# Callovian and Oxfordian echinoids of Zalas

## Jeżowce keloweju i oksfordu Zalasu

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**ABSTRACT:** Within the Callovian-to-Oxfordian sequence, transgressive upon the Variscan rhyodacite laccolith exposed at Zalas in the Cracow Upland, southern Poland, and far-known due to its ubiquitous fossils of various kinds, to this study subjected are the echinoids.

The Callovian assemblage from the variably-sized clastics is low-diversified, to contain 4 taxa of a wider regional occurrence. The Lower (up to the base of Middle) Oxfordian assemblage appears the richest in the Oxfordian of Poland. Its content is typified by the representatives of the orders Cidaroida Claus, 1880, and Phymosomatoida Mortensen, 1904. Amongst the recognised 12 species, of special attention are those first reported from the Jurassic sequences of Poland, *viz. Eosalenia miranda* Lambert, 1905, and *Heterocidaris dumortieri* Cotteau, 1871, the latter of which is still a great rarity to the science. Discussed are the life requirements of some of the recognised taxa, as apparent from the functional analysis of their tests.

#### INTRODUCTION

The Middle-to-Upper Jurassic strata exposed at Zalas in the Cracow Upland (some 20 km west of the city of Cracow) represent one of the most prolific fossiliferous sequences in Poland. The fame of the locality Zalas has burst in the early 19<sup>th</sup> century, to be continued ever since. In former years the Jurassic strata were well accessible in a series of local quarries, some natural exposures, and rural pits for sand and gravel, all abandoned now. Since the 1970's they are exposed at the top of a huge quarry of rhyodacite, the Variscan laccolith of which makes up their basement (see fig. 1).

The sedimentary sequence capping that laccolith has developed during the mid-Jurassic (Callovian) transgression which encroached upon the eroded laccolith, exposed then as a hilly monadnock. The sequence begins with a Callovian cliff, bearing large blocks/boulders of rhyodacite, and preserved as though just frozen in the surf zone (see Dżułyński 1950, fig. 2), to form a protected spot nowadays. Clastics of various grain-size and thickness (up to 5 m), sandy crinoidal limestones (encrinites, about 3 m thick), and the "Knobby Layer", capped irregularly by columnar stromatolites (from almost nil to some 30-40 cm thick), complete the Callovian succession terminated by an omission surface of the hardground type (see Giżejewska & Wieczorek 1977).

The Oxfordian succession at Zalas, far-famed due to its content of ubiquitous ammonites and sponges, starts upon a short-termed sedimentary gap. It begins with variegated marls and marly limestones (about 2 m thick) of the Lower Oxfordian Cordatum Zone, overlain by a complex facies of the carbonate buildup (cyanobacteria-sponge bioherm; now completely removed by the quarry



Fig. 1. General view of the rhyodacite quarry at Zalas in the Cracow Upland, to show exposures of the Callovian-to-Oxfordian sequence (arrowed) capping the Variscan laccolith.

works) diverging into alternated thin-bedded limestones and marls, or platy limestones (about 10 m thick) of the Middle Oxfordian Tenuicostatum Subzone of the Plicatilis Zone (see Matyja & Tarkowski 1981, figs 2-3).

The Jurassic sequence of Zalas, classical for the Polish stratigraphy, palaeogeography, and palaeontology, has subjected to numerous descriptions in regional reports, casebooks, conference abstracts, and recommended Field-Guides (e.g.: Roemer 1870; Zaręczny 1894; Wójcik 1910; Gradziński 1960; Tarkowski 1989; Gradziński & Gradziński 1994). The number of palaeontological contributions amounts far over a hundred. In such context it is amazing that the echinoderms have been noticed in faunistic lists by the two authors only (see fig. 3), viz. Siemiradzki (1893), and Wójcik (1910). There is no matter to discuss whether this is due to that the echinoderms have been overlooked/neglected by collectors of showy specimens of ammonites, sponges, and their associates (other mollusks, brachiopods), or the echinodermbearing beds have not been then exposed or accessible.

