PalZ (2024) 98:579–592
https://doi.org/10.1007/s12542-024-00709-6

RESEARCH PAPER

Morphology of the stem group echinoids *Lepidocentrus eifelianus* and *Rhenechinus hopstaetteri* from the Devonian of the Eifel region, Germany

Jeffrey R. Thompson[1,2] · **James H. Nebelsick**[3]

Received: 25 January 2024 / Accepted: 29 September 2024 / Published online: 18 December 2024

Abstract

Relatively well-preserved echinoids from Palaeozoic strata are exceptionally rare fossils. New fossil finds can thus have an important impact on our understanding of the morphology, phylogenetic relationships and history of diversification of early sea urchins. The Devonian strata of Germany have long been known to contain echinoids, predominantly through the relatively abundant record of disarticulated plates and spines. In contrast, only select articulated or semi-articulated specimens are recorded. We herein describe new specimens from the Middle and Late Devonian belonging to two Palaeozoic echinoid taxa, *Rhenechinus hopstaetteri* and *Lepidocentrus eifelianus*. These specimens are amongst the most-complete known for these two taxa, and provide novel insight into their morphology and stratigraphic range. Additionally, the record of *Rhenechinus* is the youngest occurrence of an echinocystitid echinoid in the fossil record, indicating that this family ranged from the Silurian (Aeronian or Telychian) to at least the Middle Devonian (Givetian), prior to going extinct. The morphological details provided by the new specimen of *L. eifelianus* highlights similarities between this species and other Devonian echinoids known from elsewhere in Europe and North America, and suggest that the lepidocentrids were widely dispersed and abundant during the Devonian.

Keywords Sea Urchin · Rhineland-Palatinate · Palaeozoic · Echinoderm · Devonian

Introduction

Echinoids are important and abundant members of post-Palaeozoic oceans (Lohrer et al., 2004; Nebelsick, 1996; Steneck, 2013). Despite the extensive research on their post-Palaeozoic fossil record and patterns of diversification and extinction (Hopkins & Smith, 2015; Kroh & Smith, 2010; Mongiardino Koch & Thompson, 2021; Mongiardino Koch et al., 2022; Smith & Jeffery, 1998; Thompson et al., 2017a) the macroevolutionary dynamics of Palaeozoic echinoids remain less well-known. The Palaeozoic echinoid fossil record extends back to the Ordovician (Pisera, 1994; Reich & Smith, 2009; Smith & Savill, 2001; Thompson et al., 2022a) and the Palaeozoic peak in echinoid diversity took place during the Carboniferous Period (Kier, 1965; Smith, 1984). Although the Carboniferous marks the peak in Palaeozoic echinoid diversity, significant familial turnover appears to have taken place during the preceding Devonian period (Pauly & Haude, 2024). While Silurian and Devonian echinoid faunas appear to have been dominated by echinoids from the families Echinocystitidae and Lepidocentridae (Cooper, 1931; Hawkins & Hampton, 1927; Smith et al., 2013; Thompson et al., 2022b), the Carboniferous fossil record is dominated by species from the Archaeocidaridae, Palaechinidae, Proterocidaridae and Lepidesthidae (Kier, 1965; Thompson & Bottjer, 2019; Thompson et al., 2020). While this familial turnover is easily recognized taxonomically, the relative roles of extinction of Devonian clades and pseudoextinction due to origination of new families from paraphyletic Devonian ancestors (Smith, 1994; Smith

Handling Editor: Mike Reich.

✉ Jeffrey R. Thompson
j.r.thompson@soton.ac.uk

[1] School of Biological Sciences, University of Southampton, University Road, Southampton, Hampshire SO17 1BJ, UK

[2] School of Ocean and Earth Science, University of Southampton, National Oceanography Centre, European Way, Southampton, Hampshire SO14 3ZH, UK

[3] Department of Geosciences, University of Tübingen, Schnarrenbergstr. 94-96, 72076 Tübingen, Germany

et al., 2001) are not well-constrained. A phylogenetic framework provides a means to distinguish between extinction and pseudoextinction (Smith, 1994), and in order to better understand the phylogenetic patterns associated with this Devonian–Carboniferous turnover, a keen understanding of the morphology of Devonian echinoids is paramount.

Sedimentary successions of the Rhenish Massif have yielded amongst the first described Devonian echinoids (Müller, 1856, 1857; Schultze, 1866). Despite the historical context of these taxa, most of their fossil record consists of disarticulated plates, and articulated or semi-articulated specimens are exceedingly rare. We herein describe new well-preserved specimens of *Lepidocentrus eifelianus* Müller, 1856 and *Rhenechinus hopstaetteri* Dehm, 1953 from the Middle and Late Devonian of the Eifel region, Germany. These new specimens clarify the stratigraphic distribution and morphology of these two species, providing novel information that will be necessary to subsequently unravel the phylogenetic affinities, and macroevolutionary history of Devonian–Carboniferous echinoids.

Previous work on Rhenish Devonian echinoids

Isolated finds of conjoined plates or articulated echinoid specimens from the Middle Devonian of Central Germany are rare, and only known from two species. Within the Devonian deposits of the Eifel, echinoids were first described by Müller (1856) as the species *Lepidocentrus eifelianus* Müller, 1856. This was based on disarticulated interambulacral plates and spines from material collected near Rommersheim. This material was first figured in Müller (1857) and supplemented by material described in Müller (1859). Hauser (2002) subsequently described two multi-plated and semi-articulated specimens attributed to *Lepidocentrus eifelianus* from the Prüm Syncline (along with a third specimen which is likely a cravenechinid) extending the range of the former to the late Frasnian.

Schultze (1866) monographed the echinoderms of the Devonian of the Eifel, and in doing so named a second species of *Lepidocentrus* from the Eifel, *L. muelleri* Schultze, 1866 based on a test fragment consisting of ambulacra and interambulacra. More recently, Hauser (2014) described a test as well as isolated interambulacral plates of *Lepidocentrus muelleri* from the Mühlenberg Mergel Member of the Gerolstein Syncline. While *L. eifelianus* and *L. muelleri* constitute the first records of articulated echinoids from the Eifel, additional workers have elaborated upon the taxonomic and morphological knowledge regarding these taxa. Zittel (1879) provided a short description of the morphology of *Lepidocentrus*, while Jackson and Jaggar (1896) re-described *L. muelleri* and *L. eifelianus,* and provided a comparison of these taxa to other Palaeozoic echinoids. Kier (1968) cleaned the holotype of *L. muelleri* and noted its extensive similarities to the archaeocidarid genus *Nortonechinus* Thomas, 1920, which will be discussed further below.

Although only a few articulated echinoid remains have been described from the Eifel region, isolated plates are widely distributed and can be so common that they have been the basis for eponymous lithological units—the so called "*Lepidocentrus* marls" (e.g. Hotz et al., 1955; Struve, 1955, 1992 and therein). These isolated plates have been figured together with the coronal descriptions by Schultze (1866) and Kayser (1871) additionally mentions the occurrence of plates in large numbers. In the Eifel, the presence of *Lepidocentrus* plates is also often noted within bed descriptions and/or taxonomic lists of detailed locality descriptions. For example, Hotz et al. (1955) listed ten different occurrences from at least eight different stratigraphic units of the Hillersheim and Ahdorf Synclines, almost all of Eifelian age, except for a lone occurrence from the Givetian. Similarly, Fuchs (1965) lists *Lepidocentrus* plates occurring in seven localities from six different lithological units (five Eifelian and one Givetian in age) from the Hillersheim Syncline. These *Lepidocentrus* plates occur in fine-grained sediments together with crinoidal columnals, numerous brachiopods as well as trilobites, bivalves, gastropods (including *Bellerophon*), rugose and tabulate corals and stromatoporids. The validity of these "*Lepidocentrus* marls" or horizons as lithological units has, however, been questioned as they are stratigraphically poorly constrained such that these terms are no longer in use (see detailed discussion in Hotz et al., 1955 and Struve, 1955). *Lepidocentrus* plates are also well known from the diverse Middle Devonian units of the neighboring Sauerland to the east (see Haffer & Jentsch, 1962; Müller, 1965).

In addition to plates, isolated spines attributed to echinoids are also abundant from the Eifel. Schultze (1866) described three differing spine morphotypes. Two of these were used to define the species *Xenocidaris clavigera* Schultze, 1866, with flared and expanding distal ends, and *Xenocidaris cylindrica* Schultze, 1866 which are fusiform, sculptured, and taper distally. Lastly, Schultze (1866) figured rather featureless spines of various sizes which were attributed to *Lepidocentrus muelleri*. Jackson and Jaggar (1896) tentatively placed *Xenocidaris* within the Archaeocidaridae M'Coy, 1844, though noted that the affinities of this taxon were questionable due to the poor nature of the material on which the genus was defined. He subsequently provided short descriptions of these two species of *Lepidocentrus*, and referred *Xenocidaris* to *incertae sedis* (Jackson, 1912). In some cases, these spines are associated with conjoined groups of plates (Hauser, 2002) allowing more confident taxonomic assignments, and recently, isolated lantern elements have also been figured (Hauser, 2014).

