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A new species of *Tiaracrinus* from the latest Emsian of Morocco and its phylogeny

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We describe a new species of the unusual crinoid *Tiaracrinus*, *T. jeanlemenni* sp. nov. from the latest Emsian of the famous mudmound locality Hamar Laghdad, Morocco. It differs from the previously known species in the higher number of ribs and the vaulted rib-fields, which is corroborated by the comparison of simple quantitative characters and ratios as well as by the results of a cluster analysis and a Principal Component Analysis. Based on the new material and the published specimens, we discuss the phylogeny of the genus and suggest that *T. oehlerti* and *T. moravicus* represent the ancestral forms of this small clade.

Key words: Crinoidea, mudmounds, phylogeny, morphometry, symmetry, Devonian, Morocco.

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Introduction

Palaeozoic echinoderms produced a wealth of unusual thecal morphologies, which are hard to interpret in terms of taxonomic assignment and/or functional morphology. Although this is particularly true for Early Palaeozoic clades (e.g., Sumrall and Wray 2007), it still holds true for some Devonian forms, for example pyrogocystid edrioasteroids (e.g., Bather 1915; Dehm 1961; Holloway and Jell 1983; Klug et al. 2008; De Baets et al. 2010), some crinoids (e.g., Schmidt 1934; Bohatý 2011) or late blastozoans (e.g., Dehm 1934; Rahman and Lintz 2012). Crinoids show their highest disparity in the Ordovician, but disparity remains high until the end of the Devonian (Foote 1995). Several areas of the Palaeozoic crinoid morphospace have not been reoccupied in the Mesozoic (Foote 1999).

In recent years, we have discovered the first two specimens of the genus *Tiaracrinus* in Morocco. This genus is usually thought to be restricted to Early (Lochkovian) to Middle Devonian (Eifelian; see Le Menn 1987; Prokop 1987; Haude 2008), but Kříž (1992) reported some in open nomenclature from the Late Silurian (Ludfordian). *Tiara-*

crinus is peculiar for the following reasons: (i) the calyx shows a tetramerous symmetry; (ii) so far, it has not been found with arms, although some unusual arm structures have been assigned to the genus (see further); (iii) the theca has four fields with epispines, giving it a blastozoan appearance.

Species of *Tiaracrinus* based on calices were first described in the 19th century. Schultze (1866) introduced the genus with the type species *T. quadrifrons* in his monograph on the Middle Devonian echinoderms from the Eifel Mountains. Soon thereafter, two more species of *Tiaracrinus* were described, *T. oehlerti* Schlüter, 1881 and *T. rarus* (Barrande, 1887). In the 20th century, two additional species were published based on calices, *T. tedraedra* Jaekel, 1901 and *T. moravicus* Ubaghs and Bouček, 1962. Two species based on limbrachoids, unusual arm structures, have been recently assigned to *Tiaracrinus* with some reservation (*T. ? obtusibrachialis* Haude, 1993 and *T. ? aceribrachialis* Haude, 1993). Hauser (2008: 1) listed the latter two species as *nomen dubium*. Additional specimens in open nomenclature were reported from the Ludfordian, Lockovian, Pragian and Emsian of the Czech Republic (Prokop 1987; Kříž 1992; Prokop and Petr 2002).

