth—Bittner: p. 571
1909 *Encrinus*? *radiatus*—Bather: p. 15–16
1909 *Balanocrinus radiatus* (Schauroth)—Bather: p. 16
1977 *Balanocrinus*—Głuchowski: p. 73, fig. 1m
1979 *Laevigatocrinus radiatus* (Schauroth)—Klikushin: p. 89, fig. 1

1982 *Laevigatocrinus radiatus* (Schauroth, 1859)—Klikushin: p. 302
1983 *Encrinus*? *radiatus* Schauroth, 1859—Hagdorn: p. 360, fig. 5
1985 "*Encrinus" radiatus*—Hagdorn: p. 250, figs. 1, 7–9
? 1986 *Laevigatocrinus radiatus* (Schauroth, 1859)—Klikushin: p. 103, pl. 34, fig.7
v 1986 "*Encrinus*" ? *radiatus* Schauroth, 1859—Hagdorn: p. 718, pl. 4, figs. 11–14
1992 *Laevigatocrinus radiatus* (Schauroth)—Klikushin: p. 90
v 1993 *Eckicrinus radiatus*—Hagdorn and Głuchowski: p. 170–171, 174–175, fig. 8.5
v 1996 *Eckicrinus radiatus* (Schauroth, 1859)—Hagdorn et al.: p. 62–64, figs. 5, 6; pl. 5 figs. a–u
v 1997 *Eckicrinus radiatus* (Schauroth, 1859)—Hagdorn et al.: p. 401–402, pl. 2, figs. f–j, pl. 3, fig. h
2001 *Eckicrinus*? cf. *radiatus* (Schauroth 1859)—Stiller: p. 313
2002 *Eckicrinus*? cf. *radiatus* (Schauroth 1859)—Stiller: p. 35
2005 *Eckicrinus*? *radiatus* (Schauroth 1859)—Głuchowski and Salamon: p. 87, figs. 3k–l
v 2011a *Eckicrinus radiatus* (Schauroth)—Hess (2011a): p. 25–26, figs. 7.2a–f
2017 *Eckicrinus*—Stiller: p. 296
2018 *Eckicrinus*—Hagdorn: p. 5
2019 *Eckicrinus* cf. *radiatus* (Schauroth, 1859)—Stiller: p. 556, fig. 5a–e

Lectotype. Isolated internodal NMC 2682-L designated by Hagdorn et al. (1996), from Sasso della Limpia near Recoaro (Vicentinian Prealps, Italy); Recoaro Formation, Middle Triassic, Anisian, Pelsonian; Schauroth (1859: pl. 1, fig. 4), Hagdorn et. al. (1996: fig. 5a); fig. 1a.

Diagnosis. As for genus.

Material. Recoaro Formation, Recoaro, Italy, NMC 2682-L (lectotype) and NMC 2682-P (paralectotype); 5 columnals and pluricolumnals IGPT 1623/7–1623/8, 1623/10–1623/12; 33 columnals and pluricolumnals MHI 1266/1/1–1266/1/33. Recoaro Formation, Kühwiesenkopf, Prags Dolomites, Italy: 6 columnals and pluricolumnals, MHI not catalogued. Recoaro Formation, Mte. Rite in Cadore, Italy: 3 columnals, MHI 2185. Recoaro Formation, Felsőörs, Balaton Upland, Hungary: 110 columnals and pluricolumnals, MHI 1559/1–1559/110. Vászoly Formation, Öskü, Balaton Upland, Hungary (cf. Budai et al. 2001): 21 columnals and pluricolumnals, MHI 1799/1/1–1799/1/21. Bertalanhegy and Kozór formations, Mecsek Mts., Hungary: 3 columnals, MHI 1561/271–1561/273, 1563/7. Lima striata Formation, Holy Cross Mountains, Poland: MHI 1164/1/1– 1164/1/4 and some 400 uncatalogued columnals and cirrals. Górażdże Formation, Upper Silesia, Poland: 5 columnals MHI 1257. Dziewkowice Formation (Terebratula Beds), Upper Silesia, Poland: 4 columnals MHI 1163/2. Karchowice Formation, Upper Silesia, Poland: radicular holdfast, BGR X 13379; some 130 columnals and pluricolumnals, GIUS 7–43, 5/3, MHI 1263/3, 1264/2, 1267/3. Jemielnica Formation (Diplopora Dolomite), Upper Silesia, Poland: 18 columnals GIUS 7–59-9, 13, GIUS 7–514, GIUS 7–517.

