

Lower Kimmeridgian comatulid crinoids of the Holy Cross Mountains, Central Poland

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ABSTRACT:

RADWAŃSKA, U. 2005. Lower Kimmeridgian comatulid crinoids of the Holy Cross Mountains, Central Poland. *Acta Geologica Polonica*, 55 (3), 269-282. Warszawa.

An assemblage of feather stars or comatulids (free-living crinoids of the order Comatulida A.H. CLARK, 1908) is reported for the first time from Upper Jurassic sequences of Poland, precisely from Lower Kimmeridgian strata of the Holy Cross Mountains. The major part of this assemblage comes from oolitic deposits exposed at Małogoszcz Quarry, others from oyster (*Actinostreon*, and *Nanogyra*) shellbeds higher up section at Małogoszcz, as well as from the coeval strata of the Karsy section. Taxonomically recognizable skeleton elements such as calyces, isolated centrodorsals and radials are here assigned to seven taxa, three of which are new to science: *Comatulina malogostiana* sp.nov., *Palaeocomaster karsensis* sp.nov., and *Solanocrinites sanctacrucensis* sp.nov. The majority of the material available was contained in burrows made by some ancestral stock of alpheid shrimp, closely comparable to those of present-day snapping shrimp (genus *Alpheus* WEBER, 1795), and its allies. These burrows, situated at the tops of oolitic shoals/banks at Małogoszcz, casually served both as habitats of cryptic faunas (mostly comatulids, dwarf-sized gastropods) and as preservational/taphonomic traps for others, primarily echinoderms (ten taxa of echinoids, three stalked crinoids, two ophiuroids, one asteroid) swept into by highly agitated waters, most likely during storms, to produce an *Echinodermlagerstätte*. Comatulid remains from the oyster shellbeds underwent longer periods of transport, to be entombed far from their habitats.

Key words: Crinoidea, Comatulida, Taxonomy, New Species, Eco-taphonomy, Upper Jurassic, Poland.

INTRODUCTION

The Upper Jurassic shallow-marine carbonate sequence of the Holy Cross Mountains, Central Poland, has long been known to yield ubiquitous fossils (see KUTEK 1968, 1969; MATYJA 1991; KUTEK & al. 1992a, b). Amongst echinoderms, echinoids have first been taken into investigation by the present author (RADWAŃSKA 1999, 2003a, 2004a, b), on the basis of material for a large part coming from huge exposures of cement works at Małogoszcz, established in the mid-1970s.

The present report deals with one of the more fascinating discoveries of Late Jurassic echinoderms in Poland

in recent years: the free-living crinoids of the comatulid order, or feather stars, as commonly referred to in the literature (see HENDLER & al. 1995, MESSING 1997). These tiny animals, mostly hidden from view in present-day seas due to their nocturnal mode of life, have long been unrecognized also in Jurassic deposits of Poland. The situation changed when an intense search was done in the Małogoszcz sequence of Kimmeridgian age (see KUTEK & al. 1992b; RADWAŃSKI 1995; RADWAŃSKA 1999; RADWAŃSKA & RADWAŃSKI 2003, 2004a, b, 2005).

Comatulid crinoids from the Lower Kimmeridgian portion of the sequence exposed at Małogoszcz, first recorded by RADWAŃSKI (1995, p. 12), have recently been

the subject of to a preliminary account by the present author (RADWAŃSKA 2004b). That account concerned remains of comatulid crinoids from the Upper Oolite Member, where they are confined to tiered burrows of alpheid shrimp (see RADWAŃSKA & RADWAŃSKI 2004b). Apart from this location, comatulids also occur in the marly intervals of oyster coquinas (*Actinostreon/Nanogyra* shellbeds) higher up section at Małogoszcz (see Text-fig. 1), and in coeval beds sequence exposed at Karsy near Korytnica, some 30 km away (see RADWAŃSKA 1999, pp. 297-298; MACHALSKI 1983; KIN 2005).

These two localities, Małogoszcz and Karsy, have as yet remained the only sites of the comatulid occurrence throughout all Upper Jurassic and other Mesozoic

sequences of Poland. Previous records of comatulid crinoids in Poland only involved those from Middle Miocene (Badenian) sequences along the southern slopes of the Holy Cross Mountains: the Pińczów Limestone (RADWAŃSKI 1977, p. 747 and fig. 172/8) and the Korytnica Clays (RADWAŃSKA 1987, 2003b).

SYSTEMATIC ACCOUNT

The taxonomy and terminology of comatulids used here follows that proposed by *Treatise on Invertebrate Paleontology* (WIENBERG-RASMUSSEN 1978; see comments by MESSING 1997, p. 4).

Repositories

All comatulid material described here is housed in the Department of Palaeontology, Faculty of Geology, University of Warsaw. It is kept under the collection numbers preceded by the character C (comatulids), followed by a lettered symbol Km indicative of its Kimmeridgian age.

Order Comatulida A.H. CLARK, 1908
Superfamily Solanocrinitacea JAEKEL, 1918
Family Solanocrinitidae JAEKEL, 1918

Genus *Comatulina* D'ORBIGNY, 1852

TYPE SPECIES: *Solanocrinites costatus* GOLDFUSS, 1829; *OD*

REMARKS: The genus *Comatulina* D'ORBIGNY, 1852, is diagnosed (see WIENBERG RASMUSSEN 1978, p. 7875) as featured by centrodorsals truncated conical to truncated subhemispherical, of dorsal (aboral) side flat or concave, and by closely placed cirrus sockets arranged in more than 10 (generally 11-15, exceptionally up to 20) columns in adult specimens.