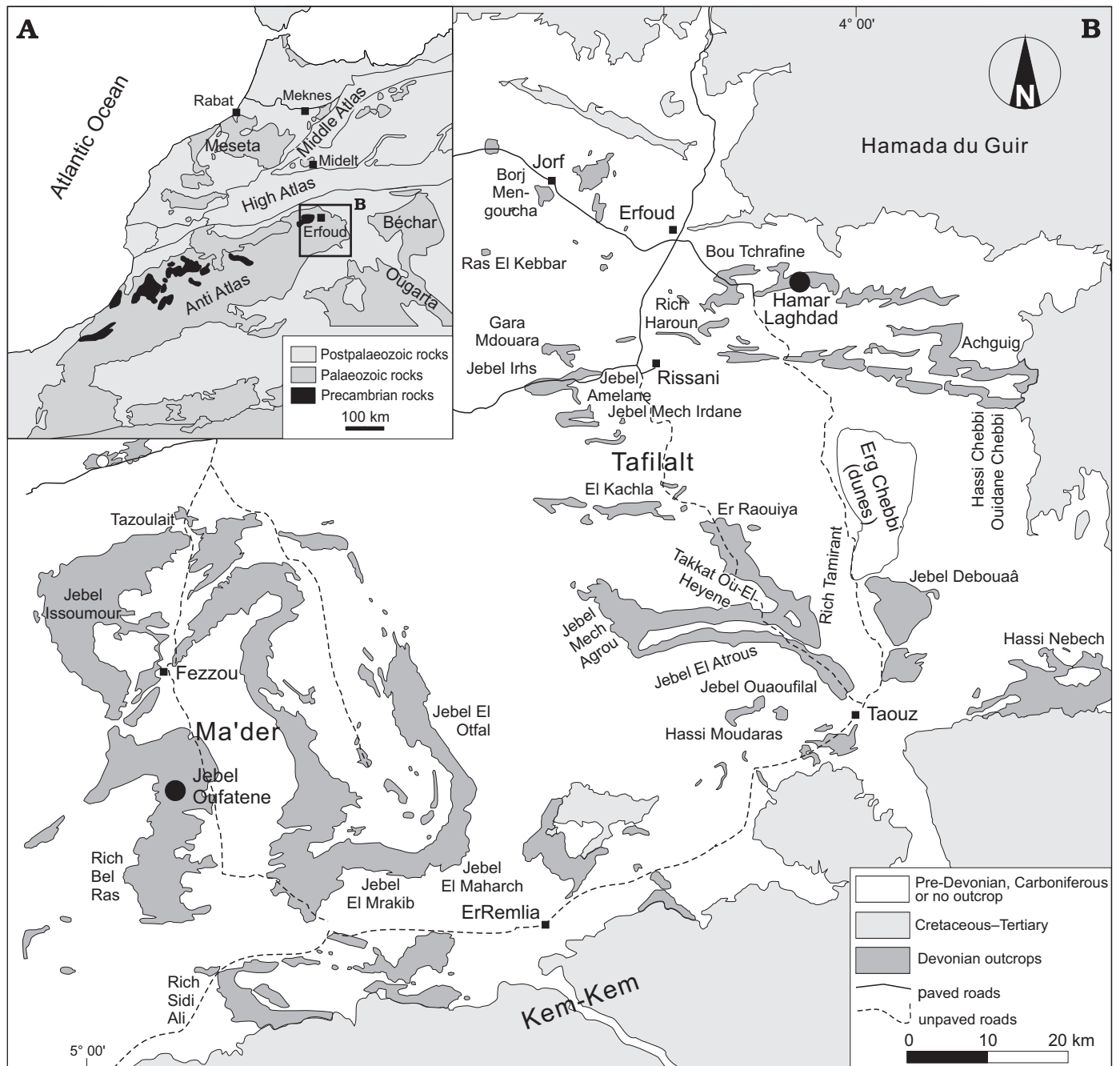


Fig. 1. Geological map (modified from Klug 2002) of the eastern Anti-Atlas showing the two localities that yielded *Tiaracrinus*.

In this study, we describe and illustrate the first two specimens of *Tiaracrinus* from the Early Devonian of Morocco. We discuss ontogenetic changes within this group as well as its phylogeny.

Institutional abbreviations.—GFCL, collection of D. Le Maître, Laboratoire de Géologie de la Faculté Catholique de Lille, France; LPB, Laboratoire de Paléontologie de Brest, France; PIMUZ, Paläontologisches Institut und Museum, Universität Zürich, Switzerland.

Other abbreviations.—PCA, Principal Component Analysis.

Material

So far, only two specimens of *Tiaracrinus* have been found in the Moroccan eastern Anti-Atlas by us. Both specimens are of latest Emsian age and were found at the southern edge of Jebel Oufatene (PIMUZ 29741) and at the “red cliff” in Hamar Laghdad (PIMUZ 29739; Fig. 1). Both specimens are stored at the Paläontologisches Institut und Museum at the University of Zurich. Both specimens (Fig. 2) are slightly corroded but well preserved otherwise. The specimen from Hamar Laghdad is slightly better preserved, probably due to

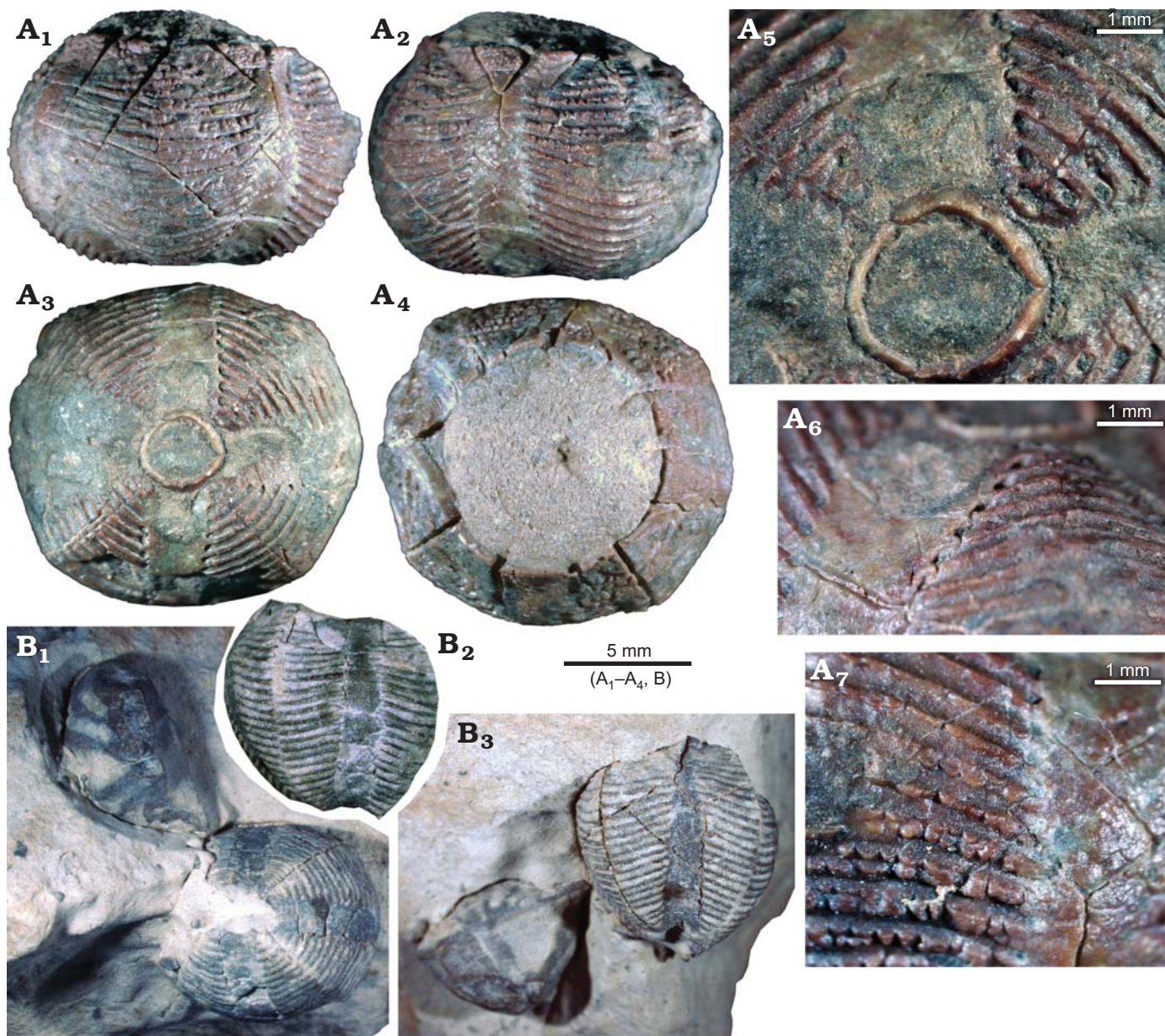
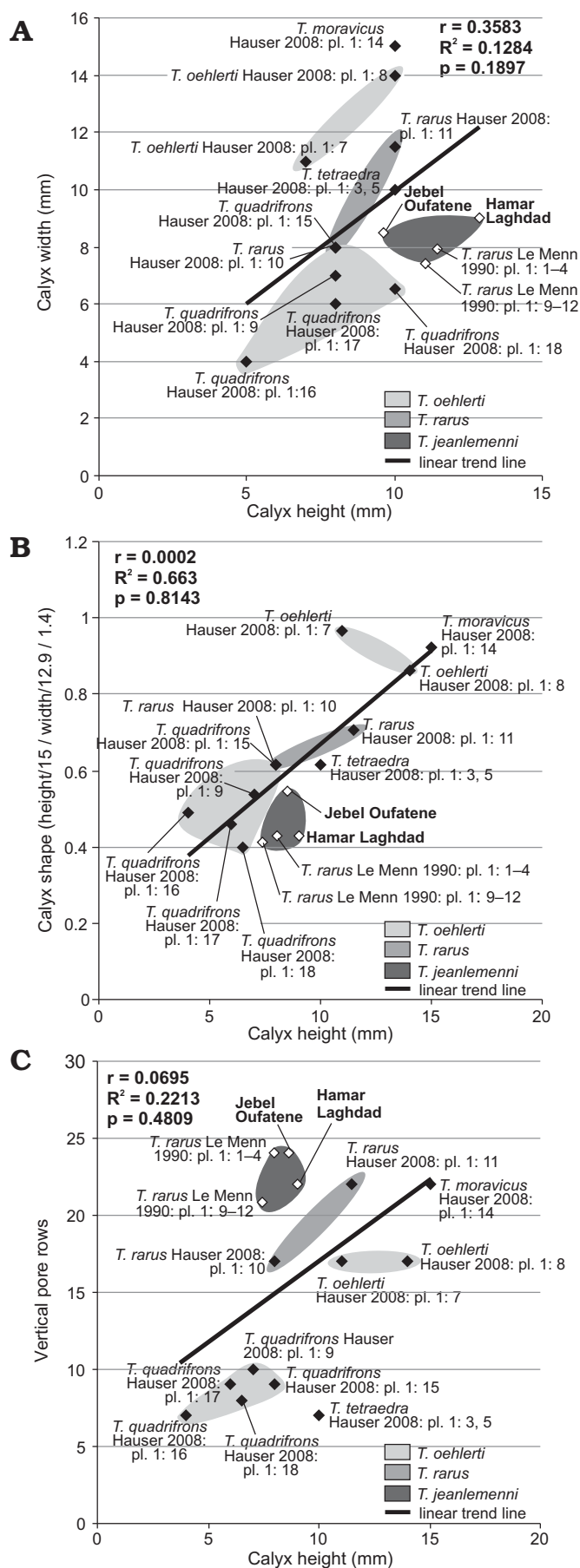