Further echinoids described from the Devonian of Germany include the echinocystitid *Rhenechinus hopstaetteri*

(Dehm, 1953; Hopstätter, 1952) and *Porechinus porosus* Dehm (1961) from the Lower Devonian Hunsrück Slate (see Smith et al., 2013 for compilations of Hunsrück slate echinoid finds), as well as *Palaechinus rhenanus* (Beyrich, 1857) and *Lepidocentrus muelleri* (Wolburg, 1933 as *L. lenneanus*), from the Middle Devonian of the Sauerland. Synonymizing *L. lenneanus* with *L. muelleri* possibly extends the stratigraphic extent of this taxon down to the Emsian as *L. lenneanus* was recovered by Wolburg (1933) from the Cultrijugatus beds, which straddle the Early/Middle Devonian boundary (Langenstrassen, 2008). A fragmentary species of the rare cravenechinid, *Cravenchinus*? *frankei* was also described from the Late Devonian of the Harz mountains by Haude (1999). Recently, Pauly and Haude (2024) have described a spectacular and diverse assemblage of Famennian echinoids which confidently extends the range of many Carboniferous families down into the Devonian.

Stratigraphic and palaeoenvironmental setting

The echinoids described in this study originated from the Eifel region, which is part of the Rhenish Massif which stretches from northeastern France across Belgium and Luxemburg into Germany. The Rhenish Massif includes a series of midsized mountains consisting of diverse rocks of Cambrian to Carboniferous age (see compilation in the Deutsche Stratigraphische Kommission 2008 and Meyer, 2013). The Eifel is especially well known for its Devonian successions and is the origin of several eponymous Devonian stage names as well as the GSSP at the base of the Eifelian.

The Middle Devonian of the Eifel region contains numerous classic fossiliferous localities leading to an expansive literature concerning stratigraphy, lithology and fossil content (see compilations in Struve, 1961, 1992; Weddige, 1996, 1998; Steingötter, 2005; Menning et al., 2006; Deutsche Stratigraphische Kommission 2008; Struve et al., 2008; Meyer, 2013; for a historical synopsis see Rath, 2005). A number of carbonate dominated synclines ("Kalkmulden") include rocks ranging from the later Emsian of the Early Devonian, through to the Eifelian and Givetian of the Middle Devonian and, in part, reaching up into the Late Devonian. These synclines show different lithological successions and facies variations such that detailed descriptions of rocks fossils have been historically given separately for each syncline. This, together with changing understanding and interpretations of biostratigraphy, lithostratigraphy and biogeography, has hampered the synthesis of facies developments with older publications replete with obsolete lithological and stratigraphic terms.

Middle Devonian rocks of the Eifel show a wide variety of lithologies and fossil content. In general, a shelf gradient is present ranging from shallow water (NW) to deeper water (SE) with variations in siliciclastic input. Fossiliferous depositional environments including massive carbonates in a reefal facies with corals and stromatoporoids, bedded carbonates dominated by brachiopods and crinoids, to marls and sandstones. A three-part facies model was developed with a facies type A dominated by shallow water proximal siliciclastics; facies type B representing higher energy, shallow water reefs and carbonates; and a deeper water, lower energy facies type C containing carbonate-marl intercalations (Faber, 1980; Meyer et al., 1977).

The lithostratigraphy and chronostratigraphy of the Middle Devonian of the Eifel area are summarized in Struve et al. (2008), see also Ernst (2008), Bohatý et al. (2012) and Ernst et al. (2014). The echinoid finds in the present study were recovered from the Givetian Zerberus Member (Fig. 1) of the Ahbach Formation of the Hillesheim Syncline. The Zerberus Member is the top lithostratigraphic unit of the Müllert Sub-Formation, which tops the Ahbach Formation. The Ahbach Formation straddles the Eifelian–Givetian boundary, with the Zerberus Member placed within the *Polygnathus hemiansatus* conodont biozone of the early Givetian. The Givetian echinoid described here originate from the Hallert Quarry locality, near Ahütte by Üxheim, Hillesheim Syncline; Zerberus Member of the Ahbach Formation.

Sedimentary environments within the Ahbach Formation range from higher energy, reefal environments to deeper, muddy marls and is very fossiliferous (see compilation in Struve, 1992; Struve et al., 2008). More recent publications on specific faunal elements of the Ahbach Formation in the Uxheim–Ahütte vicinity including palaeoecological interpretations are found in in Bohatý (2005, 2009), Bohatý and Hein (2013), Ernst et al. (2014) and Bohatý and Ausich (2021). Paleoecological reconstructions by Bohatý (2005, 2009) contrast a shallow water, higher energy stromatoporan-coral biostrome facies with a deeper water, muddy facies with soft substrates colonized by large fenestellid bryozoans, solitary rugose and favositid tabulate corals along with recapticulids, sponges, trilobites, brachiopods, crinoids and echinoids. The Zerberus Member (Struve et al., 2008), the topmost member of the Ahbach Formation (Fig. 1), consists of 30-m-thick marls with few limestone layers.

Late Devonian strata in the Eifel region are less prevalent than that of Lower and Middle Devonian and are restricted to the Prüm Syncline (Grimm et al., 2008). The locality of the upper Devonian specimen described herein is Wallersheim Loch, from which Hauser (2002) also described articulated remains of *Lepidocentrus eifelianus*. These were found within a sequence of marly black shales and limestone banks containing small pyritized goniatites and orthocone cephalopods. Following Clausen and Hauser (2005), although the stratigraphic extent of the published find locality is not conclusive, it can be correlated as a facies equivalent of the Frasnian portion of the Büdesheim Formation which

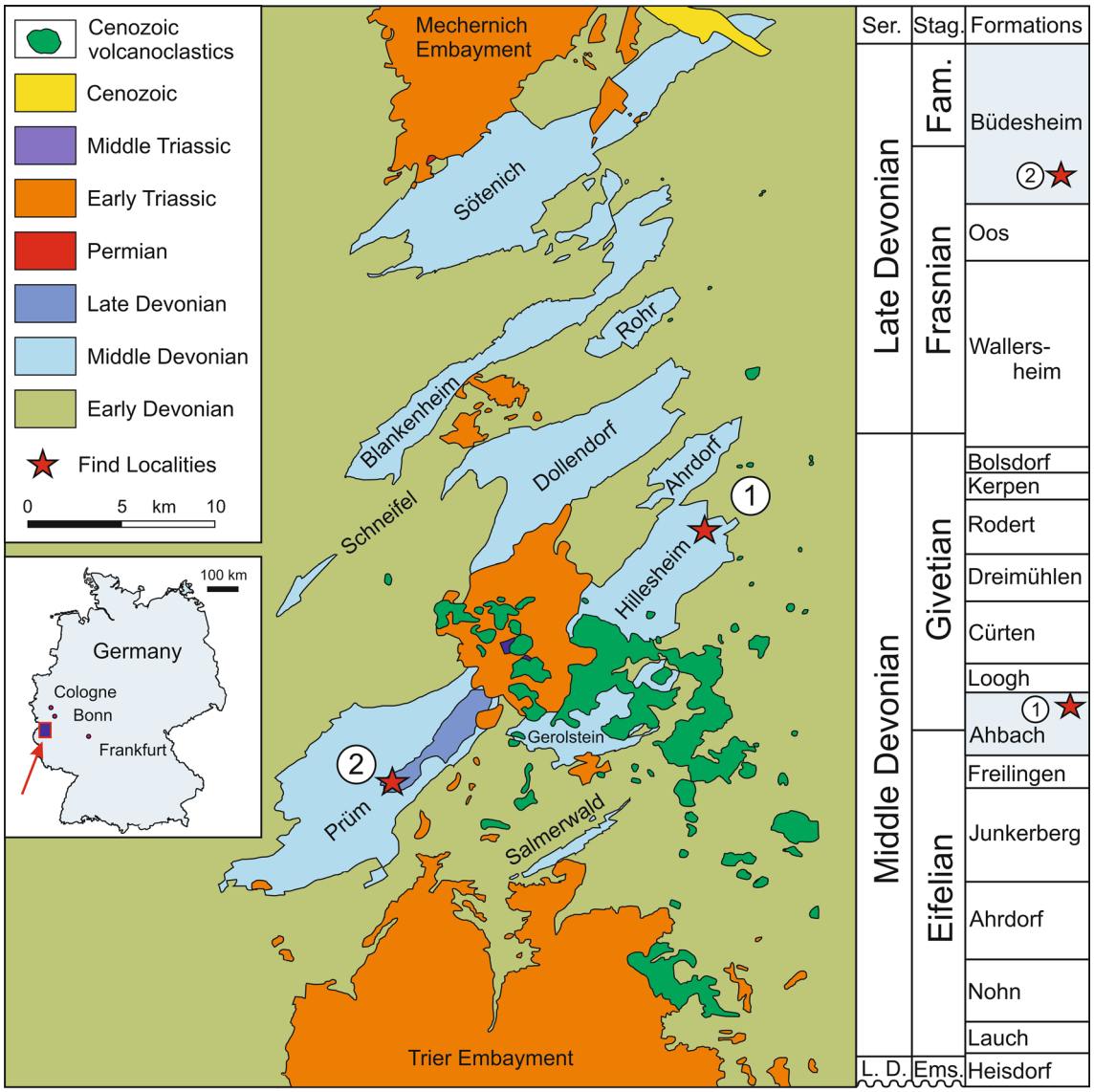

Fig. 1 Geological map of the Eifel area following Fernando-Alvarez et al. (1996) based on Ribbert (1992), Ledoux (1987) and Franke and Anderle (2001). Synclines containing Early to Late Devonian sediments are denoted. Lithostratigraphy following Bohatý and Ausich (2021) for the Middle Devonian and Clausen and Hauser (2005) for the Late Devonian. *Ser.* Series, *Stag* Stages, *E. D.* Early Devonian, *EMS.* Emsian

consists of monotonous dark, fine-grained, in part silty and marly mudstones, intercalated with subordinate grey micritic limestone layers (Grimm et al., 2008).

Systematic palaeontology

Repository. All specimens are registered with either the Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz (NHMMZ) or the Maarmuseum Manderscheid in Manderscheid, Rhineland-Palatinate, Germany (MMM). All specimens are deposited at the MMM.