In the material studied, such features are shared by four taxa, the centrodorsals of which range in shape from conically hemispherical (*C. malogostiana*), truncated conical (*C. peroni*, *C. beltremieuxi*), through to almost low cylindrical (classified below as *Comatulina* sp).

Comatulina peroni (DE LORIOL, 1889)
(Text-fig. 2 and Pl. 1, Figs 2-4)

1889. *Antedon Peroni* P. DE LORIOL, 1888; P. DE LORIOL, pp. 490-492, pl. 222, figs 2, 2a-2c.
2004b. *Comatulina peroni* (DE LORIOL, 1889); U. RADWAŃSKA, p. 126, pl. 2, fig. 11.

Małogoszcz Quarry

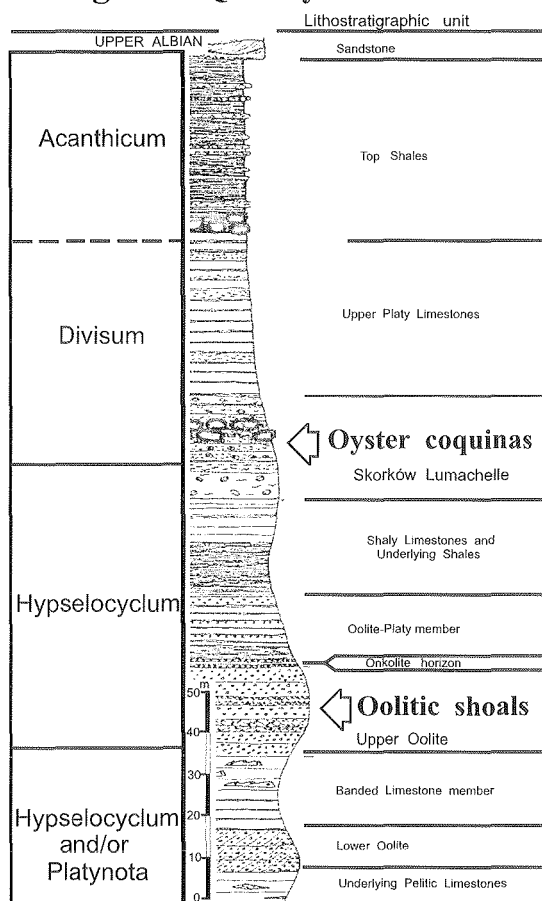


Fig. 1. Lower to low-Upper Kimmeridgian sequence exposed at Małogoszcz Quarry in the Holy Cross Mountains, Central Poland (adapted from: KUTEK & *al.* 1992b, fig. 5; MATYJA & WIERZBOWSKI 1996, fig. 3; RADWAŃSKA & RADWAŃSKI 2005, fig. 2), to show occurrence sites (arrowed) of comatulids studied from oolitic shoals (Upper Oolite Member) and onkolitic, marly oyster-coquinas (*Actinostreon/Nanogyra* shellbeds of the Skorków Lumachelle Member)

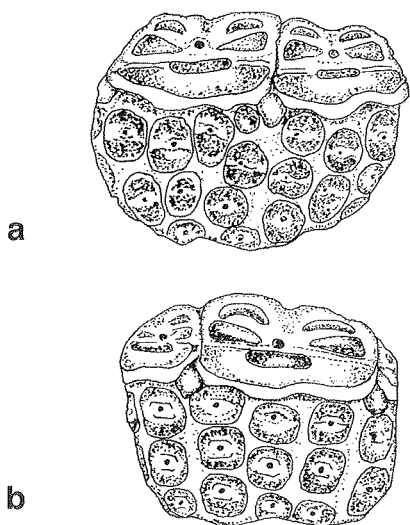


Fig. 2. *Comatulina peroni* (DE LORIO, 1889); a – lateral (interradial) view of calyx, to show basal plate; b – lateral (radial) view of calyx, to show radial plate; CKm/008; $\times 7$

MATERIAL: Four calyces and five centrodorsals; all from tiered burrows of alpheid shrimp at Małogoszcz (Upper Oolite Member).

DESCRIPTION: The centrodorsals are moderately tall, truncated conical to almost discoidal, with 15 columns of three large, closely spaced, cirrus sockets (Text-figs 2a-2b and Pl. 1, Figs 2, 3a, 4a-4b); in one specimen, the median column bifurcates to yield four sockets, what amounts 46 sockets in total (see Text-fig. 2a and Pl. 1, Fig. 4a). The aboral side of the centrodorsals is relatively large (about 75% of centrodorsal diameter), flat or slightly concave, covered by granules (Pl. 1, Fig. 3b). Cirrus sockets are oval in outline and deep, with a large lumen. The adoral side of centrodorsal has a shallow cavity, about 25% of centrodorsal diameter (Pl. 1, Fig. 3a). Basals are distinctly exposed at interradian points (Text-fig. 2a and Pl. 1, Fig. 4a). The radial ring is lower than the slightly overhanging centrodorsal (Pl. 1, Figs 4a-4b). Radials are trapezoidal, with a very low free aboral surface, and distinctly undulated aboral margin (Text-figs 2a-2b and Pl. 1, Figs 2, 3a, 4b). The articular facet of radials is moderately tall and oblique (Pl. 1, Figs 2, 3a, 4a-4b). The aboral ligament fossa is low, with a large, oval ligament pit. Interarticular ligament fossae are triangular in shape. Adoral muscular fossae are arc-shaped (Text-fig. 2b and Pl. 1, Fig. 4b).

