An Upper Mississippian echinoderm microfauna from the Genicera Formation of northern León (Carboniferous, Cantabrian Mountains, N Spain)

Joachim PABST* & Hans-Georg HERBIG

Institut für Geologie und Mineralogie, Universität zu Köln. Zülpicher Str. 49a, D-50674 Köln. jpabst2@uni-koeln.de; herbig.paleont@uni-koeln.de

* Corresponding author

Pabst, J. & Herbig, H. 2020. An Upper Mississippian echinoderm microfauna from the Genicera Formation of northern León (Carboniferous, Cantabrian Mountains, N Spain). [Microfauna de equinodermos del Misisipiense Superior de la Formación Genicera del norte de León (Carbonífero, Cordillera Cantábrica, N de España)]. Spanish Journal of Palaeontology, 35 (1), 47-76.

ABSTRACT

For the first time an echinoderm microfauna is recorded from the cephalopod limestone facies (‘griotte facies’) of the lower Carboniferous (Mississippian) Genicera Fm. (Alba Fm.). The formation is widespread in the Cantabrian Mountains in NW Spain, but the ossicles are from some sections in the surroundings of the Bernega valley in northern León. They have been derived from insoluble acetic acid residues from samples of the upper and especially of the uppermost part of the formation (Canalón Mb. and Millaró Beds). The microfauna include taxonomically treated wheel-shaped ossicles, sieve-plates and rods of holothurians, goniodonts of ophiocistioids, and ophiuroid and stenuroid skeletal elements. From the Palaeozoic of Spain Ophiocistioida, Stenuroidea, Apodida (Holothuroidea), and allagecrinids (microcrinoids) are first reported. Here, we describe two new species: Linguaserra heidii n. sp. (Ophiocistioida) and Calclyra bifida n. sp. (Ophiuroidea). Indeterminate echinoderm remains are also figured and discussed. The findings stress the importance of a diverse but still poorly documented microfauna.

RESUMEN

Por primera vez se describe una microfauna de equinodermos de las calizas nodulosas con cefalópodos (“griotte facies”) de la Formación Genicera (Formación Alba) del Carbonífero inferior (Misisipiense). Si bien esta formación es de considerable extensión en la Cordillera Cantábrica en el norte de España, los oscículos descritos solo proceden de unas secciones de los alrededores del valle de Bernega al norte de León. Tras un tratamiento con ácido acético, éstos han sido identificados en los residuos insolubles de pruebas de la parte superior y especialmente de los últimos niveles de dicha formación (Miembro Canalón y Capas de Millaró). La microfauna incluye oscículos con forma de rueda, placas perforadas y bastones de los holotúroidos, goniodontos de los ophiocistioides y elementos de ophiuroideos y stenuroides, todos ellos taxonomicamente estudiados. Varios elementos de la microfauna representan hallazgos inéditos del Paleozoico de España, incluso de sus correspondientes rangos más altos como Ophiocistioida, Stenuroidea, Apodida (Holothuroidea), y allagecrinidos (microcrinoideos). En este trabajo describimos
1. INTRODUCTION

The Cantabrian Mountains form the most external zone of the northern branch of the Spanish Variscides, named Cantabrian Zone (Lotze, 1945), which is characterized by a complex pattern of thrust slices and nappes (Julivert, 1971). During most of the Mississippian period that foreland basin passed through the pre-orogenic starved basin phase characterized by pelagic deeper water deposits (Kullmann et al., 1977; Marcos & Pulgar, 1982; Colmenero et al., 2002). During the mid and late Tournaisian, some meters thick black shales developed (Vegamían Fm.) (Comte, 1959). They are overlain by condensed pelagic nodular cephalopod limestone (‘griotte’) of the Genicera Fm. (Wagner et al., 1971), respectively Alba Fm. (Comte, 1959), including locally a subordinate package of siliceous shales and cherts. The formation does not exceed a thickness of 55 m in spite of its extended stratigraphic range, reaching from the diachronous base between latest Tournaisian and earliest Viséan (Scaliognathus anchoralis to Gnathodus texanus zone) to the late Serpukhovian (Gn. truyolsi zone). Among numerous studies, some relevant biostratigraphic papers are from van Adrichem Boogaert (1967), Higgins (1971), Higgins & Wagner-Gentis (1982), García-López & Sanz-López (2002) and Nemyrovská (2005). In the last decade, uppermost Viséan and Serpukhovian conodonts and smaller foraminifers of the Genicera Fm. gained attention due to their importance for definition of a GSSP at the Viséan–Serpukhovian boundary (e.g. Sanz-López et al., 2007; Cózar et al., 2016; Sanz-López et al., 2019). The Genicera Fm. and its lateral equivalents, e.g. the Carrión Fm. of Nemyrovská (2005) from the Palentine realm, are widespread in all tectonic units of the Cantabrian Mountains containing Mississippian rocks. Its sediments represent the largest preserved late Palaeozoic pelagic carbonate platform of the European–North African Variscides. However, analogous facies are also widespread in other South Armorican Massifs (Pyrenees, Catalan Coastal Ranges, Menorca).

The limestone of the Genicera Fm. yielded a wealth of fossils, first mentioned by Schulz (1837), Prado & de Verneuil (1850) and Barrois (1882) from the “griotte limestone”, resp. “marbre griotte”. Pelagic dwelling organisms and taxa preferring deeper-water environments predominate. These are goniatites, cyathaxonid corals, trilobites characteristic of the Kulm facies, and conodonts; opposed brachiopods are scarce (see review in Sánchez de Posada et al., 1996). Later contributions added to the knowledge of bivalves (Amler & Winkler Prins, 1999) and agglutinating foraminifers (Balthasar & Amler, 2003; Herbig et al., 2011).

Macroscopic remains of echinoderms are exceedingly rare within the formation, although articulated pelmatozoan stem ossicles occur in places, and disarticulated remains are quite common in thin sections. Herbig (1982, 1994) described an at least in part autochthonous monospecific crinoid fauna with Balearocrinus cantabricus Herbig, 1982, a genus, which is also known from time-equivalent deepwater deposits of Menorca (Bourrouilh & Termier, 1973) and the Bechar Basin of Algeria (Webster et al., 2004). A further crinoid cup from the Genicera Fm. of northern León was described by Breimer (1962, not figured); Rhabdocrinus scotocarbonarius from contemporaneous cephalopod limestones of the Palentine realm (Morris, 1992) belongs to Balearocrinus cantabricus (Herbig, 1994).

Zamora (2016) reviewed the Palaeozoic echinoderms from northern Spain and listed the few isolated Carboniferous finds. Except from crinoids, descriptions of Pennsylvanian blastoids (Sieverts-Doreck, 1951; Joysey & Breimer, 1963), asterozoans and echinoids (Bless & Sánchez de Posada, 1971) exist. Bless & Sánchez de Posada (1971) also mentioned holothurian ossicles without further specification. First short accounts on the present fauna were published by Pabst & Herbig (2018, 2019). Herein, we document these first mainly non-crinoid echinoderm remains from the Genicera Fm., namely disarticulated holothurian, ophiuroid, ophiocistoid and stenurid ossicles as well as other indeterminate echinoderm ossicles in detail. It has to be stressed that these are the first reports of ophiocistioids, of apodid holothurians, of some “arcaic ophiuroids” (Furcaster among Oegophiuroidea, Stenuroida) and of microcrinoids (allagecrinids) from the Palaeozoic of Spain. Apart...
from two Upper Devonian occurrences of actinopodian holothurians (\textit{?Microantyx} Kornicker & Imbrie, 1958 and one eucaudinid) described by García-López & Truyols (1974), no taxonomical study on holothuroid ossicles from the Palaeozoic of Spain exists at all.

All ossicles have been derived from three sections in northern León during an ongoing study linking carbonate microfacies and agglutinating foraminifers.

2. GEOLOGICAL AND STRATIGRAPHICAL SETTING

The studied sections Millaró, Olleros de Alba and Rabanal de Fenar belong to the Asturo-Leonese facies realm. They are situated in the Sobia-Bodón and Somiedo-Corecilla units, which are two of the typical thin-skinned nappe structures constituting the Cantabrian Mountains (Julivert, 1971; Pérez-Estaún et al., 1988) (Fig. 1). Detailed studies of the Millaró section are from García-López & Sanz-López (2002) and Sanz-López et al. (2007). Previous data from Olleros de Alba were summarized and supplemented by García-López & Sanz-López (2002), including the ammonoid and trilobite findings of Higgins \textit{et al.} (1964) and Gandl (1977). The section north of Rabanal de Fenar, southeastern Alba Syncline, hitherto remained unstudied. A near-by section is noteworthy due to an important, local debrisflow deposit at the top of the Genicera Fm. reworking limestone clasts of the San Adrián Mb. (Keller \textit{et al.}, 2008).

In the type locality of the Genicera Fm. Wagner \textit{et al.} (1971) distinguished three members, from below Gorgera Mb. (cephalopod limestone), Lavandera Mb. (shales and cherts) and Canalón Mb. (cephalopod limestone). However, this subdivision varies considerably in the Asturo-Leonese facies realm, as exemplified by sections in the wider surroundings of the Bernesga Valley. In the southernmost outcrops, up to 20 m red and green shale and marl appear in the uppermost Genicera Fm. (Olaja Beds, Wagner \textit{et al.}, 1971). Further north, dark grey micritic limestone occur in many sections above the Canalón Mb. (San Adrián Mb., Reuther, 1977; Kullmann \textit{et al.}, 1977), once more overlain by a thin cephalopod limestone package (Millaró Beds, Sanz-López \textit{et al.}, 2004) (Fig. 2). Like previous authors, we include the San Adrián Mb. and the overlying Millaró Beds into the uppermost Genicera Fm., contrary to Nemyrovská \textit{et al.} (2011), who proposed that both form the base of the overlying Barcaliente Fm. (Wagner \textit{et al.},

\begin{figure}
\centering
\includegraphics[width=\textwidth]{figure1.png}
\caption{Modified geological map of the Cantabrian Zone according to Julivert (1971) and Pérez-Estaún (1988) with the localization of the samples that provided remains of echinoderms.}
\end{figure}
Figure 2. Section of the Genicera Fm. at Millaró de la Tercia (Province León) with the samples that provided echinoderm remains specifying their contents. Conodont zones from García-López & Sanz-López (2002) and Sanz-López et al. (2007).
1971). Elsewhere, like in the studied section Olleros de Alba, the siliceous Lavandera Mb. is completely missing, and, like in the locality of Rabanal de Fenar, conspicuous debris flow sediments, however consisting of reworked nodular and cephalopod limestone might be intercalated in the Canalón Mb.

The differentiated development of the uppermost Genicera Fm. in northern León reflects the different segments of a vanishing, south-dipping pelagic carbonate ramp (Sanz-López et al., 2004). The shales of the Olaja Beds represent the deepest, most distal part of the ramp, where the first flysch of the Cantabrian Zone from the Variscan orogen front prograding from the South (Kullmann & Schönenberg, 1975) were deposited. The dark grey carbonates of the San Adrián Mb. correspond to the opposite, more proximal part of the ramp, receiving gravitationally redeposited, probably mostly calciturbiditic material from the foreland carbonate platform. Debrisflow sediments indicate tectonic ruptures or steepening of the ramp.

### 3. LITHOLOGY AND CARBONATE MICROFACIES

The predominantly calcareous upper Genicera Fm. (Canalón Mb. to Millaró Beds) in the studied sections consists mostly of light-grey, pinkish and cream-coloured, well-bedded to wavy bedded cephalopod limestone and subordinate red nodular and flaser bedded limestone. Beds are often separated by centimetric shale interbeds. Thin-bedded platy limestone and layers of limestone nodules in argillaceous matrix occur rarely. Locally, debrisflow sediments consisting of reworked nodular limestone occur. Besides, characteristic dark micritic limestone constitutes the San Adrián Mb.

All studied samples are cephalopod limestones from the upper and uppermost part of the Genicera Fm. (Table 1). Most of the predominant mudstones and the less frequent, mostly sparsely packed wackestones are homogenized due to bioturbation (Figs 3b, 3d, 3g, 3m). They show stirred up bioclasts (Fig. 3e) as well as defined burrows (Figs 3f, 3m).