Class **Echinoidea** Leske, 1778

Stem Group **Echinoidea**

Family **Echinocystitidae** Gregory, 1897

Genus ***Rhenechinus*** Dehm, 1953

Diagnosis. Modified from Smith et al. (2013). Echinocystitid with straight and narrow ambulacra. Plating is quadriserial throughout with every other plate a demiplate which is occluded from the adradial suture. Pore pairs are uniform and with a surrounding peripodial rim, alternately displaces

to left and right forming a biseries down the center of each half-ambulacrum. Interambulacra are broad and composed of a large number of small, polygonal plates forming semi-regular *en chevron* rows. Plates are imbricate. Basicoronal plate is present adorally. Coronal plates have small secondary tubercules or granules with short, simple, spines. Teeth are oligolamellar.

Type species. Rhenechinus hopstaetteri Dehm, 1953.

Other species. Rhenechinus ibericus (Hauser & Landeta, 2007).

Occurrence. This genus is known from the Emsian of the Hünsruck region, Germany (Rhineland-Palatinate) and Asturias, Spain as well as the Givetian of the western Eifel region, Germany (Rhineland-Palatinate).

Rhenechinus hopstaetteri Dehm, 1953

Figure 2

1952 "Ein Seeigel aus dem Hunsrückschiefer"; Hopstätter, 1952: 33.
1953 *Rhenechinus hopstätteri*; Dehm, 1953: 93, pl. 5: 1–4.
1961 *Rhenechinus hopstätteri* Dehm, 1953; Kuhn, 1961: 33, figs. 15, 16.
1966 *Rhenechinus hopstatteri* Dehm, 1953; Kier, 1966: U303, Fig. 224.2.
1970 *Rhenechinus hopstätteri* Dehm, 1953; Kutscher, 1970a: 40.
1970 *Rhenechinus hopstätteri* Dehm, 1953; Kutscher, 1970b: 96.
1980 *Rhenechinus hopstaetteri* Dehm, 1953; Mittmeyer, 1980: 38.
1990 *Rhenechinus hopstätteri* Dehm, 1953; Bartels & Brassel, 1990: 181, Fig. 169.
1997 "Seeigel *Rhenechinus hopstätteri* mit erhaltenen Stacheln "; Bartels et al., 1997: 49, Fig. 61.
1998 *Rhenechinus hopstaetteri* Dehm, 1953; Bartels et al., 1998: 210, Fig. 188.
1999 *Rhenechinus hopstätteri* Dehm, 1953; Jahnke & Bartels, 1999: 43.
2000 *Rhenechinus hopstätteri* Dehm, 1953; Jahnke & Bartels, 2000: 43.
2013 *Rhenechinus hopstaetteri* Dehm, 1953; Smith et al., 2013: 758, figs. 6, 7

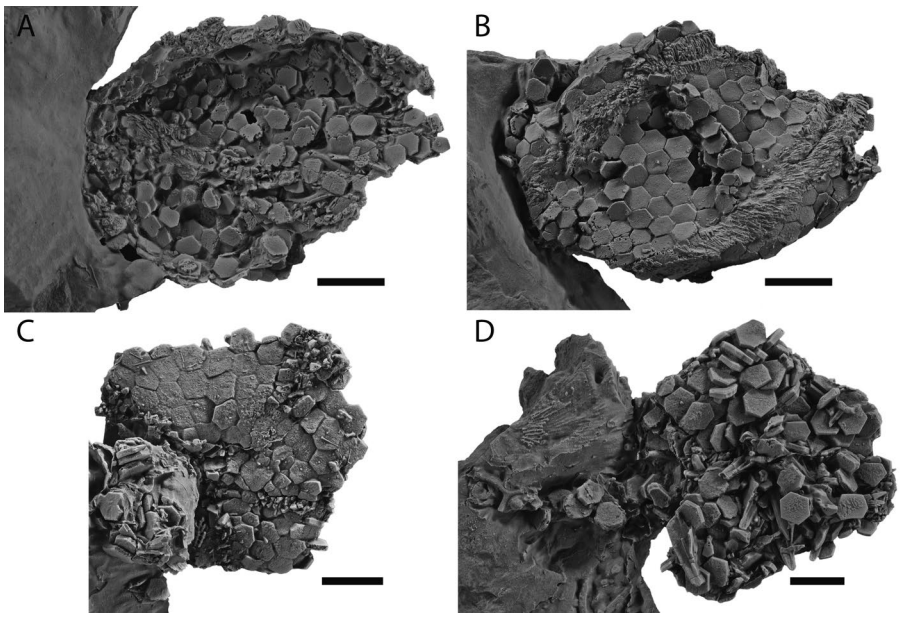

Fig. 2 Images of *Rhenechinus hopstaetteri* from the from the Hallert Quarry locality, near Ahütte by Üxheim, Hillesheim Syncline; Givetian (Middle Devonian). **A** Specimen MMM-2010–01 showing the interior of the test through a lateral view. Note the hexagonal shape of the interambulacral plating. **B** Same specimen as A, showing a lateral view of an interambulacrum and two flanking ambulacra. Ambulacra bear numerous small, dense, simple, striate spines, which obscure many of the details of the plating. Ambulacra consist of two biserial half-ambulacra with perradially located demiplates. **C** Specimen NHMMZ PWL 2023/417-LS adapical view of test showing details of ambulacral and interambulacral plating. Ambulacra are biserial with occluded demi plates. Flanges covering radial water vessel along interior of ambulacral plates can be seen in disarticulated ambulacral plates. Note the large genital plate at the summit of one interambulacrum. **D** Same specimen as C, showing disarticulated interambulacral and ambulacral plates, along with some hemipyramids and teeth from the Aristotle's lantern. Note the simple oligolamellar tooth. All scale bars are 1 cm

Occurrence. This species was first described from the Lower Emsian Hunsrück Slate from Gemünden and Bundenbach, and is now known from the Zerberus Member of the Ahbach Formation of the Hillesheim Syncline, which belongs to the early Givetian *Polygnathus hemiansatus* conodont zone (all Rhineland-Palatinate, Germany).

Diagnosis. Species of *Rhenechinus* with up to eight columns of interambulacral plates at the ambitus. Interambulacral plates polygonal and with sparse interambulacral spines. Surface of the interambulacral plates is smooth, and lacks small pits.

Description. Specimen MMM-2010-01 consists of a semi-articulated test, while specimen NHMMZ PWL 2023/417-LS is a well preserved adapical portion of the test with a crushed ambital and adoral side. Test regular, at least 54.47 mm high on MMM-2010-01, though the adoral portion of the test is missing. Plating is imbricate, though not extensively so, as many coronal plates appear to abut one another as opposed to heavily bevel over each other. The peristome and apical disc are unknown from specimen MMM-2010–01, though the apical disc is partially preserved in specimen NHMMZ PWL 2023/417-LS. Genital 2 is present and contains the madreporite. This plate is covered with small tubercles and no conspicuous genital pores are visible. This plate is about 4.87 mm wide, and 4.85 mm tall, and is rounded-triangular in outline. Genital plate 1 is also present and 4.7 mm wide and 3.04 mm tall. Ocular plates I and II are present and neither appears to be perforated with an ocular pore. Both ocular plates appear to be insert abutting the periproct. The periproct appears to consist of numerous small irregularly shaped plates, many of which appear to bear at least one tubercle.

Disarticulated elements of the lantern are present in both specimens. A hemipyramid in specimen NHMMZ PWL 2023/417-LS is 13.3 mm tall. The foramen magnum is about 3.07 mm deep, and half of its width is about 2.1 mm. Though only half of the foramen magnum is visible on this disarticulated hemipyramid, it appears to have been quite narrow. A narrow dental slide is present on the interior of the hemipyramid, which is about 7.09 mm tall. Numerous disarticulated teeth are present in both specimens. These are simple oligolamellar, and the details of individual tooth plates are visible in most preserved teeth. Teeth coming to a single point, and not serrate.

Ambulacra are composed of four columns of plates, with pore pairs arranged quadriserially. Each half-ambulacrum is about 2.6 mm wide and contains a larger, primary ambulacral plate, which reaches the perradial suture, and a smaller demi plate which is occluded from the adambulacral suture. About four primary ambulacral plates to each interambulacral plates. Primary ambulacral plates which abut the adoral and adapical sutures of interambulacral plates are enlarged and expanded along their adambulacral edge. Pore pairs in small peripodial ring. The most adambulacral pore in pore pairs on demi-plates are arranged such that they are roughly in line with the more perradial pore in the pore pair of primary plates above and below. Ambulacral plates with small secondary tubercles, each of which appears to bear a secondary spine. The preservation, and subsequent preparation of the specimen have left the number of secondary tubercles unknown, however where they were left intact, the spines densely cover the ambulacra and obscure the nature of the tubercles. Adapically and ambitally, there are no conspicuous perradial ridges on the interior of the plates of either of the specimens and thus the radial water vessel appears to have not been internal within plates in these portions of the test. Towards adoral end of specimen MMM-2010-01, some disarticulated ambulacral plates show thickenings that may be perradial ridges, though these plates are partially obscured by matrix, thus precluding definitive identification as such. Primary ambulacral plates imbricate slightly under interambulacral plates.