Description of BGR X 13379. The 22-mm-long pluricolumnal comprises 23 very low circular columnals among which 7 bear up to 5 cirrus sockets or cirrus fragments. The pluricolumnal tapers from 7.3 mm at its wider end to 3.8 mm. The multiradiate articular facet of the wider (internodal) columnal (Figs. 5f, 6b) is finely crenulated with culmina originating at a narrow areole. At one side, the crenulation is indistinct, probably caused by abrasive preparation. Towards the periphery the crenulation is augmented by multiple bifurcations and intercalations of additional culmina. The outline of the areole is indistinctly petaloid. The axial canal is also indistinct, possibly due to diagenetic calcite accretion. The articular facet of the internodal columnal at the thinner end (Figs. 5g, 6d) shows the typical petaloid *Eckicrinus* pattern with five granulated radial bands originating from a slightly raised perilumen surrounding the narrow axial canal. The pyriform petals are sunken; the petal floors are smooth. The slightly widening radial bands merge into fork- or V-shaped culmina that reach the periphery. Each interradial petal area is limited at the periphery by five to six culmina of almost equal length. In side view, the intercolumnal suture lines are indistinct, mostly smooth and only discontinuously finely crenulated (Figs. 5a–e; 6a, c). There is no discernable difference between internodal and lower nodal suture lines. Internodal and nodal latera are slightly inflated. Each second or third internodal is followed by a cirriferous nodal. Generally, the nodals are only slightly higher than the internodals. The nodals bear up to five cirrus sockets of extremely variable size. Depending on the cirrus size, nodal heights are further increased at larger cirrus sockets. The sockets of the largest cirri even extend over the neighbouring internodals. Hence, the cirrinodals are not evenly disc shaped but thickened at the larger cirrus sockets, and neighbouring internodals are thinner, respectively. Along the pluricolumnal latera, the cirri are arranged in five radial successions or sequences with the large cirri bending uniformly to one direction. Not each of the seven nodals shows the full number of five identifiable cirri but the cirrus number varies from one to five. The cirri differ considerably in shape and size, ranging between 0.5 mm wide indistinct circular scars or bud-like knobs, up to large articulated cirri with multilateral facets. Only in one radial succession or row the maximum cirrus number of seven is reached (one cirrus bud-like; Figs. 5b, c; 6a, c), in the other rows only three, four, or five cirri are discernible; among these are also small bud-like cirri with indistinct articulation patterns (Fig. 5a–d, 6a, c). The larger cirrals are up to 3.8 mm wide and 0.5 mm high. Up to seven cirrals are preserved in an individual cirrus. Hence the total length of a cirrus remains unknown. The articulation facets of the large cirrals are multiradiate with a slightly raised perilumen surrounding the narrow, circular axial canal (Figs. 5b, 6a–c). The longest culmina originate close to the perilumen; additional culmina can be intercalated towards the periphery. The large articulated cirri are uniformly bending to one direction. One cirrus succession lies opposite to the general cirrus bending direction.

Occurrence. Middle Triassic, middle Anisian (Pelsonian to Illyrian) of western Palaeo-Tethys (Italy, Hungary), eastern part of Central Europaean Basin (Poland: Silesia, Holy Cross Mountains). The pluricolumnal of *Eckicrinus* cf. *radiatus* reported by Stiller (2019) from the early late Anisian Shizishanjiao Member (lower Longtou Formation) of Southwest China proves the occurrence of this genus in the eastern Palaeo-Tethys. The impression of a circular columnal from the Ladinian of the Chabarowsk region (Amur Basin, Siberia) described as *Laevigatocrinus radiatus* by Klikushin (1986: 103, pl. 34, fig. 7) is too poorly preserved to be assigned to any crinoid taxon.

Remarks on BGR X 13379. Eck (1865) already stated that the pluricolumnal is a terminal stem fragment and the cirri are radicular attachments (‘Wurzelranken’). He also assumend that the column tapers terminally and the thinner end is distal. The enlarged cirri of BGR X 13379 were obviously bending towards a substrate that has not been preserved and remains unidentified. Similar but less illustrative *Eckicrinus* pluricolumnals have been described earlier by Hagdorn et al. (1996: figs. 6a, B) and induced Hagdorn (2011: fig. 11) to assume a ‘creeping root attachment’ for this incompletely known crinoid. The specimens figured by Quenstedt (1876: pl. 107, figs. 86 and 87) are pluricolumnals with partly enlarged cirrus scars sheathed by callus of neighbouring internodals (Fig. 1e) and with two enlarged cirrus scars that extend over the neighbouring internodals and cause an irregular columnal mosaic (Figs. 1f, 7d). Additional pluricolumnals with both bud-like and enlarged cirri were found at Öskü (Balaton Upland, Hungary; Figs. 1o, p; 7a, b). In Figs. 1o, 7a, one of three enlarged cirri is also sheathed by callus of the neighbouring internodals. The pluricolumnal with a corroded surface (Figs. 1p, 7b) has enlarged unidirectional cirri. Likewise, the pluricolumnal Figs. 1i, 7c from Recoaro shows strongly enlarged cirri with multiradiate facets pointing at one direction. Discoid or incrusting holdfasts of the encrinid type that could be assigned to *Eckicrinus* have not been found.

Hence, there is enough evidence to assume that adult *Eckicrinus* individuals were rooted by radicular cirri corresponding to the ‘rhizoidal holdfasts’ or ‘rhizoids’ in the terminology suggested by Brett (1981). Similar roots with pseudocirri or simple callus extensions (‘stolons’ Brett 1981) are common among Palaeozoic reef dwelling crinoids that clung to solid substrates, e.g., corals, and for the Ladinian/Carnian pseudoplanktonic Traumatocrinidae that were attached to driftwood logs by similar pseudocirri (Hagdorn and Wang 2015). Compared to Encrinidae and Holocrinidae, *Eckicrinus* columnals are rare in the sponge and coral reef palaeoenvironment of the Karchowice Formation in Upper Silesia (Bodzioch 1989; Morycowa and Szulc 2010; Matysik 2016, Hagdorn et al. 2021) with abundant skeletal bivalve, coral, and sponge substrates that would have allowed *Eckicrinus* to cling and to hold a favourable filtration position. The relative rarity of *Eckicrinus* columnals may be indicative of a short column or the fact that columnal accumulation after repeated shedding of distal stem parts as in *Holocrinus* (Baumiller and Hagdorn 1995) can be excluded for *Eckicrinus* with its rhizoid root. However, rhizoid roots of adult *Eckicrinus* do not necessarily exclude a primary early postlarval attachment by a discoid holdfast as documented in living comatulids (Mortensen 1920). If so, the rhizoidal holdfast would be secondary.