REMARKS: The studied calyces are concordant with those described from the Kimmeridgian of France by DE LORIO (1889) as “*Antedon peroni* P. DE LORIO,

1888”. Due to the general shape of the centrodorsal and the number of columns of cirrus sockets, they are assigned to the genus *Comatulina* D’ORBIGNY, 1852. The studied calyces of *Comatulina peroni* display a slight variability in the steepness and height of the articular facet of the radials (see Pl. 1, Figs 2, 4b). Moreover, their aboral side is relatively flat widely.

Comatulina cf. *beltremieuxi* (DE LORIO, 1889)
(Pl. 1, Figs 1a-1c)

MATERIAL: Three centrodorsals and a single radial plate; all from tiered burrows of alpheid shrimp at Małogoszcz (Upper Oolite Member).

DESCRIPTION: The centrodorsals are moderately tall, truncated conical, with 15 columns of one to three closely spaced, large cirrus sockets (Pl. 1, Fig. 1b). The aboral side of the centrodorsal is slightly concave and covered by furrows (Pl. 1, Fig. 1a). Cirrus sockets are oval in outline and deep, with a large lumen. The adoral side of the centrodorsal has a very narrow cavity, about 17% of centrodorsal diameter. Basals are not observable. The radial plate is trapezoidal, with low free aboral surface, covered by prominent granules, arranged in a single horizontal row (Pl. 1, Fig. 1c). The articular facet of the radials is moderately tall and steep. The aboral ligament fossa is low, with a large, oval ligament pit. Interarticular ligament fossae are low, and triangular in shape. Adoral muscular fossae are triangular.

REMARKS: The studied centrodorsal and the radial plate are very close to those of the species *Comatulina beltremieuxi* (DE LORIO, 1889), described from the Kimmeridgian of France. Alternatively, the single radial plate might be assigned to *Solanocrinites jutieri* (DE LORIO, 1879), from the Lower Kimmeridgian of France (see DE LORIO 1879, pp. 265-266, pl. 21, figs 1-5), but no centrodorsal which may be ascribed to that species has yet been found in the investigated material. The poor preservation of the collected specimens (isolated centrodorsal and radial plate, both with corroded surface) does not permit a precise specific determination, contrary to the previous statement (RADWAŃSKA 2004b, pl. 2, figs 3-4).

Comatulina malogostiana sp.nov.
(Text-fig. 3 and Pl. 2, Figs 1-3)

2004b. *Comatulina costata* (GOLDFUSS, 1829); U. RADWAŃSKA, p. 126, pl. 2, fig. 6.

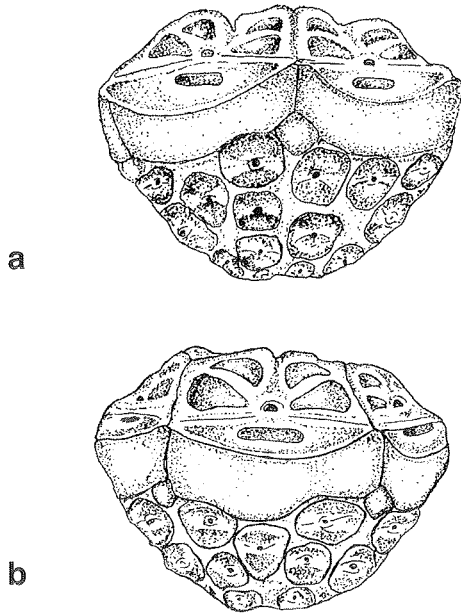


Fig. 3. *Comatulina malogostiana* sp.nov.; holotype: a – lateral (interradial) view of calyx, to show basal plate; b – lateral (radial) view of calyx, to show radial plate; CKm/001; $\times 7$

HOLOTYPE: Calyx (specimen number CKm/001), presented in Text-fig. 3 and Pl. 2, Figs 3a-3d.

PARATYPES: Centrodorsal (specimen number CKm/003) presented in Pl. 2, Fig. 1 and calyx (specimen number CKm/002), presented in Pl. 2, Fig. 2.

TYPE LOCALITY: Małogoszcz Quarry, south-western margin of the Holy Cross Mountains, Central Poland.

TYPE HORIZON: Low Kimmeridgian, Katroliceras divinum Zone; Skorków Lumachelle Member.

DERIVATION OF THE NAME: Adjectival name, from neo-Latinized name of the medieval town of Małogoszcz.

MATERIAL: The holotype calyx from oyster coquinas at Małogoszcz; the other three calyces and six centrodorsals from tiered burrows of alpheid shrimp at Małogoszcz.

DIAGNOSIS: Centrodorsal conically hemispherical, with 15 columns of one to three large, closely spaced cirrus sockets; aboral side of the centrodorsal pointed with one, centrally placed cirrus socket surrounded by five small ones; basals exposed in interradial points, rhomboidal in cross-section; radial ring a bit taller than centrodorsal, slightly overhanging; radials trapezoidal, with a very tall free aboral surface.

DESCRIPTION: The centrodorsals are moderately tall, conically hemispherical, with 15 columns of a single to three closely spaced cirrus sockets (Text-figs 3a-3b and Pl. 2, Figs 2a-2b, 3b-3c). The aboral side of centrodorsals is pointed with a single, centrally placed cirrus socket surrounded by five small ones (Pl. 2, Figs 1b, 2c, 3d). Cirrus sockets are oval in outline and deep, with a small lumen; their number is 41 in the largest specimen. Relatively distinct basals, exposed in interradial points, are rhomboidal in cross-section (Text-fig. 3a and Pl. 2, Fig. 3b). The radial ring is slightly taller than centrodorsal, slightly overhanging (Pl. 2, Figs 2a, 2b, 3b). Radials are trapezoidal, with a very high free aboral surface (Pl. 2, Fig. 3b) The articular facet of radials is moderately tall and steep at 45° . The aboral ligament fossa is large with a long, deep ligament pit. Interarticular ligament fossae are tall, and triangular in shape. Adoral muscular fossae are low, and arc-shaped (Text-fig. 3b and Pl. 2, Fig. 3c). The radial cavity is moderately large and deep, reaching about 50% of calyx diameter (Pl. 2, Fig. 3a).

