

Asteroidea from the lower Kimmeridgian of Wapienno/Bielawy, Kuyavia region, north-central Poland

MICHAŁ LOBA¹ and URSZULA RADWAŃSKA²

¹ Polish Academy of Sciences Museum of the Earth in Warsaw, Aleja na Skarpie 20/26, 27, 00-488 Warszawa, Poland. E-mail: michal.loba@mz.pan.pl

² Faculty of Geology, University of Warsaw, Żwirki i Wigury 93, 02-089 Warszawa, Poland. E-mail: u.radwanska@uw.edu.pl

ABSTRACT:

Loba, M. and Radwańska, U. 2022. Asteroidea from the lower Kimmeridgian of Wapienno/Bielawy, Kuyavia region, north-central Poland. *Acta Geologica Polonica*, **72** (1), 89–106. Warszawa.

A relatively rich assemblage of starfish is recognised from the talus facies of an Upper Jurassic (lower Kimmeridgian) biohermal, sponge-cyanobacterial build-up from the Wapienno/Bielawy succession exposed in a salt-dome anticline in Kuyavia region, north-central Poland. The paper presents 8 taxa belonging to 4 genera (one new to science): *Boxaster* gen. nov., *Noviaster* Valette, 1929, *Tylasteria* Valette, 1929, *Valettaster* Lambert, 1914, and 4 families: Astropectinidae Gray, 1840, Goniasteridae Forbes, 1841, Sphaerasteridae Schöndorf, 1906 and Stauranderasteridae Spencer, 1913. Only a very few representatives of some of these taxa have formerly been reported from the Jurassic of Poland. Two species are new: *Valettaster planus* sp. nov. and *Boxaster wapienensis* gen. et sp. nov. The Jurassic starfish assemblage recognised from the Wapienno/Bielawy succession is interpreted as an offshore starfish fauna with the admixture of allochthonous shallow-water taxa. The lithology of the source deposits indicates their transport by storm agitation and/or mass movements. This fact strongly influenced the preservation state, all collected plates being disarticulated and most of them abraded.

Key words: Asteroidea; Taxonomy; Upper Jurassic; Lower Kimmeridgian; Poland.

INTRODUCTION

Starfish (Asteroidea de Blainville, 1830) are important members of modern and fossil benthic communities (Mah and Blake 2012). Asterozoan skeletons are built from a multitude of tiny calcitic ossicles, but complete fossil starfish are usually quite rare. Most fossil starfish consist of scattered individual plates or segments of arms. This is because the skeleton is not rigid and the ossicles are relatively loosely connected by muscles and ligaments. After the death of the animal, the ossicles tend to disarticulate quickly and distribute separately into the sediment. This natural process means that fossil starfish are often found in the form of isolated ossicles.

The first reports on isolated ossicles come from

the first half of the 19th century but most taxa created then are now considered invalid or as *nomina dubia* (Villier 2008). A modern approach to the taxonomic problem has been developed in the second half of the 20th and in the beginning of the 21st century. Among the different starfish ossicles, marginal and abactinal plates are of greatest diagnostic value in valvatidan asteroids (Hess 1975a; Breton 1992; Villier *et al.* 2004b).

The present paper is focused on the taxonomic and ecologic analysis of the starfish fauna occurring in the lower Kimmeridgian marine deposits of Wapienno/Bielawy quarries in north-central Poland. The starfish from the Jurassic of Poland have hitherto been rather neglected by students of the abundant, high-diversity Jurassic fauna. Only a few au-



Text-fig. 1. Location of the Wapienno/Bielawy quarries (Zalesie Anticline) within the context of the generalised geology of Poland (without Quaternary strata). Adapted from Matyja and Wierzbowski (2002), with modifications.

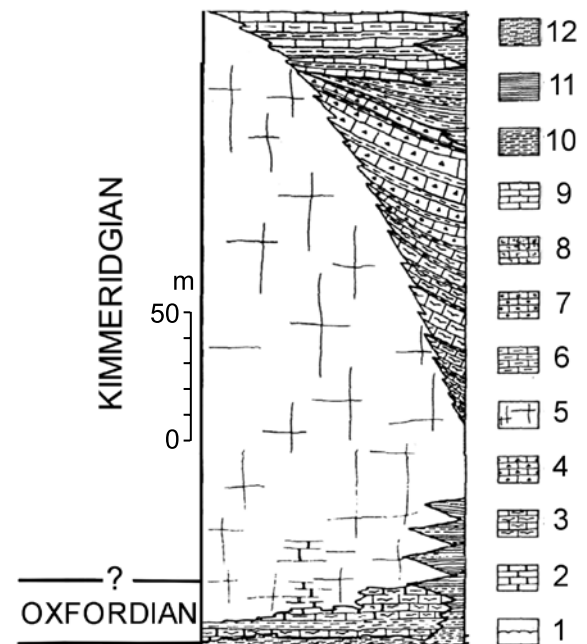
thors have contributed to the taxonomic recognition of starfish, e.g., Villier (2008) described several starfish elements from the Black Clays at Łuków in mid-eastern Poland, Radwańska (2003a) described the characteristic *Sphaeraster* Quenstedt, 1876 starfish ossicles from Wapienno/Bielawy in north-central Poland and the marginal and ambulacral plates of *Pentasteria longispina* Hess, 1968 from the lower Kimmeridgian deposits of the Małogoszcz succession in south-central Poland (see Radwańska and Radwański 2004). Zatoń *et al.* (2007) described predation marks on asteroid marginal plates from the Częstochowa region (uppermost Bajocian/lowermost Bathonian and middle Bathonian). This practically ends the list. Recently, in his unpublished Ph.D. thesis, Loba (2019) described several additional species of starfish, e.g., from the Wapienno/Bielawy locality in north-central Poland. The material from this locality includes some species and genera new to science. Here we formally describe these taxa.

GEOLOGICAL SETTING

The material studied was collected during several field trips in the first decade of the 21st century. It was

collected from two directly neighbouring quarries, Wapienno and Bielawy located within the halokinetic Zalesie Anticline, Kuyavia region, in north-central Poland (Text-fig. 1), referred to also in the literature as the Piechcin-Barcin locality (Radwańska and Radwański 2003). Due to the close distance between the quarries, and their corresponding lithology and stratigraphy, both quarries are treated herein as one locality, Wapienno/Bielawy.

In both quarries, the Upper Jurassic (Text-fig. 2) is developed as a biohermal build-up composed of massive limestones surrounded by basal facies of marls and marly limestones interlayered with detritic limestones (Matyja and Wierzbowski 1981; Matyja *et al.* 1985). The marly succession in Wapienno/Bielawy, which yielded the asteroid specimens studied, represents the upper part of the talus of the bioherm core, from where the shelly material was swept by currents and/or mass movements towards the basin (Radwańska and Radwański 2003; Radwańska 2007). The material studied comes mostly from units B3 and B4 (*sensu* Matyja *et al.* 1985). These units generally include detritic facies, in which relatively loose material (from scree and eroded surfaces) was examined for fossils.



Text-fig. 2. Generalised lithological succession of the Wapienno/Bielawy quarries. Adapted from Matyja *et al.* (1985), with modifications. 1 – stromatolite, 2 – dolomites and dolomitic limestones, 3 – layered spongy limestones, 4 – detritic spongy limestones, 5 – massive biohermal limestones, 6 – marly limestones, 7 – oolitic limestones, 8 – organic detritic limestones, 9 – micritic limestones, 10 – marls, 11 – clays and marly clays, 12 – marly mudstones.

The talus facies predominantly represented by crinoid limestones (see also Ostrowski 2003) were originally assigned to the upper Oxfordian *Epipeltoceras bimammatum* and *Idoceras planula* zones (Matyja and Wierzbowski 2002; see also Radwańska 2007). However, the Sub-Mediterranean *Epipeltoceras bimammatum* Zone in half and the *Idoceras planula* Zone in whole correspond to the Sub-Boreal *Pictonia baylei* Zone (Główniak and Wierzbowski 2007). Hence, following recent assignment (Wierzbowski *et al.* 2016), the Wapienno/Bielawy biohermal complex with associated detritic facies should be considered as representing the lower Kimmeridgian.

The starfish-bearing strata are represented primarily by the talus of a sponge-cyanobacterial calcareous build-up, composed of marly interbeds, locally covered with detritic material. Apart from starfish, the talus locally yields abundant fossils of various kinds, including the enigmatic crinoid *Cyclocrinus d'Orbigny*, 1850 and their hash (Radwańska and Radwański 2003), free-living crinoids, the very small-sized species *Semiometra petitclerci* (Cailliet, 1923) (see Radwańska 2007), echinoids (Radwańska 2000, 2003b, 2014), brachiopods (Gallinek 1896; Krawczyński 2005, 2008), tube-dwelling polychaetes (Radwańska 2004), and rare ammonites (Matyja and Wierzbowski 2002), all associated with ubiquitous siliceous sponges.

MATERIAL AND METHODS

Abundant asterozoan material was collected by UR during several field-trips to the Wapienno/Bielawy locality in the first decade of the 21st century. A total of about 200 kg of marly sediment were collected. After drying at 60°C for a week, the sediment was washed and sieved through a 1 mm sieve and the resulting residues picked for starfish ossicles under a stereomicroscope. In total, over 660 calcareous

ossicles were separated. From many different types of ossicles, we have preselected in particular the marginal and abactinal plates of asteroids, useful for taxonomic recognition. In recent years, the importance of ambulacral and adambulacral plates has also been demonstrated (e.g., Gale 2011a). However, such plates were unfortunately poorly recognisable in the material and have not been used in the current research. The selected material was cleaned from sediment residue with the use of an ultrasonic cleaner. Worth noting is that the starfish ossicles are composed of calcite, but because of redeposition, their state of preservation is rather poor. Ossicles sufficiently well preserved for taxonomic recognition were studied in detail. The best-preserved specimens have also been photographed with the use of a scanning electron microscope.

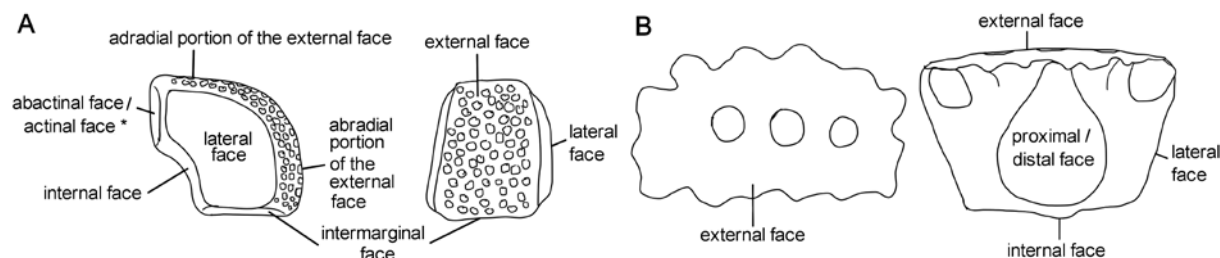
Repository

All asteroid material described here is housed in the Stanisław Józef Thugutt Geological Museum of the Faculty of Geology, University of Warsaw, with the prefix MWGUW ZI/71.

