A new brittle star from the early Carboniferous of Poland and its implications on Paleozoic modern-type ophiuroid systematics

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The fossil record of Paleozoic ophiuroids includes a number of forms which share striking similarities with modern relatives in terms of skeletal morphology. These so called modern-type Paleozoic ophiuroids yield an enormous potential for a better understanding of ophiuroid evolution, yet the scarcity of accurate and sufficiently detailed morphological descriptions available to date precludes any further-reaching assessments. Here, we describe an articulated ophiuroid specimen from the Late Tournaisian (early Carboniferous) of Czatkowice quarry, southern Poland, as a new species *Aganaster jagiellonicus* sp. nov. The good preservation of the specimen allowed for a morphological analysis at a level comparable to recent ophiuroid descriptions. It shows remarkable morphological similarities with extant former ophiolepidids *Ophiomusium* and *Ophiosphalma*. The new find thus contributes to a solid basis for future investigations on the position of the modern-type Paleozoic ophiuroid in the phylogeny of the class.

Key words: Echinodermata, Ophiuroidea, crown-group, evolution, Carboniferous, Tournaisian, Poland.

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Introduction

Brittle stars are an important component of present-day marine benthic communities (Stöhr et al. 2012), and their fossil record can be traced back at least to the Early Ordovician (Dean Shackleton 2005). Although a considerable number of ophiuroid fossils have been reported from Paleozoic (e.g., Spencer 1925; Haude and Thomas 1983), Mesozoic (e.g., Hess 1965; Jagt 2000; Thuy 2013) and Cenozoic (e.g., Rasmussen 1972; Ishida 2001) deposits, surprisingly little is known about the evolutionary history of the group. One of the main impediments in this respect is the failure of most studies of fossil ophiuroids to meaningfully reconcile these taxa with the systematics of extant brittle stars (Thuy et al. 2012). This particularly holds true for those Paleozoic ophiuroids which strikingly resemble modern relatives with respect to the ambulacral plate pairs firmly fused into vertebrae and the ambulacral groove covered by ventral arm plates and ventrally meeting lateral arm plates (Spencer and Wright 1966).

These so called modern-type Paleozoic ophiuroids are known from Silurian to Permian strata (Spencer and Wright 1966). Although a decent number of nominal species has been described so far (Chen and McNamara 2006), they were mostly compared amongst each other, in spite of the obvious similarities in skeletal morphology with extant relatives. Comparison with modern clades was further hampered by the often extremely superficial or even inaccurate morphological descriptions, using characters for distinction which are so general that they apply to the vast majority of brittle stars (e.g., Miller 1958; Morris et al. 1973; Sanchez 1983; Chen et al. 2004; Chen and McNamara 2006).

One of the very few notable exceptions in this respect is the study by Hotchkiss and Haude (2004) who re-assess the modern-type Paleozoic ophiuroids *Aganaster gregarius* (Meek and Worthen, 1869) and *Stephanoura belgica* Ubaghs, 1941. On the basis of a remarkably meticulous re-description allowing for a direct comparison with mod-

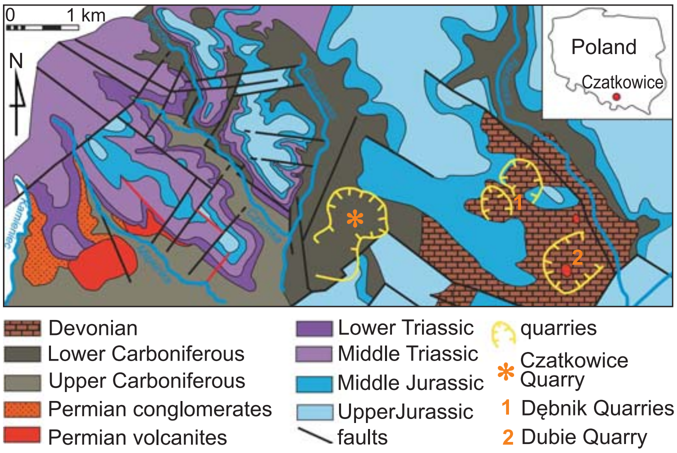

Fig. 1. Geographical position of the investigated specimen (map after Salata 2013, with modifications).

ern relatives, Hotchkiss and Haude (2004) transferred the Paleozoic taxa in question to the former extant family Ophiolepididae. Their results imply that at least part of the ophiuroid crown-group diversification took place in the Late Paleozoic, which discredits the distinction between modern-type Paleozoic ophiuroids and the Mesozoic and younger relatives as purely artificial.