REMARKS: The calyces studied are assigned to the genus *Comatulina* D'ORBIGNY, 1852. The newly established species *Comatulina malogostiana* sp.nov. differs from the closely related species, *C. costata* (GOLDFUSS, 1829), in having a lower centrodorsal, a smaller number of cirrus sockets, and a distinctly taller free aboral surface of radials. From other congeners, e.g. *C. peroni* (DE LORLIOL, 1889), it differs in its more hemispherical shape of centrodorsal, and in the more prominent basals.

Comatulina sp.
(Pl. 3, Figs 1a-1b)

MATERIAL: Two centrodorsals, from Karsy.

DESCRIPTION: The large centrodorsals (the larger reaching 13 mm in diameter) are low cylindrical, with up to 17 columns of two or three, closely spaced, large cirrus sockets (Pl. 3, Fig. 1a). The aboral side of centrodorsal is large, flattened and slightly concave, covered by radiating furrows. Cirrus sockets are large, oval in outline and deeply incised, with a large lumen; their number totals 49 in the larger specimen. The adoral side of centrodorsal has a very narrow cavity, about 14% of centrodorsal diameter (Pl. 3, Fig. 1b).

REMARKS: The studied centrodorsals are assigned to the genus *Comatulina* D'ORBIGNY, 1852. In view of their size, number and arrangement of cirrus sockets, they probably belong to the species *Comatulina lamberti* DE LORLIOL, 1889, described from the Lower Kimmeridgian of

France (see DE LORIO 1889, pp. 515-519, pl. 225, figs 2-4), but because other ossicles (basals and radials) are lacking, they are assigned to the genus level only. Amongst the congeners, these centrodorsals are extremely wide.

Genus *Palaeocomaster* GISLÉN, 1924

TYPE SPECIES: *Actinometra guirandi* DE LORIO, 1889; OD

Palaeocomaster karsensis sp.nov.
(Text-fig. 4 and Pl. 3, Figs 2a-2e)

HOLOTYPE: Calyx (specimen number CKm/011), presented in Text-fig. 4 and Pl. 3, Figs 2a-2e.

PARATYPE: Centrodorsal (specimen number CKm/014).

TYPE LOCALITY: Karsy, south-western margin of the Holy Cross Mountains, Central Poland.

TYPE HORIZON: Lower Kimmeridgian, *Katroliceras divisum* Zone; Skorków Lumachelle Member.

DERIVATION OF THE NAME: Adjectival name, from neo-Latinized name of the willage of Karsy.

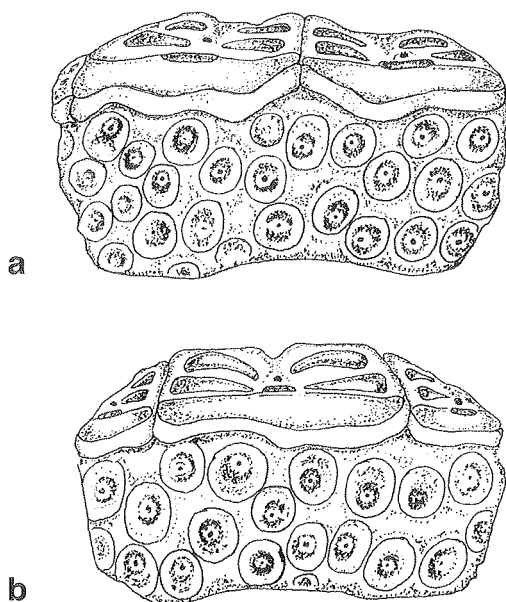


Fig. 4. *Palaeocomaster karsensis* sp.nov.; holotype: a – lateral (interradial) view of calyx, to show a lack of basal plate; b – lateral (radial) view of calyx, to show radial plate; CKm/011; $\times 7$

MATERIAL: One calyx and a single centrodorsal; both from Karsy.

DIAGNOSIS: Centrodorsal large, discoidal with numerous (c. 50) deeply incised, relatively small cirrus sockets; basals invisible; radial ring low, not overhanging; radial plates with very low free aboral surface, articular facet fairly steep at 35° .

DESCRIPTION: The large centrodorsals (the larger reaching 14.5 mm in diameter) are relatively low, slightly truncated conical to almost discoidal, with closely spaced, small cirrus sockets, not well arranged in columns (Text-figs 4a-4b and Pl. 3, Figs 2a-2b). The aboral side of centrodorsal is large, and concave, covered by radial furrows (Pl. 3, Fig. 2e). Cirrus sockets are small, deeply incised, with a small lumen; their number is about 50 in the larger specimen. Basals are invisible (Text-fig. 4a and Pl. 3, Fig. 2a). Radial ring is low, not overhanging (Pl. 3, Figs 2a-2c). Radials are trapezoidal, with very low aboral surface (Text-fig. 4b and Pl. 3, Fig. 2c). The articular facet of radials is moderately tall and fairly steep at 35° (Pl. 3, Figs 2a-2b). The aboral ligament fossa is large with a long, deep ligament pit. Interarticular ligament fossae are moderately tall, and triangular in shape. Adoral muscular fossae are low, and arc-shaped. The radial cavity is moderately large and deep, reaching about 50% of calyx diameter (Pl. 3, Fig. 2d).