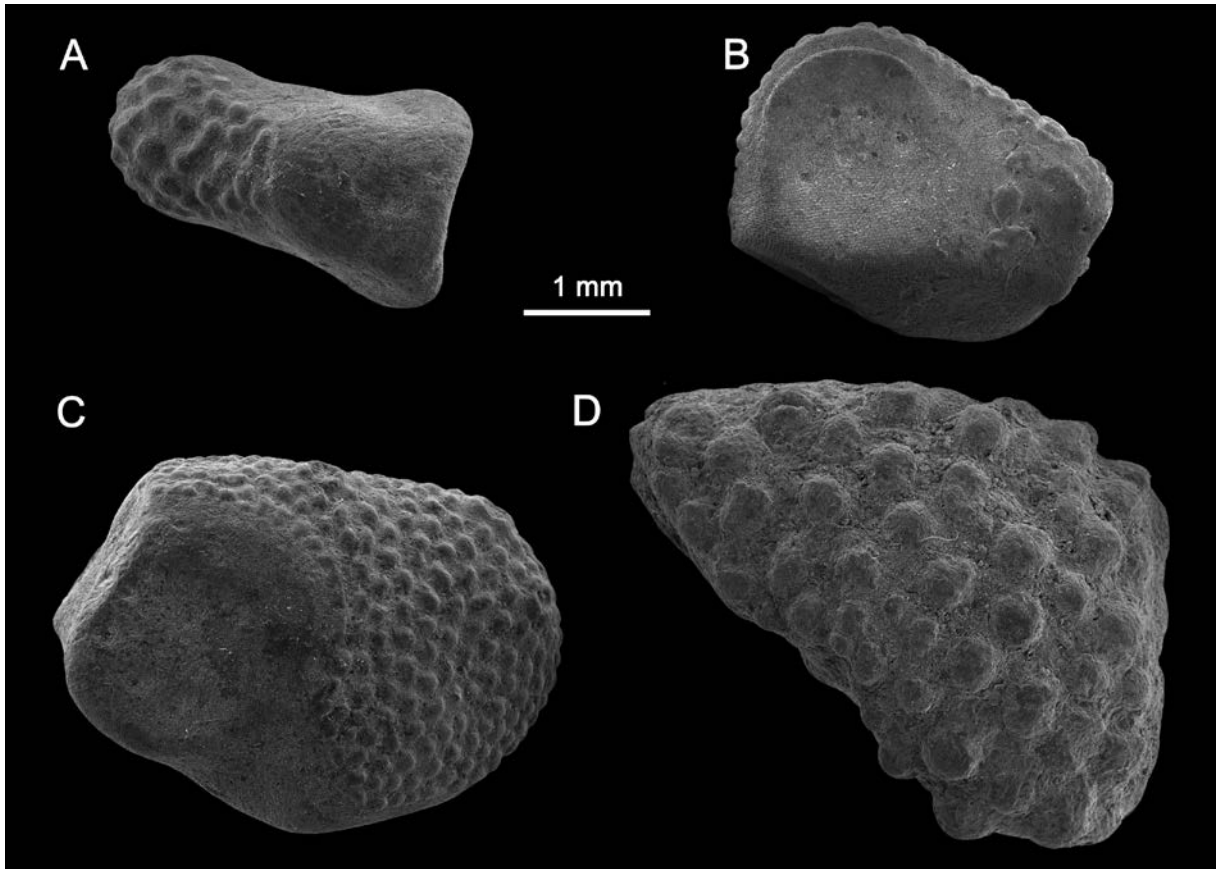
SYSTEMATIC ACCOUNT

The higher taxonomy applied in this study follows the World Register of Marine Species (WoRMS 2020). In case of completely extinct taxa which were not included in WoRMS till now, the taxonomy proposed by the original authors has been used (only for works published already in the 21st century) or adapted from Fossilworks – Gateway to the Paleobiology Database (2020).

Descriptions of taxonomically important asteroid marginal plates (Text-fig. 3) follow the nomenclature used by Breton (1992). Descriptions of abactinal plates of asteroids follow the nomenclature used by Villier (2008) and Villier *et al.* (2004b).



Text-fig. 3. Graphic explanation of the used terminology. A – Generalised marginal arm plate in proximo-distal (left) and abradial (right) views (*abactinal face occurs in the superomarginal plates, while actinal face occurs in the inferomarginal plates). B – Sphaerasterid distal abactinal plate in abactinal (left) and proximo-distal (right) views.



Text-fig. 4. *Astroidea incertae sedis*. A – MWGUW ZI/71/035, unidentified plate (probably abactinal or terminal) in external view; B – MWGUW ZI/71/037, marginal plate in internal view (due to plate's obliqueness, the lateral faces is also visible); C – MWGUW ZI/71/036, marginal plate in external view (due to plate's obliqueness, the lateral face is also visible); D – MWGUW ZI/71/038, abactinal plate in external view.

Class *Astroidea* de Blainville, 1830

Astroidea incertae sedis

(Text-fig. 4A–D)

MATERIAL: One hundred and thirty-five skeletal elements (MWGUW ZI/71/034), among which four have individual catalogue numbers (MWGUW ZI/71/035, MWGUW ZI/71/036, MWGUW ZI/71/037, MWGUW ZI/71/038).

DESCRIPTION: The material contains several types of starfish skeletal elements. The plates interpreted here as marginals (Text-fig. 4B, C) are relatively long – longer than high and longer than wide. Their lateral faces are strongly oblique suggesting an imbricating arrangement in the arm. The lateral faces are generally flat to concave and seem to bear a couple of pits, resembling granular pits. Aside from the characteristically massive tubercles, the external face tends to bear small conical spine bases. The rest of the plates (Text-

fig. 4A, D) tend to be less regular in shape, representing most likely abactinal plates from different parts of the animal's body. They are in general relatively flat, sharing with the marginals described above the ornamentation and bulbous character of the external face.

REMARKS: The fossil material containing isolated, imbricating marginals, covered with rather massive tubercles in association with spine articulations, was usually placed in the subfamily *Paleobenthopectininae* Blake, 1984 within family *Benthopectinidae* Verrill, 1899. The recognition of isolated material used to be limited to the subfamilial or familiar level, as *Paleobenthopectininae* indet. or *Benthopectinidae* indet.

However, valid species, traditionally assigned to the *Paleobenthopectininae*, were proven to belong to several unrelated groups, making the subfamily invalid (Ewin and Gale 2020; Gale and Jagt 2021). In addition, it has been shown (Gale 2011a; Gale and

Jagt 2021) that benthopectinids are characterised by very specific features of the marginals, ambulacrals and adambulacrals. This includes a clearly protruding flange, located actino-laterally on the proximal lateral face of the inferomarginals. This flange carries a distinctive band of smooth imperforate stereom (e.g., fig. 4W in Gale and Jagt 2021). No such feature has been observed on the marginals in the studied material, nor have ambulacral and adambulacral plates been recognised. Hence, we here describe the studied plates as *Asteroidea incertae sedis*.

Order Valvatida Perrier, 1884
 Family Stauranderasteridae Spencer, 1913
 Stauranderasteridae indet. 1
 (Text-fig. 5A, B)

MATERIAL: Six abactinal and/or marginal plates, catalogued together under MWGUW ZI/71/007. Two of these plates have individual catalogue numbers (MWGUW ZI/71/005, MWGUW ZI/71/008) and serve as the basis for the description.

DESCRIPTION: The studied material contains six poorly preserved stauranderasterid ossicles. They are generally massive and swollen. The abactinal plate (Text-fig. 5A) is distinctly massive. The external face of this plate has an uneven margin, having a rather convex outline on one side (in a distal/proximal orientation), whereas on the other side there are two furrows bordering the central protuberance. The external face is covered by relatively large, densely spaced granular pits.

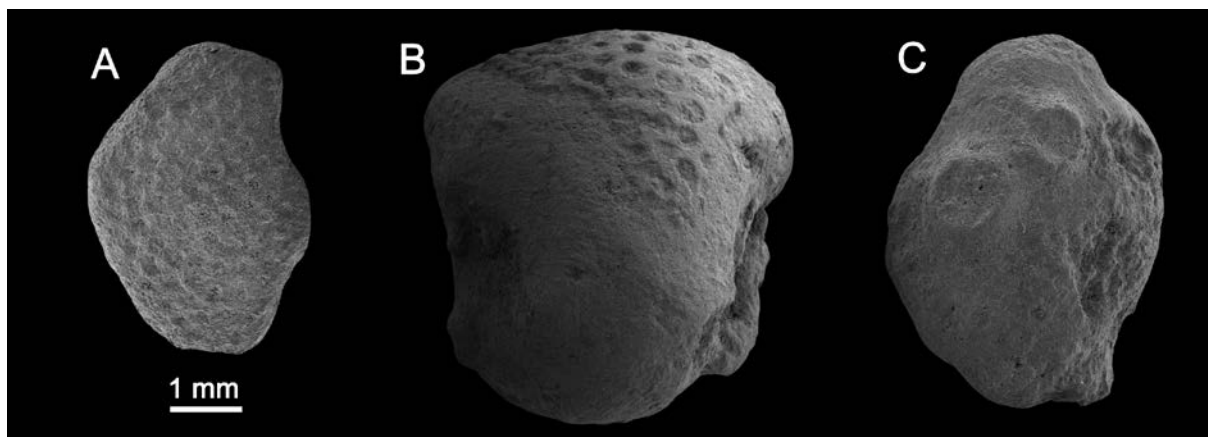
The more regular in outline second specimen

(Text-fig. 5B), probably a marginal plate, originally had an elevated external face surrounded by a depressed margin. The preserved portion of the external face is covered with relatively large, widely-spaced granular pits. All the plates lack pedicellariae pits on the external face and bear ornamentation of widely-spaced granular pits.

REMARKS: We recognise the current material as representing the Stauranderasteridae based on the massive character of the plates, and swollen shape of the marginals (Text-fig. 5B). Most of the known stauranderasterid genera possess ornamentation in the form of more or less densely spaced granular pits. The current material bears the strongest similarity to *Aspidaster* de Loriol, 1884. This Upper Jurassic genus is supposed to have abactinal plates with a weakly developed depression of the external face margin, lacks pedicellariae and has no hypertrophied primary plates. The studied plates (Text-fig. 5A, B) share most of the mentioned features. Especially specimen MWGUW ZI/71/008 (Text-fig. 5B) closely resembles a specimen described by Villier (2010, pl. 1, figs f, g) as supposedly belonging to *Aspidaster*.