Relicts of primary bedding occur. These are distinct laminae, e.g. of enriched, coarser grained bioclasts, indicating episodic influx of material prior to bioturbation (Fig. 3b). Some bioclasts might be encrusted by ferruginous microstromatolites (Fig. 3d). Also distinct, in cases ferro-manganese encrusted discontinuity surfaces occur in different microfacies. In mudstones scattered remains of planktonic organisms like radiolaria, globochaetes, ultra-thin-shelled ostracodes and larval molluscs (goniatitites, bivalves and/or brachiopods) predominate. Rare benthic elements might occur. In sample M9, section Millaró, such a microfacies is reworked in a debrisflow facies, as indicated by its completely heterogenic texture. It is characterized by a pelitized matrix, i.e. very small intraclasts of reworked mud, by scattered intraclasts up to 10 mm in diameter and by exceedingly large bioclasts, in cases with rotated geopetal structures (Figs 3a, 3k).

Sample M4, section Millaró, reveals a bioturbated, pure radiolaria mudstone from the very distal, deep ramp (Fig. 3m). Also a packstone mainly composed of globochaetes (Figs 3d, 3h, 3j, sample OLP13, section Olleros de Alba), indicates basinal environments (Vachard et al., 1994). In the less frequent wackestones, which casually might grade into packstones, remains of bentonic invertebrates are more common. They comprise fragments of echinoderms (Figs 3h–i), thick-shelled adult gastropods, bivalves and brachiopods, thick-shelled ostracodes, as well as rare trilobites (Fig. 3j) and bryozoans (Sample M13, section Millaró).

Distinct is a microbialite microfacies (Figs 3c, 3l, sample RF2, section Rabanal de Fenar), already noted from the Genicera Fm. by Mamet & Boulvain (1991) and Balthasar & Amler (2003). It consists of a meshwork of clotted peloids and irregular spar-filled fenestrae that are partly floored with peloidal internal sediment. Bioclasts are missing except for scattered radiolarians and thin-shelled ostracodes. However, agglutinating foraminifers from the Reophax biofacies in the microbialite facies indicate a basinal, oxygen-deficient environment (Gutschick & Sandberg, 1983; Sandberg & Gutschick, 1984; Herbig et al., 2011).

Macrofacies and microfacies indicate the well-known general pelagic environment of the Genicera Fm., but surprisingly a more detailed facies model does not exist except for the studies of Eichmüller & Seibert (1984) and Seibert (1986). Discontinuity surfaces and associated intraclasts result mostly from halmyrolitic processes. They indicate condensation, omission and might result in cryptohardgrounds. The mudstones with predominantly planktic organisms are from true basinal environments. However, globochaete-bearing packstones prove redeposition within the deep basin by pelagic turbidites and, hence the existence of a seafloor topography. Also the gravitationally redeposited debrisflow facies documents intrabasinal slopes or scars. Microbialites are related to the deep oxygen-deficient basin. Only the wackestone facies with higher diversity and abundance of predominantly benthic faunal elements indicates somewhat shallower, but persisting pelagic environments.

Concerning the echinoderms, apart from quite abundant columnnals and brachials of crinoids, only some transverse sections of echinoid spines were determinable. Further indeterminable echinoderm plates are present, but from the taxon groups described herein not a single element could be reliably identified in the thin-sections.
Table 1. Geographic and lithostratigraphic position of the echinoderm-ossicle bearing samples and carbonate microfacies.

| Sample | Section | Coordinates | Tectono-stratigraphic Unit | Stratigraphy | Conodont zone (chronostratigraphy after Sanz-López et al., 2007) | Microfacies |
|--------|---------|-------------|-----------------------------|--------------|---------------------------------------------------------------|-------------|
| M13    | Millaró de la Tercia | 42°58'40''N 5°38'54''W | Bodón Unit | Millaró Beds; uppermost bed (= uppermost bed of Genicera Fm.) | Gnathodus truyolsi Zone late Serpukhovian (middle/late Arnsbergian) | pelagic wackestone |
| RF2    | Rabanal de Fenar | 42°49'12''N 5°34'35''W | Somiedo-Correcilla Unit | Transition Olaja Beds/Millaró Beds; lowermost bed overlaying San Adrián Mb. | Gn. bilineatus bollandensis Zone Serpukhovian (early Arnsbergian) | microbialite |
| M9     | Millaró de la Tercia | 42°58'40''N 5°38'54''W | Bodón Unit | Canalón Mb, uppermost bed below San Adrián Mb. | Lochria nodosa Zone uppermost Viséan (Brigantian/early Serpukhovian (Pendleian) | debrite (intraclast-bearing peloidal packstone) |
| OLP13  | Olleros de Alba | 42°48'12''N 5°41'58''W | Somiedo-Correcilla Unit | Lower Canalón Mb. | Gn. bilineatus bilineatus Zone late Viséan | globochaete wackestone to packstone |
| M4     | Millaró de la Tercia | 42°58'40''N 5°38'54''W | Bodón Unit | Lowermost Canalón Mb. | Gn. praebilineatus Zone late Viséan | bioturbated radiolaria |

Figure 3. Carbonate microfacies of the echinoderm ossicles bearing samples from the upper Genicera Fm. in overview (a–d) and detail (e–m). (a, k) Debrisflow sediment consisting of bioturbated peloidal packstone with scattered dark intraclasts. (k) Detail showing dark intraclasts floating in the pelletized matrix. Millaró de la Tercia, uppermost bed of Canalón Mb. Sample M9 (GIK 1411-M9). (b, e–g) Grey, bioturbated pelagic wackestone with diverse organisms showing relictic bedding. Predominating microbioclasts and radiolarians in a strongly burrowed micritic matrix in the lower part are overlain by a bioclast-rich part with strongly fragmented shells (brachiopods and/or bivalves), goniatites, crinoid ossicles, larval shells ("filaments") and undeterminable microbioclasts. (e) Detail from the lower part with abundant radiolarian ghosts filled by micritic cement, which is also seen as geopetal infill in scarce shells. Note stacking of shells by bioturbation. (f) Detail from the lower part showing well-preserved echinoderm ossicle of unknown affinity and embryonic ammonoid in strongly bioturbated micritic matrix. (g) Detail from the upper part with abundant bioclasts, fragmented and texturally homogenized due to bioturbation. Millaró de la Tercia. Uppermost bed of the Millaró Beds (= uppermost bed of the Genicera Fm.). Sample M13 (GIK 1411-M13). (c, l) Light grey, radiolarians and planktonic ostracodes bearing microbialite. The lack of benthic biota appears to be well correlated with the basinal, oxygen depleted Reophax biofacies of the insoluble residue. (l) Detail showing sparitic fenestrae within clotted peloidal micrite. Lowermost bed of a nearly 3 m thick succession of intercalated red and green shales and cephalopod limestone below the base of the Barcaliente Fm., probably an equivalent of the Millaró Beds. Rabanal de Fenar. Sample RF2 (GIK 1411-RF2). (d, h–j) Red globochaete wackestone/packstone including other planktic biota like embryonic goniatites, ultra-thin shelled ostracodes, filaments and common radiolarians, the latter only seen as micritic "shadows" and barely discernible from the matrix. Few larger shells, trilobite and crinoid fragments redeposited from shallower environment. Note bored and ferromanganese encrusted shell at lower left. (h) Detail of a burrow fill with some micrite-filled radiolarian ghosts at its floor, well-preserved echinoderm ossicle, and uniserial globochaete colony within embryonic ammonoid. (j) Detail with well-preserved crinoid columnal. j: detail showing the general appearance of the globochaete-rich matrix and trilobite fragment. Olleros de Alba, lower Canalón Mb. Sample OLP13 (GIK 1411-OLP13). (m) Bioturbated radiolarian mudstone; additional biota missing. Millaró de la Tercia, lowermost Canalón Mb. Sample M4 (GIK 1411-M4).
4. METHODS AND MATERIALS

The herein presented echinoderm ossicles were a casual find of a research on arenaceous foraminifers. They have been derived from limestone processed with low concentrated acetic acid (8–10%) for three to four days. Hence, they were only obtained from the size fraction 0.1–0.2 mm and 0.2–0.63 mm, being aware that concerning echinoderm ossicles a study of coarser fractions up to at least 5 mm is pendent. Microfossils of the residues were, in descending order, agglutinating foraminifers, conodonts, radiolarians, few ichthyolites and hexactinellid sponge spicules, and, most rarely, not silicified echinoderm ossicles. Due to their calcareous nature, echinoderm remains are normally missing or are very rare and poorly preserved after acid treatment. However, their high-Mg calcite skeleton is transformed early in diagenesis into the chemophysical stable low-Mg calcite; moreover, the monocrystalline nature of the ossicles is largely preserved (e.g. Smith, 1990; Ausich, 2001). Both increase the resistance to acid digestion, especially within a fine-grained calcareous matrix (Zankl, 1966). A low content of argillaceous material also seems to favour a selective dissolution (Mostler, 1968a), although Boczarowski (2001) denoted that the protective function of clay particles covering the ossicles in the residue might also be considered. Anyhow, an accurately timed interruption of digestion and the very fine-grained, pure carbonate rock constituting our samples appears to be crucial for preservation of the herein presented microfauna.

The richest echinoderm fauna, including the most spectacular ossicles, were obtained from fraction 0.1–0.2 mm of sample M13, uppermost bed of the Genicera Fm. (Millaró Beds), section Millaró (Fig. 2). This fauna, albeit mostly only fragmentary and strongly corroded, comprises approximately 25% of all microfossils of the mentioned fraction: 300 g of digested limestone provided all together about 1450 microfossils, this means about 360 echinoderm ossicles. The other productive samples provided about 30 echinoderm ossicles from comparable sample weights.

5. THE ECHINODERM OSSICLES

The recovered ossicles reveal a differentiated fauna comprising “arcaic ophiuroids”, holothurians, ophiocistioids, echinoids and crinoids. About 40% of the ossicles were poorly preserved or not determinable. The remaining specimens could be assigned approximately half to holothurians, tentatively including all wheel-shaped ossicles and the majority of the sieve plates, and half to “arcaic ophiuroids”. Few were identified as remains of ophiocistioids, echinoids and crinoids.

Two Palaeozoic “arcaic ophiuroid” ossicle sets are recognizable. First, distinctive elements of the Calclyridae Frizzell & Exline, 1956 (= perforated ophiuroid spines) (Figs 4a–c) and co-occurring skeletal elements resemble assemblages reported by Boczarowski (2001) from the Middle Devonian of Poland that were attributed to the genus Furcaster Stürtz, 1886, order Oegophiurida Matsumoto, 1915. The co-occurring elements comprise vertebrae composed of two halves loosely fused along a suture (Figs 4e–f), various kinds of spines (Figs 4g–i) and possible lateral arm plates (Figs 7k–m). Mostler (1971a) described a similar fauna with Calcylyra from the Mississippian of Afghanistan. Further Calcylyra species were reported from the late Permian of Central Germany (Frizzell & Exline, 1956), SW USA (Wernlund, 1977) and Sicily/Italy (Kozur & Mostler, 1989). The Oegophiurida are regarded as Palaeozoic ophiuroids (O’Hara et al., 2017).

Second, a characteristic lateral arm plate of the genus Pectenura Haude, 1982 was found (Fig. 4d). Boczarowski (2001) still attributed the genus to the ophiuroid order Stenurida Spencer, 1951, but Blake (2013) supposed the stenurids to constitute a separate monophyletic Palaeozoic echinoderm class Stenuroida. However, paraphily of the class was not excluded by Blake (2013) and assumed by O’Hara et al. (2017). Recently, Hunter & McNamara (2018) regarded both the Oegophiurida and the Stenuroida as the “arcaic” stem group of ophiuroids. In both taxa the ambulacrales are not firmly fused to form vertebrae like in the crown group of extant ophiuroids and their Palaeozoic representants (“modern” ophiuroids). Anyhow, further morphological features place the oegophiurids much closer to the “modern” ophiuroids (e.g. basins of tube feet restricted to single ambulacral, lateral arm plates articulate directly with ambulacral).