Fig. 2. Zophocrinid crinoid *Tiaracrinus jeanlemenni* sp. nov., probably late *Polygnathus patulus* Conodont Biozone, late *Anarcestes lateseptatus* Ammonoid Biozone, latest Emsian, Early Devonian, eastern Anti-Atlas Morocco. **A.** PIMUZ 29739, holotype, “Red cliff” at Hamar Laghdad, Tafilalt. Lateral views (A₁, A₂), showing the radial channel and the rib-fields; note the ornamentation in the channel near the oral surface in A₂. Aboral view (A₃), note the small cross section of the trimeral basals and the low rim around it. Oral view (A₄), note the ornamentation in the channel near the oral surface. Detail of A₃ (A₅), note the epispires and the uniform thickness of the ribs. On the top right, the subtle striation is faintly visible between the ribs. Oblique view of the aboral side (A₆), showing the epispires. Due to weathering, the ribs obtained a tuberculate ornament (A₇). **B.** PIMUZ 29741, paratype, Jebel Oufatene, Maïder. Aboral view (B₁), the rib-fields are less vaulted and the cross section of the calyx less quadrate than in the holotype; the fossil on the top left is a spiriferid. Lateral views (B₂, B₃), showing the narrow ribs and the smooth surface of the radial channels; in the lateral aspect it looks like the radial channel is tapering towards the oral side of the cup.

a partial silicification. Holdfast, stem, brachials, arms and oral plates are not preserved in both specimens.

PIMUZ 29739, the larger specimen, was collected from scree at the “red cliff” (Klug 2002; N 30.82453°, W 4.90210°) at Hamar Laghdad in the Tafilalt region. Hamar Laghdad is situated about 18 km ESE of the town Erfoud (Fig. 1). Hamar Laghdad has become world-renowned for its mud-mounds, some of which being completely exhumed, some others are

still more or less covered by the overlying sediments (e.g., Roch 1934; Massa et al. 1965; Hollard 1974; Alberti 1982; Brachert et al. 1992; Wendt 1993; Belka 1994, 1998; Bultynck and Walliser 2000; Aitken et al. 2002; Berkowski 2006; Cavalazzi et al. 2007). As far as palaeontology is concerned, this locality yielded highly diverse trilobite associations (e.g., Alberti 1969, 1982; Klug et al. 2009), abundant cephalopods (Töneböhn 1991; Klug 2001, 2002; Klug et al. 2009) includ-



ing ammonoids infested by parasites (De Baets et al. 2011) as well as many blastozoans, crinoids (sometimes encysting corals: Berkowski and Klug 2012), brachiopods, rugose corals specialised on vent habitats (Berkowski 2004, 2006, 2008, 2012, Belka and Berkowski 2005), locally favositids in rock-forming numbers and large bivalves (*Panenka*, *Patrocardia* and similar forms). The specimen PIMUZ 29739 was collected from marl containing limestone nodules and layers of latest Emsian age. These layers contain ammonoids of the genera *Amoenophyllites*, *Anarcestes*, and *Chlupacites* (Klug et al. 2009). Immediately below these marl beds, a claystone succession of late Emsian age is present, which overly the massive mudmound limestone, also of Emsian age. The latter limestone contains *Mimagoniatites fecundus*, thus confirming their basal Dalejan age (e.g., Klug et al. 2009). Above the marl, the layers become increasingly limy. At the base of the limestone, a dark nodule layer contains abundant *Foordites veniens* (Klug 2002; Klug et al. 2009). Diagenesis and taphonomy of the red cliff are discussed in Klug et al. (2009).