REMARKS: The studied specimens with their almost discoidal shape of centrodorsal and crowded cirrus sockets, not forming distinct columns, are assigned to the genus *Palaeocomaster* GISLÉN, 1924. The newly established species *Palaeocomaster karsensis* sp.nov. differs from the most similar species *Palaeocomaster vagnasensis* (DE LORIO, 1889) by having more numerous but smaller cirrus sockets, and by showing distinctly steep articular facets of radials. From the type species, *Palaeocomaster guirandi* (DE LORIO, 1889) described from the Oxfordian of France (see DE LORIO 1889, pp. 535-537, pl. 227, figs 2, 2a-2c), it differs by the more sloping articular facets of radial plates and in the absence of exposed basals.

Palaeocomaster sp.
(Pl. 1, Figs 5a-5b)

2004b. *Palaeocomaster vagnasensis* (DE LORIO, 1889); U. RADWAŃSKA, p. 126, pl. 2, fig. 12.

MATERIAL: A single centrodorsal, from tiered burrows of alpheid shrimp at Małogoszcz (Upper Oolite Member).

DESCRIPTION: The centrodorsal is relatively large (diameter reaching 10 mm), pentagonal in outline, low discoidal, with irregularly arranged cirrus sockets, which do not form distinct columns (Pl. 1, Fig. 5b). The aboral side of centrodorsal is large, flattened and slightly concave, covered by radial furrows. Cirrus sockets are large, oval in outline, and relatively deeply incised; their number is 34. Six small cirrus sockets are developed on adoral side of centrodorsal (Pl. 1, Fig. 5a).

REMARKS: The studied specimen with its low discoidal shape and crowded cirrus sockets, not forming distinct columns, is assigned to the genus *Palaeocomaster* GISLÉN, 1924. In view of its size, and general shape, as well as number and arrangement of cirrus sockets, it probably belongs to *Palaeocomaster vagnasensis* (DE LORIO, 1889), described from the Jurassic of France (see DE LORIO 1889, pp. 538-540, pl. 227, figs 3, 3a-3b), but through a lack of other plates (basals and radials), it is assigned to the genus level only. From *Palaeocomaster karsensis* sp.nov. it differs in its lesser height, in being more pentagonal in outline, and in having cirrus sockets conspicuously larger.

Genus *Solanocrinites* GOLDFUSS, 1829

TYPE SPECIES: *Solanocrinites costatus* GOLDFUSS, 1829; *SD* DE LORIO (1889, p. 526).

Solanocrinites sanctacrucensis sp.nov. (Text-fig. 5 and Pl. 4, Figs 1-2)

2004b. *Solanocrinites* sp.; U. RADWAŃSKA, p. 126, pl. 2, figs 5a-5b.

HOLOTYPE: Calyx (specimen number CKm/012), presented in Text-figs 5a-5b and Pl. 4, Figs 1a-1d.

PARATYPE: Calyx (specimen number CKm/013), presented in Text-fig. 5c and Pl. 4, Figs 2a-2b.

TYPE LOCALITY: Małogoszcz Quarry, south-western margin of the Holy Cross Mountains, Central Poland.

TYPE HORIZON: Lower Kimmeridgian, *Ataxioceras hypselocyclum* Zone; Upper Oolite Member.

DERIVATION OF THE NAME: Adjective *sanctacrucensis* – neo-Latinized, in reference to the Holy Cross region.

MATERIAL: Six calyces, four centrodorsals, plus a single radial plate; all from tiered burrows of alpheid shrimp at Małogoszcz.

DIAGNOSIS: Centrodorsal truncated conical, with 10 columns of three, closely spaced, large cirrus sockets; aboral side of centrodorsal sharply pointed; radial ring slightly lower than centrodorsal, distinctly overhanging; radials low-trapezoidal, with moderately large, free aboral surface.

DESCRIPTION: The centrodorsals are truncated conical, with 10 columns of three, closely spaced cirrus sockets (Text-fig. 5 and Pl. 4, Figs 1d, 2b). The aboral side of centrodorsals is sharply pointed (Pl. 4, Fig. 1d). Cirrus sockets are large, oval in outline with a large lumen. Basals are inconspicuous (Text-figs 5a, 5c and Pl. 4, Figs 1b, 2a-2b). The radial ring is slightly lower than centrodorsal, distinctly overhanging (Pl. 4, Fig 1d, 2b). Radials are low trapezoidal, with moderately large aboral surface (Pl. 4, Figs 1a-1b, 1d, 2a). The articular facet of radials is relatively steep (Pl. 4, Fig. 1d). The aboral ligament fossa is large. Interarticular ligament fossae are moderately tall and triangular in outline (Text-fig. 5b-5c and Pl. 4, Figs 1a, 1d). Adoral muscular fossae are low, arc-shaped (Pl. 4, Fig. 1a). The radial cavity is deep and large, reaching 80% of calyx diameter (Pl. 4, Fig. 1c).