The present author during systematic research of Upper Jurassic echinoids of Poland (see Radwańska 1999, 2000, 2003, 2004a, b) has recognised that amongst several undescribed materials, those in hands of private collectors in particular, there are present some specimens from Zalas. To the truth, their state of preservation is usually a bit worse than that of specimens from other locations (see Radwańska 2003). Nevertheless, during fieldworks at Zalas it has soon appeared that the echinoderm content in the sequence is reasonably rich and much diversified, to contain not only echinoids, but also diverse crinoids, asteroids, and ophiuroids. Of these, some cidaroid echinoids have been reported recently (Radwańska 2003), the same as crinoids of the enigmatic genus Cyclocrinus represented by isolated columnals (Radwańska & Radwański 2003, p. 307).

Subjected to this study are solely the echinoids coming both from the Callovian, as well as from the Oxfordian interval of the Zalas sequence.

#### STRATIGRAPHIC SETTING

The sandy, basal part of the Zalas sequence, the studied echinoids come from, is contained in the Lower Callovian Macrocephalus Zone, whereas the "Knobby Layer" in the Upper Callovian Lamberti Zone (see Giżejewska & Wieczorek 1977).

The echinoid-bearing marls or marly intercalations in thin-bedded limestones are contained in the above-indicated frames of the Lower Oxfordian Cordatum Zone to the lowest part of the Middle Oxfordian Tenuicostatum Subzone of the Plicatilis Zone (see Matyja & Tarkowski 1981). Any more precise location of particular specimens in the sequence cannot be done, as most specimens collected personally were taken from the scree and/or rainfall outwash, the same as probably were the specimens of private collections.

#### THE ZALAS ECHINOIDS

All echinoids collected at Zalas, recognizable to their species level (see fig. 2 and pl. 1-3), are briefly characterised in terms of their life requirements, as apparent from the functional analysis of their tests (see Smith 1978, 1984; Radwańska 1999). The taxonomic discussion of particular species is herein omitted, having been subjected to a separate paper. Presented is, instead, a short comment on

#### **Callovian echinoids**

An echinoid assemblage collected in the Callovian sequence at Zalas is characterised by its low diversity, to contain four species only (see fig. 2 and pl. 1: 1-4), of which *Collyrites ellipticus* (Lamarck, 1816) and *Holectypus depressus* (Leske, 1778) dominate. The functional analysis of tests of these four species indicates their environmental requirements very similar, but their life habits diverse.

The functional analysis of *Holectypus depressus*, of and closely related *Holectypus corallinus*, was studied in detail by Smith (1984) and Radwańska (1999). Individuals of *Holectypus depressus* (pl. 1: 4a-4b) are thought to have been adopted to life on loose bottom sediments, mostly coarse sands, and they burrowed into vertically, using their oral spines. They buried for protection from predators during daytime and returned to the surface at night to forage; they fed using only their lantern to scoop up bottom sediment unselectively. The large periproct indicates that the volume of their faecal material was great and that the ingested particles

Species	Number of specimens	Age
Stomechinus heberti Cotteau, 1884	1 test	Je
Holectypus depressus (Leske, 1778)	17 tests	Jc
Nucleolites orbicularis Phillips, 1829	2 tests	Je
Collyrites ellipticus (Lamarck, 1816)	40 tests	Jc
<i>Polycidaris</i> sp. 2; see Radwańska 2003, p. 152	several fragments of primary spines	Jo
<i>Polycidaris? suevica</i> (Desor, 1855); see Radwańska 2003, pp. 152-153	2 fragments of tests	Jo
<i>Plegiocidaris crucifera</i> (L. Agassiz, 1840); see Radwańska 2003, pp. 154-155	several primary spines	Jo
<i>Paracidaris blumenbachi</i> (Münster in Goldfuss, 1826); see Radwańska 2003, pp. 157-159	several fragments of test	Jo
<i>Paracidaris elegans</i> (Münster in Goldfuss, 1826); see Radwańska 2003, pp. 159-160	3 tests	Jo
<i>Paracidaris laeviscula</i> (L. Agassiz, 1840); see Radwańska 2003, pp. 160-162	4 tests, ubiquitous primary spines	Jo
Eosalenia miranda Lambert, 1905	8 tests	Jo
Heterocidaris dumortieri Cotteau, 1871	4 fragments of test	Jo
Diplopodia aequale (L. Agassiz, 1840)	6 tests	Jo
Polydiadema langi (Desor, 1856)	7 tests	Jo
Pleurodiadema gauthieri Cotteau, 1884	20 tests	Jo
Magnosia decorata (L. Agassiz in Desor, 1846)	17 tests	Jo