Among the holothurians both stem groups are identified. Apodida Brandt, 1835 are characterized by the absence of tube feet and distinctive “apodid wheel-shaped” ossicles (Fig. 6) (e.g. Ludwig, 1889-1892; Gilliland, 1993; Smirnov, 1998). Contrary, Actinopoda Ludwig, 1891 possess tube feet and differentiated ossicles (Figs 5, 7n–o). Our assignment to the latter is not always unequivocal, as same morphotypes occur in different echinoderm classes and even in phyla outside of echinoderms. This is the case of branched ossicles (Figs 5h–m) that might be compared with the Palelpidia/Praeuphronides group of the Elasipodida Théel, 1882 (Gilliland, 1993). Also the assignment of sieve plates (Figs 5a–c) is equivocal in spite of the strong similarity of at least the Eocaudina septafornaminalis group to sieve plates of modern Dendrochirotida Grube, 1840 (Pawson, 1966, Gilliland, 1993).

Contrary, according to Miller et al. (2017), four-pillared table plates (Figs 5f–g) like other table plates are distinctive for the clade Pneumonophora Brandt, 1835 sensu Selenka, 1867 within the Actinopoda. According to
6. SYSTEMATIC PALAEONTOLOGY

Phylum ECHINODERMATA Bruguière, 1791 (ex Klein, 1754)
Subphylum ASTEROZOA von Zittel, 1895
Class OPHIUROIDEA Gray, 1840
Order Oegophiurida Matsumoto, 1915
Parafamily Calclyridae Frizzell & Exline, 1956
Paragenus Calclyra Frizzell & Exline, 1956
Type species Prosynapta eiseliana Spandel, 1898

[= Calclyra eiseliana (Spandel, 1898) according to Reich (2007)].

Remarks. Mostler (1971b) showed that perforated spines (“Lochstacheln”) do not belong to holothurians, as assumed with doubt in the erection of Calclyra by Frizzell & Exline (1956). They are restricted to the dorsal side of the ophiuroid disc (Mostler, 1971b) or to the proximal lateral arm plates (Boczarowski, 2001). Although Boczarowski (2001) attributed the isolated ossicles of the paragenus Calclyra to the ophiuroid genus Furcaster Stürtz, 1886, we retain Calclyra for better specific differentiation.

Calclyra bifida n. sp.
(Derivatio nominis. Derived from bifidus (Latin), meaning cleft into two parts, due to the central indentation at the upper margin of the head dividing it into two equal lobes.

Holotype. The specimen GIK 1415-8 from sample M13 (Fig. 4a).

Paratype. The specimen GIK 1413-2 from sample M13 (Fig. 4c).

Additional material. Five specimens, four from sample M13 (GIK 1412-M13-16, GIK 1415-9, GIK 1413-3, GIK 1416-2) and one from sample M9 (GIK 1414-M9-1).

Type locality, type horizon and age. Quarry near the village Millaró de la Tercia, province León, Cantabrian Mountains/NW Spain (Fig. 2, Table 1). Uppermost bed of the Millaró Beds (Genicera Fm.).

Diagnosis. In front view a nearly squared head with a central indentation at its upper margin; shaft relatively long and slender.

Description. Ophiuroid spine with a characteristic basal socle, a shaft and a head. The head consists of three subparallel running rays separating two trapezoid-shaped pores. The lateral rays form wings normal to the plane of the rays. They are bent inward at their rounded margins. The central ray is sharply bent at its top and fused with the lateral wings, resulting in front view in an almost squared, bilobate head with characteristic central indentation at its upper margin. The central ray finally turns obliquely outward and downward, ending as broad, triangle-shaped process. Thus two pores are formed in a basket-like structure. In cross-section the shaft is slightly oval and of irregular thickness.
Remarks. The oval shaft of the holotype (Fig. 4a) is only partly preserved. The slightly oblique view of the paratype (Fig. 4c) shows the real morphology of the shaft. The oblique view simulates a convex run of the lateral rays, which in fact is parallel. The connection of lateral and central rays at the upper margin of the head as well as the central triangular process are not preserved in the paratype, but bending of the central ray toward the front and further downward is still perceptible.

The late Permian *C. eiseliana* is similar to *C. bifida* but the former only has a slightly concave upper margin of the head. Moreover, it differs by the stout appearance with thicker rays and shorter shaft (Frizzell & Exline, 1956; Wernlund, 1977; Kozur & Mostler, 1989). The head of *Calclyra bifida* n. sp. differs from those of the Permian *C. gracilis* Kozur & Mostler, 1989, which are either elongate or oval to nearly circular, with almost rounded to blunt upper margin. *C. carbonica* Kozur & Mostler, 1989, originally attributed to *C. eiseliana* by Mostler (1971a), occurs in stout as well as in slender morphotypes. But his head is suboval outlined, broadest in the lower third and pointed at its upper margin. The Permian *C. triangulata*, *C. spathulata* and *C. spinata*, all erected by Wernlund (1977) from the Guadalupe Mountains/SW USA, just a little have cleft heads. Their names already indicate the differing shape of the heads, i.e. triangular, pointed upwards, spattle-shaped, and with a distinct distal spine. Boczarowski (2001) defined perforated forms from the Frasnian of Poland as *Furcaster* sp. A and compared them with *C. eiseliana*. However, according to the general shape of head and shaft, they are closer to *C. spathulata* Wernlund, 1977 or even *C. gracilis*.

Distribution. Only known from the type material, uppermost Mississippian (Serpukhovian) of the Cantabrian Mountains (NW Spain).

Vertebrae. (Figs 4e–f) Elongate axial arm ossicles with symmetrical lateral processes (wings) for muscle attachment at the thicker, supposedly adoral quarter of the ossicles. The ventral side shows the deep radial groove that carried the axial vessel of the water vascular system (Fig. 4e), the dorsal side a more compact, protecting surface (Fig. 4f). The fused halves along a recognizable axial suture point to an attribution to the genus *Furcaster* (Boczarowski, 2001).

Spines. (Figs 4g–i) Long, straight ossicles with central ridge and two lateral laminae rectangular (?) projecting on each side, either completely smooth (Fig. 4g) or with serrate margin and characteristic oblique lines originating at the central ridge (Figs 4h–i). The ridge might be characteristically braided (Fig. 4i). The extended base of the ossicles displays rapidly converging, additional longitudinal ridges. Analogous spines were reported e.g. by Boczarowski (2001) form the Devonian of Poland and attributed to the genus *Furcaster*.

?Ophiuroid ossicle. (Fig. 4j) The distinctive element is a not completely fused, bilateral symmetrical ossicle. Each half has one knob-like end, followed by a narrow rounded shaft widening above and proceeding into two long spines that project at an angle of about 30° from the axis of the ossicle. The symmetrical shape of the element is reminiscent of a vertebrum, but we are not aware of such long-spined types.

Marginal ossicles of the central disc. (Fig. 4k) A single minute skeletal element with an oval, imperforated base and an eccentrically tiny smooth vertical process; the process has a conical depression or hollow ending with irregular to zigzagged margin. Analogous elements were described by Boczarowski (2001) from the Middle and Upper Devonian of the Holy Cross Mountains/Poland and attributed to ossicles located within the dermis protecting the aboral side of the central disc.

?Ophiuroid spine. (Fig. 4l) A coarse meshed stereomal basal socle (?) with one branched “spine”, roundish in cross section. The “spine” consists of a straight main rod with right and left alternating, oblique upwards projected ridges. According to the general shape of the shaft, they are closer to *C. spathulata* Wernlund, 1977 or even *C. gracilis*.

Distribution. Only known from the type material, uppermost Mississippian (Serpukhovian) of the Cantabrian Mountains (NW Spain).

Indeterminate ophiuroid ossicles (Figs 4e–l)

Figure 4. Ophiuroids, crinoids and echinoids. All from sample M13, except specimen k, which is from sample OLP13. a–c) *Calclyra bifida* n. sp. (a) Holotype (GIK1415-8), front view. (b) Poorly preserved fragment (GIK1413-3), oblique view. (c) Paratype (GIK1413-2), oblique view. (d) Lateral arm plate of *Pectenura* sp. (GIK1413-04). e–f) Ophiuroid arm vertebrae. e: oral view (GIK1413-3). f) Aboral view (GIK1413-8). g–i) Ophiuroid spines. g) Fragment with preserved basal socle (GIK1413-14). h) Fragment with serrate laminae (GIK1412-M13-10). i) Nearly complete specimen with braided ridge (GIK1413-23). j) ?Ophiuroid element (GIK1412-OLP13-3). k) Ophiuroid marginal ossicle of the central disk (GIK1413-V2). l) Ophiuroid or crinoid spine (GIK1415-24). m–o) Crinoid ossicles. m) Columnal (GIK1413-06). n–o) Primary peristomial cover plates (“oralia”) of an allageocrinid microcrinoid. (n) External view (GIK1415-10). (o) Internal view (GIK1415-11). p) Echinoid spine (GIK1413-10). Scale bar = 0.1 mm.
Class STENUROIDEA Blake, 2013
Order Stenurida Spencer, 1951
Genus Pectenura Haude, 1982
Type species Pectenura horni Haude, 1982

**Pectenura** sp.  
(Fig. 4d)

**Material.** 1 specimen, sample M13 (GIK1413-04).

**Description.** Bone-shaped lateral arm plate. One end terminating in a club-shaped expansion. Opposite to the relatively long shaft the convexly bent end develops into two branches of different length. Faint grooves run from the club along the shaft into the coarse-meshed branches. The convex, branched end of the lateral arm plate is thought to wrap a vertebra.

**Remarks.** Very similar lateral arm plates were described by Boczarowski (2001) and attributed to *Pectenura*, which is based on completely preserved ophiuroids reported by Haude (1982) from lowermost Namurian (Serpukhovian) black shales of the Rhenish Mountains, Germany. Especially close seems to be *P. hamata* Boczarowski, 2001 from the early Givetian of the Holy Cross Mountains, Poland.

**Distribution.** Isolated ossicles of *Pectenura* were described from the Middle Devonian and early Upper Devonian of the Holy Cross Mountains (Poland, Boczarowski, 2001) and from the Upper Mississippian (Serpukhovian) of the Cantabrian Mountains (NW Spain; herein). Haude (1982) described complete specimens from the lowermost Namurian (Serpukhovian) of the Rhenish Mountains (Germany).

Subphylum ECHINOZOA von Zittel, 1895
Class HOLOTHUROIDEA de Blainville, 1834
(without rank) ACTINOPODA Ludwig, 1891
Parafamily Calclamnidae Frizzell & Exline, 1956 [pars]
Genus Eocaudina Martin, 1952 emend. Gutschick & Canis, 1971
Type species *Eocaudina septaforaminalis* Martin, 1952 emend. Gutschick & Canis, 1971

Eocaudina mccormacki Frizzell & Exline, 1956  
(Fig. 5a)

1881 Ancistrum? sp.; Etheridge, p. 5, fig. 4.
1932 Ancistrum? sp.; Croneis & McCormack, p. 142, pl. 18, fig. 29, pl. 20, figs 29, 38.
*1956 Eocaudina mccormacki* sp. nov.; Frizzell & Exline, p. 87-88, pl. 3, fig. 9.
1971 *Eocaudina mccormacki* Frizzell & Exline; Gutschick & Canis, p. 334, pl. 47, figs 26, 28, pl. 48, figs 17-30.
1973 *Eocaudina mccormacki* Frizzell & Exline, 1955 [sic!]; Matyja et al., p. 139, pl. 1, figs 3–10, 16, 21, 23, pl. 2, figs 5, 16–17 [cum syn.].
1976 *Eocaudina mccormacki* Frizzell & Exline; Kozur et al., p. 12.
1977 *Eocaudina mccormacki* Frizzell & Exline, 1955 [sic!]; Wemlund, p. 52-53, pl. 1, figs 27-29.
1983 *Thuroholia mccormacki* (Frizzel & Exline) [sic!]; Zhang, p. 333, pl. 1, 1–5.
1984b *Eocaudina gutschicki* Frizzell & Exline; Kozur, p. 63, pl. 3, 4 [only].
1985 *Thuroholia mccormacki* Frizzell & Exline; Zhang, p. 29, pl. 1, 8–9.
1985 *Eocaudina mccormacki* Frizzell & Exline, 1955 [sic!]; Ding, p. 341–342, pl. 1, figs 2-6, 8–9, 17, pl. 3, figs 1-2.
1991 *Eocaudina mccormacki* Frizzell & Exline; Langer, p. 44–45, pl. 7, figs 1, 4, 7, pl. 8, fig. 5.
1993 *Eocaudina mccormacki* Frizzell & Exline; Etheridge (1881) *fide* Gilliland, pl. 11, fig. 3.
1993 *Eocaudina mccormacki* Frizzell & Exline; Zhang, p. 107, pl. 1, fig. 27.

non 2003 *Eocudina mccormacki* Frizzell & Exline [sic!] (= *E. gutschicki vel. E. septaforaminalis*); Aboussalam, pl. 23, fig. 17.
2013 499. *mccormacki* Frizzell & Exline, 1956; *Eocaudina*; Reich, p. 42.