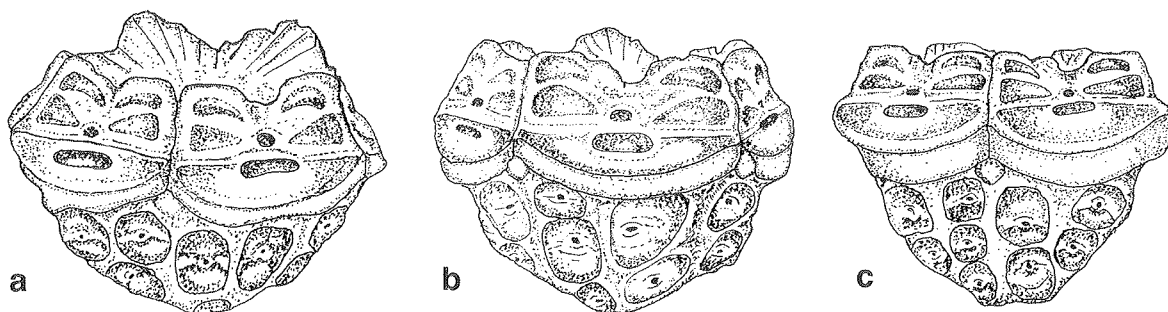


Fig. 5. *Solanocrinites sanctacrucensis* sp.nov.; a-b – holotype, a – lateral (interradial) view of calyx, to show basal plate; b – lateral (radial) view of calyx, to show radial plate; CKm/012; $\times 10$; c – paratype, lateral (interradial) view of calyx; CKm/013; $\times 10$

REMARKS: The studied calyces are assigned to the genus *Solanocrinites* GOLDFUSS, 1829. The newly established species *Solanocrinites sanctacrucensis* sp.nov. differs from the two most similar species, *S. lamberti* SIEVERTS-DORECK, 1958, and *S. costatus* (GOLDFUSS, 1829), in having a more conical centrodorsal, a distinctly overhanging radial ring, and by showing more depressed articular facet of radials.

ECO-TAPHONOMY

The majority of the comatulids studied come from one location of the alpheid burrows in oolite banks composing the Upper Oolite Member at Małogoszcz. An abundance of various echinoderms contained in these burrows, and their wide-ranging mode of preservation, justifies eco-taphonomic analysis, to recognize the pathways the comatulids and associated echinoderms have undergone from life to final burial. The alpheid burrows of Małogoszcz were long enough exposed with their openings at the sediment/water interface to become habitats for more or less cryptic faunas, and deadly traps for others (see Text-fig. 6). The burrowed surface then evolved from soft to firm (see Text-fig. 6A), and finally to the hard-bottom type (see Text-fig. 6B).

All echinoderm remains contained in the studied alpheid burrows (see Text-figs 7-8) are slightly corroded at their surface (? erosionally worn), and some are silicified to varying extent. Their mode of disarticulation and inferred taphonomic interpretation may briefly be characterized, as follows.

Comatulid crinoids. An ubiquity of comatulid remains of which only complete calyces, centrodorsals, and radial plates are diagnostic (see Pls 1-4; and WIENBERG RASMUSSEN 1978, MESSING 1997), is thought to represent a case of live specimens, skeletons of which disintegrated into component ossicles within the alpheid burrows. In these, the comatulids either lived cryptically, having been curled-up at daytime (comp. MESSING 1997, p. 18), or had been swept in with sediment by which they were suffocated, buried and disarticulated after their death. Of isolated ossicles, in majority undistinguishable in their taxonomy (radials, brachials, pinulars, cirrals), only some radials may specifically be recognized (see Pl. 1, Fig. 1c). Hundreds of isolated ossicles other than centrodorsals and/or complete calyces suggest that dead crinoids within the burrows disarticulated rapidly, in terms even of a few days (see DONOVAN 1991, pp. 245 and 254; MESSING 1997, p. 21). A part of disarticulated ossicles may have resulted from arm autotomy, a process important in present-day

comatulids living in shallow-water habitats (see MLADENOV 1983).

Echinoids. A typical feature of echinoid remains collected is the relatively high frequency of small-sized, complete tests (see Text-fig. 8.10-14). In comparison to the size of conspecific specimens from other parts of the Małogoszcz sequence (see RADWAŃSKA 1999), these may be interpreted mostly as juveniles (see Text-fig. 8.10 and 8.13). One species, *Pseudosalenia malogostiana* RADWAŃSKA, 1999, represented by both smaller and larger specimens, interpreted herein as juveniles and adults (see Text-fig. 8.11-12), is generally small-sized and has to date only been recorded from alpheid burrows of the Upper Oolite Member. These burrows may thus be regarded as habitats for a crevice fauna of some echinoids but, on the other hand, as preservational traps, the small openings of which (4-5 cm in diameter) functioned as a taphonomic filter for any skeleton swept over. A significant number of juvenile specimens is a feature typifying their assemblage as a thanatocoenosis, that was formed by catastrophic death of a live community. It is suggested that storm agitation is the most probable agent that killed the animals on the oolitic shoals studied.

Following a proposal of SMITH (1984) and results from taphonomic analyses of other echinoids, both present-day (NEBELSICK 1992) and fossil (GORDON & DONOVAN 1992), six classes of echinoid preservation are here selected, to be briefly characterized in successive order of their taphonomic significance.