Interambulacra on specimen MMM-2010-01 composed of eight columns of plates at its widest. Area is about 21.1 mm wide. Adapically and adorally the number of plate columns decreases, and on specimen 35, there appear to be five or maybe six plates in contact with genital plate 2 (the madreporite bearing plate). Interambulacral plates thin, about 0.8 mm thick. Plating imbricate, though very slightly so. Plates seem to abut each other more than bevel over each other. Plates hexagonal to subhexagonal in shape. Approximately equally high as wide, though some plates are slightly wider than high, and some are slightly higher than wide. Adambulacral interambulacral plates are often slightly higher than wide, and have one adambulacral edge expanded adorally and adapically such that there is one long, relatively flat edge imbricating over ambulacral plates. Plates on MMM-2010-01 appear to show no sculpturing, though this is likely due to sculpture having been lost during preparation of the specimen. Specimen NHMMZ PWL 2023/417-LS shows sparse tubercles or granules on interambulacral plates, which appear to have borne small spines.

Spines relatively short, and thin. Tapering to a point distally. Spines with small striations. Up to about 2.3 mm in length. Spine base consists of a small bulb, and no milled ring is present. Spines on interambulacral plates are only known from specimen NHMMZ PWL 2023/417-LS, the longest of which is about 3 mm in length. Interambulacral plates appear to have borne sparser tuberculation, and thus sparser spine coverage, than ambulacral plates.

Materials. Specimens MMM-2010-01 and NHMMZ PWL 2023/417-LS are from the Hallert Quarry locality, near Ahütte by Üxheim in the Hillesheim Syncline; from the

Zerberus Member of the Ahbach Formation; Givetian (Middle Devonian).

Remarks. Previously published specimens of *R. hopstaetteri* were collected from the Hunsrück Slate (Smith et al., 2013). The nature of preservation in the Hunsrück slate is such that specimens are preserved compressed onto slate bedding planes, thus impeding detail of morphological structures in three-dimensions. These new specimens are preserved, and have been prepared, in such a way that their morphology is visible in three dimensions. This provides novel insight into the morphology of *R. hopstaetteri*. Of particular note is the information concerning the interior of the ambulacrum, which is not obviously visible in the Hunsrück *R. hopstaetteri.* In *R. ibericus,* which is known from the Emsian of Spain, the radial water vessel is clearly covered by internal flanges. Our new *R. hopstaetteri* from the Eifel confirm that this characteristic is also present in *R. hopstaetteri,* although the covering of the radial water vessel is much less conspicuous than in *R. ibericus*.

Our new specimens appear similar to the taxon figured by Haffer and Jentsch (1962) as *Lepidocentrus rhenanus* (Beyrich). Both their specimens, which were collected from Sauerland, and our specimens from the Hillesheim Syncline have regular, primarily hexagonal, interambulacral plates, which do not exhibit much evidence of imbrication. Our material differs from those specimens, however, in the structure of the ambulacra. Our specimens clearly display biserial ambulacra in each half-ambulacrum, while those of the Haffer and Jentsch (1962) speimens display ambulacra that are uniserial in each half-ambulacrum. Regardless of the similarity of our material to the Haffer and Jentsch (1962) *Lepidocentus rhenanus,* their material clearly differs from the type specimen with regard to the shape of its interambulacral plates and the lack of imbricating plates found in their material. The plates of *L. rhenanus* are heavily imbricate, as is typical for the genus, and as this character is missing from the specimens of Haffer and Jentsch (1962), their material likely belongs to a different genus.

Family **Lepidocentridae** Lovén, 1874a, 1874b

Genus ***Lepidocentrus*** Müller, 1856

Diagnosis. Lepidocentrid with large interambulacral plates, many times larger than ambulacral plates. Interambulacral plates strongly imbricate, with rhomboidal shape, and arranged into multiple columns in each interambulacral area, typically not fewer than eight. Not all plates bearing enlarged, mamellonate primary tubercles, but in some species this is the case. Tubercles arranged towards adambulacral edge of plates. Ambulacral plates enclose radial water vessel with flange on interior of test. Pore pairs located centrally on ambulacral plates between perradial and adradial sutures. Spines lack a milled ring, and appear to be widest at their base. Spines taper distally.

Type species. Lepidocentrus eifelianus Müller, 1856.

Other species. Lepidocentrus rhenanus (Beyrich, 1857) and *Lepidocentrus muelleri* Schultze, 1866.

Occurrence. This genus is known from the Eifelian to Frasnian of the Rhenish Devonian of Germany.

Remarks. This genus was erected based off of disarticulated material described by Müller (1856) and then described again with figures a year later (Müller, 1857). Though disarticulated material typically provides poor criteria for erection of generic and species level concepts in echinoids, the morphology of disarticulated interambulacral plates in species of *Lepidocentrus* from the Devonian of the German Eifel region are distinct such that plates of different species are diagnostic. Haffer and Jentsch (1962) showed different species of *Lepidocentrus* in the Devonian of Germany with non-overlapping stratigraphic distributions with *L. muelleri* restricted to the Givetian, and *L. eifelianus* to the Eifelian. Subsequently, Hauser (2002) extended the distribution of *L. eifelianus* to the Frasnian.

In addition to the type species, three others have been described from the Eifelian and Givetian strata of the Eifel and Sauerland. *L. rhenanus* was described from an internal mould of an articulated test. Though it does display heavily imbricate plates and a fully enclosed radial water vessel, these are traits common to many lepidocentrid genera, and *L. rhenanus* could belong to another genus of lepidocentrid or, could more likely be conspecific with *L. muelleri* Schultze, 1866. *L. muelleri* differs from the type species in the shape of its interambulacral plates and the pattern of tuberculation on these plates. The fourth species reported from the German Devonian, *Lepidocentrus lenneanus* Wolburg, 1933 was described from an exceptional mouldic specimen, which was apparently lost during the second world war (Haffer & Jentsch, 1962). Haffer and Jentsch (1962) then synonymized *L. lenneanus* with *L. muelleri* based on the shape of the interambulacral plates. Although the original type material of *L. lenneanus* is lost, we think it is best to follow Haffer and Jentsch (1962) in synonomyzing *L. lenneanus* and *L. muelleri.*

In addition to taxa known from Germany, Jackson (1929) attributed material to three different species concepts within *Lepidocentrus* from the Carboniferous of Belgium. Jackson's Tournaisian *L. eifelianus* was synonymized with *Hyattechinus elegans* Jackson, 1929 by Thompson and Denayer (2017). Furthermore, the disarticulated plates from the Viséan assigned by Jackson (1929) to *Lepidocidaris* sp.

and *Lepidocidaris mammillatus* Jackson, 1929, are entirely indeterminate, and could belong to any number of taxa from the Proterocidaridae, Lepidocentridae or Archaeocidaridae.

Lepidocentrus eifelianus Müller, 1856
Figures 3, 4

1856 *Lepidocentrus eifelianus* Müller, 1856; 356
1857 *Lepidocentrus eifelianus* Müller, 1856; Müller, 1857: 258, pl. 3: 1–8
1859 *Lepidocentrus eifelianus* Müller, 1856; Müller, 1859: 197
1866 *Lepidocentrus eifelianus* Müller, 1856; Schulze, 1866: 123, pl. 13: 2
1874 *Lepidocentrus eifelianus* Müller, 1856; Lovén, 1874a, 1874b: 40
1875 *Lepidocentrus eifelianus* Müller, 1856; Quenstedt, 1875: 374: pl. 75: 14–17, 19–29

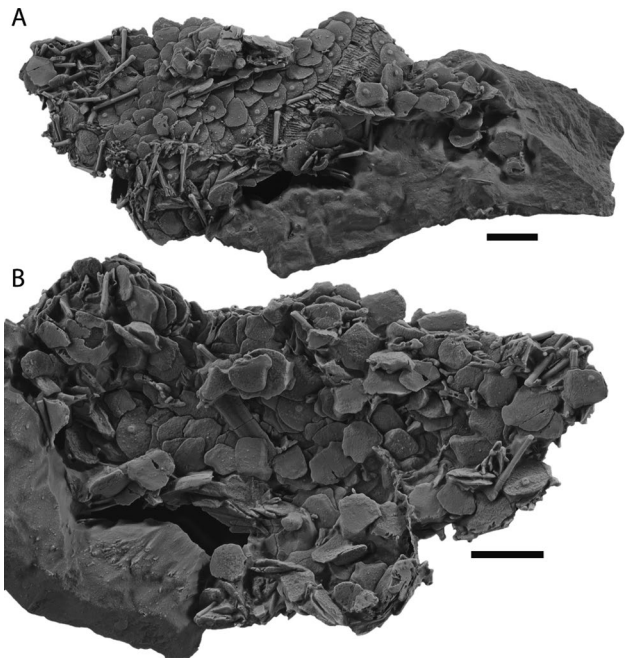

Fig. 3 Images of specimen NHMMZ PWL 2023/416-LS, a fragmentary test belonging to *Lepidocentrus eifelianus* from the Hallert Quarry locality, near Ahütte by Üxheim, Hillesheim Syncline; Givetian (Middle Devonian). **A** Lateral view of interambulacral and ambulacra with associated spines. Interambulacra are arranged into at least eight columns of imbricate plates. Most adambulacral interambulacral column bears large perforate, mamellonate tubercles arranged towards the adambulacral edge of the plate. Ambulacra are biserial, with a single column of plates in each half-ambulacrum. Spines lack obvious ornamentation and taper distally. **B** Interior of test showing disarticulated interambulacral plates, ambulacral plates, as well as teeth and spines. Note the flange located on the adradial edge of ambulacral plates which encloses the radial water vessel. Scale bars are 1 cm