General remarks. Contrary to earlier opinions (see above), assignment of *Eckicrinus* to Holocrinidae or Encrinidae and Dadocrinidae is improbable because of the multiradiate cirrus articulations and the presence of radicular cirri in the distal column, respectively. Moreover, *Holocrinus* has pentagonal to subcircular columnals with nodals wider and higher than internodals, long motile cirri with oval cirrals articulating with synarthrial facets, and more internodals per internodium than *Eckicrinus* (Fig. 8). Lateral sheathing overgrowth of cirri by neighbouring internodals, which would restrict cirrus motility, has not been observed in Holocrinidae. Encrinidae and Dadocrinidae have no cirri in distal column, and cirri in the proximal column of some Encrinidae are rudimentary, if present at all (see below and Fig. 8). Hence, until complete individuals or definitely assignable cup and arm ossicles become available, family Eckicrinidae cannot be assigned to a specific order of subclass Articulata. Similar facet patterns with long crenulae and cirrus sockets extending to adjacent columnals in *Entrochus insignis* Toula, 1877 and *Austinocrinus* depend on their general low and circular columnal shape and are regarded convergent (Hagdorn et al. 1996; Hess 2011a). The irregular pseudocirri in the rhizoid roots of the pseudoplanktonic Traumatocrinidae (Hagdorn and Wang 2015) are callus extensions ensheathing the intercolumnal fossulae and not homologous with the five true radial cirri of *Eckicrinus* nodals.