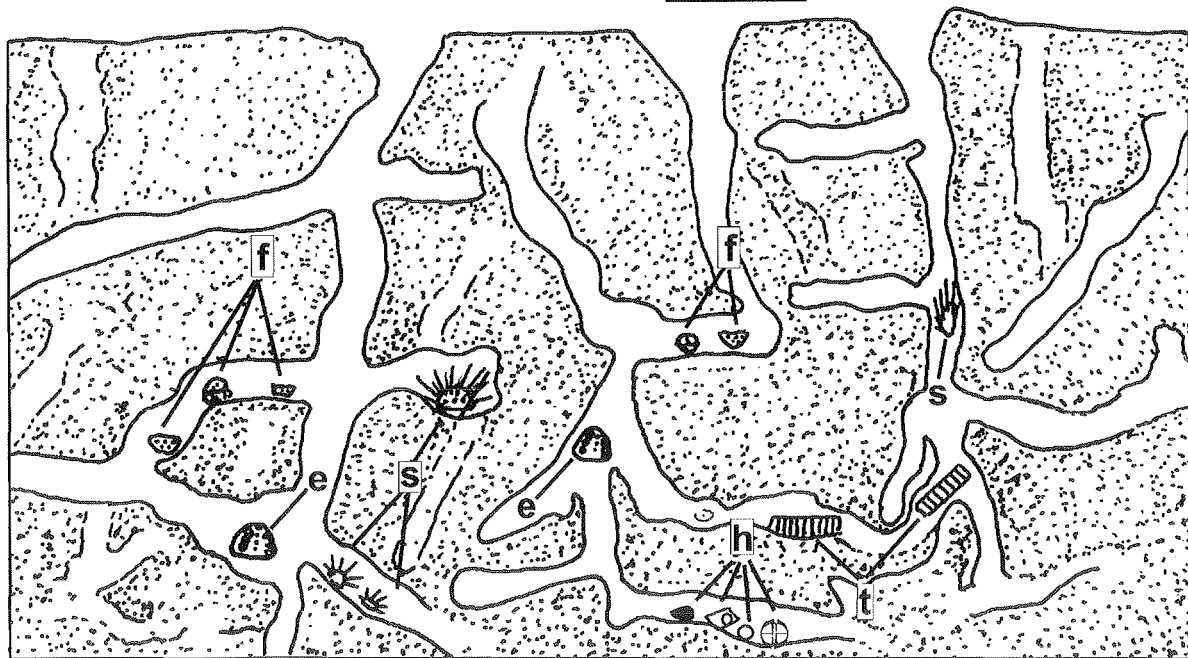
- (i) Tests, lacking spines and Aristotle's lantern, with or without apical disc, always empty (see Text-fig. 8.11-13), represent live specimens (see also ASLIN 1968) swept into burrows, where their corpses decomposed. Then, the burrows could still be empty or, possibly, inhabited by their alpheid producers.
- (ii) Tests such as above, but partially filled with ooids (see Text-fig. 8.10), represent live specimens mortally entrapped in burrows when the oolitic sediment had been swept into emptied tests.
- (iii) Tests partially filled with sediment, but with their spine canopy in position (see Text-fig. 8.14), represent live specimens violently swept into burrows, together with a bulk of sediment which buried them, and infilled tests when corpses decomposed.
- (iv) Test fragments broken across component plates (interambulacral in particular) represent those swept into burrows when their collagenous fibres were still intact; such fragments are interpreted as coming from damaged tests of live specimens that were crushed by water agitation rather than by predators.

(v) Spines, or their fragments, isolated teeth and other pieces of Aristotle's lantern, disarticulated plates of test, or larger fragments of the latter, represent either further steps in the disarticulation process of

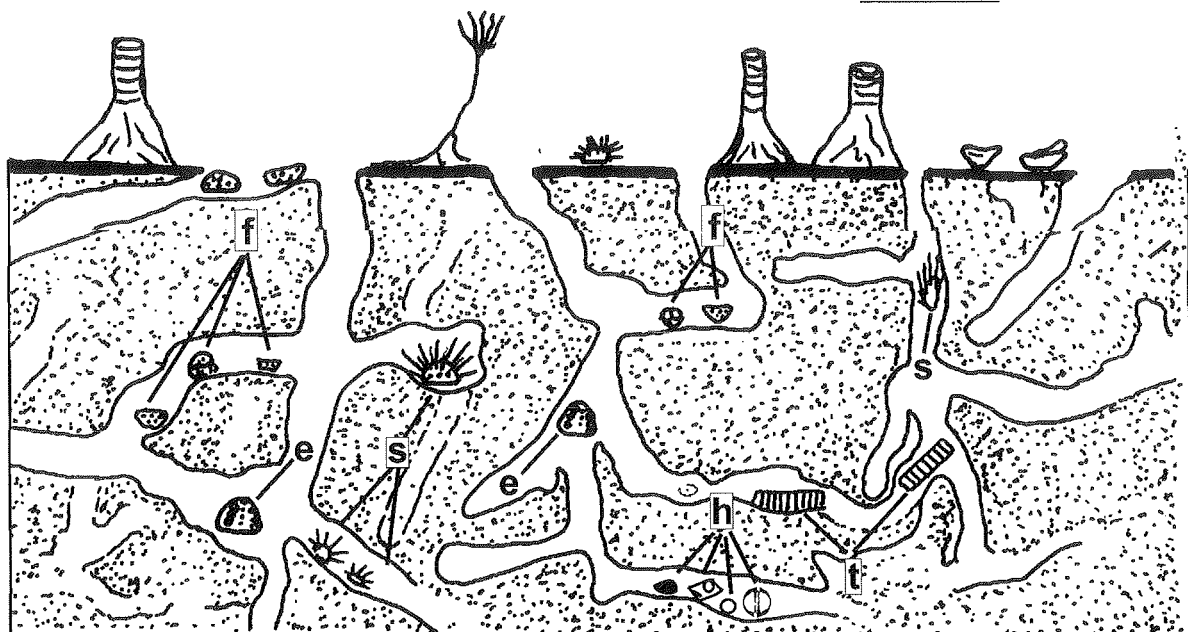
bodies/corpses swept violently into burrows, or an allochthonous detritus for which the burrows became sedimentary traps.

