

Ophiuroids from the Upper Jurassic of Kuyavia and the Kraków-Częstochowa Upland, Poland

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ABSTRACT:

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Ophiuroids from the Upper Jurassic marine deposits (upper Oxfordian–lower Kimmeridgian) of southern and north-western Poland have been studied in two sections: Zalas quarry in the Kraków-Częstochowa Upland in southern Poland and Wapienno/Bielawy quarries in the Kuyavia region of north-western Poland. Described herein are nine taxa belonging to five genera (one new to science): *Alternacantha* Thuy and Meyer, 2013; *Dermocoma* Hess, 1964; *Ophiobartia* Loba gen. nov.; *Ophioderma* Müller and Troschel, 1840; *Ophiotreta* Verrill, 1899, and three families: Ophiacanthidae and Ophiodermatidae (both of Ljungman, 1867), and Ophiotomidae Paterson, 1985. Only a few representatives of some of these taxa have previously been reported from the Jurassic of Poland. One species, *Ophiobartia radwanskii* Loba, is established as new. The ophiuroid material recognized from both Polish localities is close to those described from Western Europe at family or even genus level. Both studied ophiuroid assemblages from Zalas and Wapienno/Bielawy show similarities, being dominated by the cosmopolitan species *Ophioderma spectabile* Hess, 1966, and by different species of *Dermocoma*. The recognized ophiuroid assemblages represent a rather shallow-water environment.

Key words: Taxonomy; New species; New genus; Lateral arm plates; Lower Kimmeridgian; Upper Oxfordian.

INTRODUCTION

Brittle stars (Ophiuroidea Gray, 1840) are an important member of modern benthic communities (Stöhr *et al.* 2012). Fossils provide clues that this was also the case in the geological past.

The ophiuroid skeleton is composed of fine calcitic ossicles that are connected by muscles and ligaments. The ossicles tend to separate very quickly after the animal's death and the decomposition of its soft tissues. Hence, even semi-articulated specimens occur relatively rarely in the fossil record. In turn, isolated ophiuroid ossicles occur abundantly in Mesozoic strata, being the subject of numerous pa-

pers (e.g., Hess 1975a; Thuy and Kroh 2011; Thuy 2013; Thuy and Meyer 2013; Thuy *et al.* 2013).

So far, most of the research on ophiuroids focused on Western Europe. Till recently, the ophiuroid fossil record from Poland was very poorly documented. Radwański (2002) and Salamon and Zatoń (2004) described the massive occurrence of semi-articulated brittle stars from the Triassic of the Holy Cross Mountains and Silesia, respectively. Radwańska (in Radwańska and Radwański 2004) described two species: *Ophioderma? spectabilis* [sic] Hess, 1966 and *Ophiotreta? oertli* Hess, 1965 from tiered burrows of alpheid shrimps from the Kimmeridgian of the Holy Cross Mountains.



Text-fig. 1. Location of the Wapienno/Bielawy and Zalas quarries against the generalized geology of Poland (without Quaternary strata). Adapted from Matyja and Wierzbowski (2002), with modifications.

Recently, Loba (2019) described several asterozoan taxa from two localities in Poland, i.e., the Wapienno/Bielawy quarries complex in the Kuyavia region and the Zalas quarry in the Kraków-Częstochowa Upland, both representing the Upper Jurassic. The description of asteroid ossicles from Wapienno/Bielawy was published recently (Loba and Radwańska 2022). Here we redescribe the ophiuroid material from the Wapienno/Bielawy and Zalas quarries.

GEOLOGICAL SETTING

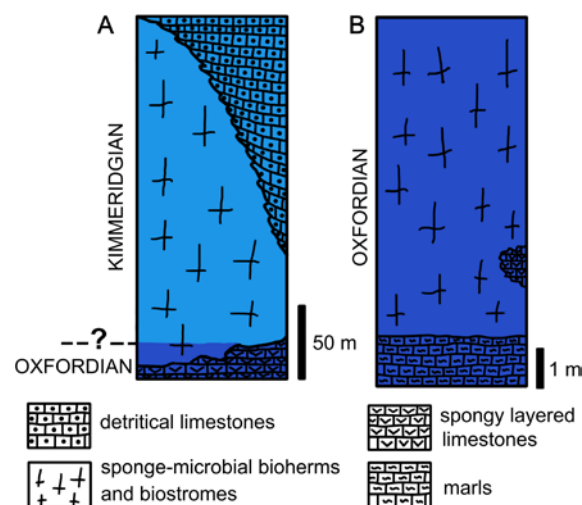
The studied material was collected during several field trips of UR in the first decade of the 21st century. Part of it comes from the complex of two quarries, Wapienno and Bielawy, also referred to as the Piechcin-Barcin locality (Radwańska and Radwański 2003), located in the Kuyavia region of north-western Poland (Text-fig. 1). Both quarries are situated in direct proximity and share the same lithology and stratigraphy, hence they are treated here as a single locality, Wapienno/Bielawy.

Wapienno/Bielawy strata are part of the Zalesie Anticline of halokinetic origin (Ineson *et al.* 1998).

Both quarries expose Upper Jurassic strata (Text-fig. 2A) of the *Epipeltoceras bimammatum* and *Idoceras planula* zones (Matyja and Wierzbowski 2002; see also Radwańska 2007). They were originally described as upper Oxfordian. However, due to correlation with the sub-boreal *Pictonia baylei* Zone (Główniak and Wierzbowski 2007), they are now considered as lower Kimmeridgian (Wierzbowski *et al.* 2016). The exposure encompasses biohermal massive limestones surrounded by detritic talus and basal facies (Matyja and Wierzbowski 1981; Matyja *et al.* 1985; see also Loba and Radwańska 2022).

The second part of the material comes from Zalas quarry in the Kraków-Częstochowa Upland in southern Poland (Text-fig. 1). Jurassic strata in Zalas overlie Permian rhyodacites that are exploited in the quarry (Jurkowska and Kołodziej 2013). The Jurassic succession begins with Callovian silico-clastic and crinoid limestones (Radwańska 2005). They are overlain by columnar stromatolites. The Oxfordian (Text-fig. 2B) starts with marls and marly limestones representing the *Cardioceras bukowskii* and *Cardioceras costicardia* subzones (Matyja and Tarkowski 1981; Górka and Bąk 2000). In their top-most part, they are quite rich in sponges, ammonites, belemnites and brachiopods. These strata gradually pass into biohermal massive limestones in the top of the succession. Due to the ongoing exploitation of the Zalas quarry, the biohermal limestones currently have been almost entirely removed.

Ophiuroid material for current research comes mainly from the talus facies of the Wapienno/Bielawy



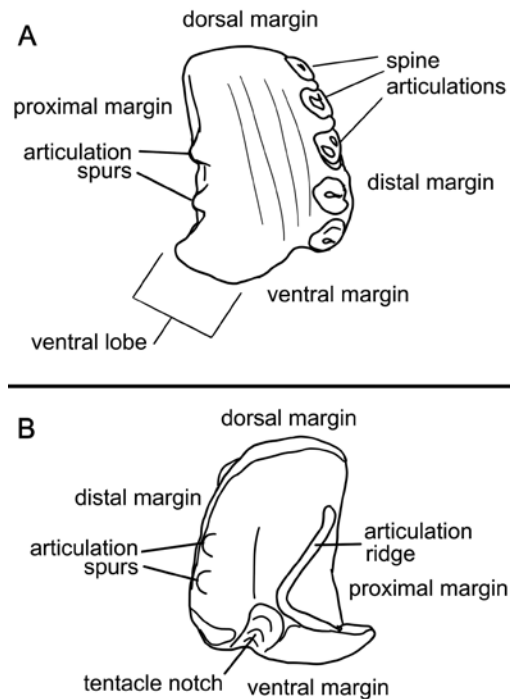
Text-fig. 2. Simplified lithological succession of the Wapienno/Bielawy and Zalas quarries (only Upper Jurassic strata are presented). A – Wapienno/Bielawy, adapted from Matyja *et al.* (1985), with modifications; B – Zalas, adapted from Jurkowska and Kołodziej (2013), with modifications.

succession (lower Kimmeridgian) and the uppermost part of the Oxfordian strata exposed in Zalas quarry. In both localities, the material was collected mainly from scree and eroded surfaces. This method of collection was chosen because it has yielded more specimens, and consumed less time and effort compared to rock sample maceration, a method that has been found to be less effective.

MATERIAL AND METHODS

The original material comprised numerous isolated ophiuroid ossicles, preselected from abundant echinoderm material, collected by UR during several field trips in the first decade of the 21st century. Over 600 kg of sediment was collected. The material was dried for a week at 60°C and then sieved through a 1 mm sieve. From such prepared material, ophiuroid Lateral Arm Plates (abbreviated further as LAPs; Text-fig. 3) were selected using a stereomicroscope. Among the isolated skeletal elements of the ophiuroids, the LAPs are of highest diagnostic value (Martynov 2010; Thuy and Stöhr 2011). The preselected LAPs were checked for their preservation state. Only LAPs preserved well enough to provide meaningful diagnostic features have been retained in the research sample. In total, 506 LAPs were preselected (387 from Wapienno/Bielawy and 119 from Zalas; Table 1). The LAPs were washed out from the rock residue using an ultrasonic cleaner and taxonomically diagnosed using a stereomicroscope. The best preserved and most representative LAPs were photographed with the use of a scanning electron microscope.

Higher taxonomy follows the World Register of Marine Species (WoRMS; www.marinespecies.org; last accessed 07.07.2022). The nomenclature used in the descriptions of the LAPs (Text-fig. 3) follows Thuy



Text-fig. 3. Graphic explanation of the used terminology. A – Ophiuroid lateral arm plate (LAP) viewed from the external side; B – Ophiuroid lateral arm plate (LAP) viewed from the internal side.

and Stöhr (2011). The term ‘sigmoidal fold’ is used in the meaning of Martynov (2010). The term ‘abaxial’ refers to the direction outwards to the ophiuroid’s arm longitudinal axis, while the term ‘adaxial’ refers to the direction towards the arm longitudinal axis.

Repository

All ophiuroid material described herein is housed in the Stanisław Józef Thugutt Geological Museum of the Faculty of Geology, University of Warsaw, with the prefix MWGUW ZI/72.

Family	Taxon	Number of LAPs	
		Wapienno/Bielawy	Zalas
<i>incertae sedis</i>	Ophiacanthida indet.	0	6
<i>incertae sedis</i>	<i>Ophiobartia radwanskii</i> Loba gen. et sp. nov.	5	0
<i>incertae sedis</i>	<i>Dermocoma</i> cf. <i>biformis</i> Hess, 1975	12	0
	<i>Dermocoma</i> sp. 1	9	0
	<i>Dermocoma</i> sp. 2	0	27
Ophiodermatidae	<i>Ophioderma spectabile</i> Hess, 1966	360	75
Ophiacanthidae	<i>Alternacantha</i> sp. 1	1	0
	<i>Alternacantha</i> sp. 2	0	1
Ophiotomidae	<i>Ophiotreta</i> cf. <i>stefaniae</i> Thuy, 2013	0	10
Total number of identified LAPs		387	119

Table 1. The count of identified LAPs from Wapienno/Bielawy and Zalas quarries following their taxonomic identity and in total.