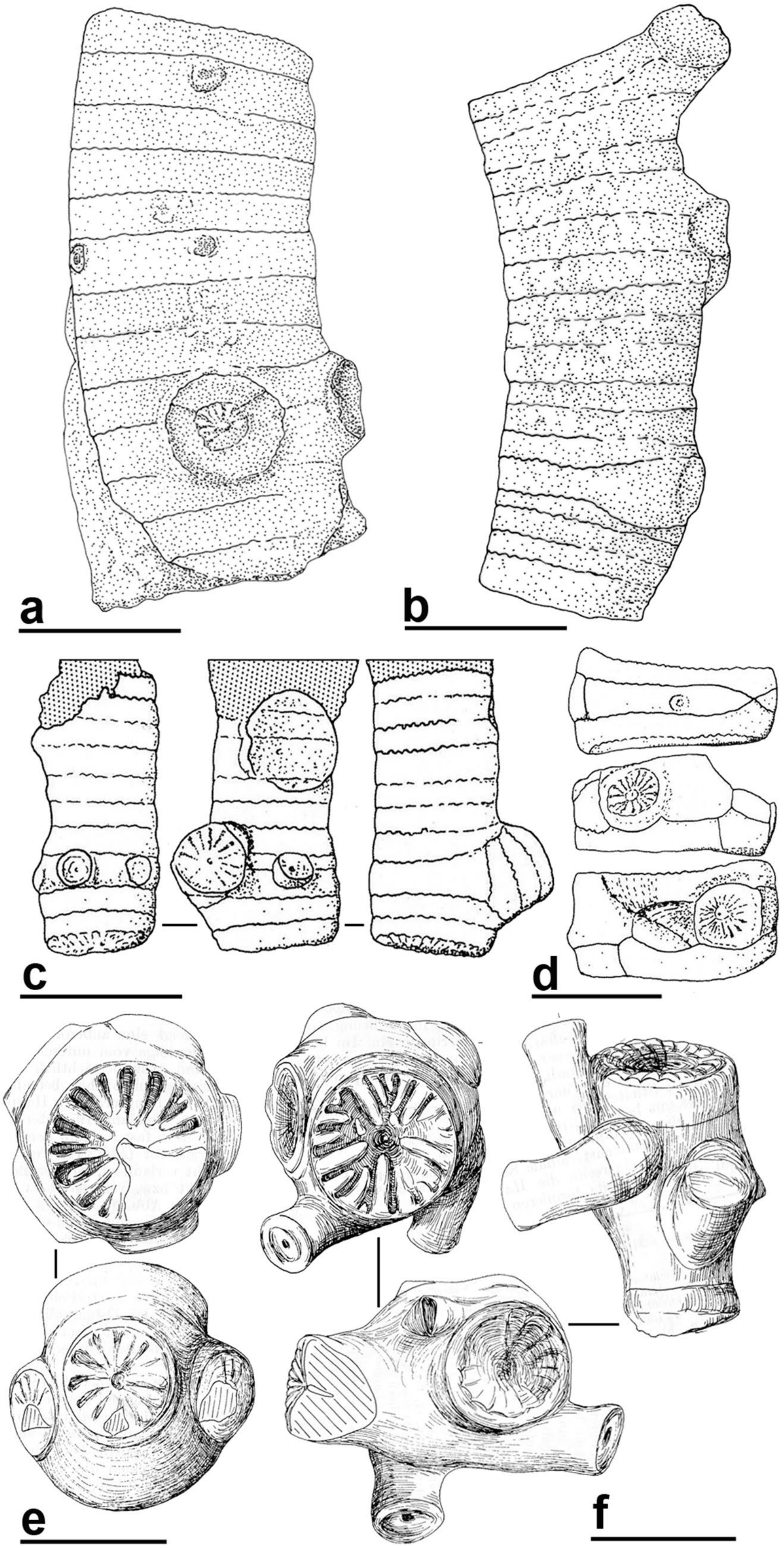

Fig. 7 Sketch drawings of *Eckicrinus* and *Tollmannicrinus* distal pluricolumnals with enlarged cirrus sockets. **a**–**b** Vászoly Formation (Avisianum subzone, late Anisian, Illyrian), Öskü (Veszprém-Plateau, Hungary). **a** Distal pluricolumnal, nodals with small indistinct and two enlarged cirrus scars, callus-sheathed by neighbouring internodals, MHI 1799/1/1, see also Fig. 1o; **b** slightly corroded distal pluricolumnal, nodals with enlarged cirri pointing to one direction, MHI 1799/1/2, see also Fig. 1p. **c**–**d** Recoaro Formation (Anisian, Pelsonian), Recoaro (Vicentinian Prealps, Italy). **c** distal pluricolumnal, nodals with circular cirrus scars two of which strongly enlarged with multiradiate articulations, MHI 1266/1/1, see also Fig. 1i; **d** distal pluricolumnal, nodal with small indistinct and two enlarged cirrus scars with multiradiate articulations, GPIT Quenstedt collection, Quenstedt (1876: pl. 107, fig. 84), see also Fig. 1f. **e**–**f** *Tollmannicrinus saklibelensis*, Hallstätter Kalk (Ladinian, Longobardian), Saklibeli (Taurus, Turkey), from Kristan-Tollmann (1975: figs. 14,1 and 13,3); **e** terminal stem part with multiradiate cirrus sockets, axial canal at lower nodal facet closed, probably due to regeneration; **f** terminal stem part, nodal with indistinct cirrus sockets and cirrus fragments. *Scale bars* 5 mm (a–d), 0.5 mm (e–f)

Eventually, there are three cases of unusual cirrinodals to be discussed.

(1) Tollmannicrinus saklibelensis (Kristan-Tollmann, 1975)—Three very small cirrinodals processed by acid from late Ladinian Hallstatt Limestones of Saklibeli (Taurus Mountains, Turkey) and described as *Entrochus saklibelensis* were regarded to be terminal (Kristan-Tollmann 1975). The line drawings (photographic documentation is not existent) show two irregular cirrinodals that were allegedly followed by a simple smooth terminal root ('einfache glatte Wurzel', Kristan-Tollmann 1975: 298, figs. 13,1 and 13,3a–c; the latter is herein reproduced in Fig. 7f). The distally rounded nodal with the axial canal closed and multiradiate cirrus facets (Kristan-Tollmann 1975: fig. 14,1 and herein reproduced in Fig. 7e) is described as a presumably regenerated terminal columnal ('regeneriertes Stielende'). This nodal induced Klikushin (1992: 73, fig. 92a) to reconstruct his new genus *Tollmannicrinus* (type species *T. saklibelensis*) with such a terminal column. Columnals of *Tollmannicrinus* differ from *Eckicrinus* in all characters except the multiradiate cirrus facets of Kristan-Tollmann's fig. 14,1a–b. *Tollmannicrinus saklibelensis* shares with *Holocrinus* the pentagonal proximal columnals, which become circular towards the dististele, long internodes, and regularly oval to circular cirrus scars with synarthrial articulations. The articulation pattern differs from *Holocrinus* in its narrow star-shaped areoles, which become indistinct in dististele, and sets of radial culmina originating at the areole. Stiller (2019) who described a slightly older (middle Anisian) species of *Tollmannicrinus* from the Qingyan Formation of Qingyan (Guizhou, Southwest China), erected the new family Tollmannicrinidae, however, without adding new data of the terminal column. It should be mentioned that the rare and incompletely known early Carnian *Pentacrinus venustus* ? Klipstein, 1843 and *Isocrinus apetalus* Zardini, 1976 from the Cassian Formation of the Dolomites have articulation facets resembling the *Tollmannicrinus* pattern. The cirrus articulation of *P. venustus* is multiradiate, and both taxa have synostosial lower nodal facets, a character diagnostic of Isocrinidae.

(2) Qingyanocrinus kueichounensis (Dubatolova and Shao, 1959)—According to Stiller (2000), the column of this Anisian crinoid from Southwest China has nodals with one to five circular cirrus sockets in the entire column. The larger cirrus sockets are crenulated around the lumen. The column terminates in a rhizoid holdfast with successive cirrinodals. The crown is unknown. Stiller (2000) erected the genus *Qingyanocrinus* and the family Qingyanocrinidae of uncertain order (see also Hess 2011c). In its rhizoid holdfast *Qingyanocrinus* resembles *Eckicrinus* but the columnal articulation pattern of short and coarse multiradiate crenulae surrounding a granulated perilumen devoid of a petaloid pattern is rather encrinid. Nevertheless, Qingyanocrinidae give evidence of a second Middle Triassic crinoid group attached by a rhizoid holdfast.

(3) Crinoidea fam. indet.—Among the Early Triassic (Olenekian, (early ?) Spathian) crinoid material from Hallstatt Limestones of Timor mentioned by Hagdorn (2018) is one exceptionally high columnal with three large multiradiate cirrus sockets (Fig. 2e). Evidence of the columnal facet pattern suggests its allocation to abundant column material from the same rock sample, which is characterized by relatively large, low, circular columnals with small pyriform petals in proxistele and long, bifurcating crenulae in dististele (Figs. 2a–d), and discoid holdfasts with the same pattern (Fig. 2f). The columnal articulation facets resemble *Eckicrinus* but the material does not comprise proximal nodals with cirrus sockets. The mixed characters point at possible relations to Encrinida (discoid holdfasts) and Eckicrinidae (columnal articulation patterns).

Hence, the incomplete and inconsistent character mixture of Eckicrinidae and the as yet unnamed Timor crinoid do not allow unequivocal assignment to specific orders. *Eckicrinus* clearly differs from *Holocrinus* and *Tollmannicrinus* in its rhizoid holdfast and the above described column characters, respectively, which suggest the erection of the new family Eckicrinidae.