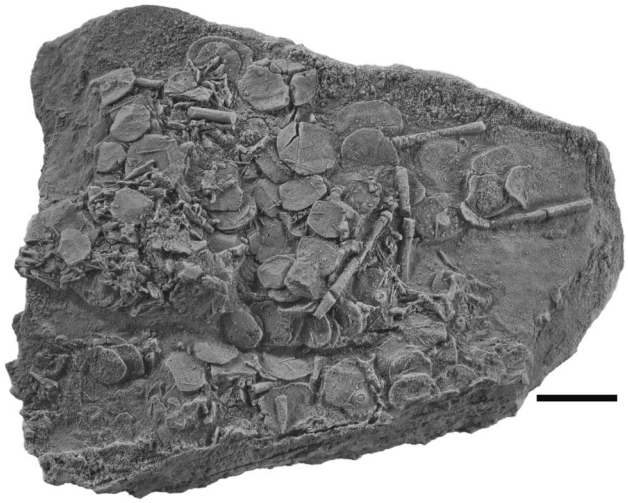

Fig. 4 Specimen NHMMZ PWL 2023/418-LS, a pile of disarticulated *Lepidocentrus eifelianus* test plates from Wallersheim/Loch locality in the Prüm Syncline; Frasnium (Late Devonian). Note the perforate tubercles on interambulacral plates. Scale bar is 1 cm

1896 *Lepidocentrus eifelianus* Müller, 1856; Jackson, 1896: 224
1904 *Lepidocentrus eifelianus* Müller, 1856; Klem, 1904: 16
1910 *Lepidocentrus eifelianus* Müller, 1856; Lambert & Thiéry, 1909–1925: 122
1912 *Lepidocentrus eifelianus* Müller, 1856; Jackson, 1912; 291, pl. 20: 14
1929 *Lepidocentrus eifelianus* Müller, 1856; Jackson, 1929; 20, pl. 5: 9a-g; pl. 10: 7a-b
1962 *Lepidocentrus eifelianus* Müller, 1856; Haffer and Jentch, 1962: 77, pl. 8: 3–6
2002 *Lepidocentrus eifelianus* Müller, 1856; Hauser, 2002: 5, pl. 4: 1–3

Occurrence. This species is known from the Givetian of the German Eifel and Sauerland. Our new specimens are from the Zerberus Member of the Ahbach Formation of the Hillesheim Syncline, which falls within the Givetian *Polygnathus hemiansatus* conodont zone.

Diagnosis. Species of *Lepidocentrus* with interambulacra arranged into at least eight columns within an interambulacrum. Adambulacral and some median interambulacral plates bearing an enlarged non-crenulate primary tubercle. All interambulacral plates bearing small, imperforate and non-crenulate secondary tubercles, which are sparsely arranged on the plate. Interambulacral plates are five-sided and subrounded in shape. Spines are cylindrical in cross section, and lack ornamentation.

Description. We provide novel insight into this species from two specimens, NHMMZ PWL 2023/416-LS, which is a semi-articulated and disarticulated ambulacral area with flanking interambulacral areas and NHMMZ PWL 2023/418-LS which is a disarticulated pile of plates and spines. In NHMMZ PWL 2023/416-LS, the apical disc and peristome are unknown, and the known lantern elements consist solely of two teeth, the tips of which are obscured by matrix and disarticulated interambulacral plates.

Ambulacra about 9.2 mm wide, arranged into two columns. Pore pairs are biserial, and are not within small peripodial ring. Ambulacral plates bearing at least two imperforate noncrenulate secondary tubercles arranged between pore pair and perradial suture on each plate, and at least one small secondary tubercle between pore pair and adambulacral suture. On some plates one or both of these perradialy located tubercles bears a small areole. More adapical ambulacral plates imbricating over more adoral plates. Interior of ambulacral plates with a small distinct arching ridge, which interlocked with the same on the opposing plate, thus enclosing the radial water vessel within the ambulacrum. A small sunken canal is also present on the interior side of the perradial side of these ambulacral plate, which leads from the perradial suture to the pore pair, and which likely housed the branch of the water vessel leading to the pore pair. Ambulacral pores are about 1.4 mm away from perradial suture, and 1.4 mm away from adambulacral suture.

The interambulacra are heavily imbricate, with the adambulacral interambulacral plates beveling over the ambulacra. The interambulacral area is arranged into at least eight columns of plates, however there are likely many more, as only the adapical portion of the interambulacra is completely known. More adoral interambulacral plates imbricating over top of more adapical plates. A median column is present in the most interradial portion of the interambulacra, which imbricates over top of two plates to either adambulacral side. Moving adambulacrally in either side from this median column, plates imbricate over more adambulacral plates. Plates are subrounded to subpolygonal in shape, and appear slightly wider than high. All interambulacral plates bear sparse, secondary tuberculation. Large, imperforate, noncrenulate primary tubercles are present however, on all adambulacral plates. These tubercles are located towards the upper, adambulacral edge of the plate. The second most adambulacral column is free from these large tubercles, however the third most adambulacral column has tubercles on some plates, and it appears that these large tubercles are present on every other plate moving adorally along the test.

Spines are present on ambulacral and interambulacral plates. Ambulacral spines are small, tapering distally and present on secondary tubercles. They are striate and at least 3.8 mm in length. Interambulacral plates bearing primary spines. These are at least 10.7 mm in length and tapir distally. The most distal end of the spines is unknown. They are widest at their base, which is a small swelling. They lack a milled ring, and appear solid.

Materials. We record two new specimens, NHMMZ PWL 2023/416-LS, and NHMMZ PWL 2023/418-LS. Specimen NHMMZ PWL 2023/416-LS (Fig. 3) is recorded from Hallert Quarry in the Hillesheim Syncline, near Ahütte by Üxheim. It occurs in the Zerberus Member of the Ahbach Formation; Givetian (Middle Devonian). Specimen NHMMZ PWL 2023/418-LS. (Fig. 4) is from the Wallersheim / Loch locality in the Prüm Syncline, Büdersheim Formation; Frasnian (Late Devonian).

Remarks. This species is differentiated from other species of *Lepidocentrus* largely based upon characters of the interambulacra. The interambulacral plates of *L. eifelianus* are rounded to subrounded and broadly five sided. The interambulacral plates of *L. muelleri*, and *L. rhenanus* are, however, rhomboidal, having four straight edges. Furthermore, Haffer and Jentsch (1962) have shown that the stratigraphic range of this taxon does not overlap with that of *L. eifelianus* in the Eifel and Sauerland. Like other known species of *Lepidocentrus*, *L. eifelianus* displays ambulacra arranged into two columns with uniserial pore pairs in each half-ambulacrum. Furthermore, it's ambulacra enclose the radial water vessel as is the case with other species of *Lepidocentrus* (Kier, 1968). This species also bears large primary tubercles on tubercles on all visible adambulacral interambulacral plates and on plates in some median columns. This indicates similarities with *Nortonechinus*, which is discussed in more detail below.

There exists some confusion as to the first date of description of *Lepidocentrus eifelianus* Müller, 1857. As mentioned by Müller (1857) the Müller, 1856 version is an extract of the version published in 1857. Both publications, in fact, deal with proceedings which took place in 1856. The species description of 1856 is shorter, somewhat rearranged, and lacks the figures of the version published in 1857. Further material from the same locality were subsequently mentioned by Müller (1859).

Müller (1857) first postulates that isolated plates and spines which were found together in fact belong together as the plates possessed knobs which fit to the base of the spines. Then expounded on the fact that the plates were not articulated but arranged in a shingled pattern which corresponds to the shape of the plates with rim parts either covering or being covered adjacent plates which is accommodated by oblique sharpened plate edges. Different sizes of plates are noted as are the details of the plate edge morphology. Tubercle differentiation is noted with larger plates possessing a one knob for a single spine and smaller knobs for

corresponding finer spines. A smooth non-raised and non-deepened periphery of the larger tubercles is noted. Spines are described with a finely striated longitudinally surface and an enlarged base and in cross sections narrow dense spokes separated by lattice like material. Müller mentions that "the microscopic structure of the plates is, as in all echinoderms, netlike and thereby it is certain that we are not dealing with an animal from another class." He also mentions that the spines have a construction common to all sea urchins.

In the plates; Müller (1857) reconstructs the plate arrangements of *Lepidocentrus eifelianus* based on the distribution of angled facets of the single plates and also following the plate arrangement of the Middle Devonian *Palaechinus rhenanus* Beyrich, 1857 which is an articulated specimen containing ambulacra, interambulacral and jaws. *Palaechinus rhenanus* was described in a single paragraph, but not figured by Beyrich (1857, again in a correspondence which took place in 1856). This specimen is thus figured for the first time by Müller (1857).

Lastly, Jackson (1929) attributed disarticulated plates from the Tournaisian of Belgium to *L. eifelianus*, however, Thompson and Denayer (2017) attributed this material to the proterocidarid *Hyattechinus elegans* Jackson, 1929.

Discussion

Echinoids from the Devonian of the Eifel

The Givetian and Eifelian age strata of the Eifel represent some of the most diverse and well-studied echinoderm-bearing deposits from the Devonian (Bohatý, 2006, 2009, 2010; Bohatý & Herbig, 2010; Haffer & Jentsch, 1962; Müller et al., 2013). Amongst these echinoderms, the echinoid fauna of the Eifel is minimally comprised of echinocystitid and lepidocentrid echinoids. In addition to the aforementioned *Lepidocentrus muelleri,* and the spine-based taxa *Xenocidaris clavigera* Schultze, 1866, and *Xenocidaris cylindrica* Schultze, 1866, we herein record for the first time the presence of *Rhenechinus hopstaetteri*, and semi-articulated material belonging to *Lepidocentrus eifelianus*.