Fig. 2. Echinoids of the Callovian and Oxfordian at Zalas.



J. Siemiradzki (1893)	K. Wójcik (1910)	Here assigned to	Age
<i>Echinobrissus Goldfussi</i> Desor	-	_	Jo
Collyrites thermarum Moesch	-	-	Jo
_	<i>Psudodiadema Langi</i> Desor	Polydiadema langi (Desor, 1856)	Jo
-	<i>Magnosia decorata</i> Desor	Magnosia decorata (L. Agassiz in Desor, 1846)	Jo
_	<i>Glypticus sulcatus</i> Gldf.	<i>Pleurodiadema gauthieri</i> Cotteau, 1884	Jo
-	Hemicidaris sp.	—	Jo
_	Cidaris filograna Agass.	<i>Paracidaris laeviscula</i> (L. Agassiz, 1840); see Radwańska (2003, pp. 160-162)	Jo
_	<i>Holectypus depressus</i> Desor	<i>Holectypus depressus</i> (Leske, 1829)	Jc
_	<i>Echinobrissus clunicularis</i> Lhwyd	Nucleolites orbicularis (L. Agassiz, 1840)	Jc

Fig. 3. Former reports of echinoids from Zalas.

were relatively large. The individuals of *Holectypus depressus* inhabited warm, shallow-water, low-energy environment.

The functional analysis of *Collyrites ellipticus* (pl. 1: 1a-1b) indicates that it was also adopted to life on loose bottom. It was a relatively shallow--ploughing species, in which the major part of the aboral side of the test was exposed above the sediment/water interface. Low profile and flattened oral side of the test, interpreted as an adaptation for more efficient locomotion on unconsolidated sediments (Smith 1984), helped in the ploughing through sediment, and provided stability against stronger currents and/or wave action. The relatively small, slightly oval peristome, positioned anteriorly on its underside, and a lack of the lantern, correspond to its mud-feeding bahaviour. The ambulacral pores crowded adorally were probably associated with moderately muscular, suckered tube feet. These tube feet were involved in taste, and in transport of bottom particles towards the mouth. The number of the tube feet was relatively small, as the volume of ingested sediment was probably limited.

The individuals of *Collyrites ellipticus* inhabited warm, shallow-water, low-energy environment.

Identical behaviour and environmental requirements have also been recognised in representatives of diverse species of the genus *Nucleolites* (see Smith 1984; Radwańska 1999). In regard with these, the species *Nucleolites orbicularis* Phillips, 1829, differs in having almost circular outline of the test, and petalodia very inconspicuous (pl. 1: 2a--2c). Such features indicate that individuals of this species presumably did not burrow deeply, contrary to its congeners, but similarly as *Holectypus*species they burrowed to shallow depths, vertically into coarse-grained bottom using their oral spines.

The only representative of regular echinoids in the Callovian assemblage belongs (pl. 1: 3a-3b) to the species *Stomechinus heberti* Cotteau, 1884. The functional analysis of tests of the genus *Stomechinus* has heretofore been presented by Radwańska (1999, pp. 346-347) for some Early Kimmeridgian species from the Holy Cross Mountains, Central Poland. The recognised Callovian species differs from the latter ones by the pronounceness and distribution of primary tubercles on

Plate 1

Callovian echinoids of Zalas: 1a-1b – *Collyrites ellipticus* (Lamarck, 1816), nat. size; 2a-2c – *Nucleolites orbicularis* Phillips, 1829, taken x2; 3a-3b – *Stomechinus heberti* Cotteau, 1884, taken x1.5 (coll. Muzeum Przyrodnicze Instytutu Systematyki i Ewolucji Zwierząt PAN w Krakowie); 4a-4b – *Holectypus depressus* (Leske, 1778), taken x2.

the test. These features, substantial for the distinction at the species lavel, are not significant in the functional analysis of the test, and thus in behavioural/environmental interpretations.