Discussion

Attachment modes

The rhizoid terminal pluricolumnals of *Eckicrinus* indicate functional cirrus modifications in distal nodals. Obviously, the bud-like cirri remained small and rudimentary as long as they assumed no attachment function. In the terminal column, contact with a solid object was likely to trigger boosting growth of those cirri closest to the substrate thus enabling the crinoid to tightly cling while other cirri remained small and devoid of attachment function. Other than branching rhizoid roots that anchor crinoids in soft bottoms, the enlarged cirri of *Eckicrinus* uniformly pointed towards a solid substrate. In other words, the hypothesized precondition of a rhizoid root was the presence of nodals with 'sleeping' cirri along the entire column, independently of the overall column length, which, however, is unknown. In terms of functional morphology, for tight and permanent attachment, the inflexible multiradiate cirral articulation was more advantageous compared to the motile synarthrial articulation of Holocrinida. The available *Eckicrinus* material does not comprise discoid or incrusting holdfasts. Hence, it remains speculative whether or not the rhizoid root is primary or secondary after loss of a hypothetical discoid holdfast of juvenile individuals. The latter hypothesis is here favoured.

The much better known Encrinidae and Dadocrinidae were permanently anchored by a discoid or incrusting holdfast (Hagdorn 1978, 1996). In some populations of the less advanced *Encrinus aculeatus, E.* cf. *E. brahli*, and *Chelocrinus schlotheimi,* proximal nodals may have cirri, which, needless to say, are devoid of attachment function (Hagdorn 1982; Hagdorn et al. 1996; Hagdorn and Schulz 1996). Discoid and rhizoid holdfasts allowed permanent and solid fixation to various skeletal substrates. However, after traumatic column fracture, encrinids and dadocrinids were unable to re-attach and hence to erect their crowns above the seafloor to attain an advantageous feeding posture. Other than these, *Eckicrinus* was hypothetically able to re-anchor by activation of 'sleeping' cirri at the new post-fracture terminal column.

In the Holocrinida–Isocrinida lineage, the attachment function is ensured by nodals with whorls of five large cirri articulating to oval cirrus sockets with a transverse ridge. Such synarthrial articulations allow cirrus motility and active grasping of objects, aided by a terminal claw-like cirral. Discoid holdfasts in an early postlarval stage of extant comatulids ('Pentacrinus stage', e.g., Mortensen 1920) likewise suggest secondary cirrus-attachment after loss of a discoid primary holdfast for the ancestral Holocrinidae. The preformed rupture points ('Sollbruchstellen') below the nodals developed by Holocrinidae, automatically placed a cirrus whorl to the column end after autotomy (Hagdorn 1983; Baumiller and Hagdorn 1995). Traces in the sediment left by *Holocrinus* arms indicate slow locomotion aided by muscular brachial articulations (Gorzelak et al. 2020) that allowed for locomotion before re-anchoring as observed among their extant isocrinid descendants.

To sum up, among Early and Middle Triassic benthic crinoids three basic attachment modes existed, represented by different lineages (Fig. 8).

(1) Discoid holdfast lineage—Permanently tight fixation by a discoid or incrusting holdfast that maintained the primary postlarval attachment. After traumatic column rupture, such a crinoid was unable to re-attach. Such holdfasts are typical for crinoids settling on hardgrounds and coarse shelly sea floors that provide suitable skeletal substrates for larval attachment. Clusters of incrusting holdfasts even acted as frame-builders consolidating bivalve-encrinid bioherms, e.g., in the Upper Muschelkalk Trochitenkalk Formation (Hagdorn 1978; Hagdorn and Ockert 1993). In the Middle Triassic, Encrinidae, Dadocrinidae, and Bangtoupocrinidae maintained this attachment mode, later on also Millericrinida and Cyrtocrinida, and the Extant Hyocrinida. Some Late Jurassic Millericrinida enlarged and modified their holdfasts to allow anchoring in softground environments (Seilacher and MacClintock 2005).

(2) Rhizoid holdfast lineage—Attachment by a rhizoid holdfast with true radicular cirri that clung permanently to skeletal substrates. In Middle Triassic times, this mode was performed by *Eckicrinus* and *Qingyanocrinus*. *Eckicrinus* inhabited coral-sponge and bivalve-encrinid bioherms, e.g., in the Lower Muschelkalk Karchowice Formation. The radicular cirri of *Eckicrinus* are regarded secondary after a hypothetical postlarval discoid holdfast stage. In *Tollmannicrinus saklibelensis* and the undescribed Early Triassic crinoid from Timor (Figs. 7e, f; 2e), radicular cirri are rather exceptional and hard to assess. Long and branching radicular rhizoids allowing anchoring in softgrounds are common and highly diversified among different Palaeozoic and—less common—in post-Palaeozoic crinoid clades (Seilacher and MacClintock 2005).

(3) Motile cirrus lineage—Actively grasping cirri with motile synarthrial articulations allowed temporary flexible attachment and re-attachment following autotomy of distal stem parts at preformed rupture points below the nodal. This mode is also regarded secondary after a presumed early postlarval discoid holdfast. The synarthrial cirrus articulation of Holocrinidae advanced in Isocrinina became the most successful attachment mode among Extant benthic crinoids (Baumiller and Hagdorn 1995; Janevski 2011). They gave rise to the eleutherozoic lifestyle, which originated in the Late Triassic Paracomatulidae (Hagdorn and Campbell 1993). Hess (2014) described Lower Jurassic comatulids, paracomatulids, and eocomatulids. However, according to genomic analyses Paracomatuloidea may not be nested in crown group Comatulida, the earliest fossil record of which is regarded Middle Jurassic by Rouse et al. (2013).