Here, we describe a recently discovered articulated ophiuroid from the early Carboniferous of Poland, which is of strikingly modern aspect. The preservation of the specimen enabled a detailed morphological description, based upon which we attempt integration into the classification of extant brittle stars.

The specimen is housed in the MZUJ. Pictures were taken using a dissecting microscope equipped with a digital imaging device. Morphological terminology follows Stöhr et al. (2012) for skeletal plates, and Thuy and Stöhr (2011) for features of lateral arm plates. Higher-level classification is adopted from Smith et al. (1995). Specimens of *Aganaster gregarius* from the lower Carboniferous Muldraugh Formation of Sugar Creek, Crawfordsville, Indiana (USA), were kindly provided by Fred Hotchkiss (Vineyard Haven, Massachusetts, USA).

Institutional abbreviations.—MZUJ, Zoological Museum of the Jagiellonian University, Kraków, Poland.

Geological setting

The described ophiuroid specimen was retrieved from a yellowish-brown, hard limestone layer, several decimetres in thickness, within a series of mainly fine-grained carbonates referred to the Mazurowe Doły Formation within the Rudawa Group, exposed in the Czatkowice quarry (coordinates 50°09.40’ N; 19°36.10’ E) in the Dębnik Massif, southern Poland (Fig. 1). The Mazurowe Doły Formation is a shallowing-upward succession of hummocky cross-stratified, oolithic-cortoid grainstone deposited on a storm-dominated carbonate ramp (Paszkowski et al. 2008). Foraminifer and rugose coral evidence indicates a late Tournaisian (Ivorian, early Carboniferous) age for the Mazurowe Doły Formation (Poty et al. 2007). Macrofossils associated include thin-shelled brachiopods, crinoid columnals, bryozoans and solitary corals. The Mazurowe Doły Formation is generally interpreted as a shallow, turbulent subtidal deposit with palaeo-depths well above storm wave base (Poty et al. 2007; Paszkowski et al. 2008).

Systematic palaeontology

Class Ophiuroidea Gray, 1840

Order Ophiurida Müller and Troschel, 1840

Suborder Ophiurina Müller and Troschel, 1840

Family unknown (formerly Ophiolepididae, see O’Hara et al. 2014)

Genus *Aganaster* Miller and Gurley, 1891

Type species: *Protaster gregarius* Meek and Worthen, 1869, by original designation; Keokuk Group, early Carboniferous, Crawfordsville, Indiana.

Emended diagnosis.—Small to medium-sized ophiuroid with disc fully covered by naked scales and radial shields; primary rosette discernible; second oral tentacle pore not superficial; lateral arm plates non-bulging and with small spine articulations and very short arm spines; tentacle pores developed as large, between-plate pores in basal arm segments, and as small within-plate perforations from the 15th arm segment towards the tip.

Stratigraphic and geographic range.—Early Carboniferous, USA, Poland.

Aganaster jagiellonicus sp. nov.

Figs. 2, 3.

Etymology: In honour of Jagiellonian University in Kraków, the oldest university in Poland and one of the oldest in Europe, and the Jagiellonian dynasty of Polish kings.

Holotype: Articulated skeleton with all five arms preserved, MZUJ T/0282 (only known specimen).

Type locality: Czatkowice quarry, Dębnik Massif, southern Poland.

Type horizon: Mazurowe Doły Formation, Rudawa Group, late Tournaisian (Ivorian, MFZ 4 to 5 foraminiferal zones or RC3α to β rugose coral zones), early Carboniferous.

Diagnosis.—Species of *Aganaster* with lateral arm plates bearing at least three minute, conical arm spines on the distal edge of the lateral arm plates, shorter than one fifth of an arm segment; ventral arm plates hexagonal and both basal and succeeding proximal arm segments.