We recognise the current material as probably belonging to several indeterminate species, but likely of the same genus, hence we have decided to treat all the plates together here.

Aspidaster delgadoi de Loriol, 1884, the type species of *Aspidaster*, is known only from the poorly preserved holotype, hence the genus as such is poorly known and in need of redescription. Because of this, we restrain ourselves from the generic assignment and tentatively recognise the current material as indeterminate stauranderasterid ossicles.



Text-fig. 5. Stauranderasteridae Spencer, 1913. **A, B** – Stauranderasteridae indet. 1, A – MWGUW ZI/71/005, radial abactinal plate in external view; B – MWGUW ZI/71/008, abactinal plate in external view. **C** – Stauranderasteridae indet. 2, MWGUW ZI/71/009, abactinal plate in external view.

Stauranderasteridae indet. 2

(Text-fig. 5C)

MATERIAL: One abactinal plate, poorly preserved (MWGUW ZI/71/009).

DESCRIPTION: The studied ossicle represents a relatively large blocky stauranderasterid abactinal plate. The external face is slightly arched and has an irregular margin. The external face is slightly elevated and bordered by a depressed margin. There are no visible signs of granular pits. A clearly visible feature is the presence of two large spine articulations on the external face. They are developed on the tops of low cones. The larger one is placed in the middle of the external face, while a slightly smaller one is located adjacent to it.

REMARKS: The massive, blocky character of the plate (Text-fig. 5C) suggests a stauranderasterid affinity. The ossicle most likely represents a radial abactinal plate.

Among known stauranderasterids, only *Aspidaster*, *Manfredaster* Villier, Breton, Margerie and Néraudeau, 2004 and *Stauranderaster* Spencer, 1907 possess an elevated central area of the external face encircled by a depressed margin. In all three genera, the external face is usually covered by more or less densely distributed granular pits. Among the indicated genera, *Stauranderaster* is known from forms with a smooth external face of the abactinal plates (Villier *et al.* 2004b), but all three genera lack spine articulations.

The spine articulations are supposed to occur occasionally (Villier *et al.* 2004b) on the abactinal and marginal plates of *Hadrandaster* Spencer, 1907. In this genus, however, the central area of the external face is not differentiated. The external face has an ornamentation of small, closely spaced and numerous granular pits. There are no observable granular pits on the external face of the studied ossicle.

The studied ossicle is clearly distinct from among all stauranderasterid ossicles recognised in the entire Wapienno/Bielawy material. Due to scanty material and poor preservation, the studied ossicle is determined at family rank only.

Family Sphaerasteridae Schöndorf, 1906

Genus *Valettaster* Lambert, 1914

TYPE SPECIES: *Oreaster ocellatus* Forbes, 1848, Upper Cretaceous, United Kingdom.

Valettaster planus sp. nov.

(Text-fig. 6A, B)

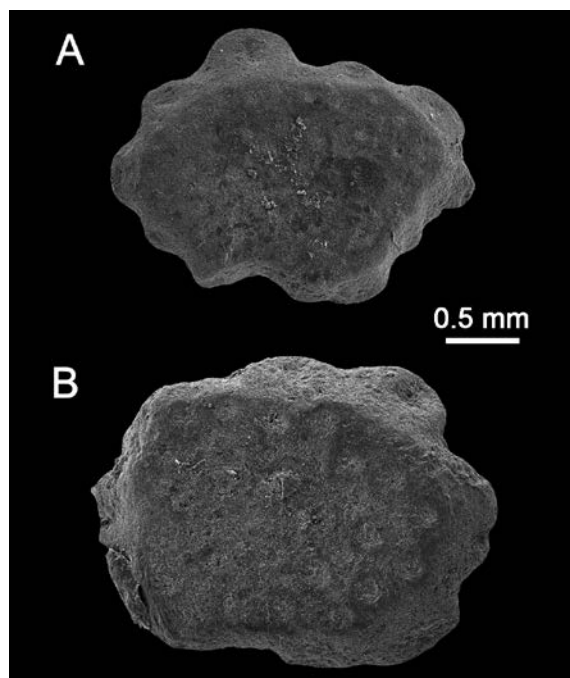
TYPE MATERIAL: Abactinal plates, holotype: MWGUW ZI/71/013, specimen presented in Text-fig. 6B, and paratype: MWGUW ZI/71/014, specimen presented in Text-fig. 6A.

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

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

DERIVATION OF THE NAME: The species name is derived from Latin *planus*, meaning flat – in correspondence to the relatively large and flat outer faces of the abactinal plates.

DIAGNOSIS: A species of *Valettaster* which is characterised by small abactinal plates with proportionally large, flat outer faces covered with relatively large and widely spaced crater-like granular pits; lateral faces irregularly digitated and short. *Valettaster planus* sp. nov. differs from *Valettaster digitatus* (Quenstedt, 1858) by smaller overall dimensions of abactinal plates, proportionally larger external faces



Text-fig. 6. *Valettaster planus* sp. nov., abactinal plates in external view. A – MWGUW ZI/71/014, paratype; B – MWGUW ZI/71/013, holotype.

of abactinal plates bearing relatively larger and more widely spaced granular pits, and by very short digitations of the lateral faces.

MATERIAL: Six abactinal plates (MWGUW ZI/71/012); among them, two have individual catalogue numbers (MWGUW ZI/71/013, MWGUW ZI/71/014). Most of them are poorly preserved.

DESCRIPTION: The studied material represents abactinal plates that are usually flattened. The specimens presented in Text-fig. 6A, B have a flat external face and an irregular, rounded shape. They bear numerous, relatively large crater-like granular pits. The lateral faces of the plates are flattened and developed as palmated outgrowths around the external face. Each of the outgrowths bears a shallow pit.

REMARKS: Due to the highly flattened character of the abactinal plates, which features a very flat external face surrounded by flattened and palmated lateral faces, we assign the studied material to *Valettaster*.

The collected ossicles are very close to those of *Valettaster digitatus* from the Jurassic of Germany. This similarity is mostly reflected in the development of densely arranged granular pits in the form

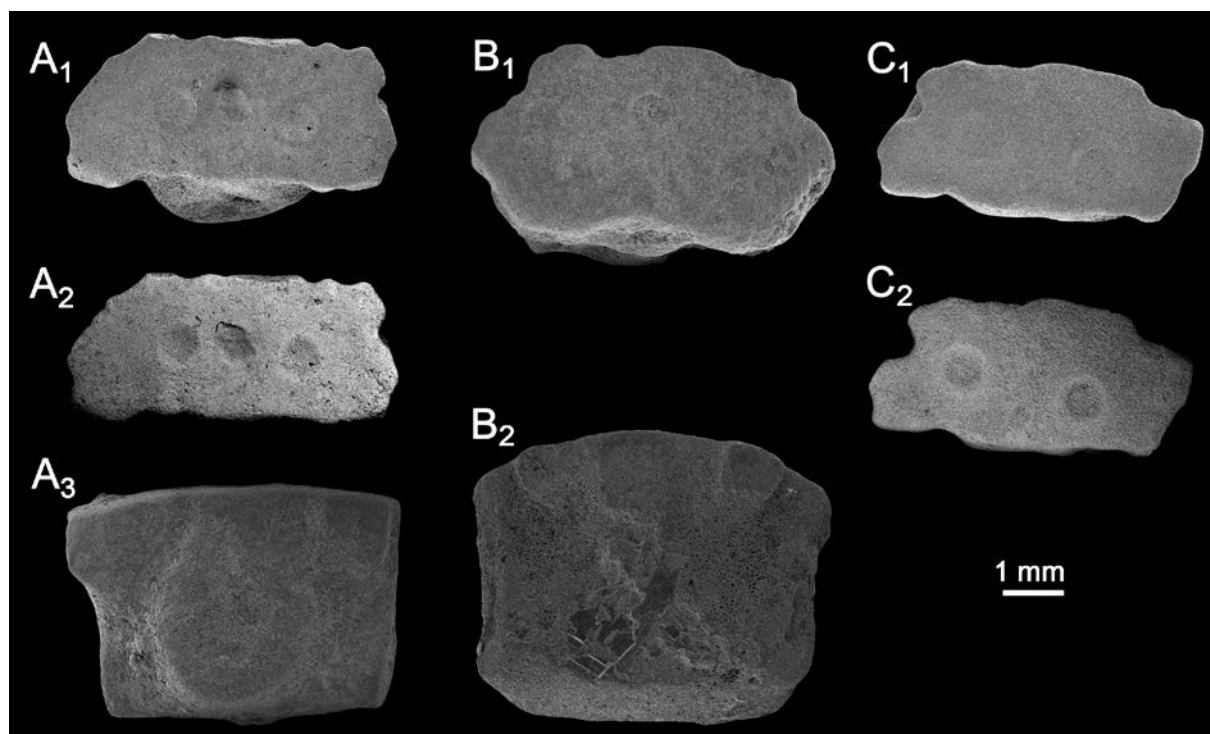
of very low crater-like cones on a flat external face. However, some differences should be emphasised. In the studied plates, the external face of the abactinal plate dominates over the lateral faces. In *V. digitatus* the external face of the abactinal plates is relatively reduced, while the digitated lateral faces surrounding it are expanded (Gale 2021). Also, the granular pits covering the outer face are proportionally larger and more widely spaced in the current material than in *V. digitatus*. Finally, the studied material consists of rather small ossicles, while the abactinal plates of *V. digitatus* used to be much larger, and regularly exceeded 5 mm in diameter (Villier 2010). Despite low numbers and generally poor preservation state of most of the abactinal plates, the described differences clearly separate the current material from *V. digitatus* and allow for the description of a new species.

Sphaerasteridae indet.

(Text-fig. 7A–C)

MATERIAL: Three abactinal radial plates, MWGUW ZI/71/002-004.

DESCRIPTION: The plate presented in Text-fig. 7A is a large blocky plate, clearly wider than long. The



Text-fig. 7. Sphaerasteridae indet., radial abactinal plates. A – MWGUW ZI/71/002, in external (A₁, A₂) and proximo-distal views (A₃). B – MWGUW ZI/71/003, in external (B₁) and proximo-distal views (B₂). C – MWGUW ZI/71/004, in external view (C₁, C₂). A₂ and C₂ made in the BEI shadow technique.

external face has a rather rectangular outline with an uneven, undulating margin. The plate is relatively tall – the height is greater than the length of the plate. The external face lacks any conspicuous ornamentation aside from the presence of three large spine bases developed in a row in the central part of the surface. The spine bases are developed as large pits, each surrounded by a raised margin creating a ridge that makes the whole spine base look like an impact crater. Distal and proximal faces are rather tall, each carrying a large, central, drop-like articular surface surrounded by two smaller, triangular articular surfaces at the sides (associated with the margin of the external face). The inner surface of the plate is rounded and lacks any significant features.