SYSTEMATIC ACCOUNT

Class Ophiuroidea Gray, 1840

Order Ophiacanthida O'Hara, Hugall, Thuy, Stöhr
and Martynov, 2017

Ophiacanthida indet.

(Text-fig. 4A–C)

MATERIAL: Six isolated LAPs (MWGUW ZI/72/011), Zalas (Oxfordian, Kraków-Częstochowa Upland, Poland). Three of them have individual catalogue numbers (MWGUW ZI/72/012, MWGUW ZI/72/013, MWGUW ZI/72/014) and were the basis of the description.

DESCRIPTION: The material encompasses LAPs with very regular proportions, with the length of proximal (Text-fig. 4B) and medial plates (Text-fig. 4C) just slightly exceeding their height. The ventral margin is relatively smooth, but the dorsal one bulges in its mid-length. Both the proximal and distal margins are gently curved, bearing small secondary undulations.

The external surface (Text-fig. 4A₁, B₁, C₁) is distally covered with an ornamentation of very fine vertical stripes. The proximal margin bears two large articular spurs, slightly protruding out of the plate's margin. The larger upper spur is rounded, while the smaller lower one is distinctly elongated horizontally. Both spurs are mirrored on the distal margin on the internal side of the plate.

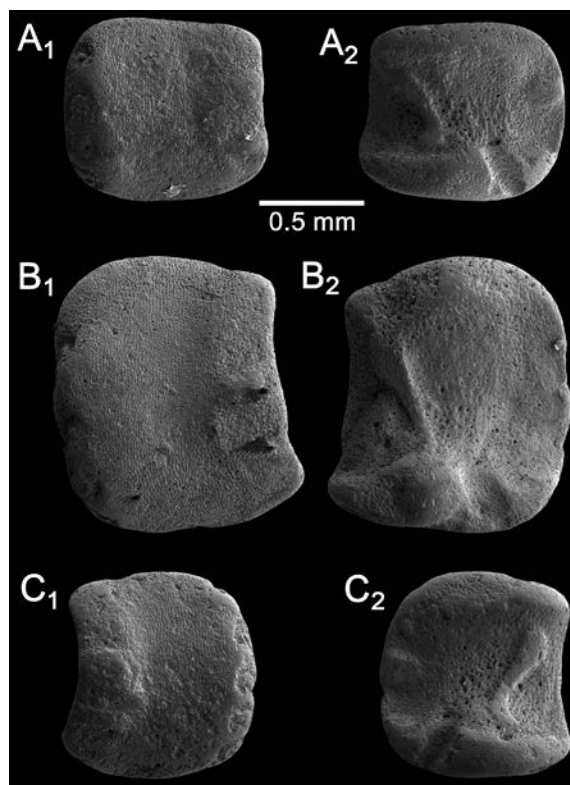
The LAPs bear not less than four (maximally five) subequal spine articulations sunken in pockets in the distal margins of the plates.

The distance between subsequent spine articulations slightly increases dorsally, while the dorsalmost articulation is separated from the others by a significantly larger distance.

The spine articulations are composed of two lobes continuously connected on the proximal side. The muscle and nerve openings are separated by a transverse ridge. The spine articulations are poorly preserved, hence it is difficult to judge if they originally had the sigmoidal fold.

The ridge on the internal side of the LAPs (Text-fig. 4A₂, B₂, C₂) is bipartite. The dorsal part traverses obliquely from the dorso-proximal corner of the plate in the ventro-distal direction. The ridge is dorsally wide and gradually narrows along the way. Before the tentacle notch, the ridge kinks in the ventro-proximal direction and begins to get broader. Tentacle notches are narrow but well developed.

The distal LAPs (Text-fig. 4A) differ in their proportions, being clearly longer than high. Their dorsal



Text-fig. 4. Lateral arm plates (LAPs) of Ophiacanthida indet., Zalas, Kraków-Częstochowa Upland, Poland (Oxfordian, Upper Jurassic). A – MWGUW ZI/72/014, distal LAP in external (A₁) and internal (A₂) views; B – MWGUW ZI/72/012, proximal LAP in external (B₁) and internal (B₂) views; C – MWGUW ZI/72/013, medial LAP in external (C₁) and internal (C₂) views.

margin does not bulge as much in its mid-length as it does in the proximal and medial plates.

REMARKS: Due to the poor state of preservation, especially in the case of spine articulations, the current material is hard to identify precisely. The general shape and dimensions are relatively similar to *Dermacantha* Thuy, 2013 (Ophionereididae Ljungman, 1867) or *Dermocoma* Hess, 1964 (Family *incertae sedis*).

The LAPs in the current material bear spine articulations that are relatively deeply sunken in the plates' distal margins and directed distally. This differs from the case in *Dermacantha*, where the spine articulations face in the lateral direction (abaxially). The dorsal and ventral lobes of the spine articulations seem to be connected continuously to one another on the proximal side in the current material, while they are separated by several knobs in *Dermacantha*. Articulation spurs on the inner-distal and outer-prox-

imal margins of the plates are well developed in the current material, while in *Dermacantha* they are absent or weakly developed. The internal ridge on the LAPs from Żalas is club-shaped, narrowing from the top to its mid-length, and then broadening backward. The internal ridge on the LAPs of *Dermacantha* lacks such demarcated changes in its breadth.

The current material bears similarities with some of the species of *Dermocoma*, e.g., *D. potti* Thuy, 2013. However, in *D. potti*, the dorsal margin of the internal ridge is pointed, while it is rounded in the current material. In the present LAPs, the external ornamentation is very fine, while in *D. potti* it consists of relatively broader vertical bands. In the current material, the distance between successive spine articulations increases dorsally, and the dorsalmost articulation is separated from the others by an especially large gap. All articulations in *D. potti* are separated from each other at equal distances.

The current material bears the strongest resemblance to *Ophiarachna? liasica* Kutscher, 1996 (Ophiomyxidae Ljungman, 1867). As in the LAPs studied, plates of *O.? liasica* bear relatively few spine articulations, the dorsalmost (if there are 4 articulations or more) being separated from the others by a gap. The external ornamentation consists of tiny tubercles aligned in fine vertical stripes. The general shape of the internal ridge in the present LAPs is also in agreement with *O.? liasica* but differs from it in details, especially in distal plates.

The internal ridge in the distal LAPs from the current material remains in agreement with the proximal plates, while the distal LAPs of *O.? liasica* (described by Kutscher 1996 as medial LAPs) bear a relatively massive and unstricted ridge. The distal LAPs in the current material bear a tentacle notch, which is developed as a perforation in the distal plates of *O.? liasica*. Finally, the current material is separated from *O.? liasica* (upper Toarcian to lower Aalenian) by a stratigraphic gap.

We recognize the morphological similarities with *O.? liasica* as meaningful. It should be noted, however, that extant species of *Ophiarachna* tend to have larger spine articulations that point more abaxially, and differently developed distal margins of the LAPs and LAPs ornamentation in the form of fine tubercles without a clear tendency to form stripes. In consequence, the assignment of *O.? liasica* to *Ophiarachna* is by itself doubtful, and this species is pending revision. Both the current material and the *O.? liasica* which present some similarities to *Dermocoma* species, however, differ from them in aspects described earlier. Bearing these doubts in mind, we

have refrained from assigning the current material to any known genus and species. At the same time, its state of preservation and the low number of identified LAPs does not permit the creation of a new taxon.

Family *incertae sedis*

Genus *Ophiobartia* Loba gen. nov.

DERIVATION OF NAME: Gender feminine. Combination of prefix ‘*ophio-*’ (snake-like, Greek) and the name Bartłomiej (Bartholomew in Polish; the name of ML’s nephew).

TYPE SPECIES: *Ophiobartia radwanskii* Loba sp. nov.

DIAGNOSIS: The same as for the type species (see below), by monotypy.

REMARKS: The intrageneric variability in the LAPs morphology among ophiuroids tends to be relatively small (Martynov 2010; Thuy and Stöhr 2011). Species of the same genus differ in such characteristics as the robustness and broadness of stripes forming the external ornamentation (if applicable) or the maximal count of spine articulations, as well as in some other details. However, the combination of characters observed in the material studied (see below for details in the remarks under the type species) does not fit any currently known genus. Due to the low intrageneric variability in the ophiuroids, we exclude the possibility that the current material may represent an unusual species of an already described genus.

Ophiobartia radwanskii Loba sp. nov.

(Text-fig. 5A–E)

TYPE MATERIAL: Proximal LAP, holotype: MWGUW ZI/72/032, presented in Text-fig. 5D, and paratypes: proximal LAP MWGUW ZI/72/033, presented in Text-fig. 5C, median LAP MWGUW ZI/72/034, presented in Text-fig. 5B.

TYPE LOCALITY: Wapienno/Bielawy quarries, Kuyavia Region, Poland.

TYPE HORIZON: *Epipeltoceras bimammatum* and *Idoceras planula* zones, lower Kimmeridgian (Upper Jurassic).

DERIVATION OF THE NAME: To honour Andrzej Radwański, an eminent geologist and palaeontologist.

DIAGNOSIS: A brittle star species having LAPs with an ornamentation of vertical stripes and no less than five spine articulations (six on the proximal LAPs) sitting in relatively shallow pockets on the distal margin of a plate. Both dorsal- and ventralmost spine articulations are enlarged, and the dorsal one sits in a characteristically widened pocket, being separated from the other articulations by a gap. There are two articulation spurs on the proximal external surface and on the distal internal surface of the LAPs. On the proximal LAPs, the dorsal spur on the internal surface is characteristically oval. The dorsal part of the articulation ridge on the internal side of a LAP is characteristically flattened and broadened into a drop-like or lens-like shape.

MATERIAL: Five LAPs (MWGUW ZI/72/032, MWGUW ZI/72/033, MWGUW ZI/72/034, MWGUW ZI/72/035, MWGUW ZI/72/036), Wapienno/Bielawy (lower Kimmeridgian, Kuyavia, Poland).

DESCRIPTION: The holotype (Text-fig. 5D) is a large proximal LAP, clearly higher than long. The dorsal margin has a slightly arched, almost straight outline. The ventral margin is developed in the form of a lobe but only slightly protrudes in the ventro-proximal direction. The distal portion of the LAP bends gently outward (abaxially). The plate is also gently bent around the longitudinal axis. The LAP is not constricted.

The external surface (Text-fig. 5D₁) bears two clear articulation spurs on the proximal margin. They are developed in form of bulges, only slightly protruding beyond the plate's proximal margin. They are generally triangular in shape, and the dorsal one is somewhat larger.

The ornamentation is largely effaced by abrasion but is preserved in the distal portion of the plate. It consists of tiny tubercles that tend to fuse in continuous vertical stripes.

At the distal margin, there are five relatively shallow pockets bearing spine articulations. The dorsal and ventralmost spine articulations are both clearly larger than the remaining three and separated from them by a small gap. In addition, the dorsal spine articulation sits in an enlarged, widened pocket. The three central spine articulations are all of similar size, separated from each other by equal spacing.