Phylogenetic implications

It has been generally accepted that all post-Palaeozoic crinoids belong to the subclass Articulata defined by a combination of characters, each of which, however, occurs also in other subclasses (Simms 1988, 1990; Hess 2011b). Simms and Sevastopulo (1993) identified several Middle to Late Palaeozoic cladid crinoids with characters of Articulata and proposed to treat them as stem group Articulata excluded from the post-Palaeozoic crown group Articulata. Webster and Jell (1999) rejected this decision and proposed to include the new Order Ampelocrinida into subclass Articulata. Discussing the coverage of Articulata and inclusion or exclusion of Ampelocrinida is beyond the scope of this paper, which follows the classification of the Revised Crinoidea Treatise (Hess et al. 2011a, b, c). The focus is here on possible phylogenetic pathways of the above discussed morphological characters of column and attachment structures. Among the nine morphological features characterizing primitive Articulata Webster and Jell (1999) specify 'cirri with multiradiate articula distally and transverse ridge articula proximally or cirri with transverse ridge articula throughout'. At first, disputed assignments of two poorly known crinoid genera have to be discussed.

(1) Webster and Jell (1999) described a single Early Permian (Artinskian) crinoid crown from West Australia as *Archaeoisocrinus occiduaustralis* and assigned it to Isocrinidae thus dating back the Order Isocrinida for at least 35 Ma. Arguing against the reportedly isocrinid characters of *Archaeoisocrinus* Twitchett and Oji (2005) and Hess (2011c) rejected its assignment to Isocrinidae. Isocrinidae are Middle Triassic offshoots of Holocrinidae with a dicyclic barrel-shaped cup with thick basal and radial plates enclosing a narrow body cavity and small upward directed radial facets. As demonstrated by Hagdorn (2011), the holocrinid cup transformed during the Middle Triassic to the

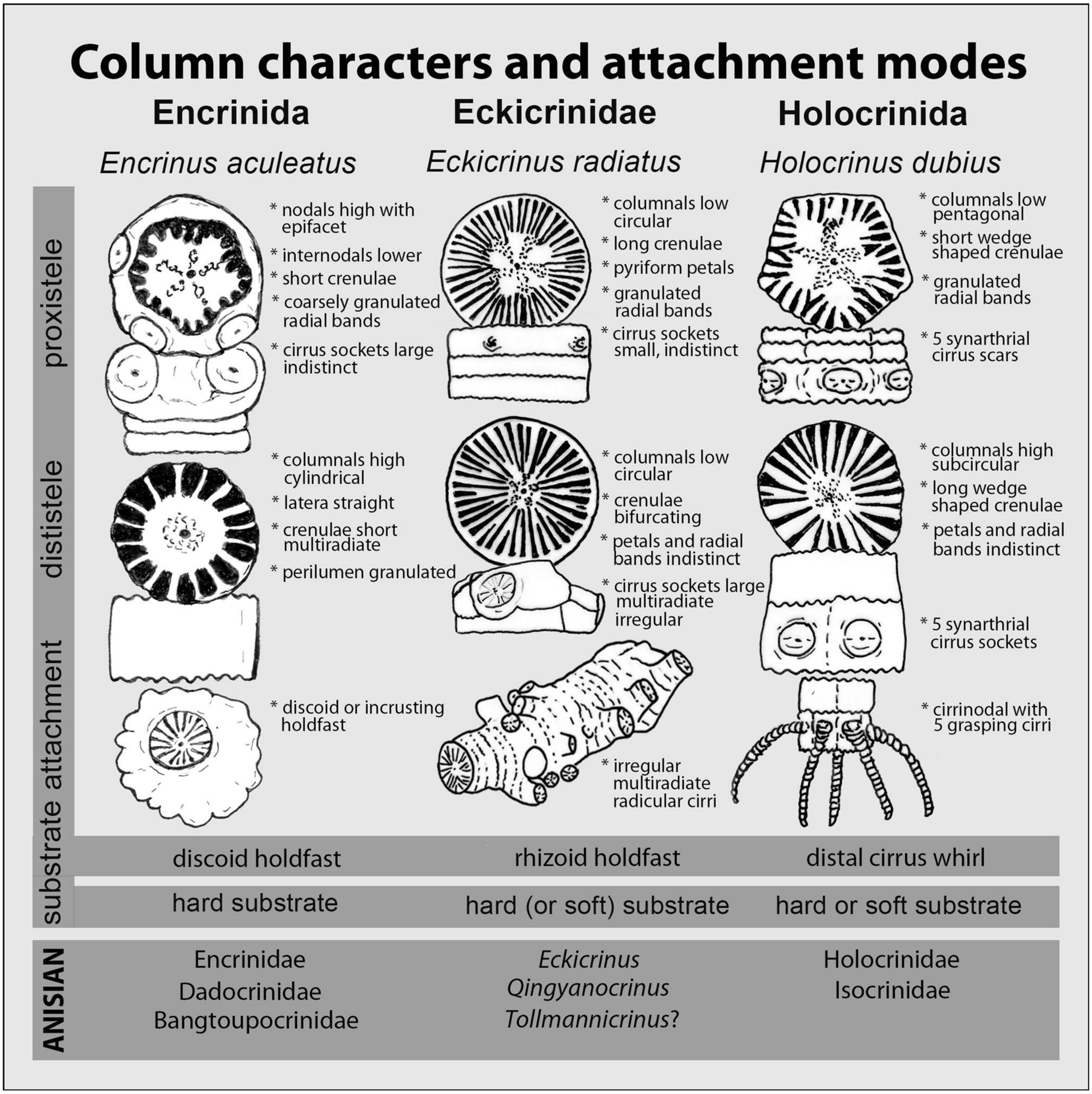

Fig. 8 Column characters provide evidence of three basic attachment modes among Middle Triassic (Anisian) benthic Crinoidea. Permanent attachment to hard substrate by a discoid holdfast is indicative of the Encrinida–Millericrinida lineage; the less advanced *Encrinus aculeatus* has still preserved rudimentary cirri in the proximal column proving descent from ancestors with a cirriferous column that terminated in a discoid holdfast. The rhizoid holdfast attachment by means of stout multiradiate cirri is documented for the otherwise incompletely known *Eckicrinus*. Whirls of motile cirri of the Holocrinida–Isocrinida lineage with grasping function allow repeated attachment to hard or soft substrates. Early post-larval attachment by a discoid holdfast is also inferred for Holocrinida and Eckicrinidae

cryptodicyclic low cone shaped isocrinid cup with basals visible in side view and wide and outward directed radial facets. Though, true isocrinid cups are not known prior to the latest Ladinian and early Carnian. Primibrachials and cup of *Archaeoisocrinus* with basals and possibly infrabasals concealed by sediment and deeply depressed in the column pit have neither isocrinid nor holocrinid affinities but rather resemble advanced encrinid cups and proximal arms. Hence, the Permian ancestor of the Holocrinidae–Isocrinidae lineage is still to be identified among Ampelocrinida with a throughout cirriferous column with synarthrial cirrus articulations and a dicyclic holocrinid-like cup.