The plate presented in Text-fig. 7B resembles closely the specimen described above, but is more massive. The external face seems to be slightly arched but remains roughly rectangular in outline. Three large spine bases are more poorly preserved than in the first plate, but still present. Smaller, lateral, triangular articular facets on the proximal and distal surfaces are better distinguishable than in the holotype. In contrast, the drop-shaped central articular surface is more poorly preserved.

The morphology of the third abactinal plate (Text-fig. 7C) does not differ substantially from the already

described plates. It is, however, slightly smaller and bears only two spine bases instead of three.

REMARKS: The studied material bears a close similarity to *Poncetaster* Villier, Kutscher and Mah, 2004 (Stauranderasteridae) in general shape, development of articulation surfaces and the character of spine bases on the outer surface. *Poncetaster* was proven to be invalid, however, encompassing indeterminate distal abactinal and actinal plates of several different sphaerasterids (Gale 2021). Hence, we recognise our material as representing a similar assembly of sphaerasterid distal ossicles.

Family Goniasteridae Forbes, 1841

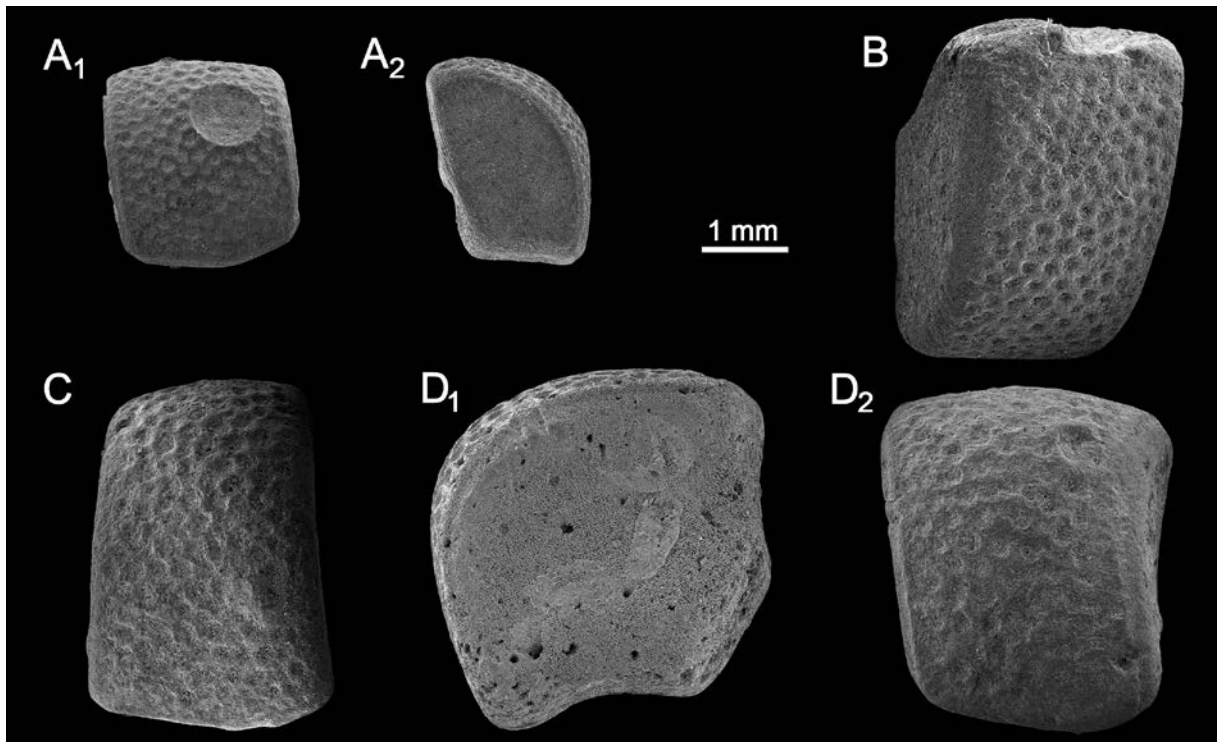
Genus *Tylasteria* Valette, 1929

TYPE SPECIES: *Asterias jurensis* Münster in Goldfuss, 1831, lower Oxfordian–upper Kimmeridgian (Upper Jurassic), France, Germany, Switzerland.

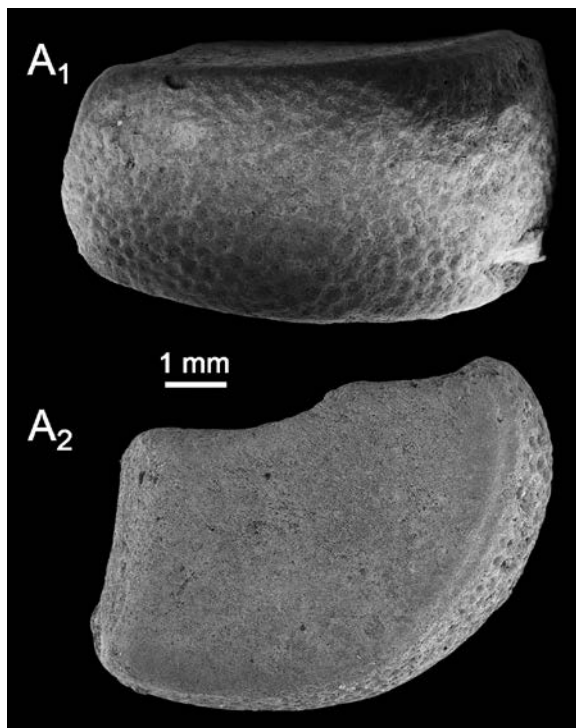
Tylasteria? sp.

(Text-figs 8A–D; 9A)

MATERIAL: Forty-one marginal plates (MWGUW ZI/71/027, MWGUW ZI/71/032), among which five



Text-fig. 8. *Tylasteria* sp., superomarginal plates. A – MWGUW ZI/71/031 (A₁ in external and A₂ in lateral view); B – MWGUW ZI/71/029 in external view; C – MWGUW ZI/71/028 in external view; D – MWGUW ZI/71/030 (D₁ in lateral and D₂ in external views).



Text-fig. 9. *Tylasteria* sp., inferomarginal plate, MWGUW ZI/71/033 (A₁ in external view and A₂ in lateral view).

have individual catalogue numbers (MWGUW ZI/71/028, MWGUW ZI/71/029, MWGUW ZI/71/030, MWGUW ZI/71/031, MWGUW ZI/71/033).

DESCRIPTION: The studied material contains several marginal plates with a very regular, cube-like shape, having very similar dimensions in every direction (Text-fig. 8A–D). These plates represent superomarginal ossicles. The external margin of the lateral face has a gently rounded outline in all plates. The collected material contains also some plates which are clearly wider than long (Text-fig. 9A₁). They also tend to taper abaxially. These possess more triangular lateral faces, but the external margin of the lateral face remains rather rounded. These plates are interpreted here as interradiar inferomarginals.

The external face is rather flat and covered with densely spaced granular pits of rounded to hexagonal shape. The external face is bordered by a fine, depressed margin. This margin is, however, too small and narrow to form fasciolar canals. There is no trace of pedicellariae articulations. Some of the plates (most probably superomarginals), as presented in Text-fig. 8A, additionally bear a large, rounded spine articulation pit.

The abactinal and adactinal faces of the plates (supero- and inferomarginals, respectively) bear several articulation facets. The intermarginal face is bipartite, bearing two articulation facets arranged against one another at a wide angle (Text-fig. 8A₁).

REMARKS: The very regular, cube-like marginal plates can occur among many valvatidans (Villier *et al.* 2004b). Among them, only goniasterids are already known from the Jurassic. Features of the marginal plates such as the regularly curved external face, ornamentation of regularly distributed hexagonal granular pits, as well as the absence of fasciolar grooves and pedicellariae, are considered (Breton 1992; Villier 2010) as plesiomorphic within the Goniasteridae.

Jurassic forms have been traditionally placed in two genera, *Comptoniaster* Breton, 1983 or *Tylasteria*. In *Comptoniaster*, the supero- and inferomarginal plates are situated directly *vis-à-vis* and have single-faced intermarginal faces (Breton 1992; Villier *et al.* 2004b). In *Tylasteria*, the supero- and inferomarginals are alternately placed, and the intermarginal face has been divided into two (Breton 1992; Villier *et al.* 2004b).

Due to the character of the intermarginal faces (divided into two angular facets), the studied plates are assigned herein to *Tylasteria*.

In the studied plates, large rounded spine pits occur on some of the superomarginals. *Tylasteria jurensis* is known to bear large conical spines placed in rounded pits on some of the superomarginal plates and has been described from the Upper Jurassic (e.g., Gale 2011b).

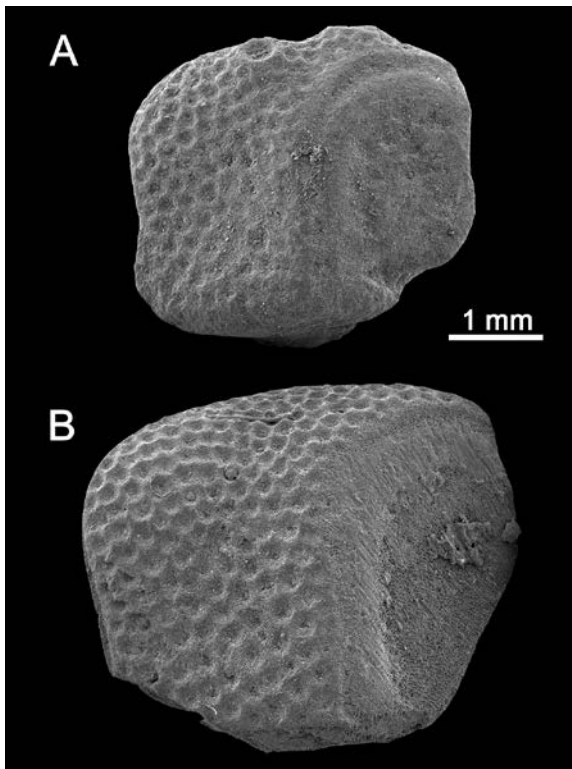
It should be emphasised that due to poor preservation of most of the plates, the frequency of spine-bearing marginals cannot be determined, nor do they represent superomarginals solely, or encompass inferomarginals as well. Due to these limitations, we restrain ourselves from the specific recognition and have decided to describe the studied material as most likely belonging to *Tylasteria*.