PIMUZ 29741 is somewhat smaller and was found at the southern edge of Jebel Oufatene (Fig. 1; compare Hollard 1974; Massa et al. 1965). This specimen is slightly deformed, probably due to compaction of the sediment. However, this deformation is minimal. We tested this by taking high and low estimates of the measurements. Therefore, we think that the overall proportions are reasonably well preserved. This is additionally corroborated by comparing the superficial visual similarities and differences of the measured specimens with PIMUZ 29741 with the clustering of forms in the PCA and in the cluster analysis (see the methods chapter). It was collected from a trench where locals had dug for late Emsian trilobites (N 30.824532°, W 4.90210°). Jebel Oufatene is about 14 km S of Fezzou in the Maïder region (eastern Anti-Atlas, Morocco). According to Kaufmann (1998), the entire Emsian is about 100 m thick in this area. The Dalejan (late Emsian) is represented by a thick claystone and clayey marl sequence, which displays increasing carbonate content near its top. For a sedimentological basin model of the Maïder Basin: see Döring (2002).

Methods

In order to distinguish between the species of this genus based on morphological differences, we produced bivariate plots (Fig. 3), a Principal Component Analysis (PCA; Fig. 4)

Fig. 3. Bivariate plots with various measurements and ratios of some published (Le Menn 1190; Hauser 2008) and the two newly described specimens of *Tiara crinus*. See the methods chapter for definition of the parameters. A. Calyx width vs. calyx height; note the clear separation of taxa. B. Calyx shape vs. calyx height. C. Number of pore rows vs. calyx height. As in A, the new taxon is also well separated from the existing taxa. The linear trendline probably reflects an ontogenetic trend. Open squares mark the values of the new species *T. jeanlemenni* sp. nov., solid squares mark all other species.

Table 1. Values used in the principal component and cluster analyses. Most of the values were taken from Hauser (1997, 2008). Values with some uncertainty are given in bold.

Specimen	Width oral surface (mm)	Calyx width (mm)	Calyx height (mm)	width pore fields (mm)	Stem width (mm)	Epispire rows (number)	Width-size class	Height-size class	Curvature	Stem to calyx-ratio	Row-ratio	Shape
Hamar Laghdad	8.7	12.9	9	9.3	3	22	1.000	0.600	0.674	0.233	0.917	0.436
Jebel Oufatene	5	9.6	8.5	5.3	2.3	24	0.744	0.567	0.521	0.240	1.000	0.590
<i>Tiaracrinus moravicus</i> Hauser 2008, pl. 1: 14	8	10	15	4	1.9	22	0.775	1.000	0.800	0.190	0.917	0.938
<i>Tiaracrinus oehlerti</i> Hauser 2008: pl. 1: 7	5	7	11	2.5	1.7	17	0.543	0.733	0.714	0.243	0.708	0.982
<i>Tiaracrinus oehlerti</i> Hauser 2008: pl. 1: 8	7.5	10	14	4	2.8	17	0.775	0.933	0.750	0.280	0.708	0.875
<i>Tiaracrinus quadrifrons</i> Hauser 2008: pl. 1: 9	6.7	8	7	4.5	1.5	10	0.620	0.467	0.838	0.188	0.417	0.547
<i>Tiaracrinus quadrifrons</i> Hauser 2008: pl. 1: 15	6	8	8	5	1.4	9	0.620	0.533	0.750	0.175	0.375	0.625
<i>Tiaracrinus quadrifrons</i> Hauser 2008: pl. 1: 16	3.5	5	4	3.7	1	7	0.388	0.267	0.700	0.200	0.292	0.500
<i>Tiaracrinus quadrifrons</i> Hauser 2008: pl. 1: 17	5.2	8	6	4.5	1.5	9	0.620	0.400	0.650	0.188	0.375	0.469
<i>Tiaracrinus quadrifrons</i> Hauser 2008: pl. 1: 18	6	10	6.5	5.5	1.5	8	0.775	0.433	0.600	0.150	0.333	0.406
<i>Tiaracrinus rarus</i> Hauser 2008: pl. 1: 10	4.5	8	8	4.5	1	17	0.620	0.533	0.563	0.125	0.708	0.625
<i>Tiaracrinus rarus</i> Hauser 2008: pl. 1: 11	5.8	10	11.5	7	1.5	22	0.775	0.767	0.580	0.150	0.917	0.719
<i>Tiaracrinus tetraedra</i> Hauser 2008, pl. 1: 3,5	7	10	10	6.5	2	7	0.775	0.667	0.700	0.200	0.292	0.625
<i>Tiaracrinus rarus</i> Le Menn 1990: pl. 1: 1–4	8	11.5	8	8	1.5	24	0.891	0.533	0.696	0.130	1.000	0.435
<i>Tiaracrinus rarus</i> Le Menn 1990: pl. 1: 9–12	8.3	11.1	7.4	6.2	1.5	21	0.860	0.493	0.748	0.135	0.875	0.417

Correlation matrix

PC	Eigenvalue	% variance
1	1.84232	48.308
2	1.18509	31.075
3	0.435917	11.43
4	0.223277	5.8546
5	0.119034	3.1212
6	0.00807011	0.21161

and a Cluster Analysis (Fig. 5) using PAST (Hammer et al. 2001) based on the following six characters (Table 1):

Calyx width size class (based on the largest width): The largest specimen was set as 1.

Calyx height size class: The largest specimen was set as 1.

Curvature of the calyx walls, calculated by dividing the largest width of the oral surface (assumed to be more or less identical with the diameter of the oral edge of the radial circlet) by the maximum width of the calyx.

Stem to calyx-ratio: The ratio between the diameter of the facet of the most proximal nodal columnal and the diameter the maximum width of the calyx.

Row ratio: The number of epispire rows divided by the maximal number of epispire rows of all known specimens.

Shape: The values of character 1 (width size class) divided by those of value 2 (height size class).