The spine articulations are in part effaced by abrasion. The muscle opening was slightly larger than the nerve opening (clearly larger in the dorsalmost articulation). In the current preservation state, both openings seem to be separated by a relatively straight ridge.

The internal side of the plate (Text-fig. 5D₂) features an articulation ridge which in its dorsal part is characteristically flattened and broadened into a drop-shape. Below this flattening, the ridge has mostly constant width and runs obliquely in the ventro-distal direction. Then it turns in the ventro-proximal direction, entering the internal side of the ventro-proximal lobe of the plate.

The distal margin of the internal side of the plate bears two articulation spurs. The ventral one is drop-shaped and stays in agreement with the sub-triangular shape of the respective spur on the proximal margin of the external side. The dorsal spur, however, is clearly oval in shape.

The tentacle notch is well developed and relatively broad.

The characteristics of the proximal paratype LAP (Text-fig. 5C) follow those of the holotype. The plate is slightly lower in relation to its length. The ventro-proximal lobe of the plate protrudes even less beyond the rest of the plate. The paratype plate has a better preserved external surface (Text-fig. 5C₁) than the holotype (aside from the most proximal part which in turn is poorly preserved). It bears the ornamentation in form of fine vertical stripes. The ornamentation terminates a little bit before the spine articulation pocket margins, leaving there a narrow band of smooth surface. The spine articulations follow the pattern seen in the holotype.

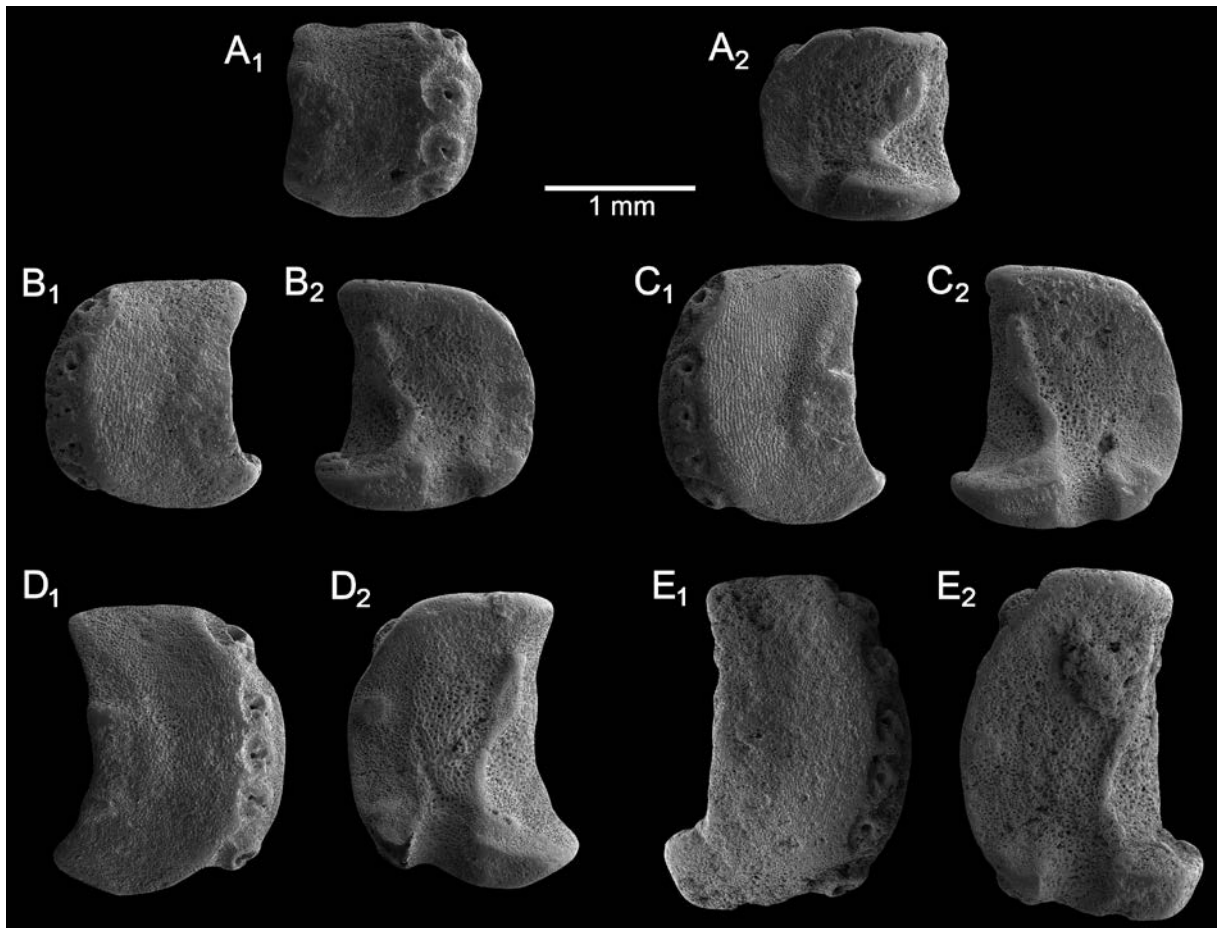
The poorly preserved proximal margin probably had two articulation spurs but the ventral one is barely visible due to abrasion.

The internal surface (Text-fig. 5C₂) is in turn more poorly preserved than in the holotype. Still, the characteristic flattening and broadening of the dorsal portion of the articulation ridge are clearly visible. The articulation spurs of the distal margin are poorly preserved.

The medial LAP (Text-fig. 5B), also included in the type series, differs from the proximal plates mainly in proportions, the length and height being of similar value. The ventro-proximal lobe can be hardly distinguished. The general preservation state seems to be worse than in both proximal plates. The external surface's ornamentation (Text-fig. 5B₁) and the development of the spine articulations stay in agreement with the holotype.

The internal side of the plate (Text-fig. 5B₂) features a characteristic drop-shaped flattening of the articulation ridge.

The material includes two other LAPs, which have not been included in the type series. One of them is a proximal plate (Text-fig. 5E). It is clearly



Text-fig. 5. Lateral arm plates (LAPs) of *Ophiobartia radwanskii* Loba gen. et sp. nov., Wapienno/Bielawy, Kuyavia, Poland (Kimmeridgian, Upper Jurassic). A – MWGUW ZI/72/036, distal LAP in external (A₁) and internal (A₂) views; B – MWGUW ZI/72/034, paratype median LAP in external (B₁) and internal (B₂) views; C – MWGUW ZI/72/033, paratype proximal LAP in external (C₁) and internal (C₂) views; D – MWGUW ZI/72/032, holotype proximal LAP in external (D₁) and internal (D₂) views; E – MWGUW ZI/72/035, proximal LAP in external (E₁) and internal (E₂) views.

higher than the holotype and has a more strongly protruding (in the proximal direction) ventro-proximal lobe. The ornamentation of the external surface (Text-fig. 5E₁) is largely obscured by abrasion. The number of spine articulations rises to six in this plate. They follow, however, the same pattern as in the holotype. The dorsal- and ventralmost articulations are visibly larger than the others. The dorsalmost one sits in a somewhat widened, enlarged pocket but this feature is not as pronounced as in the holotype. The articulation spurs on the proximal margin of the external surface are indistinguishable if present at all. The corresponding spurs on the distal margin of the internal surface (Text-fig. 5E₂) are very faintly visible. The articulation ridge on the internal side of the plate seems to be proportionally slightly thinner than in the holotype. Its ventralmost part is damaged, and

the dorsalmost part is partially obscured by sediment. Hence, it cannot be stated if the characteristic flattening of the articulation ridge was present, but if so, then it was probably proportionally narrower and smaller than in the holotype.

The last LAP (Text-fig. 5A) is probably a distal plate. It differs most significantly from the plates included in the type series. The proportions change in favour of the length over the height. Nevertheless, the differences between those two dimensions remain small. The plate is highly abraded. The character of the external surface's ornamentation (Text-fig. 5A₁) cannot be determined. Some of its traces in the ventralmost area of the plate suggest that it may have consisted of vertical stripes. The number of spine articulations falls to four. The dorsalmost articulation is not significantly larger than the others, contrary

to the previously described plates. The ventralmost articulation is not larger than the others and seems to be even a little smaller. Articulation spurs are poorly preserved on the external and internal sides. What connects the current plate most strongly with the others is the characteristic flattening of the dorsal portion of the articulation ridge on its internal side (Text-fig. 5A₂).

REMARKS: The enlargement and flattening of the dorsal portion of the articulation ridge on the internal side, seen in the current material, can be observed in many ophiidermatids, such as *Ophioderma spectabile* Hess, 1966. However, the character of this flattening is usually completely different. The entire dorsal portion of a ridge is rounded and flattened, giving it a club-like shape. In the current material, the dorsal tip of a ridge is developed normally and only then it broadens into a wedge-like form, to narrow again in a similar manner. Hence, the whole flattening has rather a drop-like or lens-like appearance (with relatively sharp points), rather than club-shaped.

A flattening or broadening of the dorsal ridge head can be observed also in some representatives of other families, for example in *Ophiogaleus* Thuy, 2013 (Ophiacanthidae). Again, the character of this broadening is significantly different.

In the available material, only five LAPs have been found. Still, the combination of the very characteristic features allows for the distinction of a new genus and species. Especially the co-occurrence of a flattened, drop-shaped dorsal portion of the articulation ridge on the internal side of the plate, an oval (almost round in the holotype) dorsal articulation spur on the distal margin of the internal side of the plate, and the development of spine articulations, with an enlarged dorsalmost one (and in proximal and median plates also the ventralmost one) placed in a widened and enlarged pocket. The combination of all these features makes the described plates very unique. We have not seen such a combination of characters so far in any genus. Hence, the creation of a new genus and species is most appropriate.

Unfortunately, in all available specimens the spine articulations are relatively poorly preserved. This makes higher systematic assignment problematic. In the current state, it is not clear whether the sigmoidal fold was present or not. By the development of spine articulations, the current material resembles to some extent some representatives of the Ophiocomidae Ljungman, 1867, such as e.g., the modern *Ophiocoma erinaceus* Müller and Troschel, 1842. The enlarged ventralmost spine articulation,

as well as the relatively huge size of all articulations, make the current material similar also to extant species of *Ophiarachna* (Ophiomyxidae). The general shape of spine articulations and the rounded shape of articulation spurs are also in agreement with modern *Ophiarachna*. In the general shape of the plates, however, and in the character of the external surface ornamentation, the current material is more similar to *Dermocoma* (Family *incertae sedis*).

Family *incertae sedis*

Genus *Dermocoma* Hess, 1964

TYPE SPECIES: *Dermocoma wrighti* Hess, 1964, Malmesbury (Wiltshire), England, Bathonian, Middle Jurassic.