Description.—Disc circular, 9 mm in diameter, exposing ventral face, dorsal disc plating unknown; ventral interradii completely covered by few (no more than ten per interradius) plates, no granules or spines discernible, plates rounded, largest near disc edge; genital slits very slender, extending

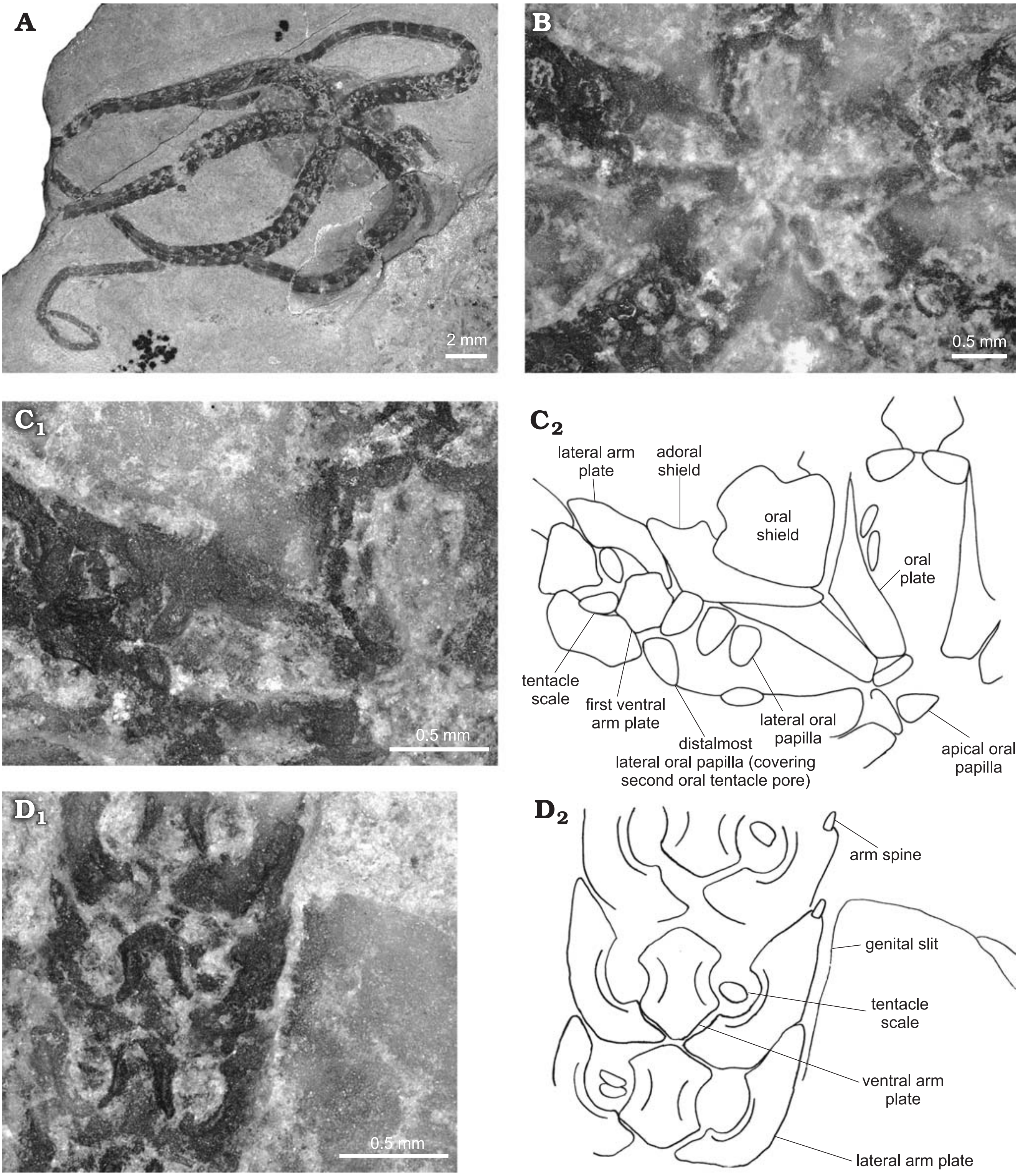

Fig. 2. Ophiurin brittle star *Aganaster jagiellonicus* sp. nov. from the upper Tournaisian to lower Visean (lower Carboniferous) Mazurowe Doły Formation, Rudawa Group of Czatkowice quarry, Dębnik Massif, southern Poland; MZUJ T/0282, holotype. **A**. General view of the specimen, exposing the ventral side (also illustrated by O'Hara et al. 2014). **B**. Oral skeleton. **C**. Detail of the oral skeleton; photograph (C_1), interpretative drawing (C_2). **D**. Detail of basal arm segments; photograph (D_1), interpretative drawing (D_2).