**Material.** 35, partly doubtful assigned specimens, all from sample M13. 12 specimens catalogued (GIK 1413-26, GIK 1413L, GIK 1413-31, GIK 1415e, GIK 1415f, GIK 1415j, GIK 1415L, GIK 1415n, 1 specimen in GIK 1416-3, 3 specimens in GIK 1416-4).

**Description.** Slightly concavo-convex subcircular to subpolygonal sieve plates with thickened outer margin; more or less equal-sized pores, relatively numerous (>50) and small, subpolygonal shaped or, if poorly formed, circular to irregular; lattices relatively thin.
Remarks. Due to their great variability, *Eocaudina* species can be very close to each other and even overlap morphologically (Boczarowski, 2001). We try to exclude at least some clearly distinct species. *E. marginata* (Langenheim & Epis, 1957) differs by its larger central pores surrounded by smaller marginal ones. The often somewhat elongated *E. croneisi* Frizzell & Exline, 1956 has clearly circular pores and an irregular outer margin. Our forms also miss the characteristic enlarged rim of *E. columcanthus* Gutschick et al., 1967. *E. gutschicki* Frizzell & Exline, 1956 has fewer pores (see Matyja et al., 1973) resembling partly small *E. septaforaminalis* with its characteristic, clearly discernible four central pores surrounded by one or more cycles of secondary pores. *E. subhexagona* Gutschick et al., 1967 has distinct hexagonal pores and could be stronger concavo-convex; *E. plaga* Boczarowski, 2001 is completely flat, irregular shaped, and has unaligned pores separated by relatively thick lattices or trabeculae. *E. ovalis* Matyja et al., 1973 has elliptical or elongate outline and more densely distributed pores; *E. gornensis* Matyja et al., 1973 is only a hexagonal variety according to Boczarowski, 2001. Other close species are *E. septaforaminalis*, *E. rimosas* Boczarowski, 2001 or even the Mesozoic *E. mortenseni* Frizzell & Exline, 1956. Similarities and overlapping morphologies led to the reinterpretations of many forms originally defined as *E. mccormacki*. Thus, Matyja et al. (1973) excluded many specimens of *E. mccormacki* originally figured by Gutschick & Canis (1971) and later Boczarowski (2001) reinterpreted all these as *E. septaforaminalis*, likewise *E. mccormacki* from Langer (1991). Additionally, he reinterpreted nearly all *E. mccormacki* retained by Matyja et al. (1973) as *E. septaforaminalis*, *E. ovalis* or *E. plagia*. In our opinion some Carboniferous specimens of Ding (1985) and Zhang (1993) and the Middle Devonian specimen of Aboussalam (2003) also need revision. Already Wernlund (1977) supposed that many species of *Eocaudina* actually are synonyms of *E. septaforaminalis*.

Distribution. *E. mccormacki* is described from the Devonian and Carboniferous of the United States (Cronies & McCormack, 1932; Summerson & Campbell, 1958; Gutschick, 1959; Gutschick & Canis, 1971), the Devonian of Poland (Matyja et al., 1973) and France (Aboussalam, 2003), the Carboniferous of Scotland (Etheridge, 1881 *fide* Gilliland, 1993), Slovakia (Kozur et al., 1976) China (Ding, 1985; Zhang, 1983; 1993), and the Cantabrian Mountains (NW Spain; herein).

**Eocaudina subhexagona** Gutschick, Canis & Brill, 1967 (Fig. 5b)

*1967 Eocaudina subhexagona* n. sp.; Gutschick et al., p. 1469, pl. 186, figs 16–21, pl. 187, fig. 18.

1968b *Eocaudina subhexagona*, Gutschick et al.; Mostler, p. 12, pl. 2, fig. 4.

1973 *Eocaudina subhexagona* Gutschick et al.; Matyła et al., p. 141–142, pl. 1, fig. 22, 24–29, pl. 2, fig. 4 [cum syn.].

1976 *Eocaudina subhexagona* Gutschick et al.; Kozur et al., p. 12.

1977 *Eocaudina subhexagona* Gutschick et al.; Matyla et al., p. 141–142, pl. 1, fig. 22, 24–29, pl. 2, fig. 4 et al.

1976 *Eocaudina subhexagona* Gutschick et al.; Kozur et al., p. 12.

1977 *Eocaudina subhexagona* Gutschick et al.; Matyla et al., p. 141–142, pl. 1, fig. 22, 24–29, pl. 2, fig. 4.

1978 *Eocaudina subhexagona* Gutschick et al.; Ebner & Fenninger, p. 6–7, pl. IV, fig. 3.

1985 *Eocaudina subhexagona* Gutschick et al.; Ding, p. 342, pl. 3, fig. 3.

2001 *Eocaudina? subhexagona* Gutschick et al.; Boczarowski, p. 145, text–fig. 66C–F.

2013 818. *subhexagona* Gutschick et al., *Eocaudina*; Reich, p. 49.

2015 *Eocaudina subhexagona*, Gutschick et al.; Nouredini et al., p. 166, pl. 1, figs 1–9.

Material. 41 fragments, all from sample M13. 3 catalogued specimens (GIK 1413-24, GIK 1413-30, GIK 1416-4).

Description. Slightly arched sieve plate; fragile skeletal lattice and well-developed hexagonal, relatively small pores; no thickened margin; always only fragmentary preserved.

Remarks. Our form is close to *Eocaudina subhexagona* Gutschick et al., 1967 although originally described as stronger curved, up to hemispherical, and with in part larger pores. The attribution to *Eocaudina* and thus to the holothurians is doubtful because similar ossicles were reported from further echinoderm classes (see Boczarowski, 2001).

Distribution. Devonian of Poland (Matyja et al., 1973; Boczarowski, 2001) and Bulgaria (Ebner & Fenninger, 1980), Mississippian of the United States (Gutschick et al., 1967) and the Cantabrian Mountains (NW Spain; herein).

**Eocaudina? sp.**

(Fig. 5c)

Material. 1 specimen, sample M13 (GIK 1413-21).

Description. Triangular, slightly concavo-convex sieve structure with typical *Eocaudina* disposition of subhexagonal to hexagonal pores. Two sides are marginal thickened; the third one is irregular (fractured ?).
Remarks. Somewhat similar is an indeterminate echinoderm remain, questionable attributed to holothurians by Kozur & Mostler (1989; pl. 2, fig. 2) from the Permian of Sicily.

Distribution. Carboniferous (Serpukhovian) of the Cantabrian Mountains (NW Spain, herein).

Genus Spicatocaudina Kozur & Mostler, 1989
Type species Eocaudina spicata (Gutschick, 1959) emend. Frizzell & Exline, 1966

Remarks. Kozur & Mostler (1989) grouped late Palaeozoic Eocaudina morphotypes with a marginal or submarginal spine-like shaft to the new genus Spicatocaudina Kozur & Mostler, 1989 of unknown taxonomic affinity. The distinctive morphology justifies separation of an own genus. However, herein we follow earlier authors who attributed the taxon to the holothurians.

Spicatocaudina spicata (Gutschick, 1959) (Fig. 5d)

*1959 Thuroholia spicatus sp. nov.; Gutschick, p. 132, pl. 25, figs 3, 4, 7–9.

1966 Eocaudina spicata (Gutschick); Frizzell & Exline, p. U659.

1967 Eocaudina spicata (Gutschick); Gutschick et al., p. 1468–1469, pl. 186, figs 35–37, pl. 187, figs 21, 25.

2012 Eocaudina spicata (Gutschick); Gao et al., p. 184, pl. 3, fig. 4.

2013 789. spicatus Gutschick, 1959; Thuroholia; Reich, p. 48.

Material. 1 specimen, sample M13 (GIK 1415-32).

Description. Only very slightly arched, elongated sieve plate with nearly 100 subcircular pores; distinct marginal spine-like pointed process, projected outwards at a small angle and also perforated. Delimited area beside the spine with equal sized small pores surrounded by larger ones; at the opposite side the eocaudina disposition is partly disrupted by fused pores forming large oval ones. Lattices relatively thin. Outer margin partly irregular due to incomplete pores.

Remarks. The marginal process of this ossicle and that of Spicatocaudina spicata are quite similar. Otherwise, the irregular sized pores differ from S. spicata. Apart from the process, the delimited area of small pores surrounded by larger ones resembles Thuroholia cribriformis Gutschick, 1954. Zhang (1983) reported a similar form with one pointed process from the Mississippian of Hunan/China as Paracucumarites sp. attributed to the Holothuroidea.

Distribution. Mississippian (Serpukhovian) of the Cantabrian Mountains (NW Spain, herein).

Parafamily Priscopedatidae Frizzell & Exline, 1956 emend. Gilliland, 1992

Priscopedatidae gen. et sp. indet. (Figs 5f–g)

Material. 1 specimen, sample M13 (GIK 1413-23).
Description. Table plate with a basal Eocaudina-like close-packed subcircular sieve plate and a prominent (eccentrically?) stirrup with height nearly the same than width of the basal plate. Several in part intertwined trabeculae at the base of the stirrup rise up and fuse to form an acute regular four-pillared hollow structure. Transversal branches between the pillars are recognizable.

Remarks. Gilliland (1992, 1993) emended the Priscopedatidae to include spired plates, as there are morphological intergradations from table plates. In fact, intertwined lattices at the base of the stirrup in our specimen are a feature of spired plates. The unique Palaeozoic priscopedatid table plates we found in literature were described by Mostler & Rahimi-Yazd (1976) from the late Permian of northern Iran: Priscopedatus quinguespinosus and Priscopedatus sp., the latter not included in the genus by Gilliland (1993) due to insufficient description and fragmentary preservation. The morphologically strongly differing Spanish form belongs to a new paragenus, but the material is not sufficient to erect a formal taxon.

Distribution. Mississippian (Serpukhovian) of the Cantabrian Mountains (NW Spain; herein).

Order ELASIPODIDA Théel, 1882

Parafamily Stichopitidae Frizzell & Exline, 1956 [pars]

“Palelpidia/Praeeuphronides group” sensu Gilliland, 1993

Genus Tetravirga Frizzell & Exline, 1956

Type species Tetravirga imperforata Frizzell & Exline, 1956

Remarks. Gilliland (1993) discussed the taxonomically enigmatic “Palelpidia/Praeeuphronides group” including as oldest genus Tetravirga from the Upper Mississippian. Already Mostler (1968b) suggested that Praeeuphronides Mostler, 1968a, Multivirga Mostler, 1968b, and Tetravirga belong to one holothurian species. However, the large morphological ranges might be due to convergences within a polyphyletic group. Therefore, further taxonomic treatment needs thorough study of additional material.

Tetravirga sp.

(Figs 5i–m)

Material. 1 specimen, sample RF2 (GIK1412-RF2-5).

Description. Flat, regular cross-shaped, moderately preserved ossicle. One shorter arm probably only fragmentary preserved. The centre of the cross has an only hardly recognizable circular impression.
of the calcareous elements remains obscure. In general, sponge macrofossils are not known from the Genicera Fm. (see e.g. García-Bellido, 2002; García-Bellido & Rigby, 2004), therefore we tend to attribute the rods to the echinoderms, and among them, following Weber (pers. comm. 2018), to the holothurians. Be that as it may, the rods are figured as a distinctive, easily recognizable faunistic element. They could represent different ontogenetic stages; larger specimens might result from extensive allometric growth of the main bar.

**Distribution.** Carboniferous of the Rhenish Mountains/Germany (Weber, pers. comm. 2018) and Cantabrian Mountains (NW Spain/herein).