Dermocoma cf. *biformis* (Hess, 1975a)
(Text-fig. 6A, B)

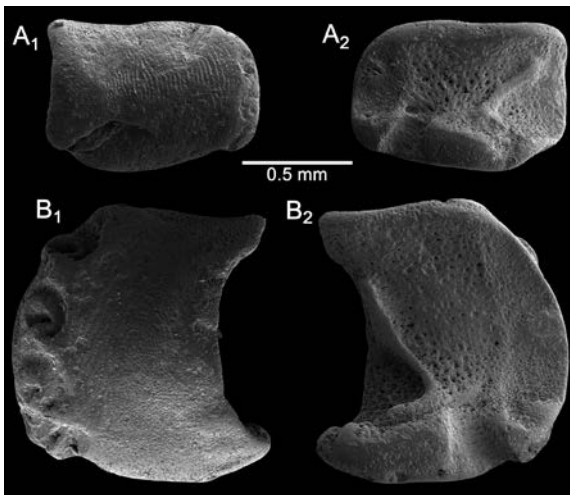
MATERIAL: 12 isolated LAPs ((MWGUW ZI/72/017), Wapienno/Bielawy (lower Kimmeridgian, Kuyavia, Poland). One median plate (MWGUW ZI/72/018) and one distal plate (MWGUW ZI/72/019) have individual catalogue numbers and were the basis of the description.

DESCRIPTION: The median plate (Text-fig. 6B) is almost equidimensional, being just slightly higher than long. The distal part of the plate bends gently outward (abaxially). The plate is unconstricted, the dorsal margin being just slightly concave.

The proximal margin follows a continuous arc in the middle of which one of the two articulation spurs is located. The spur is faint and poorly recognizable (Text-fig. 6B₁). The more ventral spur is larger and better visible but still very faint. Corresponding structures are visible on the distal margin of the internal side of the plate (Text-fig. 6B₂).

The external surface bears ornamentation in form of fine vertical and continuous stripes (Text-fig. 6B₁). The ornamentation occupies the distalmost part of the external surface obliquely, starting at the ventro-distal end of the plate and spreading out in the dorso-proximal direction. The proximalmost part of the external surface is mostly devoid of ornamentation and features the plate's stereom.

There are five spine articulations in total, occupying the distalmost portion of the external surface. They are placed in relatively deep pockets. Each pocket margin is connected with the ventral lobe of the respective spine articulation. The spine ar-



Text-fig. 6. Lateral arm plates (LAPs) of *Dermocoma* cf. *biformis* (Hess, 1975a), Wapienno/Bielawy, Kuyavia, Poland (Kimmeridgian, Upper Jurassic). A – MWGUW ZI/72/019, distal LAP in external (A₁) and internal (B₁) views; B – MWGUW ZI/72/018, median LAP in external (B₁) and internal (B₂) views.

tenticulations are large, ear-shaped and feature a sigmoidal fold. From the proximal side, the transition between the dorsal and ventral lobe is continuous. The spine articulations are all of more or less equal size, facing outward (abaxially). Only the dorsalmost one is somewhat separated from the others, facing distinctly upwards, hence it is barely visible in side view.

The internal side of the plate (Text-fig. 6B₂) features a well-developed articulation ridge, which does not reach the dorsal margin of the plate. It more or less follows the proximal margin, attaining a narrow triangular outline. In the mid-height of the plate, it starts to run obliquely in the ventro-distal direction, attaining the form of a narrow ridge. On the prolongation of this part of the ridge, there is a large tentacle notch in the ventral margin of the plate. The articulation ridge turns in the ventro-proximal direction in the ventral part of the plate, where it becomes broader.

The distal LAP (Text-fig. 6A) is clearly longer than high. The relative size of the spine articulations decreases slightly and the number of articulations falls to four.

The ornamentation of the external surface (Text-fig. 6A₁) seems to occupy a much larger area compared to the median plate, almost reaching the proximal margin. The articulation spurs at the proximal margin cannot be observed but their internal side equivalents (at the distal margin) are faintly visible

(Text-fig. 6A₂). The plate bears signs of deformation. Especially the ventro-proximal part of the external surface bears a dissolution trace left by a sediment grain (Text-fig. 6A₁).

On the internal side (Text-fig. 6A₂), the articulation ridge loses its triangular shape and in general becomes relatively more massive. The tentacle notch is clearly present on the distal plate.

REMARKS: Among the entire available material, there was no proximal plate that could be readily associated with the described plates. This makes the taxonomic recognition somewhat challenging. Because of the lack of proximal plates, the median ones were used for comparison with known species.

The material from Wapienno/Bielawy fits well into *Dermocoma*. The genus merges species very closely resembling each other in terms of LAP morphology, often differing only in very fine details.

The material at hand closely resembles *D. numbergerorum* Thuy, 2013, which is supposed to possess a similar triangular dorsal head of the internal side's articulation ridge. It also features relatively delicate ornamentation of the external surface in the form of vertical stripes, and up to two articulation spurs on the proximal margin of the external surface (and two on the distal margin of the internal surface).

However, the same description can be more or less attributed to *D. biformis*. In reality, the articulation ridge on the internal side of a plate is supposed to be broadened in the middle part in *D. biformis*, and not have a triangular head. Still, the mentioned broadening causes a similar final effect. The less developed LAP's ventral lobe, which protrudes less ventrally, advocates attribution also to *D. biformis*. In *D. numbergerorum* this part of the plate is much more developed.

In both species, however, the articulation spurs on the proximal margin of the external surface are well developed and protrude beyond the plate's proximal margin. In the current material, the spurs are barely visible and attain the form of bulges. In *D. numbergerorum*, the spurs are supposed to be relatively widely spaced in the central area of the proximal plate margin. Their relative positions and spacing in *D. biformis* resemble more closely the case observed in the current material. Hence, we recognize here the close resemblance of the current material to *D. biformis*. Still, because of the lack of proximal plates and the mentioned differences and uncertainties, we leave this tentative recognition in open nomenclature.

Dermocoma sp. 1
(Text-fig. 7A–C)

MATERIAL: Nine isolated LAPs (MWGUW ZI/72/025), Wapienno/Bielawy (lower Kimmeridgian, Kuyavia, Poland). Three of them have individual catalogue numbers (MWGUW ZI/72/026, MWGUW ZI/72/027, MWGUW ZI/72/028) and were the basis of the description.

DESCRIPTION: Of the three illustrated LAP's, the median plate (Text-fig. 7B) is probably the most representative. It is slightly higher than long. The dorsal margin is almost straight, only very gently concave. The plate lacks true constriction. The ventral margin of the plate follows a gentle convex arc.

The plate is very gently arched around the longitudinal axis. The distal part of the plate only slightly bends outwards (abaxially). It bears ornamentation in the form of fine, vertical stripes (Text-fig. 7B₁). At the distal margin, there are five spine articulations placed in pockets. Unfortunately, most of them are poorly preserved. Only the ventralmost articulation features more details. The spine articulation is generally U-shaped, having a continuous margin proximally. The neural and muscle openings seem to be separated by a straight ridge. A proper sigmoidal fold cannot be recognized.

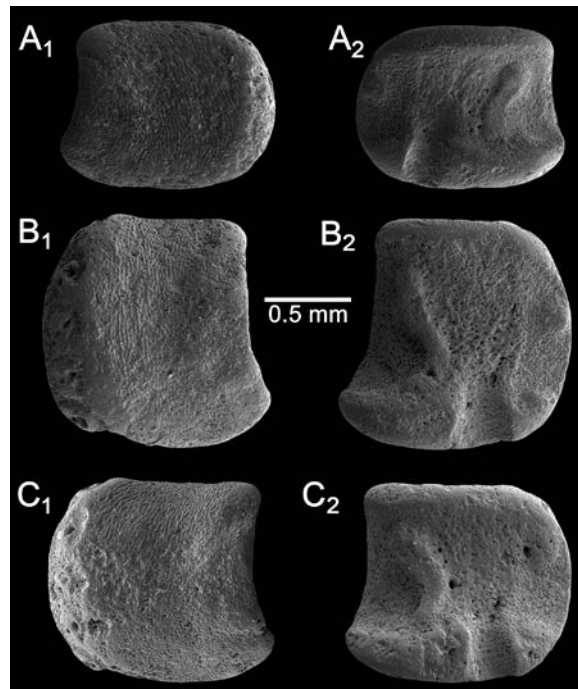
All spine articulations are of similar size and equally spaced. They face abaxially and distally. Only the dorsalmost one faces rather dorsally and distally.

The proximal margin of the plate bears two articulation spurs. They are relatively widely spaced and developed in the form of drop-like bulges. They only very slightly protrude beyond the plate's margin. Similar spurs are developed on the distal margin on the internal side of the plate (Text-fig. 7B₂).

The internal side of the plate (Text-fig. 7B₂) features a relatively short but broad articulation ridge. Generally, it follows an oblique path, being somewhat more vertical in the dorsalmost part. However, it does not reach the dorsal margin of the plate. In the ventral part, it turns gently in the ventro-proximal direction. A deep, broad tentacle notch is present in the ventral margin of the plate.

Other median and distal plates (Text-fig. 7A, C) differ from the already described one only in proportions. The median plate (Text-fig. 7C) is slightly longer than high, while the distal one (Text-fig. 7A) is clearly longer than high.

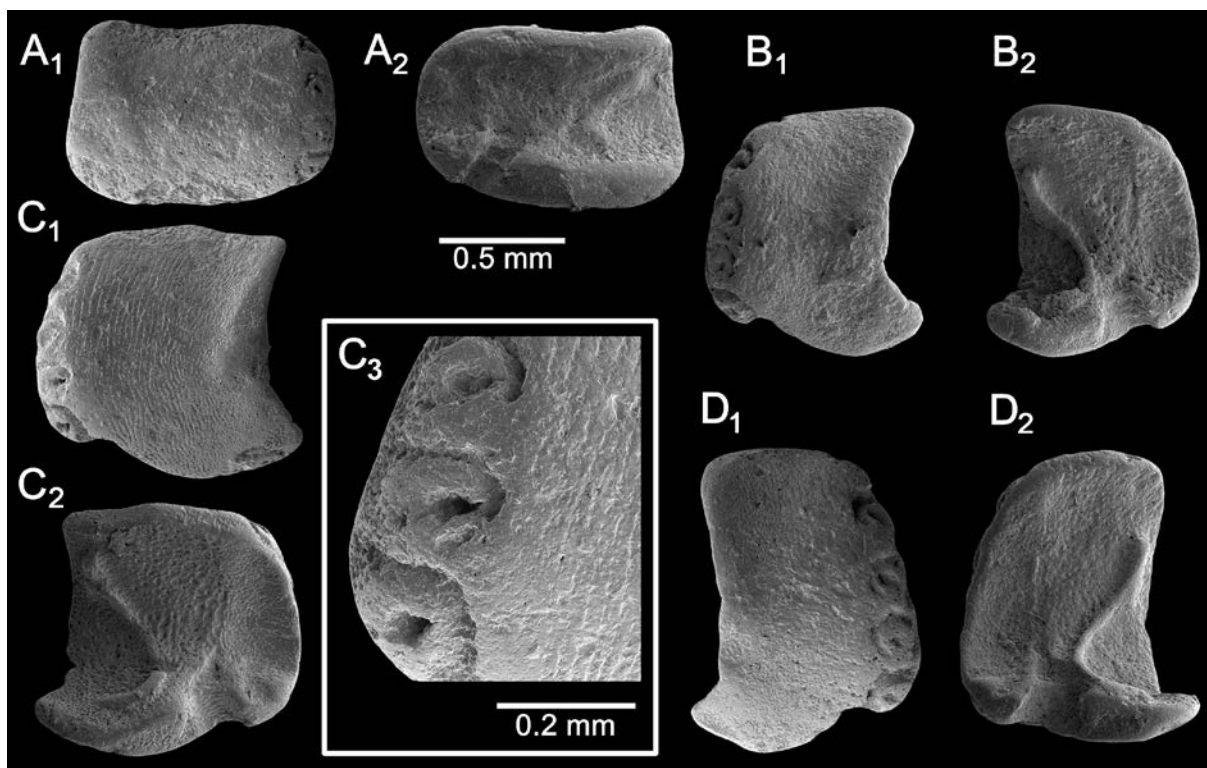
REMARKS: The present material in its general characteristics seems to resemble many fossil ophiacan-