Genus *Noviaster* Valette, 1929

TYPE SPECIES: *Noviaster lissajousi* Valette, 1929, Middle to Upper Jurassic, France and Switzerland.

Noviaster? sp.
(Text-fig. 10A, B)

MATERIAL: Seven isolated marginal plates (MWGUW ZI/71/039), two of which have individual catalogue numbers (MWGUW ZI/71/040, MWGUW ZI/71/041).



Text-fig. 10. *Noviaster* sp., marginal plates. A – MWGUW ZI/71/040 in external view; due to plate's obliqueness, the lateral face is also visible; B – MWGUW ZI/71/041 in external view; due to plate's obliqueness, the lateral face is also visible.

DESCRIPTION: The material contains several marginal plates. The plates are oblique in longitudinal aspect. The proximal lateral face (visible in external aspects of both plates presented in Text-fig. 10A, B) is flat to slightly concave. Close to the margin of the plate, it is more bulbous, forming a very low but broad ridge. Just under this ridge, there are several, mostly poorly preserved pits. The distal face is slightly convex.

The external face (Text-fig. 10A, B) is covered with rather densely spaced, round to hexagonal granular pits. Some of the plates bear also relatively small conical spine bases (Text-fig. 9A). In profile, the external face is gently arched, giving the plates a more rectangular rather than triangular outline. No pedicellariae articulations have been observed.

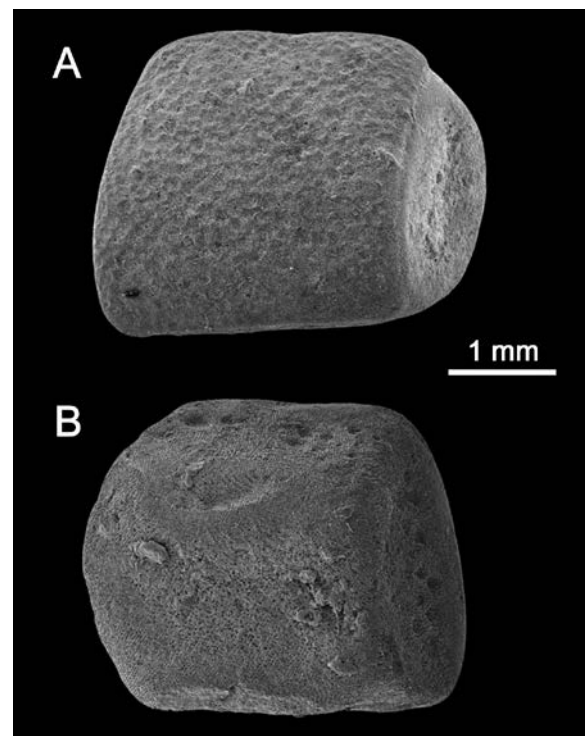
REMARKS: The general characters of the plates, including a relatively regular shape and ornamentation of round to hexagonal granular pits, allows the assignment of these plates to the Goniasteridae. However, further identification is uncertain. Marginals with

highly oblique lateral faces are known in *Noviaster*, in which the plates imbricate. Based on this similarity, the studied material is distinguished from *Tylasteria?* sp. (described above) and tentatively assigned to *Noviaster*. Due to the low number of plates and the relatively poor preservation state, this assignment remains uncertain and will need revision when new, better preserved material becomes available.

Goniasteridae indet.
(Text-fig. 11A, B)

MATERIAL: One hundred and six abactinal and marginal plates (MWGUW ZI/71/006), among which two (presented herein) have individual catalogue numbers (MWGUW ZI/71/010, MWGUW ZI/71/011).

DESCRIPTION: The collected material contains numerous blocky asteroid ossicles (Text-fig. 11A, B), most likely representing marginal plates. The plates are very regular and have rectangular external faces (Text-fig. 11A), and there is no sign of fossae or indentations for passage of papulae. The lateral faces of the plate (visible in the internal and external aspects of the plates presented in Text-fig. 11A, B) are trapezoidal in shape, where the internal margin corre-



Text-fig. 11. Goniasteridae indet., marginal plates. A – MWGUW ZI/71/010 in external view; B – MWGUW ZI/71/011 in internal view.

sponds to the shorter trapezium base and the external margin corresponds to the longer trapezium base. The external margin of the lateral face is slightly convex. Lateral faces bear several rounded pits (Text-fig. 11A, B). The external face is distinctly separated from the lateral faces by a small groove. The external face is covered by a dense mesh of relatively small granular pits (Text-fig. 5A).

REMARKS: Large blocky marginals which are very regular in shape, lacking passages for papulae or fasciole, are characteristic of the Goniasteridae.

The plate lateral faces are rather trapezoidal. Abactinal/actinal and intermarginal faces are oblique but not perpendicular to each other. Abactinal/actinal and intermarginal faces are very hard to distinguish due to their similar size and the lack of clearly defined articular facets for articulation with the abactinal or actinal plates (however, two such articulations can be barely recognised in the upper portion of Text-fig. 5B).

According to our study, the collected material represents the Family Goniasteridae and may belong to *Comptonia* Gray, 1840 on the basis of the lightly convex external face covered with relatively small, tightly packed granular pits. Due to the plesiomorphic characters of the studied plates (lack of depressed margin of the external face and no pedicellariae pits), we have decided to assign the studied material at family level only.

Order Paxillosida Perrier, 1884
Family ?Astropectinidae Gray, 1840
Genus *Boxaster* gen. nov.

DERIVATION OF THE NAME: Referring to the box-like hollow on the inner side of the marginal plates.

TYPE SPECIES: *Boxaster wapienensis* sp. nov.

DIAGNOSIS: The same as for the type species by monotypy.

REMARKS: The studied marginal plates are relatively regular and cube-like in shape and encompass differentiated ultimate superomarginals. The presence of fasciolar grooves on the inferomarginals allows for tentative assignment to the Astropectinidae, since this character has been observed so far only in this family and in the Pseudarchasteridae (Sladen, 1889). Astropectinid and pseudarchasterid isolated marginals can be very hard or even impossible to

differentiate (Gale pers. comm.) without clues from other skeletal elements, hence the assignment remains tentative. The co-occurrence of rugosities on the superomarginals and adradially protruding lateral faces – creating a hollow space between them on the inner side of a plate – is unique to *Boxaster* gen. nov. and allows for the creation of a new genus.

Boxaster wapienensis sp. nov.
(Text-figs 12A–F; 13A–D)

TYPE MATERIAL: Ultimate superomarginal plate from the latter part of the arm, holotype: MWGUW ZI/71/017, specimen presented in Text-fig. 12E, and paratypes: ultimate superomarginal plate MWGUW ZI/71/018, specimen presented in Text-fig. 13D; superomarginal plate, MWGUW ZI/71/019 specimen presented in Text-fig. 12D; superomarginal plate, MWGUW ZI/71/020, specimen presented in Text-fig. 12B; inferomarginal plate, MWGUW ZI/71/021, specimen presented in Text-fig. 12F.

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

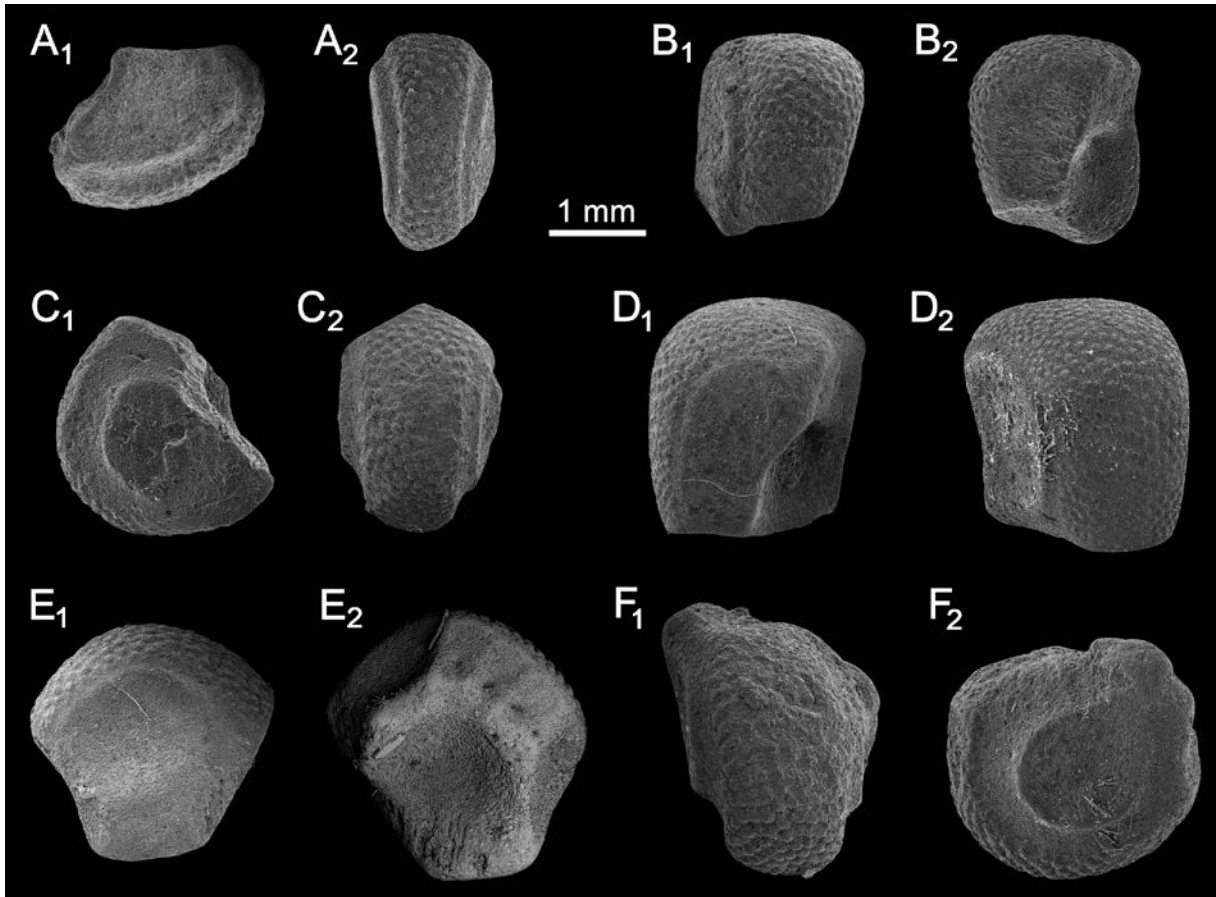
TYPE HORIZON: *Epipeltoceras bimammatum* and *Idoceras planula* zones, lower Kimmeridgian (Upper Jurassic).

DERIVATION OF THE NAME: The species is named after its type locality.