from beside the second arm segment to the edge of the disc; oral shield slightly shorter than one fourth of the disc radius, arrow-head shaped with pointed to almost right proximal angle, deeply incised latero-distal edges and rectangular distal end; madreporite indiscernible; adoral shields long and slender, extending around the lateral edge of the oral shield and separating it from the lateral arm plates of the first arm segment, proximal tips of adoral shields meeting in front of

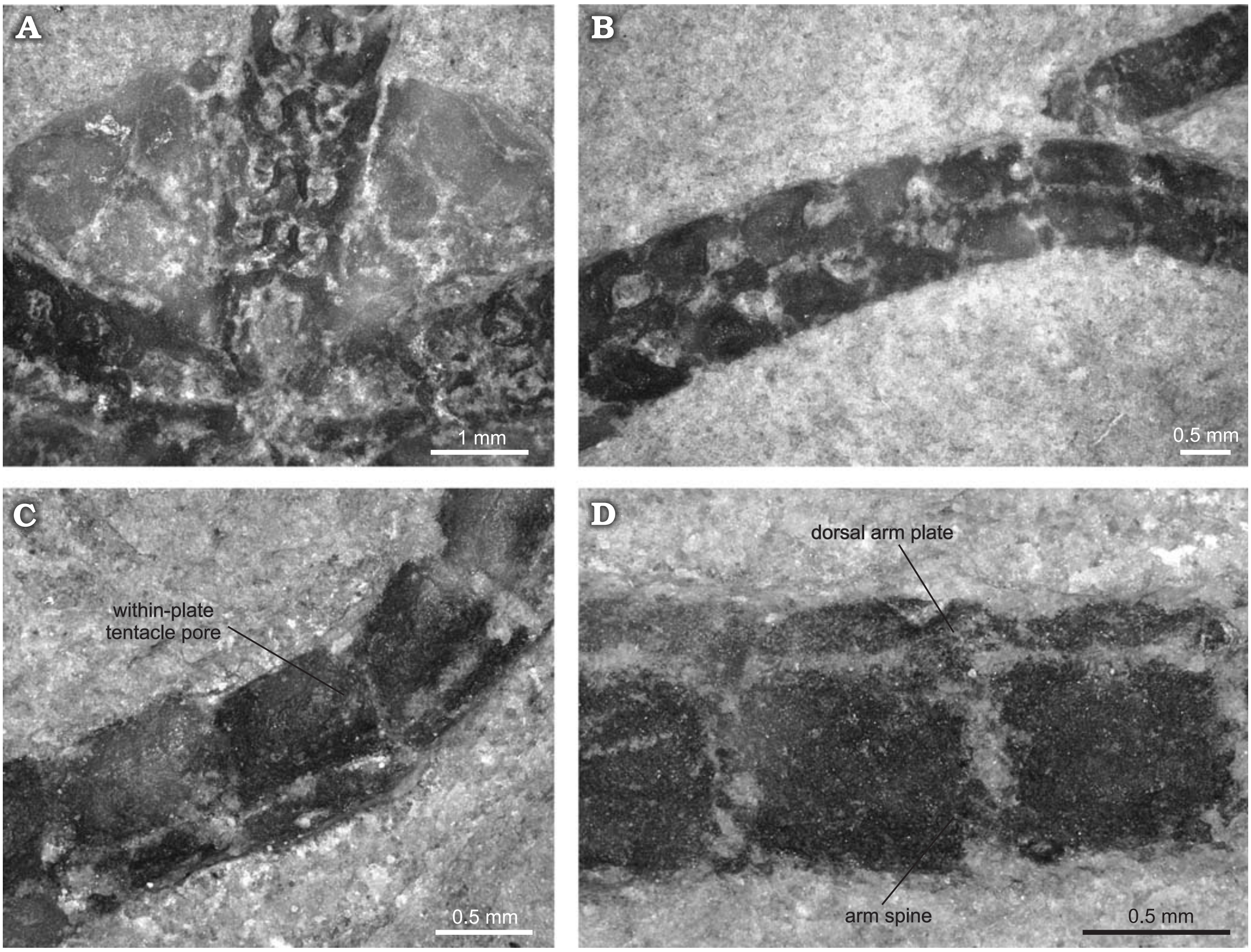

Fig. 3. Ophiurin brittle star *Aganaster jagiellonicus* sp. nov. from the upper Tournaisian to lower Visean (lower Carboniferous) Mazurowe Doły Formation, Rudawa Group of Czatkowice quarry, Dębnik Massif, southern Poland; MZUJ T/0282, holotype. Detail of ventral side (**A**); median arm segments, showing the transition from between-plate tentacle pores to within-plate tentacle pores (**B**); median arm segments in ventro-lateral view (**C**); proximal arm segments in dorso-lateral view (**D**).

oral shield; proximal portions of oral plates of rather stout aspect; jaws approximately as long as wide (distance between the tip of the jaws and the boundary between the first ventral arm plate and the adoral shield nearly equal to the distance between the first ventral arm plates on both sides of the jaws); first ventral arm plate smaller than following ventral arm plates, nearly hexagonal; second oral tentacle pore opening into the mouth slit, not superficial, covered by single leaf-like lateral papilla, slightly longer than wide, sitting on the adradial edge of the adoral shield; at least four additional, slightly larger lateral oral papillae discernible, in continuous row and contiguous, leaf-like, nearly as wide as long, sitting on adradial edge of oral shield; pointed, conical papilla, two to three times smaller than above-described papillae, discernible on lateral edge of one jaw tip, either representing the proximalmost lateral papilla or a slightly displaced apical papilla; no teeth discernible.