To summarize, the recognised irregular species, *Holectypus depressus*, *Collyrites ellipticus*, and *Nucleolites orbicularis*, were well adopted to active life on loose bottom sediments, in warm, shallow-water, low-energy environment.

#### **Oxfordian** echinoids

An echinoid assemblage from the Oxfordian sequence of Zalas is remarkably richer than the Callovian one. Of 12 taxa recognised (see fig. 2, used for transport of coarser bottom material, to comouflage against predators. The adoral tube feet arranged in small phyllodes are stronger, with well developed terminal sucker which could allow the echinoids to climb onto obstacles and to use the lantern more efficiently. The species *Pleurodiadema gauthieri* was well adopted to a not very active life on loose bottom sediments, under environmental conditions of warm water, lowenergy dynamics, situated most likely below the wave base.

The species *Magnosia decorata* (L. Agassiz in Desor, 1846), the second of the most numerous taxa (see pl. 2: 2a-2c and 3: 2a-2c), represents small-





A lack of isopores P3 or P4 type on the oral side (thus, of suckered tube feet) resulted in their being unprotected against strong waving, and they could not creep over any bottom obstacles. The presence of isopores P1 type along whole ambulacral columns, bearing the tube feet specialised for gaseous exchange, indicates their adaptation to a high temperature of water, and hence their oxygen consumption and metabolic rate must have been high. They foraged with the use of the Aristotle's lantern situated within the large, centraly placed peristome. The lantern was enough mobile to serve for rasping soft elements, e.g. algae, rather than for crushing. The Oxfordian cidaroids of Zalas lived under environmental conditions of warm water, low-energy dynamics, most likely below the wave base, and they inhabited flat areas of the finegrained and/or muddy bottom. Similar requirements are also apparent in the test analysis of the species Eosalenia miranda Lambert, 1905 (see pl. 2: 3 and 3: 1a-1c) and Heterocidaris dumortieri Cotteau, 1871 (see pl. 2: 5), the both of unclear phyletic relation to the cidaroids.

At Zalas, guite common are also representatives of the order Phymosomatoida Mortensen, 1904 (see fig. 2), such as Polydiadema langi (Desor, 1856) and Diplopodia aequale (L. Agassiz, 1840). These echinoids are characterised by a strongly flattened. relatively thick-walled test of circular or subpentagonal outline (pl. 2: 4a-4c, 6-7). The test is covered by uniform tubercles, to which attached were sharply pointed spines of equal length, used for defence. The slightly sunken and naked areas developed on the aboral side could help to channel the water and to wash the test. The presence of phyllodes with P3 isopores indicates the presence of strong. suckered tube feet which allowed the echinoids to climb onto obstacles and adhere to the bottom during higher waves. Strong flattening of the dorsal side of the test has increased greatly the number of the tube feet in contact with the bottom. These features indicate that Polydiadema and Diplopodia-species could inhabit high-energy environments. The aboral P2 isopores have been joined with the respiratory tube feet of lower efficiency. The biserial arrangement of P2 isopores on the aboral side of the test in Diplopodia-species, might have balanced their lower efficiency.

The relatively broad attachment area in P2 isopores, shows that the associated tube feet were probably strong, and possessed a terminal sucker. The presence aborally of strong, suckered tube feet indicates, like in many Recent species (see Smith 1978), that the discussed Phymosomatoida-species were able to thatch themselves, using tube feet and spines for the transport of coarser bottom materials. In this way they were able to hide, and to protect themselves from predators, the most probably seastars, the great number of which co-existed with Oxfordian echinoids at Zalas. The relatively low oxygen consumption and metabolic rate may result from adaptation not for low temperature of water but for low activity during daylight hours. They probably foraged at night with the use of the Aristotle's lantern situated within the relatively large, centraly placed peristome. The lantern was enough mobile to serve for rasping and crushing.