Text-fig. 7. Lateral arm plates (LAPs) of *Dermocoma* sp. 1, Wapienno/Bielawy, Kuyavia, Poland (Kimmeridgian, Upper Jurassic). A – MWGUW ZI/72/028, distal LAP in external (A₁) and internal (A₂) views; B – MWGUW ZI/72/026, median LAP in external (B₁) and internal (B₂) views; C – MWGUW ZI/72/027, median LAP in external (C₁) and internal (C₂) views.

thids. Especially the co-occurrence of relatively large spine articulations with vertical striations on the external surface seems to confirm this statement. In current specimens, however, the spine articulations are very poorly preserved. They also seem to bear features untypical for the Ophiacanthidae. In the current material, nerve and muscle openings of the spine articulations are of similar size, whereas the nerve opening is typically substantially smaller than the muscle opening in ophiacanthids. They also seem to be separated by a straight ridge, while ophiacanthids generally feature a sigmoidal fold, which gives the articulation an ear-shaped appearance.

Due to the above-mentioned features, the current material fits best to *Dermocoma*. The closest resemblance can be observed with *D. biformis*. The general shape of the LAPs, and the number and proportions of spine articulations point to such an interpretation. It should be noted, however, that the vertical striation contributing to the external surface ornamentation seems to be more delicate than in *D. biformis*. Similarly, in *D. biformis* the articulation spurs on the proximal external margin of a LAP tend to be



Text-fig. 8. Lateral arm plates (LAPs) of *Dermocoma* sp. 2, Zalas, Kraków-Częstochowa Upland, Poland (Oxfordian, Upper Jurassic). A – MWGUW ZI/72/023, median LAP in external (A₁) and internal (A₂) views; B – MWGUW ZI/72/021, distal LAP in external (B₁) and internal (B₂) views; C – MWGUW ZI/72/022, median LAP in external (C₁) and internal (C₂) views, C₃ – enlarged view of three ventralmost spine articulations; D – MWGUW ZI/72/024, proximal LAP in external (D₁) and internal (D₂) views.

more robustly developed than in the current material, where they are faintly visible. Those features can be explained by abrasion. Anyhow, we find the current material impossible to determine on species level with any degree of certainty, therefore it is retained in open nomenclature.

Dermocoma sp. 2
(Text-fig. 8A–D)

MATERIAL: 27 isolated LAPs (MWGUW ZI/72/020), Zalas (Oxfordian, Kraków-Częstochowa Upland, Poland). Four of the plates have individual catalogue numbers (MWGUW ZI/72/021, MWGUW ZI/72/022, MWGUW ZI/72/023, MWGUW ZI/72/024) and were the basis of the description.

DESCRIPTION: Proximal LAPs in the current material (Text-fig. 8D) are clearly higher than long. The dorsal margin is shorter than the ventral one. In the proximal half, the plates bear an enlarged ventral lobe, which is highly bent inward (towards the arm axis). Hence, it does not contribute much to the

LAP's height. Whole plates were clearly bent around the arm's longitudinal axis. There is no true constriction. The distalmost portion of the LAPs bends just slightly outwards (abaxially). Just above the ventral lobe, two articular spurs are present on the proximal margin of the plates (Text-fig. 8D₁). They are preserved as two faint bulges that do not protrude beyond the LAP's proximal margin. The LAP's external surface (Text-fig. 8D₁) was covered with an ornamentation of vertical stripes. In all specimens, this ornamentation is only partially preserved. Large portions of it have been removed, most likely due to abrasion.

The LAP's distal margin bears up to five spine articulations, placed in shallow pockets. Spine articulations increase slightly in size towards the ventral margin. Dorsal and ventral lobes of spine articulations are merged continuously on the proximal side. However, there is a small indentation in the place of the junction. The ventral lobes of the spine articulations connect with the margins of the pockets that they occupy. The tips of the spine articulations were strongly abraded and therefore the determination of

their original morphology is difficult. The presence of the sigmoidal fold can be considered quite likely.

The articular ridge on the internal side of the LAPs (Text-fig. 8D₂) is relatively narrow and does not reach the dorsal margin of the plate. Its dorsal head is slightly broader and triangular in shape. The ridge runs obliquely towards the well-developed and broad tentacle notch. Entering the plate's ventral lobe, the ridge turns in the ventro-proximal direction. Directly above the tentacle notch, there is a firm depression in the plate's internal surface.

There is only one easily recognizable articular spur on the distal margin of the internal surface of the LAPs. It is located just before the tentacle notch and has a form of a wedge-shaped bulge.

The median and distal LAPs (Text-fig. 8A–C) differ from the proximal ones mainly in proportions. The median plates (Text-fig. 8B, C) have a subquadrate shape, while the distal ones (Text-fig. 7A) are much longer than high. The median plates (Text-fig. 8B, C) bear up to five spine articulations. The dorsalmost articulation is pointed dorsally and more distally, unlike the remaining four articulations, and differently than in the proximal plates. In the distal LAPs (Text-fig. 8A), the number of spine articulations falls to four. In both, median and distal LAPs, the second articular spur on the distal margin of the plates' internal side (Text-fig. 8A₂, B₂, C₂) becomes barely recognizable, being a very thin (horizontally elongated) bulge.

REMARKS: The ornamentation (vertical stripes), shape and relative size of the spine articulations, placement of spine articulations in shallow pockets on the distal margin, which is only slightly bent outward (abaxially), and the development of the plate's ventral lobe, all point to *Dermocoma*.

Three species of *Dermocoma* have LAPs with a roughly triangular outline, with a very short dorsal and much longer ventral margin, as in the current material. Those include *D. toarcensis* (Hess, 1962), *D. longwyensis* Thuy, 2013, and *D. simonschneideri* Thuy, 2013.

The current material bears very close resemblance to the type material of *D. simonschneideri*. This is reflected in the shape and distribution of the spine articulations, as well as in the general shape of the LAPs. Similarly to the current material, there is a prominent depression directly above the tentacle notch on the internal side of the LAPs.

The LAPs from Zalas differ from *D. simonschneideri* in the higher number of spine articulations (up to five in comparison to four in the referred species). In addition, the current material possesses two horizontal articular spurs on the proximal margin of the

LAPs, while *D. simonschneideri* features a single oblique spur.

Dermocoma toarcensis and *D. longwyensis* both feature up to six spine articulations on the proximal LAPs. In the material from Zalas we have not found LAPs that would share a general morphology with those already described, and would bear six spine articulations. However, the material studied contains only the best preserved specimens, and it cannot be excluded that the more proximal but very poorly preserved plates with six spine articulations were not recognized as conspecific. Hence, the number of spine articulations alone cannot exclude *D. toarcensis* and *D. longwyensis*.

LAPs in the current material feature up to two articular spurs on the proximal margin of the plates' external surface (and similarly on the distal margin of the internal surface). In *D. toarcensis*, there are three such spurs.

The current material is indeed very similar to *D. longwyensis*. In this species, however, the LAPs are smaller on the average, and only a distal portion of the external surface was covered with an ornamentation of vertical stripes. The external surface of the LAPs in the current material is often highly abraded, but some better preserved specimens show ornamentation covering most of the area, not limited only to the distal part. Finally, as for now, *D. longwyensis* is known only from the Bajocian (Middle Jurassic), featuring a significant stratigraphic gap between this taxon and the current material (Oxfordian, Upper Jurassic).

Due to the poor preservation of most of the material we have decided to leave it in open nomenclature. It should be also emphasized that such species as *Eozonella bergeri* Thuy, Marty and Comment, 2013 (Ophiolepididae Ljungman, 1867) and *Ophiozonella stoehrae* Thuy and Kroh, 2011 (Hemieuryalidae Verrill, 1899) bear a very close similarity to the current material and the genus *Dermocoma* in general. The main differences lie in the development of spine articulations. In the two species mentioned above, the spine articulations are horse-shoe shaped and lack a typical sigmoidal fold. In the current material, the dorsal and ventral lobes of spine articulations are continuously merged on the proximal side (the place of the junction is marked by a small notch; Text-fig. 8C₃). In *Eozonella bergeri* and *Ophiozonella stoehrae* these lobes are separated by one or two knobs. In all of the specimens in the current material, the spine articulations are more or less abraded. Hence, the affinity with *Eozonella* Thuy, Marty and Comment, 2013 or *Ophiozonella* Matsumoto, 1915 cannot be excluded completely.

Family Ophiodermatidae Ljungman, 1867
 Genus *Ophioderma* Müller and Troschel, 1840

TYPE SPECIES: *Asterias longicauda* Bruzelius, 1805,
 Mediterranean Basin, recent.

Ophioderma spectabile Hess, 1966
 (Text-fig. 9A–C)

1966. *Ophioderma?* *spectabilis* [sic]; Hess, pp. 1051–1052,
 figs 63, 64.

1975b. *Ophioderma?* *spectabilis* [sic]; Hess, p. 608, fig. 11;
 tab. 2, figs 5–7.

1975c. *Ophioderma?* *spectabilis* [sic]; Hess, p. 592, figs
 5–9, 13; tab. 1, figs 3, 4.

2004. *Ophioderma?* *spectabilis* [sic]; Radwańska in Rad-
 wańska and Radwański, p. 126, pl. 2, fig. 10.