The standardisation was made for several purposes: (i) standardisation reduces the bias caused by differences in di-

mensions of the respective parameter; (ii) it eliminates the bias in scaling errors in those cases, where morphometric values were taken from the literature. We thus performed a PCA on the correlation matrix. The intraspecific variability is mainly caused by differences in ontogenetic trajectories (see Fig. 3) and, to a minor degree, by preservational biases such as the differences between internal moulds versus specimens that preserve the skeleton.

In the bivariate plots (Fig. 3), which were made using Excel, trendlines are given, which are supposed to show the predominant ontogenetic trend (correlation with calyx height, i.e., size). These were also produced with Excel.

The choice of specimens is based on their availability and preservation mainly. Not many well-preserved specimens of *Tiaracrinus* are sufficiently well documented and show all characters needed for our analyses, hence the low number of data.

Systematic palaeontology

Phylum Echinodermata Klein, 1754

Class Crinoidea Miller, 1821

Order Disparida Moore and Laudon, 1943

Superfamily Belemnocrinaceae Miller, 1883

Family Zophocrinidae Miller, 1892?

Type genus: *Zophocrinus* Miller, 1891.

Discussion.—In spite of the overall similarity in cup-shape and the organisation of the oral surface, it still appears questionable to include morphologically quite different genera such as *Zophocrinus* and *Tiaracrinus* in the same family. As far as we understand, the evolution or evolutionary reduction of epispires is probably not fully understood. We therefore keep this historical family assignment in agreement with the Treatise (Moore et al. 1978) as well as crinoid experts such as Le Menn (1990) and Hauser (2008).

Genus *Tiaracrinus* Schultze, 1866

Type species: *Tiaracrinus quadrifrons* Schultze, 1866, original designation; Stinava near Plumlov, Moravia, Czech Republic, Emsian, Early Devonian.

Species included: *Tiaracrinus moravicus* Ubags and Bouček, 1962; *Tiaracrinus oehlerti* Schlüter, 1881; “*Staurosoma rarum*” Barrande, 1887; *Tiaracrinus quadrifrons* Schultze, 1866; *Tiaracrinus tetraedra* Jaekel in Lotz, 1901; *Tiaracrinus jeanlemenni* sp. nov.; “*Tiaracrinus*” sp. (sic!) Kříž, 1992.

Discussion.—Initially described as a crinoid, *Tiaracrinus* was occasionally attributed to the Rhombifera (Blastozoa) by some early palaeontologists (Jaekel 1899, 1918; Bather 1900). Subsequently it has been consistently assigned to the crinoids (e.g., Frech 1902; Springer 1926; Bassler 1938; Moore et al. 1978; Le Menn 1990; Haude 1993; Hauser 2008). This confusion was probably largely related with its peculiar symmetry, the possible absence of arms and the presence of pores (epispires) on the theca. Here, we briefly discuss these features, their possible implications and problems associated with them:

(i) *Symmetry:* *Tiaracrinus* has three basals and four radials, thus determining the tetrameral symmetry of the calyx (Le Menn 1990). The oral surface is rarely preserved but has been discussed in detail by Le Menn (1990). The calyx shows five different plate numbers per circlet in the calyx. The base shows three plates while the cup is tetrameral. On the oral surface, 13 fields with brachial platelets and eight interoral fields can be seen, which surround the five oral plates (Le Menn 1990).

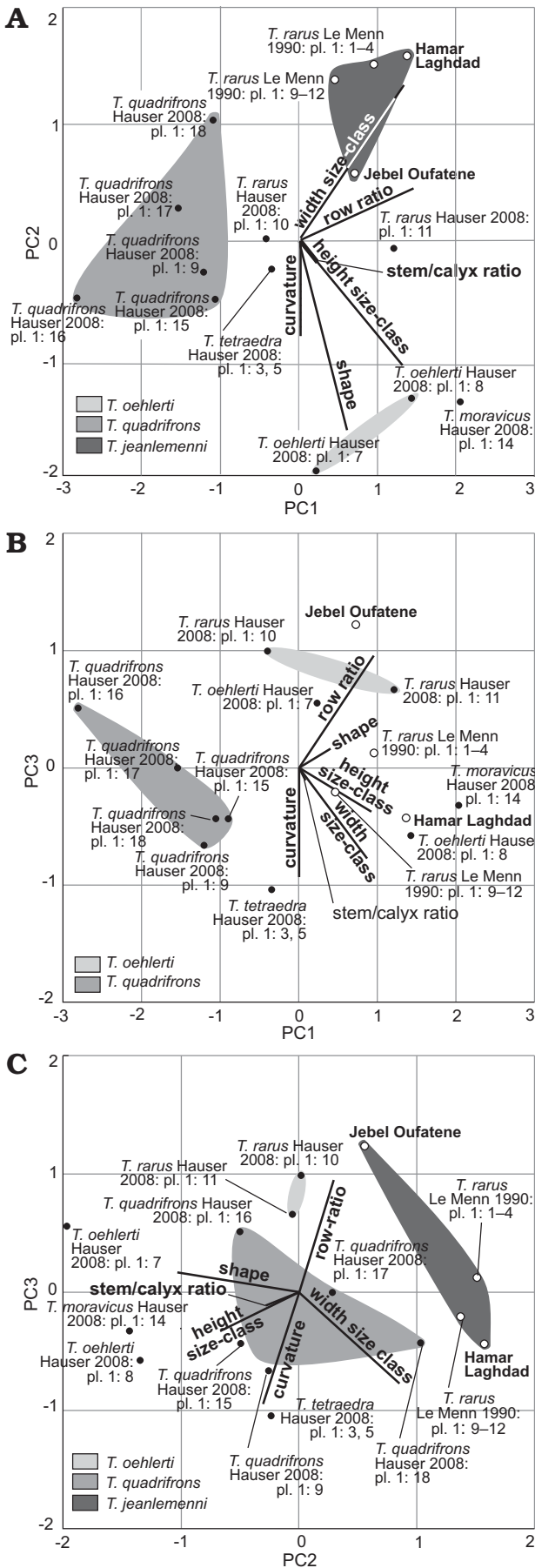


Fig. 4. PCA of some published (Le Menn 1990; Hauser 2008) and the two newly described specimens of *Tiaracrinus* (see Table 1). See Methods for definition of the parameters. **A.** Plot of principal components 1 and 2; note, how the new species separates well from the previously known ones. **B.** Plot of principal components 1 and 3. **C.** Plot of principal components 2 and 3; again, the new species is morphologically separated from the others. Open circles mark the values of the new species *T. jeanlemenni* sp. nov., solid squares mark all other species.