(without rank) APODIDA Brandt, 1835 (*sensu* Östergren, 1907)

*Parafamily* Palaeochiridotidae Frizzell & Exline, 1966 emend. Gutschick et al., 1967 [pars]

*Genus* Langepis Kozur & Mostler, 2008

Type species *Rota campbelli* Gutschick, 1959

**Remarks.** Kozur & Mostler (2008) introduced the monotypic genus *Langepis* for wheel-shaped ossicles with 4–10 short spokes, a single central perforation and a smooth rim without additional peripheral rings of pores, establishing “*Rota campbelli*” Gutschick, 1959 as the type species. They restricted the likewise monotypic genus *Rota* to wheel-shaped ossicles with two, rarely three peripheral rings of pores with *Rota martini* Langenheim & Epis, 1957 remaining as type species. Initially, Gutschick et al. (1967) proposed both species to be synonymous, an issue also mentioned but not further discussed by Gilliland (1993).

*Langepis campbelli* (Gutschick, 1959)

(Figs 6a–c)

pars 1957 *Rota martini* n. sp.; Langenheim & Epis, p. 170, pl. 1, figs 17–18, 20, 23, 25 [only].

*1959 Rota campbelli*, n. sp.; Gutschick, p. 135–136, pl. 26, figs 1–21, 26, 27, 32–35, text-fig. 4.

1967 *Rota campbelli* Gutschick; Gutschick et al., p. 1474, pl. 187, figs 1–6, 23, pl. 188, figs 1–2, 8–9, 14–15, 21–23, 28–31, 36, 40–43, text-fig. 4 (1, 5, 15, 21–22, 27–28, 33, 36).

1984 *Rota campbelli* Gutschick; Sandberg & Gutschick, pl. 8, fig. G.

2013 121. *campbelli* Gutschick, 1959; *Rota*; Reich, p. 34.

**Material.** 3 specimens, sample M13 (GIK 1415-5, GIK 1415-7, GIK 1412-M13-3).

**Description.** Wheel-shaped ossicles with 6–8 spokes separated by subtriangular to suboval spoke interspaces with radial orientated long axis; spokes slightly arched towards the dorsal side and tapering towards the undulated to polygonal outer line; smooth rim. Concavo-convex relatively small central area with a perforation in the middle (in Fig. 6b diagenetically obscured); diameter 190–250 µm.

**Remarks.** The finding of wheel-shaped ossicles within ophiocistioids by Haude & Langenstrassen (1976a) led to confusion concerning their taxonomic assignment. One essential differing feature is a tripartite central structure at the ventral side of the ophiocistioid wheels. Boczarowski (1997) revised and reassigned several taxa, supposing inter alia that the specimen figured by Sandberg & Gutschick (1984) as *Rota campbelli* might belong to the ophiocistioid *Protocaudina* Croneis in Croneis & Mccormack, 1932. However, several authors like Reich & Mostler (2002), Reich (2010a, 2012), and Nouredini et al. (2015) continued to assign wheel-shaped ossicles with a tripartite or tetrapartite central ventral structure like *Protocaudina* and *Microantyx* to the holothurians. Reich (2012) stressed the fact that similar post-Triassic wheel-shaped ossicles, not considered by Boczarowski (1997), are unequivocal holothurians, as ophiocistioids became extinct during the Triassic (Reich et al., 2018).

**Distribution.** Lower Mississippian of Arizona, Indiana, Missouri and Montana (USA). Apart from our Serpukhovian findings in the Cantabrian Mountains (Spain), also Kozur and Mostler (2008) mentioned Mississippian occurrences in Europe, but without further details. Reich (pers. comm. 2018) mentioned an unpublished occurrence from the Viséan of the Rügen Island (Baltic Sea, core Dranske 1/68).

*Genus* Rotoides Gutschick et al., 1967

Type species *Rotoides tretomesota* Gutschick et al., 1967

**Remarks.** According to Gutschick et al. (1967) the genus *Rotoides* is similar to the genus *Langepis*, but the first has more spokes (8 to 12) and a larger central area without any perforation or central dome. The smooth rim and the lack of an accentuated dorsal central dome differentiate *Rotoides* from Carboniferous Theeliidae Frizzell & Exline, 1956.
Rotoides sp.  
(Figs 6d–j)

**Material.** 7 specimens. 1 of sample M4 (GIK 1414-M4-R1), 1 of sample M9 (GIK 1414-M9-R1) and 5 of sample M13 (GIK 1415-6, GIK 1413-4, GIK 1413-5, GIK 1413-6, GIK 1413-7).

**Description.** Circular, mostly slight undulated ossicles; 8–12 spokes, slightly arched and getting thinner towards the rim; spoke interspaces triangular to subtriangular; smooth rim bent in different rates inward towards the dorsal side. Central area nearly half the diameter of the ossicle, slightly domed towards the dorsal side and without any perforation or ornamentation, neither on the ventral side, nor on the dorsal side. Diameters from 180–280 µm, in average 200 µm.

**Remarks.** Very similar is *Rotoides imperforata* Gutschick et al., 1967. Our specimens differ by a smaller central area and bigger spoke interspaces. Concerning *Rotoides imperforata*, Kozur (1984a) postulated that the species cannot be distinguished from *Theelia Schlumberger*, 1890 and called a single Moscovian specimen from the Bükk Mountains/Hungary *Theelia imperforata* (Gutschick et al., 1967), not followed by Reich (2013). Remarkable is the great similitude between our forms and wheel-shaped ossicles of the ophiocistioid *Rotasaccus dentifer* Haude & Langenstrassen, 1976a, only discernible by the characteristic central tripartite ornamentation on the ventral side of the latter (see Haude & Langenstrassen, 1976a). *Rotoides* sp. also resembles *Microantyx* morphotypes, but in this case a tetrapartite central structure on the ventral side of the latter is the differencing feature (e.g. Boczarowski, 1997; Bohatý & Herbig, 2010; Nouredini et al., 2015).

**Distribution.** Mississippian of the USA (Indiana, Missouri, Montana), Serpukhovian of Spain (Cantabrian Mountains, herein).

Paleochiridotidae gen. et sp. indet.  
(Figs 6k–m)

**Material.** 2 specimens, sample M13 (GIK 1412-M13-8, GIK 1415-4).

**Description.** Flat, circular ossicles with respectively 12 and 14 short and thick spokes separated by triangular interspaces; turned-up rim with regular continuous fine denticulation (Fig. 6m); large central area, more than half the diameter of the ossicle. Considerable size range: 160–310 µm.

**Remarks.** We did not find similar wheel-shaped ossicles in literature and kept the sparse material in open nomenclature. General characters, especially the fine regular and continuous denticulation of the rim, resembles modern wheel-shaped ossicles of the Apodida (compare e.g. Gilliland, 1993; Smirnov, 1998).

**Distribution.** Serpukhovian of the Cantabrian Mountains (Spain, herein).

Class OPHIOCISTIOIDEA Sollas, 1899
Order unnamed
Family Linguaserridae Reich & Haude, 2004
Genus Linguaserra Langer, 1991 emend. Reich, 2007
Type species Linguaserra ligula Langer, 1991

**Remarks.** *Linguaserra* was earlier placed in the Rotasaccidae Haude & Langenstrassen, 1976a, but separated by Reich & Haude (2004) in an own family, which is interpreted to be a conservative stem-line of the ophiocistioids, reaching from the early Silurian to the Upper Triassic (Reich & Haude, 2004; Reich, 2010a; Reich et al., 2018). The supposed second genus of the family, Rogeriserra (in Reich & Smith, 2009), remained a nomen nudum, and was excluded from Linguaserridae by Reich (2007). Its exact systematic position is unknown, but is supposed intermediate between ophiuroids and ophiocistioids (Reich & Smith, 2009).

Figure 6. Apodid wheel-shaped ossicles.  
(a–c) *Langepis campbelli* (Gutschick, 1959). Sample M13. (a) Specimen with 6 spokes, ventral view (GIK1415-5). (b) Specimen with 7 spokes, ventral view (GIK1415-7). (c) Specimen with 8 spokes, dorsal view (GIK1412-M13-3).  
(d–j) *Rotoides* sp. (d) Fractured specimen with originally 10 spokes, ventral view (GIK1415-6). Sample M13. (e–f) Specimen with 9 spokes, dorsal view (e), lateral view (f) (GIK1413-4). Sample M13. (g) Specimen with 8 spokes, ventral view (GIK1413-5). Sample M13. (h) Fractured specimen with originally up to 12 spokes, dorsal view (GIK1414-M9-R1). Sample M9. (i) Specimen with 10 spokes, ventral view (GIK1414-M4-R1). Sample M4. (j) Specimen with 9 spokes, ventral view (GIK1413-6). Sample M13.  
(k–m) Paleochiridotidae gen. et sp. indet. Dorsal views. Sample M13. (k) Specimen with 14 spokes (GIK1412-M13-8). (l) Specimen with 12 spokes, majority of spoke interspaces obscured by infilling (GIK1415-4). (m) Amplified (x2) detail of specimen 6l with hardly recognizable but definitely uniformly very fine denticulated rim. Scale bars = 0.1 mm.
Linguaserra heidii n. sp.  
(Figs 7a–b)

1997 Linguaserra sp.; Weber, p. 489, pl. 1, fig. 1.
2004 sp. sensu Weber (1997), Linguaserra; Reich & Haude, p. 494.
2014 Linguaserra. sp. sensu Weber (1997); Reich & Kutscher, fig. 2(3).
2018 Linguaserra. sp. sensu Weber (1997); Reich et al., p. 5, fig. 5(3).

**Remarks.** The genus Linguaserra includes five known species. These are L. franzeneae Reich & Kutscher, 2014 from the Llandovery (early Silurian) of Gotland (Sweden), L. ligula Langer, 1991 from the Eifelian to Givetian (Middle Devonian) of the Rhenish Mountains (Germany), L. spandeli Reich, 2007 from the Zechstein (uppermost Permian) of Thuringia (Germany), L. triassica Reich in Reich et al., 2018 from the Upper Triassic of the Dolomites (N Italy) and the new species L. heidii n. sp., which hitherto was known from the uppermost Tournaisian (Mississippian) of the Rhenish Mountains (Richrath Mb. of Heiligenhaus Fm., see latest biostratigraphic and sequence stratigraphic data in Bábek et al., 2010 and Herbig, 2016).

Linguaserra heidii n. sp. is the smallest and most slender lanceolate species with an expressed pinched abaxial part (Table 2). L. franzeneae is tongue-shaped, L. ligula acute pole-shaped, and L. spandeli is similar in outline to L. heidii n. sp., but wider and more compact. In outline, L. triassica is related to L. spandeli, but distinct from all other species by its ridged lateral denticles. Compared to all other species, the long teeth of L. heidii n. sp. are exceptionally discrete.

**Distribution.** Uppermost Tournaisian of the Rhenish Mountains (Germany) and Serpukhovian of the Cantabrian Mountains (NW Spain).

Linguaserra cf. heidii  
(Fig. 7c)

**Material.** 1 specimen, sample M13 (GIK 1415-2).

**Description.** Small, extremely slender, nearly flat, symmetrical goniodont; acute central main tooth, four acute divergent and discrete lateral teeth on each flank (partly broken) nearly as big as the main tooth; long and slender, pinched abaxial part, fine-pored. For measurements see Table 2.

**Figure 7.** Ophiocistioids and indeterminate echinoderm ossicles. Sample M13. a–b) Linguaserra heidii n. sp., aboral views. (a) Holotype (GIK1415-3), (b) paratype (GIK1413-1). c) Linguaserra cf. heidii (GIK1415-2), aboral view. d) Linguaserra n. sp. (GIK1415-1), aboral view. e–f) Ossicle type A. Ophiocistioid perradialia? (GIK1413-01, 1415-02). g–i) Ossicle type B. Affinity unknown. (g) Oblique view of smooth surface (GIK1415-14). (h) Lateral view (GIK1415-15). (i) Oblique view of opposite side with central furrow and parallel running ridge ending in a crest, fractured; lower half is not preserved (GIK1415-13). j) Ossicle type C. Plate of a crinoid calyx? (GIK1413-08). k–m) Ossicle type D. Ophiuroid lateral arm plates? (k) GIK1413-05. (l) GIK1415-12. (m) GIK1415-16. n–o) Ossicle type E. Holothurian anal teeth? (n) with spiny processes, inner (?) view (GIK1413-12), (o) without processes, lateral view (GIK1413-13). p–q) Ossicle type F. ?Eocaudina irregularis. (p) Circular outlined (GIK1413-25). (q) Biconcave-convex outlined (GIK1413-28). r–t) Ossicle type G. ?Mortensenites teat. (r) Fragment? (GIK1413-27). (s–t) GIK1413-20. (s) Outer (?) surface. (t) Lateral view. Scale bars = 0.1 mm.
Remarks. The specimen strongly resembles *L. heidii* n. sp., but is still more slender and has only four discrete teeth on each flank.