The echinoids described here expand upon the known environmental distribution of *R. hopstaetteri*. Smith et al. (2013) hypothesized that echinoids from the Emsian Hunsruck slate, which represents an environment just below storm wave-base (Raiswell et al., 2008), were transported into these environments from shallower water ecosystems. The occurrences of *R. hopstaetteri* and *Lepidocentrus eifelianus* from the Ahbach formation are thought to represent occurrences in fossiliferous deeper water, muddy facies with soft substrates (Bohatý (2005, 2009). The finds from *Lepidocentrus eifelianus* from the Frasnian are interpreted to represent even deeper water, cephalopod-dominated environments (Grimm et al., 2008). The occurrence of well-preserved, articulated, specimens of these echinoids was likely because specimens at these taphonomic grades are likely to have a higher chance of preservation in lower energy environments. The observed distribution of taxa in these deep water environments most likely represents a taphonomic artifact as the distribution of isolated disarticulated plate material in the Devonian of Germany shows a much wider distribution (Haffer & Jentsch, 1962).

The only non-German species of *Rhenechinus* is *Rhenechinus ibericus* Hauser and Landeta (2007). This taxon is known from shallow water deposits, replete with bryozoans, brachiopods and pelmatozoans (Smith et al., 2013), and the paleoenvironment in which it inhabited is more akin to that of *R. hopstaetteri* from the Eifel. Additionally, the Givetian occurrence of *R. hopstaetteri* from the Eifel thus extends the stratigraphic range of this species from the Emsian into the Givetian, and furthermore marks the youngest occurrence in the fossil record of the family Echinocystitidae.

In addition to *Rhenechinus*, the echinoid fauna of the Eifel also includes the two lepidocentrid species *L. eifelianus,* and *L. muelleri.* These taxa are relatively common in Eifelian and Givetian strata in the Eifel where they occur primarily as disarticulated plates and spines (Haffer & Jentsch, 1962). The morphology of the interambulacral plates and spines of these taxa is similar to other disarticulated lepidocentrid remains assigned to numerous species of *Xenocidaris* from the Frasnian of Belgium (Maillieux, 1935, 1940), and furthermore (as discussed in more detail below), the morphology of these plates is similar to those of *Nortonechinus*, and *Albertechinus* from the Devonian of North America (Kier, 1968; Stearn, 1956; Thomas, 1920, 1921). The widespread occurrence of lepidocentrid echinoids with this morphology in the Devonian may indicate that they were one of the more abundant and widely-dispersed groups of echinoids in the Devonian.

Implications of Eifelian echinoid morphology for stem group echinoid phylogeny

We describe herein the morphology of *Lepidocentrus eifelianus* based on semi-articulated test material. This has allowed for more accurate comparisons of this taxon to other Devonian echinoids, which has important implications for understanding the phylogenetic relationships of stem group echinoids. Of note is the close similarity in morphology between *L. eifelianus* and the archaeocidarid echinoid *Nortonechinus welleri* Thomas, 1920, from the Frasnian of Iowa (Thomas, 1921). Both of these taxa have numerous columns of imbricate interambulacral plates bearing large tubercle and spines, and have ambulacral plates which enclose the radial water vessel. The similarities between *Lepidocentrus* and *Nortonechinus* were highlighted by Kier (1968), who

proposed that *Nortonechinus* gave rise to the archaeocidarid echinoids, and by extension the entire crown group. Kier's arguments were largely based on comparisons between *L. muelleri* and *Nortonechinus*, who chose to place *Nortonechinus* within the Archaeocidaridae based upon the large primary tubercles found on its interambulacral plates. Our updated characterization of *L. eifelianus* indicates even closer similarities between *Lepidocentrus* and *Nortonechinus,* and suggests a morphologically intermediate position for *L. eifelianus* between *L. muelleri* and *Nortonechinus*. The large tubercles which dominated the interambulacral plates of *Nortonechinus,* and which were the primary basis for Kier's (1968) proposition that *Nortonechinus* was ancestral to the archaeocidarid echinoids, are herein shown to have also been present in *Lepidocentrus*. This could suggest that the character used to align *Nortonechinus* with the archaeocidarids, large interambulacral tubercles and spines, involved independently across a number of stem group echinoids, and that in fact *Nortonechinus* is not in a clade with the archaeocidarid echinoids and other members of the crown group. Following the work of Kier (1968) *Nortonechinus* has recently been used as an outgroup for phylogenetic analyses of archaeocidarids and other crown group echinoids (Thompson et al., 2020). The morphology seen in *L. eifelianus* could thus cast doubt on the appropriateness of *Nortonechinus* as the outgroup to the archaeocidarids. Conversely, if *Nortonechinus* is still shown to have close affinities with the archaeocidarids, then the large tubercles seen in archaeocidarids and many crown group echinoids can trace their origin to lepidocentrids like *L. eifelianus*, which supports the hypothesis of Thompson et al., (2020, 2017b) that the acquisition of characters leading to the echinoid crown group was step-wise. In order to fully realize the implications of this new material from the Eifel, a phylogenetic analysis including other Palaeozoic and stem group echinoid taxa is necessary. Future work will aim to do just that.

Acknowledgements JRT was funded by a Leverhulme Trust Early Career Fellowship. We would like to thank Dr. Martin Koziol, director of the Maarmuseum Manderscheid in Manderscheid, Rhineland-Palatinate, Germany for making specimens available for study and providing information concerning their origin. We also thank Wolfgang Gerber, formally of the Department of Earth Sciences, University of Tübingen, for the excellent photographs, and our reviewers Samuel Zamora and Mike Reich for comments which improved upon the clarity and utility of the manuscript.

Funding JRT was funded by a Leverhulme Trust Early Career Fellowship.

Data availability All data is available within the manuscript.

Declarations

Conflict of interest We have no conflicts of interest.

References

Bartels, C., & Brassel, G. (1990). Fossilien im Hunsrückschiefer. *Museum Idar– Oberstein, 7*, 1–231.

Bartels, C., Lutz, H., Blind, W., & Opel, A. (1997). *Schatzkammer Dachschiefer. Die Lebenswelt des Hunsrückschiefer Meeres* (p. 82). Landessamlung für Naturkunde Rheinland−Pfalz, Mainz and Deutsches Bergbau−Museum.

Bartels, C., Briggs, D. E. G., & Brassel, G. (1998). The fossils of the Hunsrück Slate. Marine life in the Devonian. *Cambridge Palaeobiology Series, 3*, 1–309.

Beyrich, E. (1857). Über ein zu den Palechiniden gehöriges Petrefakt. *Zeitschrift der Deutschen Geologischen Gesellschaft, 9*, 4.

Bohatý, J. (2005). Doppellagige Kronenplatten: Ein neues anatomisches Merkmal paläozoischer Crinoiden und Revision der Familie Cupressocrinitidae (Devon). *Paläontologische Zeitschrift, 79*(2), 201–225.

Bohatý, J. (2006). A new Middle Devonian Hexacrinites (Crinoidea, Camerata) from the Gerolstein syncline (Eifel Hills, Germany). *Neues Jahrbuch Für Geologie und Paläontologie, Abhandlungen, 242*(2–3), 261–274.

Bohatý, J. (2009). *Palaeodiversity, palaeobiology and palaeoecology of Middle Devonian crinoids from the Eifel type region*. Unpublished PhD Thesis, University of Cologne. 253 pp.

Bohatý, J. (2010). Revision of the Hexacrinitidae (Crinoidea) based on a classical Lower Givetian crinoid deposit (Gerolstein, Eifel/Germany). *Neues Jahrbuch Für Geologie und Paläontologie, Abhandlungen, 257*(1), 23–54.

Bohatý, J., & Ausich, W. I. (2021). Revision of two Devonian cupressocrinitids from the Schultze collection (Museum of Comparative Zoology, Harvard University) and description of a new Halocrinites (Crinoidea, Eucladida). *Journal of Paleontology, 96*(1), 196–212.

Bohatý, J., Ausich, W. I., Nardin, E., Nyhuis, C., & Schröder, S. (2012). Coral-crinoid biocoenosis and resulting trace fossils from the Middle Devonian of the Eifel Synclines (Rhenish Massif, Germany). *Journal of Paleontology, 86*(2), 282–301.

Bohatý, J., & Herbig, H.-G. (2010). Middle Givetian echinoderms from the Schlade Valley (Rhenish Massif, Germany): Habitats, taxonomy and ecostratigraphy. *Paläontologische Zeitschrift, 84*(3), 365–385.

Bohatý, J., & Hein, U. (2013). Ein neuer camerater Crinoidea (Echinodermata) aus der `Mimatrypa-Biofacies´ (Mittel Devon) des Steinbruchs `Wotan´ bei Üxheim-Ahütte (Hillesheimer Eifelkalkmulde, Rheinische Schiefergebirge). *Mainzer Naturwissenschaftliche Archiv, 50*, 99–119.

Clausen, C.-D., & Hauser, J. (2005). Cyrto- und orthocone Nautiloideen aus dem Oberdevon der Wallersheimer Mulde (Wallersheim/Loch, Prümer Mulde; Eifel). *Senckenbergiana Lethaea, 85*(1), 63–79.

Cooper, G. A. (1931). *Lepidechinoides* Olsson, a genus of Devonian echinoids. *Journal of Paleontology, 5*(2), 127–142.

Dehm, R. (1953). *Rhenechinus hopstätteri* nov. gen. nov. sp., ein Seeigel aus dem rheinischen Unter-Devon. *Notizblatt Des Hessischen Landesamtes Für Bodenforschung, 81*, 88–95.

Dehm, R. (1961). Ein zweiter Seeigel, *Porechinus porosus* nov. gen. nov. spec., aus dem rheinischen Unter-Devon. *Mitteilungen der Bayerischen Staatssammlung Für Paläontologie und Historische Geologie, 1*, 1–8.

Deutsche Stratigraphische Kommission. (2008). Stratigraphie von Deutschland VIII Devon. *Schriftenreihe der Deutsche Gesellschaft Für Geowissenschaften, 52*, 1–578.