(2) Oji and Twitchett (2015) described several isolated columnals extracted from an olistolithic block of Induan age (Griesbachian, *Isarciella isarcica* Zone) of Oman as *Baudicrinus krystyni* and assigned this genus to Dadocrinidae thus dating the Order Encrinida back to ca. 1 Ma after the extinction event. *Baudicrinus* is currently the oldest known post-Palaeozoic crinoid but cirrals with synarthrial articulations recovered from a second Griesbachian block from Oman, prove that *Baudicrinus* is, in fact, a holocrinid (Brosse et al. 2018). Hence, Holocrinidae remain the oldest verified clade of crown group Articulata. The assignment of *Baudicrinus* to Dadocrinidae induced Oji and Twitchett (2015) to discuss the evolution of Articulata. They conclude either a dramatic radiation in the immediate aftermath of the extinction, or multiple lineages of crown group Articulata that survived. Due to the poor fossil record, there is no strict evidence for either hypothesis.

However, the synarthrial cirral articulations of the earliest holocrinids and corresponding articulations among several Ampelocrinida (Webster and Jell 1999) constrain that this character is not a holocrinid synapomorphy but ancestral. Cirri with transverse ridges must otherwise have developed a second time separately. Other than cirri, the preformed rupture point in the holocrinid column below the nodal was likely a post-extinction adaptation, which was improved by isocrinids during the Middle Triassic. A suitable Permian ancestor of the Holocrinida has not yet been identified.

Although not verified for the earliest Triassic, the late Olenekian and early Anisian Dadocrinidae are the oldest known representatives of the Order Encrinida. They share discoid holdfasts with all other Encrinida. Their dicyclic or cryptodicyclic, high conical cup clearly differs from the holocrinid cup in its basals and radials with deep ligament pits, wide radial facets, and a more voluminous body cavity (Hagdorn 2011). Less advanced Encrinidae, especially juvenile and semiadult individuals, share these characters with the Dadocrinidae. Cirrinodals with indistinct articulations in the proximal column of such encrinids corroborate the descendence of Encrinida from a crinoid with a discoid holdfast and with cirri. The characters distinguishing Encrinida and Holocrinida were already developed in the Early Triassic (Smithian). For the time of the divergence, two scenarios are conceivable: (1) Encrinida descended from the holocrinid lineage prior to Smithan times either in the earliest Triassic or in the Late Permian. Hence, depending on the date of divergence, one or two lineages survived the extinction event. (2) Encrinida descended from a separate ampelocrinid Permian ancestor with a cirriferous column but attached by a discoid holdfast. In this case, more than one crinoid lineage passed the Permian–Triassic boundary. With respect of the short Early Triassic epoch the latter scenario is apparently more realistic (Fig. 9).

Genomic analyses of Extant Crinoidea by Rouse et al. (2013) revealed Isocrinida, Cyrtocrinida, and Hyocrinida as clades, with Isocrinida as presumable sister group of all other existing crinoids. The extant stalked Bourgueticrinina and Guillecrinina are nested among the Comatulida the fossil record of which goes back to the Middle Jurassic. Molecular clock analyses suggest 231–252 Ma in the Middle to Early Triassic for the most recent common ancestor of Articulata (Rouse et al. 2013). This data are in accordance with the fossil record of the basic divergence of Articulata in a cirrus lineage and a holdfast lineage prior to late Early Triassic. The molecular data support this scenario, assuming that the Cyrtocrinida are offshoots of the extinct Millericrinida and these be rooted in the discoid holdfast lineage Encrinida.

As delineated above, discoid holdfasts and rudimentary cirri are documented for Middle Triassic Encrinidae and discoid holdfasts inferred for early post-larval stages of cirrus-attached Holocrinidae. Hence, Encrinida maintained the ancestral holdfasts and reduced cirri to rudimentary appendages in proximal nodals devoid of attachment function (less advanced Encrinidae) or lost them entirely (Dadocrinidae). Holocrinida lost the inferred postlarval holdfasts maintaining cirri throughout the column and adapting them for temporary attachment.

The origin of Eckicrinidae and its systematic position remains even more obscure because of its unknown crown morphology. Its rhizoid holdfast suggests descent from Ampelocrinida with multiradiate distal cirri rather than a Triassic offspring from either Holocrinida or Encrinida. The column of the Late Permian (Wuchiapingian–Changhsingian) *'Cyathocrinites' ramosus* from the Zechstein reefs of Thuringia and North England (Schlotheim 1820; King 1850; Geinitz 1861; Spandel 1898) resembles *Eckicrinus* in general appearance. From the British Ford Formation reef facies of the Zechstein Cycle 1 Donovan et al. (1986) re-described this crinoid, which, however, differs from *Cyathocrinites* s. s. and could not be assigned to a taxon below order level. With *Eckicrinus,* it shares the low circular columnals and cirrinodals with indistinct small and large multiradiate facets. The columnal articulations are multiradiate, but the axial canal is wider and the numbers of internodals per internodium