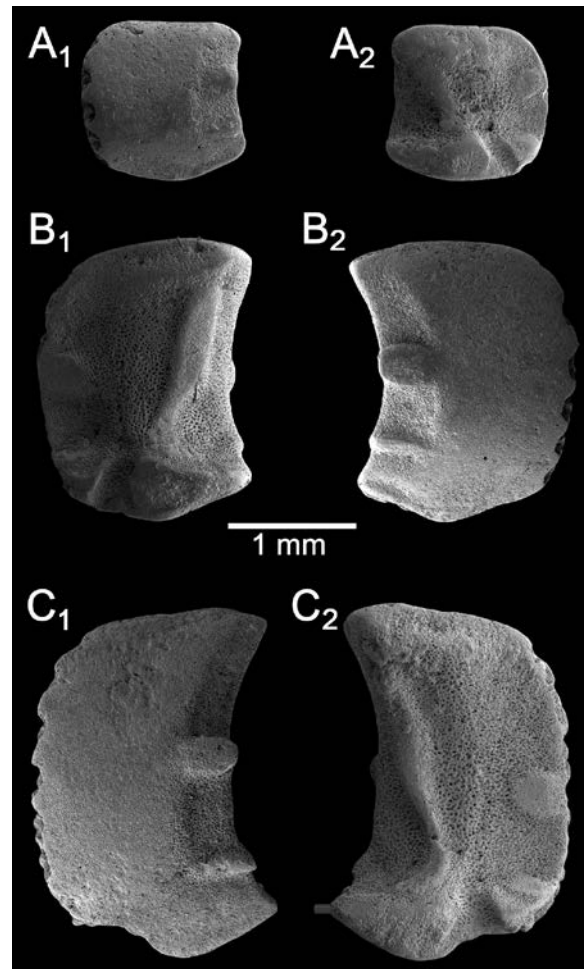
MATERIAL: 360 isolated LAPs (MWGUW ZI/72/
 001), Wapienno/Bielawy (lower Kimmeridgian, Ku-
 yavia, Poland). Three of them have individual cat-
 alogue numbers (MWGUW ZI/72/005, MWGUW
 ZI/72/009, MWGUW ZI/72/010) and were the ba-
 sis of the description. 75 isolated LAPs (MWGUW
 ZI/72/002), Zalas (Oxfordian, Kraków-Częstochowa
 Upland, Poland).

DESCRIPTION: The material consists of relatively
 large and massive LAPs. The proximal plates (Text-
 fig. 9C) reach up to about 4 mm in height. They bear
 seven to eight small spine articulations sunken in
 pockets at the distal margin of the plate. This number
 falls to about five to six articulations in the median
 plates, and to four in the distal ones. The spine ar-
 ticulations face distally, suggesting that spines were
 directed along the arm axis.

The external surface is covered with minute
 tubercles visible under magnifications equal to or
 greater than 32x. Under lower magnifications (Text-
 fig. 9C₁), the external surface seems to be virtually
 smooth. The dorsal margin features a facet for dor-
 sal plate articulation. It seems that the right and left
 lateral plates were separated from one another by a
 dorsal plate on their entire length.

The proximal margin of the plates is somewhat
 recessed inwardly (towards the arm axis), creating
 a distinguishing band in that part of the plate. In the
 middle, and in the ventral half, this band is disturbed
 by the presence of two firm articulation spurs. The
 more dorsal one is bigger and more rounded, while
 the ventral one is smaller and more longitudinal.
 Both are clearly visible.

In the proximal plates (Text-fig. 9C), their ventro-



Text-fig. 9. Lateral arm plates (LAPs) of *Ophioderma spectabile*
 Hess, 1966, Wapienno/Bielawy, Kuyavia, Poland (Kimmeridgian,
 Upper Jurassic). A – MWGUW ZI/72/005, distal LAP in external
 (A₁) and internal (A₂) views; B – MWGUW ZI/72/010, median LAP
 in internal (B₁) and external (B₂) views; C – MWGUW ZI/72/009,
 proximal LAP in external (C₁) and internal (C₂) views.

proximal part is developed into a lobe visibly en-
 hancing the plate's height. A similar lobe is present
 to some extent in the median (Text-fig. 9B) and dis-
 tal plates (Text-fig. 9A) also, but in them it is more
 arched around the longitudinal axis, hence it does not
 contribute to the plate's height so clearly.

The internal side of the plates (Text-fig. 9A₂, B₁,
 C₂) features a large, firm articular ridge developed
 alongside the proximal margin. It consists of a club-
 like, rather flat dorsal part that transverses obliquely
 towards the ventro-distal margin. It constricts along
 the way and finally bends in the ventro-proximal
 direction, entering the internal surface of a ventro-
 proximal lobe. On that surface it expands again.

The tentacle notches are present on all plates in the mid-ventral to ventro-distal margin. The distal half of the plate's internal side bears articular spurs that correspond to those developed on the proximal margin of the external surface.

REMARKS: The current material perfectly fits the diagnosis of *Ophiderma spectabile*, a species described from the Oxfordian of Switzerland (Hess 1975b) and France (Hess 1966, 1975c).

There are some general similarities with *Palaeocoma* d'Orbigny, 1850. This genus features multiple tiny articular spurs on the proximal margin as opposed to two large ones in the current material. The articular ridge on the internal side of the plate is placed more centrally and relatively broader. In the current material, it occupies the proximal part of the plate and is relatively narrower than in *Palaeocoma*, even in its dorsal, club-like part.

Other genera bearing some similarities are *Ophiopetra* Enay and Hess, 1962 and *Eozonella*. In comparison with *O. lithographica* Enay and Hess, 1962, the LAPs in the current material are larger on the average and bear numerous spine articulations. *Ophiopetra lithographica* features up to three spine articulations and has no articular spurs on the proximal margin. The LAPs of *Eozonella oertlii* (Hess, 1965) bear free-standing spine articulations and always a singular articular spur on the proximal margin. In the current material, the spine articulations are sunken in pockets in the distal margin of the plate and bear two spurs on the proximal margin.

The material at hand closely resembles some modern species of *Ophiderma*, e.g., *O. panamensis* Lütken, 1859. This is a strong argument for placing *O. spectabile* in this genus. It should be noted, however, that the LAPs of recent *Ophiderma* bear also large similarities (Thuy and Stöhr 2011) with *Ophiopsis* Müller and Troschel, 1840. What more, *Ophiderma* includes extant species, the LAPs of which are highly similar to each other, making their differentiation very difficult (Thuy and Stöhr 2011). It cannot be excluded that the Jurassic *O. spectabile* actually represents a group of cryptic species and not a single taxon.

Family Ophiacanthidae Ljungman, 1867

Genus *Alternacantha* Thuy and Meyer, 2013

TYPE SPECIES: *Alternacantha occulta* Thuy and Meyer, 2013, Sichtern near Liestal, Canton Basel, Switzerland, middle Bathonian (Middle Jurassic).

Alternacantha sp. 1

(Text-fig. 10B)

MATERIAL: One isolated LAP (MWGUW ZI/72/015), Wapienno/Bielawy (lower Kimmeridgian, Kuyavia, Poland).

DESCRIPTION: The large, unconstricted proximal LAP (Text-fig. 10B) is clearly higher than long. The plate is highly arched around the longitudinal axis. The dorsal margin is almost straight and much longer than the ventral one. The most ventro-proximal part of the plate is developed in a lobe, bent inwardly and proximally.

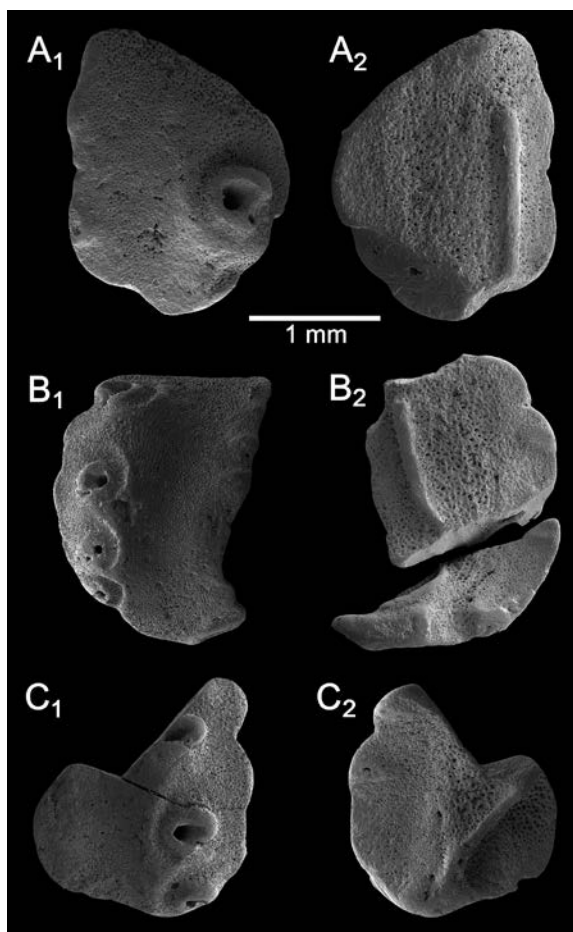
The proximal margin of the plate is only slightly oblique, heading from the dorso-proximal to the ventro-distal direction, but turns sharply in the ventro-proximal direction when entering the ventro-proximal lobe. The dorsal part of the proximal margin bears three articulation spurs, which protrude slightly out of the plate's margin (Text-fig. 10B₁). The dorsalmost spur is poorly visible; however, the other two are clearly distinct. The ventralmost spur is the largest and occupies the space just above the proximal margin's transition into the ventro-proximal lobe.

The spurs correspond to similar structures on the distal margin of the internal side of the plate (Text-fig. 10B₂). However, only two spurs can be distinguished on the internal side. There is no sign of a spur that would correspond to the dorsalmost spur on the external surface.

The external surface features an ornamentation composed of fine tubercles (Text-fig. 10B₁). Those tend to align in vertical rows, especially in the distal part of the plate. They do not connect into continuous stripes. Such ornamentation covers most of the external surface apart from the most proximal band.

The distal part of the plate bears four spine articulations featuring a sigmoidal. They point abaxially and are placed along a low ridge. Each spine articulation sits in a shallow pocket. There is a ridge connecting the ventral lobe of the spine articulation with the margin of the corresponding pocket. The three ventralmost spine articulations feature slight gradation in size, which increases towards the dorsal margin. The fourth, dorsalmost spine articulation is distinctly larger and separated by a larger gap from the others.

The spine articulations are somewhat shifted from the plate's distal margin at a distance roughly corresponding to the half-diameter of a given articulation. This is specifically true for the middle two spine articulations. The dorsal- and ventralmost



Text-fig. 10. Lateral arm plates (LAPs) of **A, C** – *Alternacantha* sp. 2, Żalas, Kraków-Częstochowa Upland, Poland (Oxfordian, Upper Jurassic). **A** – MWGUW ZI/72/016, dorsal LAP's fragment in external (A_1) and internal (A_2) views; **C** – MWGUW ZI/72/016, ventral LAP's fragment in external (C_1) and internal (C_2) views; **B** – *Alternacantha* sp. 1, MWGUW ZI/72/015, in external (B_1) and internal (B_2) views (the plate was broken during processing). Wapienno/Bielawy, Kuyavia, Poland (Kimmeridgian, Upper Jurassic).

articulations are rather closely associated with the plate's distal margin. The distal margin is undulating in character.

The articular ridge on the internal side of the plate (Text-fig. 10B₂) is rather narrow along most of its length. In the dorsal part, it is almost vertical, following the contour of the plate's proximal margin. In the central part, it bends in the ventro-distal direction. On the prolongation of this part of the ridge, there is a tentacle notch developed in the plate's ventral margin. Before reaching it, the ridge bends in the ventro-proximal direction entering the internal side of the ventro-proximal lobe. In this part, the articulation ridge is the broadest.