DIAGNOSIS: Paxillosid starfish possessing both supero- and inferomarginals covered with rugosities; superomarginals lateral faces flanging adradially, creating a hollow space on the internal side of the plate; fasciolar grooves present on the inferomarginal plates; shallower and narrower fasciolar grooves are present also on proximal sides of intermediate superomarginals.

MATERIAL: Three hundred and fifty-two marginal plates (MWGUW ZI/71/015, MWGUW ZI/71/016); among them, ten with individual catalogue numbers (MWGUW ZI/71/017-026).

DESCRIPTION: The holotype (Text-fig. 12E) represents an ultimate superomarginal plate, which is similar in size to the other marginal plates but distinctly asymmetrical in shape. The external face of this plate is relatively wide, covered by tubercles. In lateral view, the margin of the external face gently



Text-fig. 12. *Boxaster wapienensis* gen. et sp. nov. A – MWGUW ZI/71/022, inferomarginal plate in lateral (A₁) and external (A₂) views. B – MWGUW ZI/71/020, paratype superomarginal plate in external (B₁) and lateral (B₂) views. C – MWGUW ZI/71/023, inferomarginal plate in lateral (C₁) and external (C₂) views. D – MWGUW ZI/71/019, paratype superomarginal plate in lateral (D₁) and external (D₂) views. E – MWGUW ZI/71/017, holotype ultimate superomarginal plate in lateral-proximal (E₁) and internal views (E₂). E₂ has been made in the BEI shadow technique. F – MWGUW ZI/71/021, paratype inferomarginal in external (F₁) and lateral (F₂) views.

bends and is moderately convex. The proximal lateral surface (Text-fig. 12E₁) is bordered by a weakly depressed margin. The size of the proximal lateral face and its general characteristics are concordant with the other marginals in the material. In contrast, the distal lateral face (Text-fig. 12E₂) is much smaller and oblique to the proximal surface. The distal lateral face most probably was in contact with the terminal plate, while the area directly opposite the proximal face is occupied rather by the internal face of the plate.

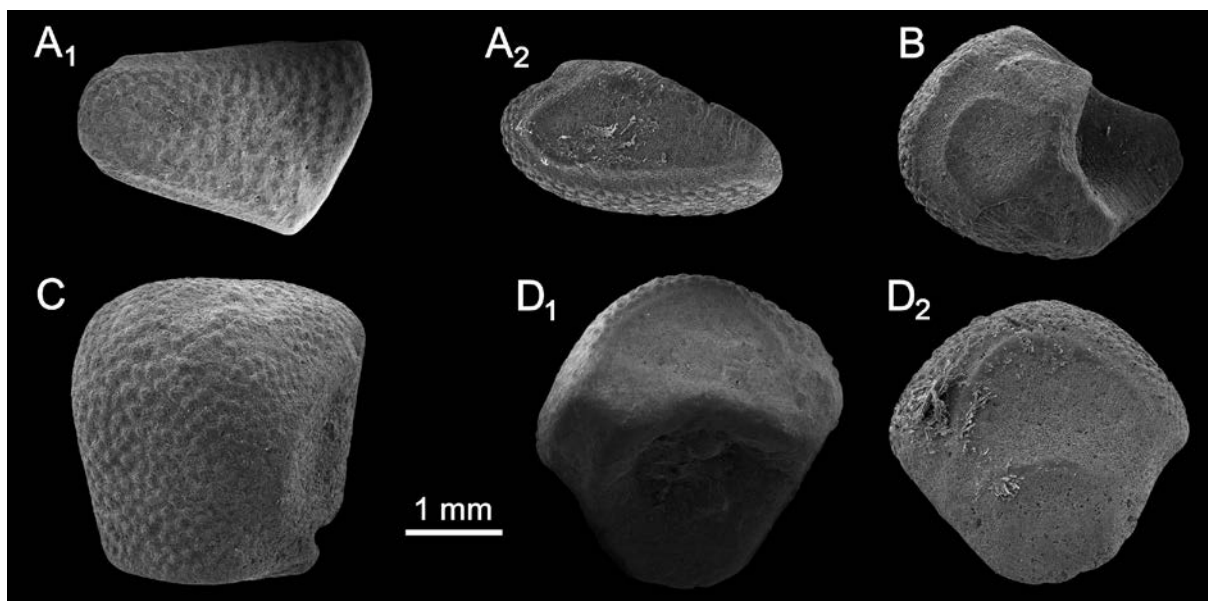
Directly adjacent and proximally to the distal lateral surface, occurs a large articular surface, rectangular in shape, which was probably in contact with the ultimate superomarginal plate from the opposite row in an arm. Proximally to this articular surface occur three small facets, which were probably in con-

tact with the abactinal plates, hence as a whole, they correspond to the abactinal face in the other superomarginals.

The intermarginal face is poorly preserved but it was probably in contact with a single inferomarginal plate.

Among the paratypes, another ultimate superomarginal plate is presented in Text-fig. 13D. Its morphology is consistent with that of the holotype. The studied plate is slightly larger and has a wider external face than in the holotype. The articular surface for connection with the opposite ultimate superomarginal plate is larger, more kidney-shaped than in the holotype. It is rather flat while being slightly concave in the holotype. Articular facets of abactinal plates are more poorly preserved than in the holotype.

Another paratype is represented by a superomar-



Text-fig. 13. *Boxaster wapienensis* gen. et sp. nov. A – MWGUW ZI/71/024, inferomarginal plate in external (A₁) and lateral (A₂) views. B – MWGUW ZI/71/025, distal inferomarginal plate in lateral-distal view. C – MWGUW ZI/71/026, superomarginal plate in external view. D – MWGUW ZI/71/018, paratype ultimate superomarginal plate in internal (D₁) and lateral-proximal (D₂) views.

ginal plate (Text-fig. 12D), which was positioned in the more proximal part of the arm. This plate is clearly box-shaped. The external face is distinctly broader in the abradial-adradial direction and longer in the proximo-distal direction than in the previously described ultimate plates but bears the same type of ornamentation in the form of tubercles. In lateral view (Text-fig. 12D₁), the plate has a strongly arched, hooked profile.

The lateral faces are distinctly asymmetrical (Text-fig. 12D₁). The smaller one, most probably distal, is slightly kidney-shaped. The larger, proximal face is more rectangular in outline mainly due to the development of an adradially protruding flange. Due to the presence of this flange, there is a hollow space on the internal side of the plate (Text-fig. 12D₁). The proximal face also slightly protrudes in the proximo-distal direction, creating a very narrow and shallow fasciolar groove.

The specimen presented in Text-fig. 12B represents another intermediate superomarginal plate. It is very similar to those shown in Text-fig. 12D but slightly smaller. The asymmetry of the lateral surfaces is even more strongly pronounced. The wing-like protrusion of the proximal lateral face is proportionally bigger.

The last paratype presented in Text-fig. 12F is very similar to the previously described plates among

the type series. This plate possesses the external face ornamentation in the form of tubercles. The lateral faces are characteristically asymmetrical, the proximal one being distinctly larger than the distal one. In lateral view, however, the plate profile is more rounded than hooked (Text-fig. 12F₂). The plate is almost round in this view.

The studied plate can be distinguished from the previously described plates by the possession of strongly pronounced proximo-distally protruding lateral faces, creating deep and wide fasciolar canals between the external faces of subsequent plates (Text-fig. 12F₁). Specimen MWGUW ZI/71/021 (Text-fig. 12F) and other similar plates not included in the type series, are treated here as inferomarginal plates of the same species as the previously described plates.

The studied material comprises many other plates of similar morphology as the paratype presented in Text-fig. 12F. Three of them have been presented in Text-figs 12A, C and 13A. These plates are not distinctly asymmetrical (and lack a hollow, concave space on their inner sides). In one of them (Text-fig. 13A), lateral surfaces do not protrude as clearly as those in the paratype (Text-fig. 12F), and this plate represents an intraspecific variety.

In the studied material there are also plates (Text-fig. 13B) very similar to those described as inferomarginal plates (Text-figs 12A, C, F and 13A). They

differ, however, by the presence of an additional, triangular-shaped articular surface, developed above the distal lateral face. Such plates are interpreted here as distal inferomarginals corresponding to ultimate superomarginals. However, due to the difficulties with their interpretation and assignment, they were excluded from the type series.

REMARKS: The studied material comprises several different morphotypes of marginal plates, with a continuous transition between them. All these plates bear also the same type of ornamentation.

The superomarginals in the studied material co-occur with inferomarginal plates that bear the same type of ornamentation in the form of rugosities (tubercles). The rugosities are of similar size and have a similar spacing on both types of plates, hence most likely the inferomarginals represent the same species as superomarginals. Among both types of plates occurs a relatively large variability of shapes but there are continuous transitions between the morphotypes, suggesting intraspecific variation (due to the exact position in an arm). Inferomarginals are also characterised by strongly protruding lateral faces that create fasciolar grooves between the adjacent plates. To a much lesser degree, the fasciolar grooves are developed also by proximal lateral faces of intermediate superomarginals. Such grooves have been observed so far only in the two paxilloid families – Astropectinidae and Pseudarchasteridae.

Astropectinids and pseudarchasterids can be very hard or even impossible to differentiate based solely on the isolated marginals, without aid from the spination characteristics and adambulacral morphology (Gale, pers. comm.).

Astropectinids tend to have clearly differentiated supero- and inferomarginals (Hess 1955; Gale 2020). The superomarginals usually bear granular pits while the inferomarginals are covered by rugosities (tubercles). Among the rugosities, there is also a row of larger horseshoe-shaped (or rounded) spine articulations running obliquely or transversely across the external face. Among the fossil representatives, there are, however, exceptions from this rule. Recently, Gale (2020) has described a new astropectinid genus and species – *Eoastropecten sechuanensis* Gale, 2020 – which bears ornamentation composed of rugosities on both, supero- and inferomarginals. *Eoastropecten sechuanensis* is Carnian in age (Upper Triassic), however Gale (2020) noted the presence of similarly sculpted marginals also in the Upper Jurassic (Oxfordian; fig. 2I in Gale 2020). Our specimen illustrated in Text-fig. 13A bears also close simi-

larity to the series of inferomarginals described from the Oxfordian of Savigna in France as *Pentasteria longispina* Hess, 1968 (figs 3g, h in Gale 2011b).

Our material bears a strong similarity to the specimens described by Gale (2011b, 2020), hence we tentatively assign it to the Astropectinidae. However, their pseudarchasterid affinities cannot be decisively excluded. The Pseudarchasteridae have been traditionally considered as a subfamily among the Goniasteridae, however recent studies (Blake and Jagt 2005; Mah and Foltz 2011) have placed them firmly among the Paxillosoida. Marginal plates of the pseudarchasterids can bear fasciolar grooves similar to those in the astropectinids, while other skeletal characteristics can be more goniasterid-like. Intermediate superomarginals in the current material have indeed very regular shapes and a hooked profile giving them a ‘goniasterid-like’ appearance.