Ernst, A. (2008). Non-fenestrate bryozoans from the Middle Devonian of the Eifel (western Rhenish Massif, Germany). *Neus Jahrbuch Für Geologie und Paläontologie, Abhandlungen, 250*(3), 313–379.

Ernst, A., Taylor, P. D., & Bohatý, J. (2014). A new Middle Devonian cystoporate bryozoan from Germany containing a new symbiont bioclaustration. *Acta Palaeontologica Polonica, 59*, 173–183.

Faber, P. (1980). Fazies-Gliederung und -Entwicklung im Mittel-Devon der Eifel (Rheinisches Schiefergebirge). *Mainzer Geowissenschaftliche Mitteilungen, 8*, 83–149.

Fernando-Alvarez, C., Brunton, H. C., & Struve, W. W. (1996). On *Athyris* (Brachiopoda) and its type species `*Terebratula´ concentrica* von Buch. *Senckenbergiana Lethaea, 76*(1–2), 65–105.

Franke W. R., & Anderle, H.-J. (2001). *Geologische Übersichtskarte der Bundesrepublik Deutschland 1:200 000, CC 6310 Frankfurt a.M. Bundesanstalt für Geowissenschaften und Rohstoffe in Zusammenarbeit mit den Staatlichen Geologische Diensten der Bundesrepublik Deutschland.*

Fuchs, G. (1965). Geologie des Westteils der Hillesheimer Mulde (Mitteldevon, Eifel). *Fortschritte in der Geologie Von Rheinland und Westfalen, 9*, 323–448.

Gregory, J. W. (1897). On the affinities of the Echinothuriidae. *Quarterly Journal of the Geological Society, 53*, 112–122.

Grimm, M. C., Piecha, M., Prick, R., & Joachimski, M. (2008). Höheres Mitteldevon und Oberdevon der Prümer Mulde (Givetium bis tiefes Fammennium/Eifel). *Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften, 52*, 375–391.

Haffer, J., & Jentsch, S. (1962). Über die *Lepidocentrus*-Arten (Echinoidea) des rheinischen Mitteldevon. *Paläontologische Zeitschrift, 36*, 77–85.

Haude, R. (1999). Ein seltener paläozoischer Seeigel aus der Endzeit des Iberg-Atolls (Harz, Adorf-Stufe). *Neues Jahrbuch Für Geologie und Paläontologie, Abhandlungen, 214*, 149–167.

Hauser, J. (2002). *Lepidocentrus* J. Mueller, 1856 und andere Echiniden-Reste aus dem hohen Frasnium (Ober-Devon) von Wallersheim-Loch (Prümer Mulde, Eifel). In J. Hauser & A. A. Hauser (Eds.), *Oberdevonische Echinodermen aus den Dolomitsteinbrüchen von Wallersheim/Loch (Rheinisches Schiefergebirge, Prümer Mulde; Eifel)* (p. 13). Privately published by the authors.

Hauser, J. (2014). *Die Echinodermen und Begleitfauna des Mühlenberg-Mergel-Members (Givetium) der Gerolsteiner Mulde*. Privately Published by the author.

Hauser, J., & Landeta, F. G. (2007). *Neue Crinoiden aus dem Paläozoikum von Nordspanian* (p. 78). Privately published by the authors.

Hawkins, H. L., & Hampton, S. M. (1927). The occurrence, structure, and affinities of *Echinocystis* and *Palaeodiscus*. *Quarterly Journal of the Geological Society, 83*, 574–603.

Hopkins, M. J., & Smith, A. B. (2015). Dynamic evolutionary change in post-Paleozoic echinoids and the importance of scale when interpreting changes in rates of evolution. *Proceedings of the National Academy of Sciences, 112*(12), 3758–3763.

Hopstätter, H. (1952). Ein Seeigel aus dem Hunsrückschiefer. *Notizblatt Des Hessischen Landesamtes Für Bodenforschung, VI*(3), 33–34.

Hotz, E.-E., Kräusel, W., & Struve, W. (1955). Zur Geologie der Eifelkalkmulden II. Die Eifel-Mulden von Hillesheim und Ahrdorf. *Beihefte, Geologisches Jahrbuch, 17*, 44–204.

Jackson, R. T. (1896). Studies on Palæchinioidea. *Bulletin of the Geological Society of America, 7*, 171–246.

Jackson, R. T. (1912). Phylogeny of the Echini: With a revision of Palaeozoic species. *Memoirees of the Boston Society of Natural History, 7*, 1–491.

Jackson, R. T. (1929). Palaeozoic Echini of Belgium. *Mémoires Du Musée Royal D'histoire Naturelle De Belgique, 38*, 1–74.

Jackson, R. T., & Jaggar, T. A. (1896). Studies of *Melonites multiporus*. *Bulletin of the Geological Society of America, 7*, 135–170.

Jahnke, H., & Bartels, C. (1999). LArdesia di Hunsrück. In G. Pinna (Ed.), *Alle radici della storia naturale d'Europa* (pp. 36–44). Jaca Books.

Jahnke, H., & Bartels, C. (2000). Der Hunsrückschiefer und seine Fossilien, Unter−Devon. In D. Meischner (Ed.), *Europäische Fossillagerstätten* (pp. 36–44). Springer.

Kayser, E. (1871). Studien aus dem Gebiete des rheinischen Devon. II. Die devonischen Bildungen der Eifel. *Zeitschrift der Deutschen Geologischen Gesellschaft, 33*, 289–374.

Kier, P. M. (1965). Evolutionary trends in Paleozoic echinoids. *Journal of Paleontology*, *39*(3), 436−465.

Kier, P. M. (1966). Noncidaroid Paleozoic echinoids. In R. C. Moore (Ed.), *Treatise on invertebrate paleontology: Part U Echinodermata 3.* The Geological Society of America, Inc. and The University of Kansas Press.

Kier, P. M. (1968). *Nortonechinus* and the ancestry of the cidarid echinoids. *Journal of Paleontology,*, *42*(5) 1163−1170.

Klem, M. J. (1904). A revision of the Palaeozoic Palaeechinoidea with a synopsis of all known species. *Transactions of the Academy of Science of St Louis, 14*(1), 1–98.

Kroh, A., & Smith, A. B. (2010). The phylogeny and classification of post-Palaeozoic echinoids. *Journal of Systematic Palaeontology, 8*(2), 147–212.

Kuhn, O. (1961). Die Tierwelt der Bundenbacher Schiefer. *Die Neue Brehm– Bücherei, 274*, 1–48.

Kutscher, F. (1970a). Die Echinodermen des Hunsrückschiefer−Meeres. In Festschrift zum 60. Geburtstag von Horst Falke. *Abhandlungen des Hessischen Landesamtes für Bodenforschung*, *56*, 37–48.

Kutscher, F. (1970b). Die Versteinerungen des Hunsrückschiefers. Erinnerungen an Walther Maximilian Lehmann. In: W. Lieber, (Eds.), *Idar-Oberstein, Der Aufschluss, Sonderheft*, *19*, 87–100.

Lambert, J., & Thiéry, P. (1909–1925). Essai de Nomenclature. Raisonnée des Echinides. L. Ferrière, Chaumont.

Langenstrassen. F. (2008). 4.1.14 Unter- und Mitteldevon in Sauerland. In: Deutsche Stratigraphische Kommission, (Eds.), *Stratigraphie von Deutschland VIII Devon*, *Schriftenriehe der Deutschen Gesellschaft für Geowissenschaften*, *52*, 417–439.

Ledoux, H. (1987). *Blatt C 5506 Bonn. Geologische Karte von Nordrhein-Westfalen 1 100 000*. Geologisches Landesamt Nordrhein-Westfalen.

Leske, N. G. (1778). *Iacobi Theodori Klein Naturalis disposito Echinodermatum, Edita et aucta a N. G. Leske*. G. E. Beer

Lohrer, A. M., Thrush, S. F., & Gibbs, M. M. (2004). Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature, 431*(7012), 1092–1095.

Lovén, S. (1874a). L Etudes sur les echinoidees. *Kongelige. Svenska. Vetenskaps-Akademiens. Handlingar, 11*, 1–91.

Lovén, S. (1874b). Études sur les Échinoidés. *Kongliga Svenska Vetenskaps-Akademiens Handlingar, 2*(7), 1–91.

Maillieux, E. (1935). Contribution á L'étude des Échinoides du Frasnien de la Belgique. *Mémoires Du Musée Royal D'histoire Naturelle De Belgique, 65*, 3–16.

Maillieux, E. (1940). Les Échinodermes du Frasnien de la Belgique. *Mémoires Du Musée Royal D'histoire Naturelle De Belgique, 92*, 1–47.

M'Coy, F. (1844). *A synopsis of the characters of the carboniferous limestone fossils of Ireland,* viii + 274 pp. M. H. Gill.

Menning, M., Alekseev, A. S., Chuvashov, B. I., Davydov, V. I., Devuyst, F.-X., Forke, H. C., Grunt, T. A., Hance, L., Heckel, P. H., Izokh, N. G., Jin, Y.-G., Jones, P. J., Kotlyar, G. V., Kozur, H. W., Nemyrovska, T. I., Schneider, J. W., Wang, X.-D., Weddige, K., Weyer, D., & Work, D. M. (2006). Global time scale and regional stratigraphic reference scales of Central and West Europe, East Europe, Tethys, South China, and North America as used in the Devonian–Carboniferous–Permian Correlation Chart 2003 (DCP 2003). *Palaeogeography, Palaeoclimatology, Palaeoecology, 240*, 318–372.

Meyer, W. (2013). *Geologie der Eifel* (4th ed.). Schweizerbart Science Publishers.