REMARKS: The character of the large spine articulations, with a sigmoidal fold, size gradation, and a distinct placement and size of the dorsalmost one allows the placing of the current LAP within *Alternacantha*.

The only species of this genus that does not possess ornamentation on the external surface in form of continuous stripes is *A. arges* Thuy, 2013. LAPs of *A. arges* tend to be distinctly larger than the current plate. In the described LAP, the dorsal margin is straight, while in *A. arges* it is developed into a triangle. The proximal margin articulation spurs in *A. arges* are clearly demarcated, extended horizontally, and occupy a distinctly more ventral position. Only two of the three spurs in the described plate are readily recognizable and even they are quite faint compared to *A. arges*. They are rather oval in shape and occupy the dorsal portion of the plate.

Regardless of the lack of vertical stripes (this feature may result from the preservation state), the described LAP is very similar to *A. dilionessa* Thuy, 2013. A striking similarity can be observed in the paratype specimen of a proximal plate (see Thuy 2013, fig. 24: 4). In both cases, the area between the dorsalmost spine articulation and other articulations is built from denser stereom, and the margin of the spine articulation pocket is faint.

Two articular spurs on the proximal margin have similar shapes and positions. However, in *A. dilionessa*, the distal margin of the plate seems to be more widely separated from the spine articulations, and particularly it overhangs distally over the plate's area bearing a tentacle notch. In the material at hand, the distal margin gently transverses into the ventro-proximal lobe.

The described LAP may represent a species new to science. Because of its singular occurrence and a large similarity to *A. dilionessa* we refrain from a formal description of a new taxon.

Alternacantha sp. 2
(Text-fig. 10A, C)

MATERIAL: Two fragments of a supposedly single proximal LAP (MWGUW ZI/72/016), Żalas (Oxfordian, Kraków-Częstochowa Upland, Poland).

DESCRIPTION: The material consists of two fragments of a supposedly single proximal LAP (Text-fig. 10A, C). The first fragment represents the dorsalmost portion of a LAP (Text-fig. 10A). It bears a large spine articulation sitting in a shallow pocket. The margin of the pocket is recessed from the spine

articulation. The spine articulation consists of two lobes (dorsal and ventral), merged continuously on the proximal side. The dorsal lobe is larger than the ventral one. The muscle and nerve openings are separated by a sigmoidal fold. The external surface of the LAP (Text-fig. 10A₁) does not bear ornamentation and is built of fine stereom. The internal side of the LAP (Text-fig. 10A₂) preserves only the dorsalmost portion of the articular ridge. The ridge is narrow and parallel to the proximal margin of the LAP. It runs in immediate proximity to the LAP's proximal margin.

The second fragment (Text-fig. 10C) represents the ventralmost portion of a LAP. It bears three large spine articulations (Text-fig. 10C₁) with a morphology consistent with the one described from the dorsal LAP's fragment. The spine articulations and the spacing between them increase in size in the dorsal direction. As in the dorsal fragment, spine articulations sit in spacious but shallow pockets. The ventral lobes of the spine articulations are not connected with the pocket margins by any means. The spine articulations are recessed from the LAP's distal margin by a space equal to half to full diameter of a given articulation. The internal side of the fragment (Text-fig. 10C₂) preserves the ventralmost portion of the articular ridge that runs obliquely in the ventro-distal direction. It remains very narrow. The internal side of the LAP's distal margin bears two wedge-shaped articulation spurs. Spurs on the proximal margin of the LAP's external side have not been identified. While the LAP's ventral margin seems to be preserved completely, a tentacle notch has not been identified.

REMARKS: Due to the size of the spine articulations, their shape, gradual increase in size in the dorsal direction, their placement in spacious pockets, and shape of the internal ridge (which was most likely narrow along its whole length), the current material represents *Alternacantha*. Among the *Alternacantha* species, the current material bears the closest similarity to *A. arges*. No other *Alternacantha* plates have been found in the Zalas ophiuroid material. The material consists only of two fragments of a single or even two different LAPs. Hence, the material is assigned at generic level only.

Family Ophiotomidae Paterson, 1985
 Genus *Ophiotreta* Verrill, 1899

TYPE SPECIES: *Ophiacantha lineolata* Lyman, 1883, Western Atlantic Ocean, recent.

Ophiotreta cf. *stefaniae* Thuy, 2013
 (Text-fig. 11A, B)

MATERIAL: Ten isolated LAPs (MWGUW ZI/72/029), Zalas (Oxfordian, Kraków-Częstochowa Upland, Poland). Two of them have individual catalogue numbers (MWGUW ZI/72/030, MWGUW ZI/72/031) and were the basis of the description.

DESCRIPTION: The proximal plate (Text-fig. 11B) is proportionally very narrow and high. The dorsal margin of the plate is virtually straight and perpendicular to the proximal and distal margin. The proximal and distal margins are very gently arched, almost straight. The entire plate is bent strongly around the longitudinal axis. There is no recognizable ornamentation on the external surface (Text-fig. 11B₁).

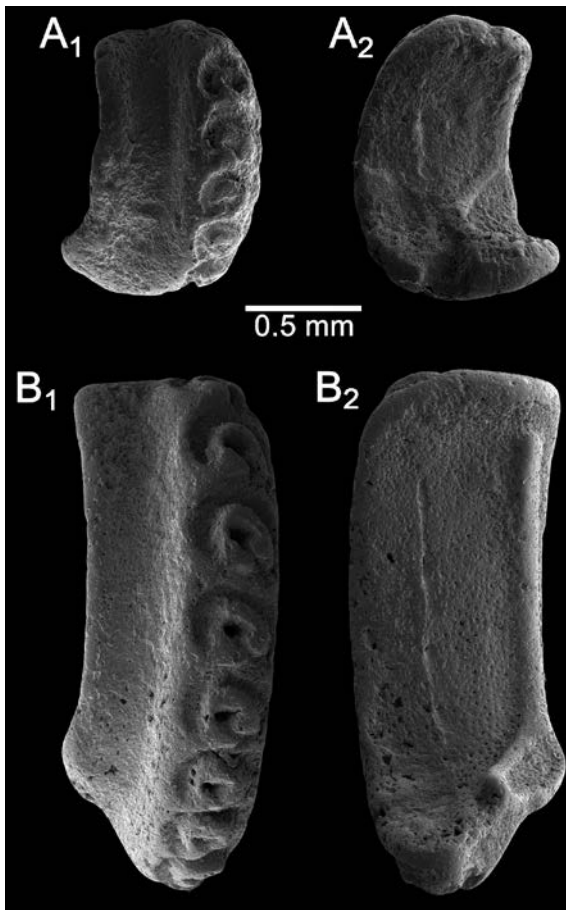
Longitudinally, the plate is split into two areas. The proximal portion is more or less flat, while the distal half of the plate is developed into an abaxially bulging ridge. The height of the ridge increases ventrally. The ventralmost portion of the plate is developed as a ventrally protruding lobe, created mostly by the plate's distal ridge.

The distal ridge bears nine large spine articulations sitting in relatively shallow pockets. The spine articulations are ear-shaped and feature a sigmoidal fold. The dorsal and ventral lobes of each articulation are connected continuously from the proximal side. A small, rounded indentation can be observed in some articulations, but it never entirely disconnects both lobes. The ventral lobe of each of the articulations merges with the corresponding pocket margin.

No articulation spurs can be observed on the proximal external (Text-fig. 11B₁) or the distal internal surface (Text-fig. 11B₂) of the plate. The internal side of the plate features a very slender articulation ridge (Text-fig. 11B₂). It can be divided into two parts. The dorsal one is very long and very closely follows the proximal margin of the plate. The short ventral part quite abruptly turns obliquely in the ventro-distal direction and at the end, turns backward slightly in the ventro-proximal direction. The tentacle notch is very narrow and shallow.

The median plate (Text-fig. 11A) has more regular proportions than the described proximal plate but it is still visibly higher than long. The plate surface increases gently from top to bottom, hence the dorsal margin is somewhat shorter than the ventral one. Both are more arched than in the proximal plate.

The bulging ridge in the distal portion of the plate does not contribute to the plate's ventral lobe, as it did in the proximal LAP. The lobe itself is much smaller



Text-fig. 11. Lateral arm plates (LAPs) of *Ophiotreta cf. stefaniae* Thuy, 2013, Zalas, Kraków-Częstochowa Upland, Poland (Oxfordian, Upper Jurassic). A – MWGUW ZI/72/031, median LAP in external (A₁) and internal (A₂) views; B – MWGUW ZI/72/030, proximal LAP in external (B₁) and internal (B₂) views.

and does not protrude much beyond the plate's general outline.

The number of spine articulations is reduced to six. They are developed in the same fashion as in the proximal plate. The plate's distal ridge is highest in the mid-dorsal portion, rather than in the ventralmost part.

On the internal side of the plate (Text-fig. 11A₂), there is an articulation ridge, which is developed in an analogous way as in the proximal LAP. In contrast to the proximal plate, the triangular articulation spur is faintly visible on the distal margin of the plate's internal side. The tentacle notch is much deeper and broader than in the proximal plate.

REMARKS: The general characteristics of the current material, especially the features of the large

spine articulations with a sigmoidal fold, allow us with a high degree of confidence to place it in the *Ophiacanthina* O'Hara, Hugall, Thuy, Stöhr and Martynov, 2017.

There are several genera known from the fossil record possessing relatively very short LAPs compared to their height. One of them is *Manfredura* Thuy, 2013. However, *M. curvata* (Kutscher and Jagt, 2000), the sole species described so far, lacks a bulging ridge in the distal portion of the plate. The spine articulations in *M. curvata* are free. They are depressed slightly against the external surface of the plate but are not supposed to sit in characteristic pockets. Compared to the current material, *M. curvata* has also a completely different morphology of the articulation ridge on the internal side of the plate.

An articulation ridge on the internal side of the plate is developed similarly to the current material in a number of genera, e.g., *Ophiotreta*, *Ophiogaleus* and *Hanshessia* Thuy and Meyer, 2013. *Ophiogaleus* differs from the two other genera and from the current material in having a broadened, triangular dorsal head of an articulation ridge.

Both *Hanshessia* and *Ophiotreta* possess very similar LAP morphology. *Hanshessia* is supposed to have a smooth, rounded transgression between the dorsal-vertical and ventral-oblique portion of the articulation ridge. In *Ophiotreta* there is a sharp, pointy kink on the ventro-proximal side of the transgression. The situation in the current material more closely resembles the *Ophiotreta* condition.

Ophiotreta seems to be almost identical with *Ophiopristis* Verrill, 1899, but the connection between the ventral lobes of spine articulations and the pocket margins they are sitting in occurs more often in *Ophiotreta* (Thuy 2013). Hence the assignment of the current material to *Ophiotreta*.