The current material differs from all other known astropectinids (including *E. sechuanensis*) and pseudarchasterids in having box-like intermediate superomarginals bearing lateral faces protruding adradially in such a way that they create a hollow space between them on the inner side of a plate. Also, no other paxilloid described so far is characterised by the presence of differentiated ultimate superomarginals of complex morphology as in the current material. Rugosities on the inferomarginals of *E. sechuanensis* are arranged in oblique rows, while there is no such pattern observable on the inferomarginals described herein. All the described differences allow for naming a new genus and species.

DISCUSSION

The relatively rich starfish material from Wapienno/Bielawy contains representatives of families recognised also in other Jurassic localities known from Western Europe. The Savigna locality (upper Oxfordian) in the Jura Mountains of France (Gale 2011a, b) is closest to Wapienno/Bielawy in its geological age. Both localities share the presence of astropectinids and goniasterids. However, the asteroid fauna at Savigna is much more diverse than at Wapienno/Bielawy. The Savigna assemblage comprises also representatives of such families as the Gonioplectinidae Verill, 1899, Pterasteridae Perrier, 1875, Plumasteridae Gale 2011b, Asteriidae Gray, 1840, and Terminasteridae Gale, 2011a, which have been not found at Wapienno/Bielawy. On the contrary, Savigna does not yield stauranderasterid remains, which are present at Wapienno/Bielawy, however sparsely.

It should be emphasised that Savigna represents quite a different palaeoecological setting than the Polish locality. Savigna strata are developed as thin beds of marly limestones separated from each other by thick beds of calcareous clays (Gale 2011b). The last ones contain rich asterozoan faunas. This lithology is interpreted as an effect of slow sedimentation on a low energy bottom of a shallow inland sea (between 50 and 60 m deep; Gale 2011b). Such conditions assured good preservation of abundant ossicles, as well as creating a favourable environment for a rich starfish fauna. On the contrary, the Wapienno/Bielawy site represents a bioherm slope that reached the normal wave base. The material at Wapienno/Bielawy was deposited in a shallow marine setting with evidence of wave and current activity, and was subjected to redeposition. This resulted in the generally poor preservation of the material.

The studied assemblage from Wapienno/Bielawy resembles more closely the remains described from the Toarcian of the French 'Seuil du Poitou' locality near Sainte-Verge (Villier *et al.* 2004b). This locality represents a succession deposited in a relatively shallow environment, situated close to the Armorican and Central massifs (which were the source of material for the clastic sedimentation). 'Seuil du Poitou' yields a poorly diversified mix of goniasterid, stauranderasterid and astropectinid taxa, similarly to Wapienno/Bielawy. 'Seuil du Poitou' strata are, however, of Toarcian age leaving a big stratigraphic gap between this site and Wapienno/Bielawy.

A relatively rich starfish fauna has been described by Villier (2008) from the Black Clays of Łuków (Callovian) in mid-eastern Poland. This setting is interpreted as a deep offshore environment with the admixture of allochthonous fossil material brought by storms and currents. This assemblage indicates some similarities to Wapienno/Bielawy when compared at family level. The Łuków assemblage, aside from Savigna, is one of the richest and most diverse among known Jurassic localities. It contains, for example 'Poncetaster', recognised also in Wapienno/Bielawy (as Sphaerasteridae indet.), and bears some other stauranderasterid and goniasterid remains. Łuków yields also specimens of *Pentasteria* Valette, 1929 (Astropectinidae) that were not recognised in the material from Wapienno/Bielawy, but astropectinids are most likely represented here by *Boxaster wapienensis* gen. et sp. nov.

Other localities with a similar stratigraphic position include Latrecey from the Callovian and Oxfordian of Eastern France (Courville and Villier 2003), as well as Guldenthal and Le Bémont from the Oxfordian of

Switzerland (Hess 1960, 1975a, b). They generally yield a mixture of goniasterid and stauranderasterid taxa with the addition of *Pentasteria* sp. (Astropectinidae), with the exception of Le Bémont, from where only goniasterids have been described. *Terminaster cancriformis* (Quenstedt, 1876) (Terminasteridae) has been also reported from Guldenthal.

At generic and species levels, Wapienno/Bielawy is somewhat unique. The most numerous among the identified ossicles are marginals of *Boxaster wapienensis* gen. et sp. nov. This most-likely astropectinid taxon bears features validating its recognition as a new genus and species. Due to the gradual transition between the morphological variants of the ossicles, all referred material likely represents the same taxon. It cannot be excluded, however, that some of the ossicles (excluded from the type series) should be recognised as a separate species.

The Wapienno/Bielawy locality yields also abundant ossicles of 'benthopectinid-like' appearance that cannot be assigned with any certainty to any known taxon within the Asteroidea based on the current material. Future research, focused on ambulacral and adambulacral ossicles, may shed some light on their true affinities. At the moment, however, they can be recognised only as Asteroidea *incertae sedis*.

Goniasterids have a quite wide bathymetric range. The representatives of *Tylasteria* and *Noviaster*, recognised at Wapienno/Bielawy are usually found in deposits interpreted as the sub-tidal zone but may occur also in deep offshore settings (Fossilworks 2020).

The Family Stauranderasteridae is interpreted (Villier 2008) as an ecological counterpart of the recent Oreasteridae Fischer, 1911, representatives of which settle in high energy shallow tropical waters. However, stauranderasterids are known to occur in shallow-water to offshore settings. As such, they may indicate a high-energy setting, but they do not indicate clearly a shallow-water environment. Stauranderasterids are surely present in the material studied herein, however, only a couple of ossicles are preserved well enough to warrant their familial assignment.

Astropectinids tend to have a similarly wide bathymetric range as the goniasterids. Modern representatives live mostly in soft-bottom settings, where they tend to bury themselves in the sediment. Most of the fossil forms are interpreted to have a similar mode of life. *Boxaster wapienensis* gen. et sp. nov. seems to be a highly derived astropectinid (or pseudarchasterid) which likely had a rather robust, swollen morphology in life. These features may have served as adaptations to live in an environment

containing coarser sediment present on the bioherm slopes in the Wapienno/Bielawy setting.

Considering that the studied material comes from debris and eroded surfaces of the bioherm talus, the described data suggest that the studied assemblage may represent a mixture of autochthonous offshore fauna and shallow water taxa coming from the destruction of the bioherm top (in the active wave zone). This conclusion remains in agreement with suggestions made by previous authors (Krawczyński 2005, 2008; Radwańska 2007).

CONCLUSIONS

The starfish material recognised from the Wapienno/Bielawy quarries is at family level close to the starfish faunas described from Western Europe. The starfish assemblage studied is relatively rich with regard to volume, but rather poor concerning its diversity. This may be the effect of taphonomic conditions which strongly influenced the preservation state. Most of the collected plates are abraded, making precise taxonomic recognition difficult or impossible. In this assemblage, 658 specimens belonging to 8 taxa of 4 families have been recognised. Two species are new to science, *Boxaster wapienensis* gen. et sp. nov. (?Astropectinidae) and *Valettaster planus* sp. nov. (Sphaerasteridae). The Jurassic starfish assemblage from Wapienno/Bielawy is interpreted as an offshore starfish fauna with the admixture of allochthonous shallow water taxa.

According to the present state of research, it is impossible to ascertain whether the newly discovered species were endemic to the Wapienno/Bielawy bioherm area, or were more broadly distributed in the Polish Jura Chain. The new study clearly shows that Late Jurassic asterozoan faunas still require intensive research.

Acknowledgements

We would like to sincerely thank our reviewers, Andrew Gale and Loic Villier, for many precious hints and advice. We would like to thank also Anna Żylińska for her assistance throughout the publication process and her editorial comments.

REFERENCES

Blainville, H.-M. de. 1830. Zoophytes. *Dictionnaire de Sciences Naturelles*, **60**, 546 pp.

- Blake, D.B. 1984. The Benthopectinidae (Asteroidea: Echinodermata) of the Jurassic of Switzerland. *Eclogae geologicae Helvetiae*, **77** (3), 631–647.
- Blake, D.B. and Jagt, J.W.M. 2005. New latest Cretaceous and earliest Paleogene asteroids (Echinodermata) from the Netherlands and Denmark and their paleobiological significance. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique*, **75**, 183–200.
- Breton, G. 1983. *Comptoniaster*, gen. nov. de Goniasteridae du Mésozoïque. *Symbioses*, **15** (4), 244–245.
- Breton, G. 1992. Les Goniasteridae (Asteroidea, Echinodermata) jurassiques et crétacés de France: taphonomie, systématique, paléobiogéographie, évolution. *Bulletin trimestriel de la Société Géologique de Normandie et des Amis du Muséum du Havre*, **78** (hors-série), 590 pp.
- Caillet, H. 1923. Note sur un Antedon nouveau del'Oxfordien. *Bulletin de la Société Belfontaine d'Emulation*, **38** (for 1922), 125–127.
- Courville, P. and Villier, L. 2003. L'Oxfordien moyen et supérieur de l'est du Bassin Parisien (France). L'exemple de Latrecey (Haute-Marne): aspects fauniques, paléoenvironnementaux et stratigraphiques. *Revue de Paléobiologie*, **22**, 175–196.
- Ewin, T.A.M. and Gale, A.S. 2020. Asteroids (Echinodermata) from the Barremian (Lower Cretaceous) of the Agadir Basin, west Morocco. *Journal of Paleontology*, **94** (5), 931–954.
- Fischer, W.K. 1911. Asteroidea of the North Pacific and adjacent waters. 1 – Phanerozoia and Spinulosa. *Bulletin of the United States National Museum*, **76**, 420 pp.
- Forbes, E. 1841. A history of British starfish and other animals of the class Echinodermata, 267 pp. John Van Voorst; London.
- Forbes, E. 1848. On the Asteriadae found fossil in British strata. *Memoirs of the Geological Survey of Great Britain, and of the Museum of Practical Geology in London*, **2** (2), 457–482.
- Fossilworks – Gateway to the Paleobiology Database, <http://fossilworks.org> (last accessed 10.04.2020).
- Gale, A.S. 2011a. The phylogeny of post-Palaeozoic Asteroidea (Neoasteroidea, Echinodermata). *Special Papers in Palaeontology*, **85**, 112 pp.
- Gale, A.S. 2011b. Asteroidea (Echinodermata) from the Oxfordian (Late Jurassic) of Savigna, Department du Jura, France. *Swiss Journal of Palaeontology*, **130**, 69–89.
- Gale, A.S. 2020. A new comb-star (Asteroidea, Astropectinidae) from the Upper Triassic (Carnian) of China. *Zootaxa*, **4861** (1), 139–144.
- Gale, A.S. 2021. Taxonomy and phylogeny of the 'football stars' (Asteroidea, Sphaerasteridae). *Journal of Systematic Palaeontology*, <https://doi.org/10.1080/14772019.2021.1960911>
- Gale, A.S. and Jagt, J.W.M. 2021. The fossil record of the family Benthopectinidae (Echinodermata, Asteroidea), a reappraisal. *European Journal of Taxonomy*, **755** (1), 149–190.
- Gallinek, E. 1896. Der Obere Jura bei Inowrazlaw in Posen. *Verhandlungen der Kaiserlichen Russischen Mineralo-*