All five arms preserved intact until median to distal arm segments; longest arm approximately 45 mm long (measured from the proximal edge of the first arm segment) and preserving at least 46 arm segments including those incorporated into the disc; arms very slightly increasing in width at the basalmost freestanding segments, then very slowly tapering over the next 10 segments, more quickly tapering over the following few segments and again very gently tapering towards tip of the arms; arm segments not bulging; lateral arm plates of thick aspect, devoid of conspicuous outer surface ornamentation or constriction, non-bulging, meeting ventrally from the first arm segments not incorporated into the disc; distal edge of lateral arm plates with three or more very small spine articulations, either sunken into depressions of distal lateral arm plate edge or integrated into outer surface stereom, structural details of spine articulations not discernible; very small, conical arm spines, parallel to the arm axis, shorter than one fifth of an arm segment.

Lateral arm plates of proximalmost 15 arm segments including those incorporated into the disc with deep, conspicuous between-plate tentacle pores (3 arms scorable); ventro-distal edge of tentacle notch in lateral arm plates lined by a thin, thickened and sharply defined ridge; lateral arm plates of following arm segments with a small, hardly discernible within-plate tentacle pore near ventro-distal tip; two large, leaf-like tentacle scales on most (1st to 14th) of arm segments with between-plate tentacle pores, probably only one tentacle scale on distalmost (15th) segment with between-plate tentacle pore, no scales discernible on (16th and more distal) arm segments with within-plate tentacle pores; tentacle scales slightly oblique to arm axis, most probably pointing proximalwards or towards the arm midline and borne by the edge of the tentacle notch of the lateral arm plate; ventral arm plates of the proximalmost 14 to 15 arm segments (including those incorporated into the disc) approximately hexagonal, with slightly obtuse distal angle, concave and conspicuously thickened and bulging lateral edges, with longitudinal central groove as a result of the bulging lateral edges; proximal angle of ventral arm plates nearly right, truncated in proximalmost segments; ventral arm plates approximately 1.5 times longer than wide in proximal segments, slightly longer in median to distal ones; ventral arm plates separating lateral arm plates in segments incorporated into the disc; successive ventral arm plates separated by lateral arm plates.