**Distribution.** Only known from the Upper Mississippian (Serpukhovian) of the Cantabrian Mountains, NW Spain.

**Linguaserra** n. sp.

(Fig. 7d)

**Material.** 1 specimen, sample M13 (GIK 1415-1).

**Description.** Lance-shaped nearly symmetrical, only very slightly arched goniodont. Acute long central tooth, about double size than the lateral teeth; six lateral teeth on each side, fused at their bases, width and length approximately equal, all running subparallel to the median axis, resulting in a regular triangular-shaped outline of the serrate part of the goniodont. Abaxial and axial part of nearly equal length; width of abaxial part tapering slightly towards the fine-pored distal end. Negative impression of the subsequent goniodont of the teeth battery recognizable: the distance between the tips of the main denticles of two consecutive goniodonts (Haude & Langenstrassen, 1976b) is 0.1 mm. For further measurements see Table 2.

**Remarks.** *Linguaserra* n. sp. is clearly separated from the slender *L. heidii* n. sp. It is the second species of the rare genus recognized in the Carboniferous. As only a single specimen is available we keep it in open nomenclature. Using the published plot of Reich *et al.* (2018) of denticle index (DI) versus total length/maximum width (Z'/B), *Linguaserra* n. sp. (Z'/B = 2.0, DI = 3.3) would plot just between *L. ligula* and *L. spandeli*. However, considering the typical lance-shaped outline of late Palaeozoic Linguaserridae (Reich & Kutscher, 2014), *Linguaserra* n. sp. is closer to *L. spandeli*.

**Distribution.** Upper Mississippian (Serpukhovian) of the Cantabrian Mountains (NW Spain, herein).

**Table 2** Measurements of discussed *Linguaserra* species using parameters defined by Haude & Langenstrassen (1976b) and Reich *et al.* (2018). Z': maximum length. z': length of the serrate axial part. B: maximum width. R: width axial part/width abaxial part ratio; > 1 means that the abaxial part is pinched (lance-shaped), < 1 the opposite (tongue-shaped). n: number of denticles per flank. F: length of serrate flank (without main denticle). DI: denticle index for small goniodonts (number of denticles at flank per 0.1 mm). *Own measurements of specimens figured without corresponding values. In brackets values of Reich (2018).

| species or specimen | Z' (μm) | z' (μm) | B (μm) | R | Z'/B | n | F (μm) | DI |
|---------------------|---------|---------|--------|---|------|---|--------|----|
| *Linguaserra heidii* n. sp. (holotype, herein) | 333 | 180 | 186 | >1 | 1.79 | 5 | 162 | 3.1 |
| *Linguaserra* sp. *sensu* Weber, 1997 | 246* | 100* | 126* | >1 | (1.95) | 5-6 | 113* | (5.1) |
| *L. cf. heidii* (herein) | 340 | 150 | 120 | >1 | 1.8 | 4 | 113 | 3.5 |
| *L. spandeli* Reich, 2007 (holotype) | 316* | 157* | 184* | >1 | (2.4) | 6-7 | 152* | (4.1) |
| *L. ligula* Langer, 1991 (holotype) | 670* | 380* | 340* | <1 | (1.95) | 9-10* | 360* | (2.8) |
| *L. franzeneae* Reich & Kutscher, 2014 (holotype) | 823 | 485* | 486 | <1 | 1.69 | 7-8 | 523 | (1.6) |
| *L. triassica* Reich, 2018 (holotype) | 484 | 230 | 284 | >1 | 1.7 | 11 | 253 | 4.4 |
| *Linguaserra* n. sp. (herein) | 420 | 210 | 210 | >1 | 2 | 6 | 180 | 3.3 |
Ossicle type A. (Figs 7e–f) Elongate planar ossicle, symmetrical along long axis and short axis as well, strongly biconcave along long axis and with bluntly acute tips with slightly concave margins. Raised rims along the indentations on the longitudinal sides only on supposed external face of the ossicle (Fig. 7e), but missing on the supposed internal face (Fig. 7f). Such indentations with a slightly raised border are characteristic for podial pores, i.e. the passage for tube feet between ambulacralia. On the one hand, they remind flooring plates of some edrioasteroids (Zamora, pers. comm. 2019). On the other hand, the similitude with perradialia of ophiocistioids is tempting. According to Ubags (1966) their perradialia are typically cross-shaped and tetraconcave. The shape is independent from integration as plates in a hard corona in phylogenetic old groups or as isolated ossicles in younger groups from the Middle Devonian onwards (see reconstruction of the Middle Devonian (Givetian) Rotasaccus dentifer in Haude & Langenstrassen, 1976a). However, Reich & Mostler (2002) noted that from the Carboniferous and Permian from ophiocistioids hitherto only isolated goniodonts are known.

Ossicle type B. (Figs 7g–i) The slightly concavo-convex ossicles have a convex outer surface with a very dense stereom (Fig. 7g), and a concave inner surface with a coarse-meshed labyrinthic stereom (Figs 7h–i). A ridge and an adjacent furrow run along the inner surface (Fig. 7i). The ridge ends on both extremes in a crest, being one more accentuated. This quite frequent ossicle in the residues of sample M13 remains of unknown affinity.

Ossicle type C. (Figs 7j) Pentagonal flat plate resembling a calyx plate of a crinoid, but also echinoids and edrioasteroids have similar plates.

Ossicle type D. (Figs 7k–m) Different views of a curved to corrugated ossicle resembling lateral arm plates of ophiuroids, which might wrap the vertebral column.

Ossicle type E. (Figs 7n–o) Elongate, half-tube shaped ossicles seen from its inner side (Fig. 7n) and laterally (Fig. 7o) with numerous pores; without or with small spiny process projected asymmetrical on each side. Somewhat similar structures were reported by Boczarowski (2001) from the Devonian of Poland and interpreted as anal teeth of holothurians, concretely of Dendrochirotida, even though the spiny processes of his elements are mostly arranged symmetricaly on each side. H.M. Weber (pers. comm. 2018) supports this attribution regarding our structures. Due to scarce material and the missing of commonly Y-shaped outlines, we opt to remain them among the indeterminate ossicles.

Ossicle type F. (Figs 7p–q) Sieve plates with many small, concentrically arranged pores, mostly with circular outline (Fig. 7p). A single ossicle with biconcave inner (?) margin ending in acute tips, and convex outer (?) margin (Fig. 7q). The ossicles resemble Eocaudina irregularis (Summerson & Campbell, 1958) and Eocaudina sp. of Gao et al. (2012), which probably also belongs to E. irregularis.

Ossicle type G. (Figs 7r–t) Multilayered ossicles with relatively coarse-meshed stereom; complete elements circular in outline, but with one conspicuous indentation. On the outer (?) surface three prominent nodes arranged in a slightly arched row, which mimics the orientation of the indentation. Opposite surface plane. The tentatively assigned, relictic preserved ossicle from Figure 7r shows an identical stereom structure. Zhang (1983) introduced similar ossicles from the early Carboniferous (Touraisian) of China as Mortensenites teat. The taxon was also described by Ding (1985) from the late Carboniferous of China. The assignment of Mortensenites ossicles to holothurians was rejected by e.g. Pawson (1980) and Reich (2013).

7. RESULTS AND CONCLUSIONS

The microfacies of the studied samples of the upper and uppermost Genicera Fm. (Canalón Mb. and Millaró Beds) of North León confirms subphotic pelagic deeper water environments well below storm-wave base with a sufficiently oxygenated sea floor, which was a soft bottom according to the prevalence of mudstones and wackestones. Unexpectedly, they provided a diversified late Viséan to Serpukhovian autochthonous echinoderm fauna consisting of micro-ossicles of at least holothurians, stenurids, ophiuroids, ophiocistioids, echinoids and pelmatozoans.

The holothurians comprise ossicles of both stem clades: The wheel-shaped ossicles, represented by the genera Langepis and Rotoide and by indeterminate palaeochiridotids reveal the presence of the Apodida; the sieve-plates, table plates and branched ossicles (Tetravirga) represent the sister clade Actinopoda. Within the Actinopoda, the Pneumonophora as well as the Elasipodida, which both should arise in the Devonian (Miller et al., 2017) are present. The Pneumonophora probably are proved by table ossicles and sieve plates; the Elasipodida at least by Tetravirga. The diversity of the Cantabrian fauna corroborates Reich (2010b), who stated the early diversification of the taxonomic higher ranks already during the Ordovician–Silurian interval, and the acme in the Middle Devonian with the appearance of the elasipodids. The fauna also supports Kozur & Mostler (2008) who claimed that already one third of the present-day holothurian diversity existed in early Carboniferous times. Also Reich (2013) noted that the Carboniferous yielded the richest holothurian diversity of the Palaeozoic,
altogether 65 paraspecies, but like before Reich (2010b), stressed the fact of a biased record due to taxonomic problems and widely missing studies.

Besides the holothurians, “arcaic” ophiuroids provided the most frequent ossicles. They, too, are represented by the known Palaeozoic stem groups. The Oegophiurida are proved by characteristic skeletal elements of Furcaster, including a new species of the paragenus Calclyra, the Stenurida by a distinct lateral arm plate of Pectenura. Elements of the ophiocistioids are very rare. They are represented by goniodonts assigned to Linguaserra, including the new species Linguaserra heidii n. sp.

Within the pelmatozoans an allagecrinid microcrinoid was distinguished. Further indeterminate echinoderm ossicles are abundant and diverse.

In summary, the fauna stresses the importance of a pelagic deeper water echinoderm community of vagile and sessile taxa during the Carboniferous. It strongly reminds of the abundance and diversity of echinoderms in modern pelagic, psychrospheric environments. Therefore, the roots of this exceptionally conservative community are in the Palaeozoic (Pabst & Herbig, 2018, 2019).

However, the Mississippian pelagic environment is strongly underexplored, as most echinoderm ossicles have been derived from shallow-water environments and even description of these associations are rare. They are known from Scotland (Etheridge, 1881), Belgium (Weber & Aretz, 2000), Germany (Haude & Thomas, 1994; Weber, 1997), Austria (Schraut, 1995), Poland (Alexandrowicz, 1971), Slovakia (Kozur et al., 1976), Iran (Nouredini et al., 2015), Afghanistan (Mostler, 1971a; Reich & Mostler, 2002), China (Zhang, 1983, 1985, 1986a, 1986b, 1993), and the USA (e.g. Craneis & McCormack, 1932; Gutschick, 1959; Gutschick et al., 1967). However, opposed to the herein first reported Upper Mississippian fauna of the Cantabrian Mountains, they belong to tropical carbonate platforms. The same is true for the Pennsylvanian, e.g. for non-crinoid faunas described from Hungary (Kozur, 1984a, 1984b), USA (e.g. Frizzell & Exline, 1956, 1966), China (e.g. Ding, 1985; Zhang, 1993) and North Spain (Bless & Sánchez de Posada, 1971; Zamora, 2016).

**ACKNOWLEDGEMENTS**

We are indebted to M. Reich (Munich) for his valuable advices and comments on an earlier version of the manuscript and to H.M. Weber (Bergisch-Gladbach) for several taxonomical precisions. G.D. Sevastopulo is acknowledged for his hint to the occurrence of the allagecrinid ossicles. We are also much obliged to the reviewers M. Reich (Munich) and S. Zamora (Zaragoza) for detailed and useful comments and suggestions. We thank D. Lutzenkirchen for engaged assistance in the laboratory during his internship, and last, but not least, R. Bäumler for thorough preparation of the thin-sections and H. Ciezynski for splendid SEM photographs.