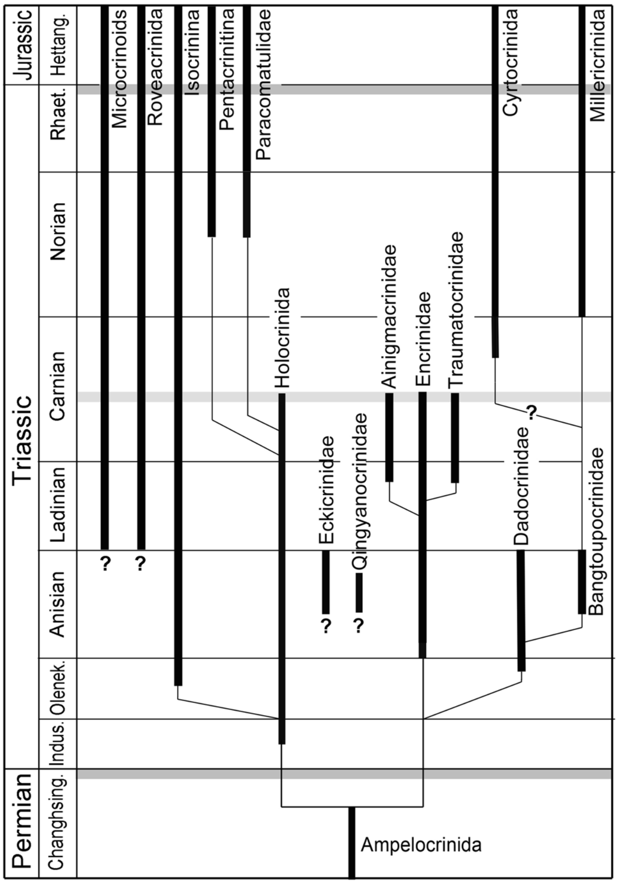

Fig. 9 Stratigraphic ranges (thick lines) and inferred phylogenetic relations (thin lines) of the Triassic Crinoidea. Regarding the short Early Triassic epoch of less than 5 Ma the divergence of the Holocrinida and Encrinida lineages is suggested in the Late Permian rather than in the earliest Triassic. The insufficiently known Eckicrinidae and Qingyanocrinidae, respectively, could be offsprings of Early Triassic Holocrinida or Encrinida, possibly also of a separate lineage of Late Permian Ampelocrinida. Grey bars: end-Permian and mid-Carnian extinction events. Modified from Hagdorn (1995)

are irregular but always higher than in *Eckicrinus*. Interestingly, there is evidence for discoid holdfast attachment of juveniles (Spandel 1898: pl. 12, fig. 20 and Donovan et al. 1986: pl. 71, fig. 4). The cryptodicyclic cup of *'C.' ramosus* is broad bowl-shaped with wide radial facets resembling a juvenile encrinid cup but has an anal X incorporated in the CD interray. With its rhizoid cirri, which may be incrusted by bryozoans, *'C.' ramosus* was anchored in the Zechstein bryozoan reefs of Thuringia (Schlotheim 1820). However, it was not necessarily ancestral of *Eckicrinus*. Well oxygenated seamounds in tropical areas of the central or eastern Tethys were certainly more suitable environments for crinoids to survive the Permian–Triassic crisis (Oji and Twitchett 2015) and to produce crinoidal limestones thus contributing significantly to the biomass (Brosse et al. 2018).

The hypothetical phylogenetic scenarios of crown group Articulata are far from being fully understood. Hence, the search for crinoid remains along the Permian–Triassic boundary must be continued and even dissociated ossicles can contribute to better understanding the early phylogeny of crown group Articulata. Suitable boundary sections that yielded unidentified crinoid remains have been listed by Klikushin (1987) and Twitchett and Oji (2005).

Conclusions

As long as the incomplete fossil record of many Triassic crinoids obscures the phylogenetic relations, their systematic positions remain debatable. Convergently developed morphological similarities may furthermore hamper completing this puzzle with so many pieces lacking. Nevertheless, among Middle Triassic crinoids terminal column morphologies indicate three different attachment strategies persisting in different extant Articulata. The discoid holdfast attachment of many Palaeozoic crinoid clades was also most successful in the Mesozoic as long as they preferentially inhabited shallow water environments with biohermal structures (Encrinida–Millericrinida). Even more successful up to the present is the temporary attachment to various substrates by actively grasping cirri with synarthrial articulations combined with preformed rupture points at lower nodal facets that allow detachment and re-attachment (Holocrinida–Isocrinida). The third attachment strategy, in the Middle Triassic represented by *Eckicrinus* and *Qingyanocrinus* is by rhizoid holdfasts with stout radicular cirri. This strategy allowed anchoring by clinging to solid objects and also rooting deep into soft substrates if cirri grew long enough to all directions for safely anchoring the crinoid. Regarding these attachment strategies, the fossil record suggests the descent of crown group Articulata from at least two different clades of Late Permian Ampelocrinida. A third lineage, represented in the Middle Triassic by the as yet unassigned family Eckicrinidae, could be derived in Early Triassic times from either Encrinida or Holocrinida, but possibly also from a Permian ancestor with rhizoid cirri.

The above presented data further contribute to challenging the mantra of an extreme bottleneck in echinoderm phylogeny. Thuy et al. (2017) already provided evidence of more than a single lineage of asteroids, ophiuroids, and echinoids that passed the Permian–Triassic boundary, which was documented in more detail by Hagdorn (2017) and Thompson et al. (2018). Moreover, the ophiocistioid teeth of Carnian age described by Reich et al. (2018) from the Cassian Formation of the Dolomites even prove the survival of a sixth echinoderm class until at least Late Triassic times.

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