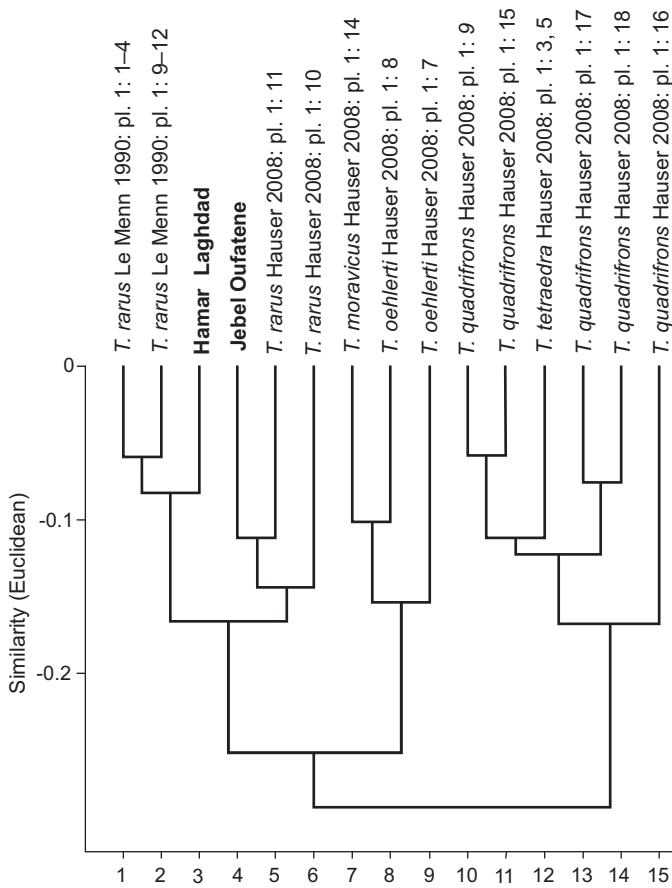


Fig. 5. Cluster analysis (Euclidean, paired group) of some published specimens and the two newly described specimens (see Table 1). The cluster on the right including *Tiaracrinus quadrifrons* and *Tiaracrinus tetraedra* is supported by the bootstrap (at 500 replicates; 59% with past); the *Tiaracrinus oehlerti* and *Tiaracrinus moravicus*-group (59 and 64%) and the *Tiaracrinus jeanlemenni* and *Tiaracrinus rarus*-group (62 and 72%) are also reasonably well supported. See also the methods chapter for definition of the parameters.

(ii) Arms: *Tiaracrinus* is commonly found without arms and has been described in the Treatise on Invertebrate Paleontology (Moore et al. 1978: 562) as follows: “Arm facets obscure or absent. Arms and columns unknown”. Later, Haude (1993) assigned limbrachoids from the Middle Devonian of Germany to this genus. He discussed the problems of the systematic position of this genus: “Immerhin ist die Theka so ungewöhnlich gebaut, dass selbst bedeutende Kenner der Pelmatozoen wie Bather (1900: 57) und Jaekel (1918: 99) *Tiaracrinus* zu den Cystoiden stellten. (An einem Cystoiden wären im übrigen die Limbrachioide wesentlich leichter als [biseriale] versteifte Brachiolen zu interpretieren.)” [Translation: “After all, the theca is constructed in such an unusual way that even important adepts of the pelmatozoans such as Bather (1900: 57) and Jaekel (1918: 99) have assigned *Tiaracrinus* to the cystoids. (On a cystoid, by the way, the limbrachoids would be much easier to interpret as stiffened [biseriale] brachiolen.)”]

Le Menn (1990: 163) also discussed this issue: “Le nombre de bras demeure difficile à établir” [Translation: “The

number of arms remains difficult to identify”]. While Le Maître (1958a–c) had suggested 18 arms based on 18 ditches on the oral surface, Le Menn (1990) thinks that these ditches were formed by erosion. The latter author discussed the possibilities of five or eight arms, based on the number and arrangement of oral, interoral, and brachial plates. It appears like this question has to stay unanswered until a complete, articulated specimen is found.

(iii) Pores on the calyx: *Tiaracrinus* displays four fields with epispires (Fig. 2). These epispires have been interpreted as representing a plesiomorphic character by Guensburg and Sprinkle (2007: 287): “Crinoid respiratory folds, for instance, are symmetrical internally and externally, whereas rhombiferan internal folds are extended forming interior bulges. Folds of most crinoids occur at triple junctures of plate corners, whereas those of rhombiferans cross plate sides.”

The origin of the type material is unknown according to Hauser (2008), but Le Menn (1987) described similar specimens from the Saint Céneré Formation (Pragian) of the “Tranchée de la voie Sablé”; Massif Armoricain (France).

Stratigraphic and geographic range.—Species of *Tiaracrinus* are recorded from: the Emsian of Plumlov (Moravia, Czech Republic), the late Emsian (according to Prokop 1987) of Koňeprusy (Bohemia, Czech Republic), the Freilingen Formation (Eifelian) of Nollenbach (Eifel, Germany), the Greifensteiner Kalk (near Emsian–Eifelian boundary) of Greifenstein (Lahn-Dill-Kreis, Germany), the Amerboh Group (late Emsian) of the eastern Anti-Atlas (Morocco), the Kopanina Formation (Ludfordian, Silurian) of Mušlovka quarry (Bohemia, Czech Republic).

Tiaracrinus jeanlemenni sp. nov.

Fig. 2.

1990 *Tiaracrinus rarus* (Barrande, 1887); Le Menn 1990: 162, pl. 1.

Etymology: After Jean Le Menn, honouring his work on Palaeozoic echinoderms and his thorough description of the genus in Africa.