**REFERENCES**

Aboussalam, Z.S. 2003. Das “Taghanic-Event” im höheren Mittel-Devon von West-Europa und Marokko. *Münstersche Forschungen zur Geologie und Paläontologie*, 97, 1-332.

Alexandrowicz, Z. 1971. Carboniferous Holothuroidea sclerites in the Upper Silesia Coal Basin (Southern Poland). *Rocznik Polskiego Towarzystwa Geologicznego [= Annales de la Société Géologique de Pologne]*, 41, 281–291.

Amler, M.R.W. & Winkler Prins, C.F. 1999. Lower Carboniferous marine bivalves from the Cantabrian Mountains (Spain). *Scripta Geologica*, 120, 1–35.

Ausch, W.I. 2001. Echinoderm taphonomy. In: *Echinoderm Studies* (eds Jangoux, M. & Lawrence, J.M.), A.A. Balkema, Rotterdam, 6, 171–227.

Balthasar, U. & Amler, M.R.W. 2003. Silicified foraminifera from the Lower Carboniferous Genicera Formation (Cantabrian Mountains, Northern Spain) and their palaeoenvironmental interpretation. *Courier Forschungsinstitut Senckenberg*, 242, 1–19.

Bábek, O., Kalvoda, J., Aretz, M., Cossey, P.J., Devuyst, X., Herbig, H.-G. & Sevastopulo, G. 2010. The correlation potential of magnetic susceptibility and outcrop gamma-ray logs at Tournaisian–Viséan boundary sections in Western Europe. *Geologica Belgica*, 13, 291–208.

Barrois, Ch. 1882. Recherches sur les terrains anciens de Asturies et de la Galice. *Mémoirs de la Société Géologique du Nord*, 2, 1–630.

Blake, D.B. 2013. Early Asterozoan (Echinodermata) diversification: a paleontologic quandary. *Journal of Paleontology*, 87, 353–372; doi: 10.1666/12-042.1.

Bless, M.J.M. & Sánchez de Posada, L. 1971. Restos de Asterozoa en el Westfaliense superior de Asturias. *Breviora Geológica Asturica*, 15, 13–16.

Boczarowski, A. 1997. Mistaken identity of wheel-shaped sclerites of Ophiocistioidea and Holothuroidea. *Slovak Geological Magazine*, 3, 331–340.

Boczarowski, A. 2001. Isolated sclerites of Devonian non-Pelmatozoan echinoderms. *Palaeontologica Polonica*, 59, 1–219.

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

Bourrouilh, R. & Termier, G. 1973. *Baleacrinus breimeri*, crinoide nouveau du Viséen supérieur de Minorca (Baleares). *Annales de la Société géologique du Nord*, 93, 225–232.

Brandt, J.F. 1835. Prodromus descriptionis animalium ab H. Mertensio in orbis terrarum circumnavigatone
observatorium. In: Animalia Mertensii. St. Petersburg, Fasc. 1, 75 pp.

Breimer, A. 1962. A monograph on Spanish Paleozoic Crinoidea. Leidse Geologische Mededelingen, 27, 1-190.

Bruguière, J.G. 1791. Tableau Encyclopédique et Méthodique des Trois Règles de la Nature. Contenant l’Helmintologie, ou les vers Infusoirés, les vers Intestins, les vers Mollusques, etc. Septième Livraison. C.F. Panckoucke, Paris, viii + 132 pp.

Colmenero, J.R., Fernández, L.P., Moreno, C., Bahamonde, J.R., Barba, P., Heredia, N. & González, F. 2002. Carboniferous. In: The Geology of Spain (eds Gibbons, W. & Moreno, M.T.). Geological Society, London, 93–116.

Comte, P. 1959. Recherches sur les terrains anciens de la Cordillère Cantabrique. Memorias del Instituto Geológico y Minero de España, 60, 1–440.

Cózar, P., Somerville, I.D., Sanz-López, J. & Blanco-Ferrera, S. 2016. Foraminiferal biostratigraphy across the Visean/Serpukhovian boundary in the Vegas de Sotres section (Cantabrian Mountains, Spain). Journal of Foraminiferal Research, 46, 171–192; doi: 10.2113/gsjfr46.2.171.

Crones, C. & McCormack, J. 1932. Fossil Holothuroidea. Journal of Paleontology, 6, 111–148.

de Blainville, H.M.D. 1834. Manuel d’Actinologie ou de Zoophytologie. F.G. Levraut, Paris, 695 pp.

Ding, H. 1985. Discovery of holothurian sclerites from the Taiyuan Formation (Upper Carboniferous), Henan, China. Acta Micropalaeontologica Sinica, 2, 339–348 (in Chinese with English abstract).

Ebner, F. & Fenninger, A. 1980. Mikrofazies and Biostratigraphie der Kalkgerölle von Falcovce (NW Bulgarien). Paleontologiya, Stratigrafiya i Lithologiya, Bulgarska Akademii Na Naukite, 12, 3–12.

Eichmüller, K. & Seibert, P. 1984. Faziesentwicklung zwischen Tournais und Westfal D im Kantabrischen Gebirge (NW-Spanien). Zeitschrift der Deutschen Geologischen Gesellschaft, 135, 163–191.

Etheridge, R., Jr. 1881. On the presence of the scattered skeletal remains of Holothuroidea in the Carboniferous Limestones Series of Scotland. Proceedings of the Royal Philosophical Society of Edinburgh, 6, 183–193.

Frizzell, D. & Exline, H. 1956. Monograph of fossil holothurian sclerites. Bulletin of the Missouri University School of Metallurgy and Mines, Technical Series, 89 [1955], 1–204.

Frizzell, D. & Exline, H. 1966. Holothuroidea – fossil record. In: Treatise on Invertebrate Paleontology. Part U. Echinodermata (ed. Moore, R. C.). Geological Society of America and University of Kansas Press, 3 (2), U646–U672.

Gandl, J. 1977. Die Trilobiten der Alba-Schichten (Unter-Visé bis Namur A). Senckenbergiana lethaea, 58, 113–217.

Gao, L., Ding, H., Zhang, P., Wang, Y. & Sun, J. 2012. Discovery of Carboniferous holothurian sclerites from the Benxi Formation, Pingshuo Mining Area, Shanxi Province. Acta Micropalaeontologica Sinica, 29, 179–194.

García-Bellido, D. 2002. Poríferos fósiles del Paleozoico de la Península Ibérica. Ph.D. Thesis, Universidad Complutense de Madrid, 183 pp.

García-Bellido, D. & Rigby, J. 2004. Devonian and Carboniferous sponges from Spain. Journal of Paleontology, 78, 431–455.

García-López, S. & Sanz-López, J. 2002. Devonian to Lower Carboniferous conodont biostratigraphy of the Bernesga Valley section (Cantabrian Zone, NW-Spain). In: Palaeozoic Conodonts from Northern Spain (eds García-López, S. & Bastida, F.). Cuadernos del Museo Geominero, 1, 125–162.

García-López, S. & Truyols, J. 1974. Presencia de escleritos de holoturoideos en las calizas Devónicas de la Cordillera Cantábrica. Breviora Geológica Astúrica, 27, 1–190.

Gray, J.E. 1840. A synopsis of the genera and species of the class Hypostoma Asterias (Linn.). Annals and Magazine of Natural History, 6, 275–290.

Grube, A.E. 1840. Actinien, Echinodermen und Würmer des Adriatischen-und Mittelmeers. J. H. Bon, Königsberg, 92 pp.

Gutschick, R.C. 1954. Holothurian sclerites of the Middle Ordovician of northern Illinois. Journal of Paleontology, 28, 827–829.

Gutschick, R.C. 1959. Lower Mississippian holothurian sclerites from the Rockford Limestone of northern Indiana. Journal of Paleontology, 33, 130–137.

Gutschick, R.C. & Canis, W.F. 1971. The holothurian sclerite genera Cucumarites, Eooauidina, and Thuroholia. Re-study of Eooauidina and Protocaudina from the Devonian of Iowa. Journal of Paleontology, 45, 327–337.

Gutschick, R.C. & Sandberg, C.A. 1983. Mississippian continental margins of the conterminous United States. In: The Shelfbreak: Critical Interface on Continental Margins (eds Stanley, D.J. & Moore, G.T.). Society of Economic Paleontologists and Mineralogists, Special Publication, 33, 79–96.

Gutschick, R.C., Canis, W.F. & Brill, K.G., Jr. 1967. Kinderhookian (Mississippian) holothurian sclerites from Montana and Missouri. Journal of Paleontology, 41, 1461–1480.

Haude, R. 1982. Ophiuren (Echinodermata) aus dem Karbon des Rheinischen Schiefergebirges. Geologisches Jahrbuch Hessen, 110, 5–26.

Haude, R. & Langenstrassen, F. 1976a. Rotasaccus dentifer n. g. n. sp., ein devonischer Ophiocistioide (Echinodermata) mit holothuroiden Wandskleriten und echinoidem Kauapparat. Paläontologische Zeitschrift, 50, 130–150.

Haude, R. & Langenstrassen, F. 1976b. Winkelzähne und Ophiocistioide aus Silur, Devon und Karbon. Lethaia, 9, 179–184.

Haude, R. & Thomas, E. 1994. Eleutherozoen (Echinodermata) aus dem Unterkarbon von Aprath im Bergischen Land. Archäologie im Ruhrgebiet, 2, 115–132.

Herbig, H.-G. 1982. Balearocrinus cantabricus n. sp. (Crinoidae, Inadunata) aus dem Visé des Kantabrischen...
Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1982, 476–484.

Herbig, H.-G. 1994. Remarks on the Late Viséan crinoids from the Cantabrian Mountains and Menorca (NW Spain and Balearic Islands). *Revista Española de Paleontología*, 9, 24–28.

Herbig, H.-G. 2016. Mississippian (Early Carboniferous) sequence stratigraphy of the Rhenish Kulm Basin, Germany. *Geologica Belgica*, 1984b. A Nagybátony-324. sz. fúrás oligocén Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 114, 61–79 (in Hungarian with German abstract).

Herbig, H.-G. 1994. Remarks on the Late Viséan crinoids Kozur, H. & Mostler, H. 1989. Echinoderm remains from the Middle Permian (Wordian) from Sosio Valley (Western and Balearic Islands). *Jahrbuch der Geologischen Bundesanstalt Wien*, 9, 24–28.

Herbig, H.-G. 2016. Mississippian (Early Carboniferous) sequence stratigraphy of the Rhenish Kulm Basin, Germany. *Geologica Belgica*, 1984b. A Nagybátony-324. sz. fúrás oligocén Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 114, 61–79 (in Hungarian with German abstract).

Herbig, H.-G. 2016. Mississippian (Early Carboniferous) sequence stratigraphy of the Rhenish Kulm Basin, Germany. *Geologica Belgica*, 1984b. A Nagybátony-324. sz. fúrás oligocén Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 114, 61–79 (in Hungarian with German abstract).

Herbig, H.-G. 2016. Mississippian (Early Carboniferous) sequence stratigraphy of the Rhenish Kulm Basin, Germany. *Geologica Belgica*, 1984b. A Nagybátony-324. sz. fúrás oligocén Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 114, 61–79 (in Hungarian with German abstract).

Herbig, H.-G. 2016. Mississippian (Early Carboniferous) sequence stratigraphy of the Rhenish Kulm Basin, Germany. *Geologica Belgica*, 1984b. A Nagybátony-324. sz. fúrás oligocén Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 114, 61–79 (in Hungarian with German abstract).

Herbig, H.-G. 2016. Mississippian (Early Carboniferous) sequence stratigraphy of the Rhenish Kulm Basin, Germany. *Geologica Belgica*, 1984b. A Nagybátony-324. sz. fúrás oligocén Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 114, 61–79 (in Hungarian with German abstract).

Herbig, H.-G. 2016. Mississippian (Early Carboniferous) sequence stratigraphy of the Rhenish Kulm Basin, Germany. *Geologica Belgica*, 1984b. A Nagybátony-324. sz. fúrás oligocén Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 114, 61–79 (in Hungarian with German abstract).

Herbig, H.-G. 2016. Mississippian (Early Carboniferous) sequence stratigraphy of the Rhenish Kulm Basin, Germany. *Geologica Belgica*, 1984b. A Nagybátony-324. sz. fúrás oligocén Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 114, 61–79 (in Hungarian with German abstract).