To summarize, the recognised species of the order Phymosomatoida were well adopted to a not very active life on loose bottom sediments, in warm, shallow-water, moderately high-energy environment.

#### Previous assignments updated

The taxonomic recognition of the currently collectable echinoids of Zalas, both of Callovian and Oxfordian age (see fig. 2), allows to correct/update the previous assignments of Siemiradz-ki (1893) and Wójcik (1910) as follows (fig. 3).

#### REGIONAL COMMENT

The Callovian assemblage of echinoids from Zalas (see fig. 2) is very similar to those from other localities in the Cracow Upland (see Wójcik 1910; Jesionek-Szymańska 1963), and particularly to that one from the famous site of Balin Oolite (see Roemer 1870, pl. 21: 19-21). All Callovian assemblages are typified by small-sized irregular echinoids, amongst which the large-sized, previously unknown regular, *Stomechinus heberti* Cotteau, 1884, becomes evidently a showy rarity (see pl. 1: 3a-3c).

Plate 3

Close-up views of tests of the Oxfordian echinoids of Zalas: 1a-1c – *Eosalenia miranda* Lambert, 1905; 2a-2c – *Magnosia decorata* (L. Agassiz in Desor, 1846); 3a-3b – *Pleurodiadema gauthieri* Cotteau, 1884.

The Oxfordian assemblage of echinoids from Zalas, comprising 12 species, appears the richest in the Oxfordian sequences of Poland (*cf.* Radwańska 2000, 2003, 2004b). Apart from 6 species of cidaroids (see Radwańska 2003, and fig. 2), it contains 3 species of phymosomatoids, and the other 3 species of the genera of uncertain taxonomic position (*Eosalenia*, *Heterocidaris*, *Magnosia*). The non-cidaroid genera are represented both by these previously reported by Wójcik (1910), that is *Polydiadema*, *Pleurodiadema*, and *Magnosia* (see revised items, fig. 3), as well as those unknown as yet from Poland (*Eosalenia*, *Heterocidaris*). Of the recognised taxa, several need a special comment.

First, the assemblage is dominated (see fig. 2) by three small-sized species, Pleurodiadema gauthieri Cotteau, 1884, Magnosia decorata (L. Agassiz in Desor, 1846), and Polydiadema langi Desor, 1856, the life requirements of which are slightly different (see above). Nevertheless, they all are guite frequent in many Lower Oxfordian localities of the Cracow Upland, and Polydiadema langi having been present almost everywhere (Wójcik 1910). The cooccurrence of echinoids of slightly more or less diverse life requirements may be interpreted either as an effect of their lifetime not coeval, with bottom conditions having been in more or less permanent change, or as a result of variable bottom topography of microhabitats featured by the dominance of sponges, both living as well as of their mummies and/or initial buildups (Matyja & Tarkowski 1981, fig. 2-3; and restoration of comparable Oxfordian seascape in Switzerland – Hess 1975, fig. 27).

Second, the cidaroid *Paracidaris laeviscula* (Agassiz, 1840), reported previously as *"filograna"* L. Agassiz, 1840, being a *nomen nudum* (see Radwańska 2003, pp. 160-162), is represented primarily (fig. 2) by ubiquitous isolated primary spines, which in some layers of the Lower Oxfordian sequence are mass-accumulated.

Third, of special interest is the occurrence of fragments of the peculiarly sculptured (pl. 2: 5), large-sized *Heterocidaris dumortieri* Cotteau, 1871, a species of the genus still very poorly known, of unclear systematic position, and extremely rare in Europe (Cotteau 1860, 1882; Fell 1966). This species, as well as its congeners, are relatively thinwalled, but of quite large size (over 10 cm in diameter), what certainly makes their preservational potential very poor. Up to now, neither this species nor genus have ever been recorded in Poland.