Remarks.—The described specimen is characterised by ventral disc plates lacking granules or spines, a continuous series of block-like lateral oral papillae, second oral tentacle pores opening into the mouth slit, thick and non-bulging lateral arm plates, very small appressed arm spines, and within-plate tentacle pores from median arm segments onwards. This combination of characters typically occurs in the extant genus *Ophiomusium* Lyman, 1869, formerly assigned to the family Ophiolepididae but recently found to be sister to the Ophiuridae instead (O'Hara et al. 2014), and the morphologically very similar extant *Ophiosphalma* Clark, 1941. In these two genera, however, the within-plate tentacle pores replace between-plate ones in almost all arm segments, whereas this new species displays between-plate tentacle pores until median arm segments. In this respect, the described specimen has greater similarities with Jurassic and Cretaceous forms commonly regarded as closely related to extant *Ophiomusium*, in particular the Lower Jurassic *Ophiomusium*? *murravii* (Forbes, 1843) (Thuy et al. 2011) and the Late Jurassic *Ophiomusium gagnebini* Thurman, 1851 (Hess 1960), which both display within-plate tentacle pores from median arm segments onwards. The genus *Mesophiomusium* Kutscher and Jagt, 2000 was established on the basis of dissociated lateral arm plate fossils from the Late Cretaceous of Denmark to accommodate fossil *Ophiomusium*-like forms with within-plate tentacle pores in median to distal arm segments. The lateral arm plates of the type species *M. moenense* Kutscher and Jagt, 2000, however, are more reminiscent of those found in another extant ophiolepidid genus *Ophiomastus* Lyman, 1878, rather than *Ophiomusium* or *Ophiosphalma* (BT unpublished material). Clearly, most of the Jurassic and Cretaceous *Ophiomusium*-like forms, including the above-mentioned *Ophiomusium* and *Mesophiomusium* species, need thorough reappraisal as to their generic assignment and relation with extant relatives. However, they almost certainly belong to different genera than the Carboniferous specimen described herein on account of its non-bulging distal portion of the lateral arm plates, the grooved, nearly hexagonal proximal ventral arm plates and the very large basal tentacle pores.

Among the modern-type Paleozoic ophiuroids known to date, the described specimen shares closest similarities with species of the genera *Aganaster* and *Archaeophiomusium* Hattin, 1967, both assigned to the Ophiolepididae (Hattin 1967; Hotchkiss and Haude 2004). In *Stephanoura belgica*, in contrast, proximal arm segments display spine articulations on a strongly elevated ridge, resulting in an undulating ventro-lateral arm profile, and bear needle-like spines which exceed the length of an arm segment (Haude and Thomas 1983). Furthermore, the lateral arm plates of *S. belgica* are composed of coarsely meshed stereom. The type species *Aganaster gregarius* from the early Carboniferous of North America differs from the described specimen in bearing the arm spine articulations on a slightly elevated ridge at some distance from the distal edge of the lateral arm plates. It furthermore has smaller basal tentacle pores and nearly hexagonal ventral arm plates only in the basalmost segments, followed by bell-shaped ones in succeeding segments. The other species assigned to *Aganaster* (*Aganaster cingulatus* Easton, 1943, from the Carboniferous of Arkansas, USA; *A.*? *fujiaensis* Liao and Wang, 2002 and *A. huaanensis* Wu, 1982, from the Permian of China), although poorly known, also do not display the combination of characters found in the described specimen. *Archaeophiomusium burrisi* (Miller, 1958) from the Permian of Kansas, USA, the type species of the genus, differs in having bulging lateral arm plates, smaller tentacle pores on the basal arm segments, and non-grooved ventral arm plates which are bell-shaped rather than hexagonal. These differences hold true for *Archaeophiomusium bispinosum* Mayou, 1969, from the Permian of Nevada, USA, which, in addition, displays superficial second oral tentacle pores and minute papillae on the distal tip of a plate pair that seem to correspond to the genital plates. *Archaeophiomusium andinum* Sanchez, 1983 from the Permian of Venezuela, and *Ophiomusium calathospongum* Berry, 1939 from the Late Devonian of Pennsylvania, USA which may possibly belong to *Archaeophiomusium*, are both poorly known. The descriptions and illustrations available fail to convincingly diagnose the respective species. Due to the poor preservation of the type material, it is likely that the species in question are, in fact, nomina dubia. The scarce morphological details at hand, in particular with respect to the shape of the lateral arm plates, however, preclude confusion with the here-described specimen. Since no currently known species is compatible with the specimen in question, we describe it as a new species.