In most *Ophiotreta* species, the ventral portion of the articulation ridge on the internal side of the plate is developed in form of a more or less straight ridge following obliquely in the ventro-distal direction, and is clearly disconnected from a smaller knob occupying a more ventro-proximal position. In the current material, there is a continuous transgression between the dorsal and ventral portions of the ridge. Such case occurs in the two so far described species, i.e., *O. stefaniae* and *O. striata* (Kutscher and Jagt, 2000).

There are no clear marks of ornamentation on the external surface in the current material. It should be noted, however, that this may result from abrasion, since all recognized LAPs are poorly preserved. Both *O. stefaniae* and *O. striata* feature the ornamentation of vertical lath-like bands. In *O. striata* they are sup-

posed to be more weakly developed, which theoretically may be more in line with the current material. Similarly, a large number of spine articulations and the lack of articulation spurs speaks for *O. striata*.

The last feature, however, as in the case of ornamentation, may represent a preservational issue. The triangular articulation spur can be vaguely observed on the distal margin of the internal side of the LAP recognized as a median one. *Ophiotreta stefaniae* is supposed to possess one articulation spur on the proximal external and distal internal margin of the LAPs, respectively.

In addition, the connection between spine articulation ventral lobes and respective pocket margins is weakly developed in *O. striata*, while it is easily observable in *O. stefaniae* and in the current material.

Due to the described features, the current material should be described as *O. stefaniae*. However, some minor differences and the poor preservation state do not allow for certainty, hence we leave the recognition in open nomenclature.

DISCUSSION

The ophiuroid material described herein derives from two localities in Poland, representing different palaeogeographic and palaeoenvironmental conditions. The Zalas strata fit into the long Upper Jurassic biohermal chain associated with the southern margin of the northern continental shelf of the Tethys Ocean (Matyszkiewicz *et al.* 2012). Especially interesting is the position of the Wapienno/Bielawy environment. The bioherm, which developed here in the Kimmeridgian, arose on the top of an elevation of halokinetic origin (Matyja and Wierzbowski 1985). The bioherm was surrounded by relatively deep water areas and separated from other biohermal structures, lying far to the south on the continental shelf margin, e.g., such as Zalas.

Despite the stratigraphic and geographic gaps, both Polish localities bear close similarities. The ophiuroid record (Table 1) is highly dominated by *Ophioderma spectabile*. Especially in Wapienno/Bielawy, this species comprises about 93% of all identified LAPs. In Zalas, this dominance is less pronounced; LAPs of *O. spectabile* account for about 63% of the identified plates. The second most numerous taxon in Zalas is *Dermocoma* sp. 2 (22.7%). Representatives of *Dermocoma* are represented in Wapienno/Bielawy by a similar total number of identified LAPs. However, their percentage count (about 5.5%) is much lower than in Zalas due to the domi-

nance of *O. spectabile*. Both localities yielded LAPs of *Alternacantha*. This genus, however, is represented only by solitary plates.

In both localities, the number of taxonomically recognized specimens may be influenced by preservational bias. LAPs of *O. spectabile* are relatively large and robust, and both those features may enhance their chances to be preserved in good condition. Other LAPs in the study samples are also fairly robust. On the other hand, species having more fragile LAPs may have been preserved in a condition not good enough to be kept in the study sample. Some may not have been preserved in the fossil record at all or may have been left unrecognized as ophiuroid LAPs (collecting bias). These possibilities cannot be entirely excluded. Still, comparisons with other localities yielding better-preserved specimens (provided later in this section) allow us to conclude that our sample stands for a good approximation of real taxonomic diversity at the Wapienno/Bielawy and Zalas sites. While the amounts of identified LAPs should not be treated as reflecting true palaeopopulation dynamics, nonetheless, *O. spectabile* was probably the most abundant and cosmopolitan species.

The Wapienno/Bielawy and Zalas sites differ in the occurrence of some genera and species. *Ophiotreta* has been recognized only in Zalas, where it accounts for about 8.4% of all identified LAPs. Similarly, indeterminate Ophiacanthida LAPs that bear a resemblance to *Ophiarachna? liasica* occurs only in Zalas (about 5% of all LAPs). *Ophiobartia radwanskii* Loba gen. et sp. nov. has been recognized only in Wapienno/Bielawy, and accounts for only about 1.3% of the identified LAPs.

It seems that the main difference between the Wapienno/Bielawy and Zalas localities lies in the proportions of *Ophioderma spectabile* and *Dermocoma* spp. The LAPs of these two taxa are the most crucial ophiuroid representatives in both sites. This difference is probably enhanced by the slightly different taphonomic conditions but may be suspected to represent a true difference in the palaeopopulation dynamics. Present-day ophiodermatids, aside from a few exceptions, tend to live mostly in shallow and warm tropical waters (Stöhr *et al.* 2012). The LAPs of the Jurassic *O. spectabile* have been also documented as fillings of shrimp burrows (Kimmeridgian in age) in the Małogoszcz quarry in the Holy Cross Mountains (Radwańska and Radwański 2004). Present-day shrimps of the genus *Alpheus* Fabricius, 1798 are known to live in tropical warm waters, burrowing in calcareous muds of the tidal and subtidal zones.

On the contrary, most extant ophiacanthids live in deep-water settings (Stöhr *et al.* 2012; Thuy 2013). Nonetheless, ophiuroids have been shown to possess a relatively high bathymetric plasticity in a geological time scale, and many Jurassic ophiacanthids have been reported from clearly shallow-water settings (Thuy 2013; Thuy and Meyer 2013). *Ophioderma spectabile* and *Dermocoma* spp. have been shown to co-occur at depths of about 50–60 m (Gale 2011). It cannot be excluded that the differences between the Wapienno/Bielawy and Zalas localities (both relatively shallow-water and biohermal/biostromal in nature) are dictated by a somewhat different bathymetry and environmental energy, as well as palaeobiogeography, but those are hard to assess with any degree of certainty.

The ophiuroid material recognized from both Polish localities is close to those described from Western Europe at the family or even genus level. The studied material shows the closest affinity to that described from Guldentäl (Oxfordian of Switzerland). Hess (1975a) described several ophiuroids from this locality based on isolated skeletal elements. As in the Zalas and Wapienno/Bielawy localities, the Günsberg formation of Guldentäl developed in relatively shallow-water settings, allowing for the development of biohermal structures (Hess 1975a). Ophiuroid diversity at Guldentäl is relatively low. *Ophioderma spectabile* and some species of *Dermocoma* (including *D. biformis*) dominate the assemblage. A very similar situation occurs in the Zalas and Wapienno/Bielawy settings. This supports our conclusion our samples are not heavily influenced by preservational or collecting bias.

A similar assemblage of ophiuroids was observed by Hess (1975b) from Raedersdorf (Oxfordian of France). The Bure Member of the Vellerat Formation in Raedersdorf is composed mainly of marls (Gygi 2000) and developed in a somewhat deeper setting than the Guldentäl, Zalas and Wapienno/Bielawy localities.

One of the best-described settings yielding well preserved ophiuroid material is Savigna (Oxfordian of France). Hess (1966) recognized from there two taxa of ophiacanthids, originally described as: ‘*Ophiacantha? jurassica*’ and ‘*Ophiacantha? constricta*’. However, the revisions by Thuy (2013), and Thuy and Meyer (2013) point to a larger diversity of the specimens described by Hess (1966), and different familial affinities. Those authors recognized several species at Savigna: *Ophiocamax dorotheae* Thuy, 2013 (Ophiocamacidae O’Hara, Stöhr, Hugall, Thuy and Martynov, 2018); *Ophiogaleus constrictus*

(Hess, 1966), *Alternacantha schwermannorum* Thuy, 2013 and *Ophiojagtus argoviensis* (Hess, 1966) (Ophiacanthidae). Beside the taxa mentioned above, other species from Savigna include (Hess 1966): *Enakomusium* cf. *gagnebini* (Thurmann, 1851) (Ophiomusina *incertae sedis*); *Ophiomusium praecisum* Hess, 1966 (Ophiosphalmidae O’Hara, Stöhr, Hugall, Thuy and Martynov, 2018); *Eozonella oertlii* (Ophiolepididae); *Sinosura wolburgi* (Hess, 1960) (Ophioleucidae Matsumoto, 1915); and *Ophioderma spectabile* (Ophiodermatidae). From among the listed taxa, only *O. spectabile* and *Alternacantha* spp. occur in Zalas and Wapienno/Bielawy. In contrary to Savigna, most of the LAPs from the Polish material are relatively poorly preserved.

We have not identified *Eozonella oertlii* in the Zalas and Wapienno/Bielawy sites, but its presence cannot be fully excluded. The LAPs of *E. oertlii* and *Ophioderma spectabile* have close similarities, and the features allowing for a clear differentiation between them are removed by abrasion in many LAPs, possibly leading to the misidentification of the discussed species (*E. oertlii* as *O. spectabile*).

The strata in Savigna consist mostly of thick calcareous mudstones interlayered with thinner marly limestones (Gale 2011). The type of sediment and fossil assemblages suggests a depth of deposition of about 50–60 m in a calm environment, far from the source of clastic material or biohermal buildups. By contrast, the Wapienno/Bielawy and Zalas settings both represent biohermal and/or biostromal facies, accompanied by relatively higher current energy. These environmental differences are the most probable causes of faunal discordance between the Savigna and Polish material. A similar discrepancy has been noted in the previous study (Loba and Radwańska 2022) among starfish ossicles.

The ophiuroid assemblages from Zalas and Wapienno/Bielawy reflect palaeoenvironmental conditions and are concordant with other European upper Oxfordian localities characterized by similar environmental and sedimentary regimes (e.g., Guldentäl in Switzerland).

The material studied is comparable with other Upper Jurassic European assemblages on family and genus levels. Unfortunately, the collected ophiuroid material is rather poorly preserved. The poor state of preservation makes the recognition of valid diagnostic features often very difficult, and hampers the precise determination of the taxonomic position of the studied specimens. Except LAPs referable to *O. spectabile*, other taxa are represented by a very limited number of plates; most of them have been

described under open nomenclature. It cannot be excluded that some of the taxa described herein in open nomenclature represent species new to science. More and better preserved material would be needed to test this supposition.

Some ophiuroid LAPs recognized from Wapienno/Bielawy are unique enough to create a new genus and species, i.e., *Ophiobartia radwanskii* Loba gen. et sp. nov. Previously we have described (Loba and Radwańska 2022) a new species of starfish from the same locality. This shows that there is high potential for species diversity in the eastern part of the German Basin, represented by the Upper Jurassic formations of Poland.

CONCLUSIONS

The ophiuroid material from Zalas and Wapienno/Bielawy quarries, in regard to its volume and diversity, represents the richest assemblage among those hitherto described from the Upper Jurassic of Poland. This assemblage is close to those recognized from Western Europe at family and even genus level. Most of the collected plates are abraded making their precise taxonomic recognition difficult or impossible. In this assemblage, 506 specimens have been identified as belonging to nine species. Four of those species can be assigned to three known families. Five other species cannot be currently assigned to any specific family. One species, i.e., *Ophiobartia radwanskii* Loba gen. et sp. nov. (Family *incertae sedis*) is new to science. Most of the recognized species preferred shallow-water environments (depths of about 50–60 m).

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