Meyer, W., Stoltidis, I., & Winter, J. (1977). Exkursionsbericht. Geologische Exkursion in den Raum Weyer – Schuld – Heyroth – Niederehe – Üxheim-Ahütte. *Decheniana, 130*, 322–334.

Mittmeyer, H.−G. (1980). Vorläufige Gesamtliste der Hunsrückschiefer− Fossilien. In: W. Stürmer, F. Schaarschmidt, & H.−G. Mittmeyer (Eds.), *Versteinertes Leben im Röntgenlicht*. *Kleine Senckenberg−Reihe*, (Vol 11, pp. 34–39)

Mongiardino Koch, N., & Thompson, J. R. (2021). A total-evidence dated phylogeny of Echinoidea combining phylogenomic and paleontological data. *Systematic Biology, 70*(3), 421–439.

Mongiardino Koch, N., Thompson, J. R., Hiley, A. S., McCowin, M. F., Armstrong, A. F., Coppard, S. E., Aguilera, F., Bronstein, O., Kroh, A., & Mooi, R. (2022). Phylogenomic analyses of echinoid diversification prompt a re-evaluation of their fossil record. *eLife, 11*, e72460.

Müller, H. (1965). Zur Stratigraphie der Eifel/Givet-Grenze im östlichen Sauerland. *Fortschritte in der Geologie von Rheinland und Westfalen, 9*, 755–806.

Müller, J. (1856). Über ein Echinoderm mit schuppenförmigen Tafeln und Echinidstacheln im Eifeler Kalk. *Monatsberichte der Königlichen Preußischen Akademie der Wissenschaften zu Berlin, 1856*, 356–361.

Müller, J. (1857). Über neue Echinodermen des Eifeler Kalkes. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin, 1856*, 243–268.

Müller, J. (1859). Über einige Echinodermen der Rheinischen Grauwacke und des Eifeler Kalkes. *Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin, 1858*, 185–198.

Müller, P., Hahn, G., & Bohatý, J. (2013). Agelacrinitid Edrioasteroidea (Echinodermata) from the Middle Devonian of the Eifel (Rhenish Massif, Germany). *Paläontologische Zeitschrift, 87*(4), 455–472.

Nebelsick, J. H. (1996). Biodiversity of shallow-water Red Sea echinoids: Implications for the fossil record. *Journal of the Marine Biological Association of the United Kingdom, 76*(01), 185–194.

Pauly, L. & Haude, R. (2024) New sea urchins (Echinodermata: Echinoidea) from the Famennian of Velbert (W Germany): Evidence for echinoid faunal turnover in the Late Devonian. *Palaeobiodiversity and Palaeoenvironments*, *104*, 571–628.

Pisera, A. (1994). Echinoderms of the Mojcza limestone. In: J. Dzik, E. Olempska, & A. Pisera (Eds) *Ordovician carbonate platform ecosystem of the Holy Cross Mountains, Poland. Palaeontologia Polonica*, *53*, 283–307.

Quenstedt, F. A. (1875). *Petrefactenkunde Deutschlands. Echinodermen (Echiniden)*. Fues´s Verlag (R. Reisland).

Raiswell, R., Newton, R., Bottrell, S. H., Coburn, P. M., Briggs, D. E. G., Bond, D. P., & Poulton, S. W. (2008). Turbidite depositional influences on the diagenesis of Beecher's Trilobite Bed and the Hunsrück Slate; sites of soft tissue pyritization. *American Journal of Science, 308*(2), 105–129.

Rath, S. (2005). *Die Erforschungsgeschichte der Eifel-Geologie. -200 Jahre ein klassisches Gebiet geologischer Forschung.* Ph. D. Thesis, Technical University of Aachen, vi + 239 pp.

Reich, M., & Smith, A. B. (2009). Origins and biomechanical evolution of teeth in echinoids and their relatives. *Palaeontology, 52*(5), 1149–1168.

Ribbert, K. -H. (1992). *Blatt C 5502 Aachen. Geologische Karte von Nordrhein-Westphalen 1 : 100 000.* Geologisches Landesamt Nordrhein-Westphalen.

Schultze, L. (1866). Monographie der Echinodermen des Eifeler Kalkes. *Denkschriften der Kaiserlichen Akademia der Wissenschaften (Mathematisch-Naturwissenschaftlichen Classe), 26*, 113–230.

Smith, A. B. (1984). Echinoid palaeobiology. *Special Topics in Palaeontology, 1*, xii–190.

Smith, A. B. (1994). *Systematics and the fossil record: Documenting evolutionary patterns*. Blackwell Scientific Publications.

Smith, A. B., & Jeffery, C. H. (1998). Selectivity of extinction among sea urchins at the end of the Cretaceous period. *Nature, 392*(6671), 69–71.

Smith, A. B., Gale, A. S., & Monks, N. E. (2001). Sea-level change and rock-record bias in the Cretaceous: A problem for extinction and biodiversity studies. *Paleobiology, 27*(02), 241–253.

Smith, A. B., Reich, M., & Zamora, S. (2013). Morphology and ecological setting of the basal echinoid genus *Rhenechinus* from the early Devonian of Spain and Germany. *Acta Palaeontologica Polonica, 58*(4), 751–762.

Smith, A. B., & Savill, J. J. (2001). *Bromidechinus*, a new Ordovician echinozoan (Echinodermata), and its bearing on the early history of echinoids. *Transactions of the Royal Society of Edinburgh: Earth Sciences, 92*(02), 137–147.

Stearn, C. W. (1956). A new Echinoid from the upper Devonian of Alberta. *Journal of Paleontology, 30*(3), 741–746.

Steingötter, K. (2005). *Geologie von Rheinland-Pfalz,* vii+400 pp. Schweizerbart.

Steneck, R. S. (2013). Sea urchins as drivers of shallow benthic marine community structure. In J. M. Lawrence (Ed.), *Sea urchins: Biology and ecology* (pp. 195–207). Academic Press.

Struve, W. (1955). Die Frage der Eifler Crinoiden-Schicht (Mittel-Devon) im Lichte feinstratigraphischer Untersuchungen. *Senckenbergiana Lethaea, 35*, 279–316.

Struve, W. (1961). Zur Stratigraphie der südlichen Eifler Kalkmulden: (Devon: Emsium, Eifelium, Givetium). *Senckenbergiana Lethaea, 42*, 291–345.

Struve, W. (1992). Neues zur Stratigraphie und Fauna des rhenotypen Mittel-Devon. *Senckenbergiana Lethaea, 71*, 503–624.

Struve, W., Basse, M., & Weddige, K. (2008). 4.1.10 Prädevon, Ober-Emsium und Mitteldevon der Eifeler Kalkmulden-Zone. *Stratigraphie Von Deutschland VIII Devon, 52*, 297–374.

Thomas, A. O. (1920). Echinoderms of the Iowa Devonian. *Bulletin of the Geological Society of America, 31*, 211–213.

Thomas, A. O. (1921). Echinoderms of the Iowa Devonian. *Iowa Geological Survey Annual Report, 29*, 385–552.

Thompson, J. R., & Bottjer, D. J. (2019). Quantitative analysis of substrate preference in Carboniferous stem group echinoids. *Palaeogeography, Palaeoclimatology, Palaeoecology, 513*, 35–51.

Thompson, J. R., Cotton, L. J., Candela, Y., Kutscher, M., Reich, M., & Bottjer, D. J. (2022a). The Ordovician diversification of sea urchins: Systematics of the Bothriocidaroida (Echinodermata:

Echinoidea). *Journal of Systematic Palaeontology, 19*(20), 1395–1448.

Thompson, J. R., Ausich, W. I., & Cournoyer, M. E. (2022b). The morphologic and paleobiogeographic implications of a new early Silurian echinoid from Anticosti Island, Quebec. *Canada. Canadian Journal of Earth Sciences, 59*(12), 973–983.

Thompson, J. R., & Denayer, J. (2017). Revision of echinoids from the Tournaisian (Mississippian) of Belgium and the importance of disarticulated material in assessing palaeodiversity. *Geological Journal, 52*(4), 529–538.

Thompson, J. R., Erkenbrack, E. M., Hinman, V. F., McCauley, B. S., Petsios, E., & Bottjer, D. J. (2017a). Paleogenomics of echinoids reveals an ancient origin for the double-negative specification of micromeres in sea urchins. *Proceedings of the National Academy of Sciences, 114*(23), 5870–5877.

Thompson, J. R., Petsios, E., & Bottjer, D. J. (2017b). A diverse assemblage of Permian echinoids (Echinodermata, Echinoidea) and implications for character evolution in early crown group echinoids. *Journal of Paleontology, 91*(4), 767–780.

Thompson, J. R., Mirantsev, G. V., Petsios, E., & Bottjer, D. J. (2020). Phylogenetic analysis of the Archaeocidaridae and Palaeozoic Miocidaridae (Echinodermata: Echinoidea) and the origin of crown group echinoids. *Papers in Palaeontology, 6*(2), 217–249.

Weddige, K. (1996). Devon-Korrelationstabelle. *Senckenbergiana Lethaea, 76*, 267–286.

Weddige, K. (1998). Devon-Korrelationstabelle. Ergänzungen 1998. *Senckenbergiana Lethaea, 78*, 243–265.

Wolburg, J. (1933). Das Devon im Gebiet der oberen Lenne. *Abhandlungen der Preußischen Geologischen Landesanstalt, Neue Folge, 151*, 1–70.

Zittel, K.A. (1879). *Handbuch der Palaeontologie. I. Band, Paleozoologie. Abtheilung, Protozoa, Coelenterata, Echinodermata und Molluscoidea*, viii +765 pp. R. Oldenbourg.