Type material: Holotype: PIMUZ 29739, a well-preserved calyx but lacking the oral surface. Paratypes: PIMUZ 29741, GFCL 2152–2153, LPB 16795.

Type locality: “Red cliff” at Hamar Laghdad (eastern Anti-Atlas, Morocco).

Type horizon: Probably late *Polygnathus patulus* Conodont Biozone, late *Anarcestes lateseptatus* Ammonoid Biozone, latest Emsian, Early Devonian (Bultynck and Walliser 2000; Klug 2002).

Diagnosis.—*Tiaracrinus* with a more or less spherical calyx, with four very broad rhomboid radial rib-fields, which are strongly vaulted and which carry a large number of slender ribs (>20), a small and narrow radial ring, narrow and with slightly concave radial channels.

Description.—For the description of the Algerian specimens see Le Menn (1990). The two new Moroccan specimens are described below. Specimen PIMUZ 29739, holotype (Fig. 2A). The specimen preserves only the broad subglobular calyx and measures 9 mm in height and maximally 12.9 mm in

width. At the oral surface, the width of the calyx is reduced to 8.7 mm, but the oral surface is not preserved. The radial rib-field is up to 9.3 mm wide and it carries up to 22 ribs with pores at the end. In some parts, the ribs carry tubercles, but this might be due to weathering. The four radial channels form a perfect cross when seen from the aboral side. Specimen PIMUZ 29741, paratype (Fig. 2B). This calyx also lacks the oral surface, arms, and the stem. With a calyx height of 8.5 mm, this specimen is only 9.6 mm wide and therefore more slender than the holotype and the Algerian specimens. Although this specimen is slightly deformed, this difference in shape is probably original rather than a taphonomic artefact. At the oral surface, it measures only 5 mm while the other three specimens measure 8 mm or more. The ribs in the diamond-shaped rib-field appear finer but are more numerous (24) than in the other specimens. The radial channels also form a perfect cross when seen from the oral side and the rib-fields form a right angle where the channels meet.

Discussion.—Le Menn (1990) listed the five species *Tiaracrinus moravicus*, *T. rarus*, *T. quadrifrons*, *T. soyei*, and *T. tedraedra*. His assignment of the three Algerian calices to Barrande's (1887) species *T. rarus* was based on the globular calyx with the large number of ribs and the rhomboid rib-fields, which are similar to the European species *T. rarus*. Both the bivariate plots (Fig. 3) and the PCA-plots of principal component 1 and 2 as well as of principal component 2 and 3 (Fig. 4) revealed, however, that all specimens of the new species plot in a field separate from those of *T. rarus* and the other species. By contrast, both in the cluster analysis (Fig. 5) and in the plot of principal component 1 and 3 (Fig. 4), the specimen from Jebel Oufatene (PIMUZ 29741) falls in the field of *T. rarus*.

The results of this cluster analysis (Fig. 5) of 15 specimens revealed three pairs of species, which plot in the same respective clusters (see also the phylogeny chapter). In this analysis (Fig. 5), *T. rarus* is the sister species of *T. jeanlemenni*. This is also supported by the PCA (especially the principal component 3, i.e., the width size-class and the row ratio) and the bivariate plots (Figs. 3, 4). The separation of *T. jeanlemenni* from *T. rarus* is based mainly on the higher number of pore rows (Fig. 3C) and the lower height to width ratio in the new species.

Morphologically, the Algerian specimens (Le Menn 1990: pl. 1: 1–12) strongly resemble PIMUZ 29739 from Hamar Laghdad, while the slightly smaller specimen PIMUZ 29741 from Jebel Oufatene looks slightly different (Fig. 2). The question arises, whether this last mentioned specimen belongs to a separate species because it has more ribs with epispire than the other four specimens and the calyx is more slender, which might, however, be due to the slight traces of compaction or due to intraspecific variability (which cannot be quantified due to the low number of available specimens). It resembles *T. rarus* in the narrower oral surface but it differs from this Bohemian species in the adorally converging radial channels. Nevertheless, most of its measurements and

values (Fig. 3; pore rows in relation to size, height in relation to width) plot very close to the other specimens assigned to the new species (Fig. 3, 4), and therefore we conclude that it belongs to the new species and simply represents a morphological variant.

Stratigraphic and geographic range.—Late Emsian of the eastern Anti-Atlas (Morocco) and Monts d'Ougarta (Algeria).

Growth

As already pointed out by Le Menn (1990: 165), some of the characters of *Tiaracrinus*, such as the number of ribs, vary through ontogeny. The correlation of calyx width and height in the bivariate graph of Fig. 3A is not significant ($r = 0.358$, $R^2 = 0.128$, $p = 0.1897$), which is probably due to the fact that the graph depicts specimens from several species. Evaluation of a possible correlation with single species is, however, not possible at this point because of the lack of material and thus data. In spite of the lack of data, it is still clear that with increasing height, the width is also increasing, apparently to differing degrees in different species, but this hypothesis requires much more material to be tested. The number of ribs and epispire increases more or less constantly through ontogeny (Fig. 3B; $r = 0.0695$, $R^2 = 0.2213$, $p = 0.4809$), namely from 7 to 10 in *T. quadrifrons* from a calyx height of around 4 to around 8 mm, and in *T. rarus* from 17 to 22 at heights from about 8 to 11.5 mm, although the new species has more ribs than representatives of the other species at comparable sizes. We have printed a linear trendline to these epispire row-data, although the distribution of data points vaguely suggest an exponential correlation; the number of specimens and thus data is too low to draw conclusions on the exponential increase in row number. Nevertheless, a nonlinear increase in epispire rows would not be surprising since the volume of a sphere (and the calyx of *Tiaracrinus* is nearly spherical) also increases exponentially when compared to diameter (calyx height) increase; an exponentially growing body would probably have an exponentially growing respiration, hence the possibly exponential increase in epispire rows. The variation in strength of the ribs and size of the epispire within one specimen appears to be low (compare Hauser 2008: pl. 1).