Geographic and stratigraphic range.—Type locality and horizon only.

Concluding remarks

The classification of the new species on genus level poses problem because almost all currently known *Ophiomusium*-like genera with between-plate tentacle pores developed until median arm segments, whether of Paleozoic or Mesozoic age, are poorly diagnosed and unite mostly heterogeneous amalgams of species. We therefore refer to the type species of the available genera in order to assess the systematic position of the new species. Although the shape of the proximal to median ventral arm plates and the size of the basal tentacle pores are more reminiscent of *Stephanoura*, the shape of the lateral arm plates and of the basalmost ventral arm plates, and the position of the change from between-plate to within-plate tentacle pores (or the number of segments with between-plate tentacle pores) suggests assignment to *Aganaster*. The systematic relevance of the last-mentioned character requires further investigation. In fact, while being the key character to separate *Ophiomusium* and *Ophiosphalma*, it can show considerable intraspecific variability, e.g., in *Stephanoura belgica* (Hotchkiss and Haude 2004).

Given the presently very limited knowledge on the morphology of the other superficially similar genera, the new species seems best placed in the genus *Aganaster*. It must be reminded, however, that the dorsal side of the new species remains unknown and that assignment to the genus *Aganaster* should thus be considered as tentative. Clearly, more research based on well preserved modern-type Palezoic ophiuroid specimens is necessary to meaningfully delimit genus concepts and eventually elucidate the relationships between the different forms.

The present study adds to the diverse and stratigraphically long-lasting record of modern-type Paleozoic ophiuroids, currently including more than 15 nominal species ranging from the Devonian to the Permian. In spite of the potentially tremendous significance for the understanding of early crown-group ophiuroid diversification, however, studies on the taxa in question have produced little more than a loose collection of superficial descriptions, except for very few notable exceptions (e.g., Hotchkiss and Haude 2004). The term "modern-type" quite accurately circumscribes the core of the problem: does the similarity with some extant ophiuroid forms, indeed, reflect close phylogenetics tie, pushing early radiation of the crown group deep into the Paleozoic, as suggested by Hotchkiss and Haude (2004), or are the modern-looking Paleozoic forms only extinct homeomorphs of their extant counterparts with no direct phylogenetic ties?

Unfortunately, the current state of knowledge precludes any conclusion in this respect. The hypothesis of an early Paleozoic crown-group radiation is implicit in the assignment of certain genera to the extant Ophiolepididae, although the family in question has been recently rejected as polyphyletic (O'Hara et al. 2014). Other modern-type Paleozoic genera are grouped in the extinct family Ophiurinidae assumed to belong to the extant suborder Chilophiurina (Spencer and Wright 1966). The Ophiurinidae is an ill-defined taxon and reflects differences in approach between palaeontologists and neontologists rather than phylogenetic relationships.

Any attempt to meaningfully interpret the fossil record of the modern-type Paleozoic ophiuroids with respect to their probable significance for crown-group diversification will have to involve meticulous, material-based re-assessment of the skeletal characters at a level as close to recent ophiuroid descriptions as possible. Descriptions should be based on well preserved specimens, and special emphasis should be put on larger specimens, like the one described herein, as they tend to display pivotal characters more clearly. On the basis of the here described specimen, it seems likely that at least some of the modern-type Paleozoic ophiuroids, indeed, are early crown-group representatives. If so, the discovery of *Aganaster jagiellonicus* adds to the growing evidence that *Ophiomusium*-like forms, rather than *Ophiobyrsa* or ophiomyxids in general (Smith et al. 1995), are at the origin of the modern ophiuroid radiation (Hotchkiss and Haude 2004; O'Hara et al. 2014).

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