#### Tomy Jurajskie, tom III

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#### STRESZCZENIE

Profil osadów jurajskich odsłaniający się w stropie wielkiego kamieniołomu waryscyjskich riodacytów Zalasu (patrz fig. 1) okazuje się znaczącym ze względu na bogactwo szczątków różnorodnych szkarłupni (liliowców, rozgwiazd, weżowideł), spośród których na szczególna uwage zasługują jeżowce. W dotychczasowych opracowaniach profilu Zalasu, dostępnego dawniej w niewielkich odsłonięciach naturalnych lub lokalnych łomikach, jeżowce były notowane sporadycznie, jako towarzyszące obfitej faunie gabek, amonitów i innych mięczaków, oraz ramienionogów (patrz Siemieradzki 1893; Wójcik 1910). Rozległe odsłonięcie w kamieniołomie riodacytów, rozbudowywanym od lat 1970-tych, umożliwiło szczegółowe rozpoznanie wykształcenia facjalnego osadów jurajskich, ich inwentarza faunistycznego i przede wszystkim ich biostratygrafii wyznaczającej pozycję stratygraficzną profilu w przedziale dolny kelowej – niższa część oksfordu środkowego (patrz Giżejewska i Wieczorek 1977; Matyja i Tarkowski 1991; Tarkowski 1989).

Badane przez autorkę jeżowce, pochodzące częściowo z rozmaitych kolekcji (publicznych i prywatnych), a w większości zebrane osobiście, stanowią w sumie dosyć istotny element w rozpoznaniu faun jurajskich Polski.

Zespół jeżowców z osadów keloweju (patrz pl. 1) obejmuje tylko 4 gatunki (patrz fig. 2) o różnych wymaganiach życiowych wskazujących na nieustabilizowane warunki środowiskowe w czasie postępującej transgresji morskiej. Oprócz dość banalnych form nieregularnych pojawia się tutaj (patrz pl. 1: 3a-3b) duży osobnik regularny, *Stomechinus heberti* Cotteau, 1884, nieznany dotąd w środkowej jurze Polski.

Zespół jeżowców z osadów oksfordu (patrz pl. 2-3) składa się z 12 taksonów (patrz fig. 2), spośród których sześć z podgromady Cidaroidea Claus, 1880. zostało omówionych wcześniej (Radwańska 2003). Zespół ten obejmuje wyłącznie jeżowce regularne o zbliżonych wymaganiach życiowych wskazujace na ujednolicenje warunków środowiskowych w czasie rozszerzającej się transgresji. Uwagę zwraca w nim gatunek Heterocidaris dumortieri Cotteau, 1871, o wprawdzie niejasnej pozycji systematycznej (patrz Fell 1966), a reprezentowany niestety tylko w postaci ułamków pancerzy (pl. 2: 5) znacznych rozmiarów (średnicy ponad 10 cm), ale bedacy niezmierna rzadkościa w jurze europejskiej (patrz Cotteau 1860, 1871; Fell 1966) i nieznany dotychczas z obszaru Polski.

Analiza funkcjonalna pancerzy (patrz Smith 1978, 1984; Radwańska 1999) pozwoliła na bardziej szczegółowe rozpatrzenie sposobu życia i wymogów środowiskowych badanych gatunków jeżowców z keloweju i oksfordu Zalasu, zaś analiza taksonomiczna na unacześnienie rozpoznań autorów wcześniejszych (Siemiradzki 1893; Wójcik 1910; patrz fig. 3).

Zespół jeżowców oksfordzkich Zalasu okazuje się najbogatszym spośród wszystkich dotychczas badanych stanowisk oksfordu w Polsce (por. Radwańska 2000, 2003, 2004b), zaś jego środowiskowe siedlisko – wśród obfitych gąbek, ich mumii i budowli (por. Matyja i Tarkowski 1981, fig. 2B-3) – nadzwyczaj podobne do przedstawionego dla środkowego oksfordu Szwajcarii (patrz Hess 1975, fig. 27).