Phylogeny

Some of the relationships within the genus are undoubtedly as proposed by Le Menn (1990). Accordingly, *T. oehlerti* and *T. moravicus* with their elongate and slightly ornamented calices represent a small monophylum (supported by the results of our cluster analysis in Fig. 5). Intrageneric variability is dominated by the significant ontogenetic increase in the number of epispire rows. A possible correlation between calyx width and height through ontogeny lacks statistical support, which is probably due to the low amount of data.

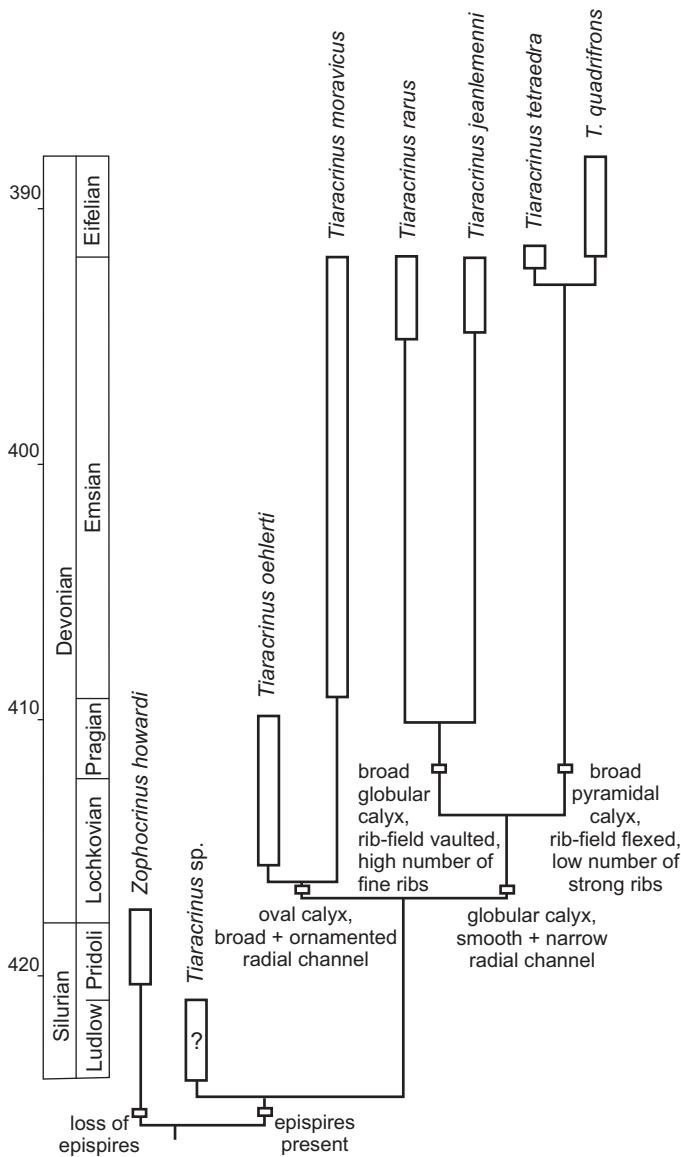


Fig. 6. Reconstruction of the phylogeny of the species of *Tiaracrinus*, based on their morphology and stratigraphic occurrences. Devonian timescale after Kaufmann (2006). All ranges of species lack precision and are thus indicated by open boxes.

Alternatively, as proposed by Hauser (2008: 2), *T. oehlerti* and *T. moravicus* could be conspecific and were assigned to different species because of differences in preservation. The same question is open with respect to *T. tetraedra* and *T. quadrifrons*, two superficially similar species with profoundly different preservation (Hauser 2008: 5), which also form one cluster. *T. jeanlemenni*, *T. rarus*, *T. tetraedra*, and *T. quadrifrons* share the broader calyx with the narrower radial channels and might thus be closely related (see Fig. 3).

The question arises, which of the various kinds of morphology represents the more plesiomorphic state. The age (Pragian to earliest Eifelian) of most of the reasonably well-known species does not differ significantly. Since *T. oehlerti* appears to be the oldest of the better known species, we suggest that the morphology with the elongate calyx and the

more ornamented radial channels represent the more ancestral morphology (Fig. 6). At least the calyx shape is more similar to the genus *Zophocrinus*, which is one of the few genera in the same family according to the crinoid Treatise (Moore et al. 1978). Remarkably, all the other genera assigned to the Zophocrinidae lack epispires. Following Guensburg and Sprinkle (2007: 287), the presence of epispires in crinoids can be considered as a plesiomorphic character and thus, the morphology of *Zophocrinus* and *Parazophocrinus* would be more derived, if we accept the taxonomy of Moore et al. (1978). By contrast, it could be argued that the *Tiaracrinus*-lineage had evolved convergently, an assumption, which is less parsimonious. For a test of this latter hypothesis, material and data are not available at this point. Such material would have to show a transition between the epispire-free *Zophocrinus* and early *Tiaracrinus* with epispires, for instance with a very low number of rows.

Conclusions

Based on the higher number of ribs in the rhomboid rib-fields and the globular calyx-shape, we describe the new species *Tiaracrinus jeanlemenni* sp. nov., which resembles the Czech species *T. rarus*. The species pair *T. jeanlemenni* sp. nov. and *T. rarus* differs from the other *Tiaracrinus* species in the greater number of more narrow epispire rows and from the pair *T. oehlerti* and *T. moravicus* in the more globular calyx with the more narrow radial channels. Morphometric analyses (PCA and Cluster Analyses) support the closer relationships between the species pairs *Tiaracrinus jeanlemenni* sp. nov. and *T. rarus*, between *T. tetraedra* and *T. quadrifrons*, as well as between *T. oehlerti* and *T. moravicus*. In the cases of the latter two pairs, two explanations are at hand: Either, (i) *T. tetraedra* and *T. moravicus* represent junior synonyms with the type materials of both species-pairs being differently preserved or (ii) all four species, are closely related to the respective other species of the two species-pairs, representing two two-species monophyla. Based on their younger age and the much higher than wide calyx (reminiscent of the outgroup-genus *Zophocrinus*), we interpret the species-pair *T. oehlerti* and *T. moravicus* as the most plesiomorphic one within the genus, from which the other four species are derived.

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