- gischen Gesellschaft zu St. Petersburg, Zweite Serie*, **33** (2), 353–427.
- Główniak, E. and Wierzbowski, A. 2007. Taxonomical revision of the perisphinctid ammonites of the Upper Jurassic (Plicatilis to Planula zones) described by Józef Siemiradzki (1891) from Kraków Upland. *Volumina Jurassica*, **5** (1), 27–138.
- Goldfuss, G.A. 1831. *Petrefacta Germaniae*, p. 3, pp. 165–240. Arnz & Comp.; Düsseldorf.
- Gray, J.E. 1840. A synopsis of the genera and species of the class Hypostoma Asterias (Linn.). *Annals and Magazine of Natural History*, **6**, 275–290.
- Hess, H. 1955. Die fossilen Astropectiniden (Asteroidea). Neue Beobachtungen und Übersicht über die bekannten Arten. *Schweizerische Palaeontologische Abhandlungen, Birkhäuser Verlag, Basel*, **71**, 113 pp.
- Hess, H. 1960. Ophiurenreste aus dem Malm des Schweizer Juras und des Departements Haut-Rhin. *Eclogae geologicae Helvetiae*, **35**, 385–421.
- Hess, H. 1968. Ein neuer Seestern (*Pentasteria longispina* n. sp.) aus den Effingerschichten des Weissensteins (Kt. Solothurn). *Eclogae geologicae Helvetiae*, **61** (2), 607–614.
- Hess, H. 1975a. Die fossilen Echinodermen des Schweizer Juras. *Veröffentlichungen aus dem Naturhistorischen Museum Basel*, **8**, 130 pp.
- Hess, H. 1975b. Mikropalaontologische Untersuchungen an Ophiuren. VI. Die Ophiuren aus den Gunsberg-Schichten (oberes Oxford) vom Guldental (Kt Solothurn). *Eclogae geologicae Helvetiae*, **68** (3), 591–601.
- Krawczyński, C. 2005. Representatives of the genus *Craniscus* Dall, 1871, from the Upper Oxfordian of Bielawy and Wapienno in Kujawy area. *Volumina Jurassica*, **3** (1), 75–85. [In Polish]
- Krawczyński, C. 2008. The Upper Oxfordian (Jurassic) thecideide brachiopods from the Kujawy area, Poland. *Acta Geologica Polonica*, **58**, 395–406.
- Lambert, J. 1914. Echinodermes. *Revue Critique de Paléozoologie*, **18**, 25–32.
- Loba, M. 2019. Asteroidea and Ophiuroidea from selected Jurassic localities of Poland. Unpublished PhD thesis, 137 pp. University of Warsaw; Warszawa. [In Polish with English abstract].
- Loriol, P. de. 1884. Notes pour servir à l'étude des échinodermes. *Recueil Zoologique Suisse*, **1**, 605–643.
- Mah, C.L. and Blake, D.B. 2012. Global Diversity and Phylogeny of the Asteroidea (Echinodermata). *PLoS ONE*, **7** (4), e35644.
- Mah, C.L. and Foltz, D. 2011. Molecular phylogeny of the Valvatacea (Asteroidea: Echinodermata). *Zoological Journal of the Linnean Society*, **161** (4), 769–788.
- Matyja, B.A., Merta, T. and Wierzbowski, A. 1985. Stratygrafia i litologia utworów jurajskich struktury Zalesia. In: Matyja, B.A. and Wierzbowski, A. (Eds). *Utwory jurajskie struktury Zalesia na Kujawach i ich znaczenie surowcowe*, 19–29. Wydawnictwa Geologiczne: Warszawa. [In Polish]
- Matyja, B.A. and Wierzbowski, A. 1981. The Upper Jurassic Rocks at Barcin and Piechcin; Their stratigraphy and facies as compared with neighbouring areas. *Geological Quarterly*, **25**, 513–523. [In Polish]
- Matyja, B.A. and Wierzbowski, A. 2002. Boreal and Subboreal ammonites in the Submediterranean uppermost Oxfordian in the Bielawy section (northern Poland) and their correlation value. *Acta Geologica Polonica*, **52**, 411–421.
- Orbigny, A. d' 1850. *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés*, 1, 394 pp. Victor Masson; Paris.
- Ostrowski, S. 2003. Krawędzie bioherm mikrobialitowo-gąbkowych miejscem znacznego nagromadzenia płytek szkarłupni. *Volumina Jurassica*, **1** (1), 59–62.
- Perrier, E. 1875. Révision de la collection de Stellérides du Muséum d'histoire naturelle de Paris, 384 pp. Reinwald; Paris.
- Perrier, E. 1884. Mémoire sur les étoiles de mer recueillies dans la mer des Antilles et le Golf du Mexique. *Nouvelles Archives du Muséum d'Histoire Naturelle*, **6** (2), 127–276.
- Quenstedt, F.A. 1858. *Der Jura*, 842 pp. H. Laupp'schen; Tübingen.
- Quenstedt, F.A. 1876. *Petrefaktenkunde Deutschlands*, 1 abt. Echinodermen (Asteriden und Encriniden), 742 pp. L.F. Fues; Leipzig.
- Radwańska, U. 2000. Analiza funkcjonalna pancerza jeżowca regularnego *Rhabdocidaris nobilis* (Münster, 1826) i jej znaczenie paleoekologiczne. In: Wierzbowski, A., Matyja, B.A. and Grabowski, J. (Eds), Polish Working Group of the Jurassic system – Jurassica, 1st meeting, Wiktorowo (Poland), 28–29 September 2000, p. 22. Polskie Towarzystwo Geologiczne; Warszawa.
- Radwańska, U. 2003a. Aberrantne rozgwiazdy z rodzaju *Sphaeraster* Quenstedt, 1875, w profilu oksfordu Wapienno/Bielawy na Kujawach. *Volumina Jurassica*, **1** (1), 63–69.
- Radwańska, U. 2003b. A monograph of the Polish Oxfordian echinoids: Part 1, Subclass Cidaroida Claus, 1880. *Acta Geologica Polonica*, **53**, 143–165.
- Radwańska, U. 2004. Tube-dwelling polychaetes from the Upper Oxfordian of Wapienno/Bielawy, Couiavia region, north-central Poland. *Acta Geologica Polonica*, **54**, 35–52.
- Radwańska, U. 2007. A rare comatulid crinoid, *Semiometra petitielerci* (Caillet, 1923), from the Upper Oxfordian of Poland. *Acta Geologica Polonica*, **57**, 161–167.
- Radwańska, U. 2014. A monograph of the Polish Oxfordian echinoids: Part 2, Subclass Euchinoidea Bronn, 1860. *Acta Geologica Polonica*, **64**, 325–349.
- Radwańska, U. and Radwański, A. 2003. The Jurassic crinoid genus *Cyclocrinus* d'Orbigny, 1850: still an enigma. *Acta Geologica Polonica*, **53**, 301–320.

- Radwańska, U. and Radwański, A. 2004. Tiered burrows of alpheid shrimps and their eco-taphonomic significance in the Oxfordian and Kimmeridgian of the Holy Cross Mountains. *Volumina Jurassica*, **2** (1), 113–130. [In Polish with English abstract]
- Schöndorf, F. 1906. Das Genus Sphaeraster und seine Beziehungen zu rezenten Seesternen. *Jahrbücher des Nassauischen Vereins für Naturkunde*, **59**, 249–256.
- Sladen, W.P. 1889. The Asteroidea. *Report of the Scientific Results of the Voyage of the H.M.S. Challenger 1873–1876, Zoology*, **30**, 935 pp.
- Spencer, W.K. 1907. A Monograph of the British Fossil Echinodermata from the Cretaceous Formations. Volume second: The Asteroidea and Ophiuroidea. *Paleontographical Society Monographs*, **2** (4), 91–132.
- Spencer, W.K. 1913. The evolution of Cretaceous Asteroidea. *Philosophical Transactions of the Royal Society of London, serie B*, **204**, 99–177.
- Valette, A. 1929. Note sur quelques stellerides jurassiques du laboratoire de géologie de la Faculté des Sciences de Lyon. *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon*, **16** (13), 1–62.
- Verrill, A.E. 1899. Revision of certain genera and species of starfishes with description of new forms. *Transactions of the Connecticut Academy of Arts and Sciences*, **10**, 145–234.
- Villier, L. 2008. Sea star ossicles from the Callovian black clays of the Łuków area, eastern Poland. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **247**, 147–160.
- Villier, L. 2010. Asteroids from Barremian calciturbidites of the Serre de Bleyton (Drôme, SE France). *Annalen des Naturhistorischen Museums in Wien, Serie A*, **112**, 701–732.
- Villier, L., Breton, G., Margerie, P. and Néraudeau, D. 2004a. *Manfredaster* nov. gen. *cariniferus* nov. sp. un astéride original du Coniacien de Seine-Maritime et révision systématique de la famille des Stauranderasteridae (Echinodermata, Asteroidea). *Bulletin trimestriel de la Société géologique de Normandie et amis du Muséum du Havre*, **90** (2), 29–41.
- Villier, L., Kutscher, M. and Mah, C. 2004b. Systematics, palaeoecology, and evolutionary significance of Middle Toarcian Asteroidea (Echinodermata) from the ‘Seuil du Poitou’, Western France. *Géobios*, **37**, 807–825.
- Wierzbowski, A., Atrops, F., Grabowski, J., Hounslow, M.W., Matyja, B.A., Olóriz, F., Page, K.N., Parent, H., Rogov, M.A., Schweigert, G., Villaseñor, A.B., Wierzbowski, H. and Wright, J.K. 2016. Towards a consistent Oxfordian/Kimmeridgian global boundary: current state of knowledge. *Volumina Jurassica*, **14** (1), 15–50.
- WoRMS – World Register of Marine species, <http://www.marinespecies.org/> (last accessed 10.04.2020).
- Zatoń, M., Villier, L. and Salamon, M. 2007. Signs of predation in the Middle Jurassic of south-central Poland: evidence from echinoderm taphonomy. *Lethaia*, **40** (2), 139–151.

Manuscript submitted: 22nd May 2021

Revised version accepted: 27th September 2021