Herbig, H.-G. 2016. Mississippian (Early Carboniferous) sequence stratigraphy of the Rhenish Kulm Basin, Germany. *Geologica Belgica*, 1984b. A Nagybátony-324. sz. fúrás oligocén Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 114, 61–79 (in Hungarian with German abstract).

Herbig, H.-G. 2016. Mississippian (Early Carboniferous) sequence stratigraphy of the Rhenish Kulm Basin, Germany. *Geologica Belgica*, 1984b. A Nagybátony-324. sz. fúrás oligocén Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 114, 61–79 (in Hungarian with German abstract).

Herbig, H.-G. 2016. Mississippian (Early Carboniferous) sequence stratigraphy of the Rhenish Kulm Basin, Germany. *Geologica Belgica*, 1984b. A Nagybátony-324. sz. fúrás oligocén Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 114, 61–79 (in Hungarian with German abstract).

Herbig, H.-G. 2016. Mississippian (Early Carboniferous) sequence stratigraphy of the Rhenish Kulm Basin, Germany. *Geologica Belgica*, 1984b. A Nagybátony-324. sz. fúrás oligocén Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 114, 61–79 (in Hungarian with German abstract).

Herbig, H.-G. 2016. Mississippian (Early Carboniferous) sequence stratigraphy of the Rhenish Kulm Basin, Germany. *Geologica Belgica*, 1984b. A Nagybátony-324. sz. fúrás oligocén Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 114, 61–79 (in Hungarian with German abstract).

Herbig, H.-G. 2016. Mississippian (Early Carboniferous) sequence stratigraphy of the Rhenish Kulm Basin, Germany. *Geologica Belgica*, 1984b. A Nagybátony-324. sz. fúrás oligocén Gebirges (Alba-Formation, Prov. León/NW-Spanien). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 114, 61–79 (in Hungarian with German abstract).
Matsumoto, H. 1915. A new classification of Ophiuroidea: with description of genera and species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 67, 43–92.

Matyja, B.A., Matyja, H. & Szulczewski, M. 1973. The genus *Eocaudina* Martin (Holothuroidea) from the Devonian of Poland. *Acta Geologica Polonica*, 23, 135–147.

Miller, A.K., Kerr, A.M., Paulay, G., Reich, M., Wilson, N.G., Carvajal, J.I. & Rouse, G.W. 2017. Molecular phylogeny of extant Holothuroidea (Echinodermata). *Molecular Phylogenetics and Evolution*, 111, 100–131; doi: 10.1016/j.ympev.2017.02.014.

Morris, P.G. 1992. *Rhabdocrinites scotocarbonarius* (Wright), a crinoid from the Carboniferous “griotte” limestone of Palencia, Northwest Spain. *Revista Española de Paleontología*, 7, 181–184.

Mostler, H. 1968a. Neue Holothurien-Sklerite aus den norischen Hallstätter Kalken (Nördlichen Kalkalpen). *Berichte des Naturwissenschaftlichen-Medizinischen Vereins Innsbruck*, 56, 427–441.

Mostler, H. 1968b. Holothurien-Sklerite aus oberanischen Hallstätterkalken (Ostalpen, Bosnien, Türkei). *Veröffentlichungen der Universität Innsbruck–Alpenkundliche Studien*, 2, 5–45.

Mostler, H. 1971a. Mikrofauna aus dem Unter-Karson vom Hindukusch. *Geologisch-Paläontologische Mitteilungen Innsbruck*, 1, 1–19.

Mostler, H. 1971b. Ophiuren skelettelemente (äußere Skelettanhänge) aus der alpinen Trias. *Geologisch-Paläontologische Mitteilungen Innsbruck*, 1, 1–35.

Mostler, M. & Rahimi-Yazd, A. 1976. Neue Holothuriensklerite aus dem Oberperm von Julfa im Nordiran. *Geologisch-Paläontologische Mitteilungen Innsbruck*, 5, 1–35.

Nemyrovska, T.I. 2005. Late Viséan/early Sepukhovian conodont succession from the Triolli section, Palencia (Cantabrian Mountains, Spain). *Scripta Geologica*, 129, 13–89.

Nemyrovska, T.I., Wagner, R.H., Winkler Prins, C.F. & Montañez, I. 2011. Conodont faunas across the mid-Carboniferous boundary from the Barcaliente Formation at La Lastra (Palentian Zone, Cantabrian Mountains, northwest Spain); geological setting, sedimentological characters and faunal descriptions. *Scripta Geologica*, 143, 127–183.

Nouredini, M., Yazdi, M., Ashouri, A.R., & Rahmanti, S. 2017. Restructuring higher taxonomy using broad-scale phylogenomics: the living Ophiuroidea. *Molecular Phylogenetics and Evolution*, 107, 415–430; doi: 10.1016/j.ympev.2016.12.006.

Östergren, H.J. 1907. Zur Phylogenie und Systematik der Seewalzen. *Sätryck ur Zoologiska Studier*, 1, 191–215.

Pabst, J. & Herbig, H.-G. 2018. Vagile echinoderms from a Carboniferous pelagic environment – Evidence for the antiquity of the modern deep-water fauna. In: *Book of Abstracts: GeoBonn 2018 – Living Earth*, 2–6 September 2018, Bonn. Dachverband Geowissenschaften, p. 264.

Pabst, J. & Herbig, H.-G. 2019. A pelagic echinoderm microfauna from the Serpukhovian of the southern Cantabrian Mountains (Province León, NW Spain). In: *19th International Congress on the Carboniferous and Permian*, Cologne, July 29–August 2, 2019. *Abstracts* (eds Hartenfels, S., Herbig, H.-G., Amler, M.R.W. & Aretz, M.). Kölner Forum für Geologie und Paläontologie, 23, 252–253.

Pawson, D.L. 1966. Phylogeny and evolution of holothuroids. In: *Treatise on Invertebrate Paleontology. Part U, Echinodermata* (ed. Moore, R.C.). Geological Society of America and University of Kansas Press, Boulder/Colorado and Lawrence/Kansas, 3 (2), U641–U646.

Pawson, D.L. 1980. Holothuroidea. In: *Echinoderms: Notes for a Short Course* (eds Broadhead, T.W. & Waters, J.A.). University of Tennessee, Department of Geological Sciences, Studies in Geology, 1, 175–189.

Pérez-Estaún, A., Bastida, F., Alonso, J.L., Marquínez, J., Aller, J., Alvarez-Marrón, J., Marcos, A. & Pulgar, J.A. 1988. A thin-skinned tectonics model for an arcuate fold and thrust belt: The Cantabrian Zone (Variscan Ibero-Armorican Arc). *Tectonics*, 7, 517–537; doi: 10.1029/TT007i003p00517.

Prado, C. & de Verneuil, E. 1850. Sur les terrains de Sabero et des environs dans les Montagnes de León (Espagne). *Bulletin de la Société Géologique de France*, 2ème série, 7, 137–155.

Reich, M. 2007. *Linguaserra spandeli* sp. nov. (Echinodermata: Ophiocistioida) from the Late Permian (Zechstein) of Thuringia, Germany. *Annales de Paléontologie*, 93, 137–155; doi: 10.1016/j.annpal.2007.09.007.

Reich, M. 2010a. Evolution and diversification of ophiocistioids (Echinodermata: Echinozoa). In: *Echinoderms: Durham*. *Proceedings of the 12th International Echinoderm Conference*, 7–11 August 2006, Durham/New Hampshire (eds Harris, L.G., Böttcher, S.A., Walker, C.W. & Lesser, M.P.). CRC Press, Taylor & Francis, 51–54.

Reich, M. 2010b. The early evolution and diversification of holothurians (Echinozoa). In: *Echinoderms: Durham*. *Proceedings of the 12th International Echinoderm Conference*, 7–11 August 2006, Durham/New Hampshire (eds Harris, L.G., Böttcher, S.A., Walker, C.W. & Lesser, M.P.). CRC Press, Taylor & Francis, 55–59.

Reich, M. 2012. On Mesoozoic laetomgonid sea cucumbers (Echinodermata: Holothuroidea: Elasipodida). *Zoosymposia*, 7, 185–212; doi: 10.11646/zoosymposia.7.1.18.

Reich, M. 2013. How many species of fossil holothurians are there? In: *Echinoderms in a Changing World. Proceedings of the 13th International Echinoderm Conference*, 5–9 January 2009, Hobart/Tasmania (ed. Johnson, C.). CRC Press, Taylor & Francis, 23–51.

Reich, M. & Hau de, R. 2004. Ophiocistioida (fossil Echinodermata): an overview. In: *Echinoderms: München*. *Proceedings of the 11th international Echinoderm Conference*, 6–10 October 2003, Munich (eds Heinzeller,
(Spain) and their stratigraphic application. *Leidse Geologische Mededelingen*, 39, 129–192.

von Zittel, K.A. 1895. *Grundzüge der Palaeontologie*. 971 pp.

Wagner, R.H., Winkler Prins, C.F., Riding, R.E. & Wagner-Gentis, C.H.T. 1971. Lithostratigraphic units of the lower part of the Carboniferous in northern León, Spain (with a note on some goniatite faunas). *Trabajos de Geología, Universidad de Oviedo*, 4, 603–663.

Weber, H.M. 1997. Holothurien- und Ophiocistioiden-Reste (Echinodermata) aus dem Unterkarbon des Velberter Sattels (Rheinisches Schiefergebirge). *Sonderveröffentlichungen des Geologischen Instituts der Universität zu Köln*, 114, 485–497.

Weber, H.M. & Aretz, M. 2000. Außergewöhnliche Funde mikroskopischer Echinodermen-Reste aus dem belgischen Kohlenkalk (Unterkarbon). *Terra Nostra*, 2000/3 (70. Jahrestagung der Paläontologischen Gesellschaft. Vorträge und Poster. 24–30 September 2000 in Coburg), p. 123.

Webster, G.D., Maples, C.G., Sevastopulo, G.D., Frest, T. & Waters, J.A. 2004. Carboniferous (Viséan–Moscovian) echinoderms from the Béchar Basin area of western Algeria. *Bulletin of American Paleontology*, 369, 1-98.

Wernlund, R.J. 1977. *Biostratigraphy and paleoecology of holothurian sclerites from the Pinery Member, Bell Canyon Formation (Permian) of the Delaware Basin of West Texas*. M.Sc. Thesis, Geosciences Faculty of Texas Tech University. 122 pp.

Wernlund, R.J. 1996. *Taxonomy, distribution, and paleoecology of holothurians (Echinodermata) sclerites in Upper Pennsylvanian cyclothem shales, North-Central Texas and South-Central Kansas*. Ph.D. Thesis, Graduate Faculty of the Texas Tech University, 122 pp.

Zamora, S. 2016. Equinodermos del Paleozoico del norte de España. In: *Actas de las XXXII Jornadas de la Sociedad Española de Paleontología* (eds Meléndez, G., Núñez, A. & Tomás, M.). Cuadernos del Museo Geominero, 20, 11–23.

Zankl, H. 1966. Holothurien-Sklerite aus dem Dachsteinkalk (Ober-Trias) der nördlichen Kalkalpen. *Paläontologische Zeitschrift*, 40, 70–88.

Zhang, J.-J. 1983. Some Holothuroidea fossils of early Carboniferous from Linwu, Hunan province. *Oil & Gas Geology*, 4, 332–334 (in Chinese with English abstract).

Zhang, J.-J. 1985. Some Middle Devonian and Lower Carboniferous holothurian sclerites from Hunan. *Hunan Geology [= Hunan dizhi]*, 4, 27–37 (in Chinese with English abstract).

Zhang, J.-J. 1986a. Lower Carboniferous holothurian sclerites from Hunan Province. *Acta Micropalaeontologica Sinica*, 3, 399–408 (in Chinese with English abstract).

Zhang, J.-J. 1986b. Lower Carboniferous holothurian sclerites from Menggongao Formation of central Hunan. *Earth Science. Journal of Wuhan College of Geology [= Diqiu-kexue. Wuhuan Dishi-xueyuan-xuebao]*, 11, 547–550.

Zhang, J.-J. 1993. Late Early Carboniferous Holothuroidea from Dushan, Guizhou. *Acta Palaeontologica Sinica*, 32, 105–114 (in Chinese with English abstract).