(vi) Isolated copepod cysts, composed of echinoid cal-

A



B



cite, some with echinoid test fragments (see RADWAŃSKA & RADWAŃSKI 2005), suggest a weakened structure of echinoid plates to which they adhered and, moreover, a relatively high parasite pressure of copepods upon echinoids from the Upper Oolite habitats.

Stalked crinoids. The most common remains of echinoderms in the alpheid burrows are from stalked crinoids, represented largely by isolated columnals, pluricolumnals, holdfasts, as well as cirrals and radials, the latter not distinguishable from those of comatulids. Nevertheless, two ecotypes of stalked crinoids are recognized (cf. KLIKUSHIN 1996), viz. (i) long-stemmed ones, adorned with cirri, living 'freely' on soft bottoms, and (ii) long- or short-stemmed ones, devoid of cirri, cemented to a hard substrate (organic skeletons, hardground).

The first ecotype is represented (see Text-fig. 8.4-5) by columnals of *Isocrinus amblyscalaris* (THURMANN, 1861), the species according to HESS (1975a, p. 55) synonymous with crowns of *I. pendulus* VON MEYER, which lived more or less freely, having been either anchored/stilted with its cirri in a stable place (see HESS 1975a, fig. 8; 1999a, p. 209 and fig. 212; 1999b, figs 235-236), or supported by cirri distributed along a longer stem that could float over the bottom (see WIENBERG RASMUSSEN 1977, fig. 2; KLIKUSHIN 1996, fig. 3). Some present-day isocrinids are even able to relocate actively when irritated (see MESSING & al. 1988). The studied species had certainly the ability to autotomize its parts (see MLADENOV 1983, OJI 2001, OJI & OKAMOTO 1994) when seriously disturbed by hydrodynamic agents and/or predators. Its remains in the alpheid burrows should thus be regarded as having been swept into those from more distant surroundings.

The second ecotype is characterized by smaller-sized species, such as *Angulocrinus echinatus*

(SCHLOTHEIM, 1820) whose longer stem fragments and holdfasts are present (see Text-fig. 8.8-9), and as large-sized specimens attributable to the genus *Liliocrinus* (see Text-fig. 8.6-7) and/or *Apiocrinites* and *Millerocrinus*. Of the latter, a stem fragment infested by a myzostomidan polychaete is discussed separately (RADWAŃSKA & RADWAŃSKI 2005), and a large holdfast of *Apiocrinites* grazed by echinoids to produce

Fig. 6. A unique site of the *Echinodermlagerstätte* in the Lower Kimmeridgian oolitic banks (Upper Oolite Member) at Malogoszcz.

A – Soft-bottom stage: tiered burrows of alpheid shrimp in highly bioturbated oolite become refuges for cryptic forms (living and/or hiding at daytime), and taphonomic traps for others, either alive or dead, swept into them by agitated waters. **B** – Hard-bottom stage: the erosionally truncated and lithified burrows of alpheids are still open at the sediment/water interface and encrusted by stalked crinoids and oysters, to become the taphonomic traps for all biota (living and dead specimens, disarticulated remains) swept in by agitated waters of storm origin that had sabred or uprooted some stalked crinoids. The echinoderm remains are distinguished as follows: **f** – Comatulid crinoids, **e** – Empty tests of echinoids, **s** – Echinoid tests with attached spines, **t** – Columnals/pluricolumnals of stalked crinoids, **h** – Echinoderm hash of isolated ossicles (crinoids, echinoids, ophiuroids, asteroids)

COMATULID CRINOIDS		Material		
		CC	CD	R
1	<i>Comatulina peroni</i> (DE LORIO, 1889)	4	5	-
2	<i>Comatulina cf. betremieuxi</i> (DE LORIO, 1889)	-	3	1
3	<i>Comatulina malogostiana</i> sp.n.	4	6	-
4	<i>Palaecomaster</i> sp.	-	1	-
5	<i>Solanocrinites sanctacrucensis</i> sp.n.	6	4	1
ECHINOIDS		Material		
		Tc	Tf	Sp
6	<i>Rhabdocidaris orbignyana</i> (L. AGASSIZ, 1840)	-	4	26
7	<i>Plegiocidaris crucifera</i> (L. AGASSIZ, 1840)	-	-	3
8	<i>Acrosalenia angularis</i> (L. AGASSIZ, 1840)	2	1	-
9	<i>Pseudosalenia malogostiana</i> RADWAŃSKA, 1999	2	-	-
10	<i>Hemicidaris intermedia</i> (FLEMING, 1828)	2	44	22
11	<i>Pseudocidaris sanctacrucensis</i> RADWAŃSKA, 1999	-	-	10
12	<i>Trochotiara kongieli</i> RADWAŃSKA, 1999	2	-	-
13	<i>Phymosoma supracorallinum</i> (COTTEAU, 1865)	1	-	-
14	<i>Polycyphus distinctus</i> (L. AGASSIZ, 1840)	-	3	-
15	<i>Pygaster morrissi</i> WRIGHT, 1851	-	3	-
STALKED CRINOIDS		Material		
		St	Co	H
16	<i>Isocrinus amblyscalaris</i> (THURMANN, 1861)	23	6	-
17	<i>Angulocrinus echinatus</i> (SCHLOTHEIM, 1820)	6	-	2
18	<i>Liliocrinus/Apiocrinites</i> sp.	55	10	n̄
OPHIUROIDS		Material		
		Bv	Ba	
19	<i>Ophioderma? spectabilis</i> HESS, 1966	-	12	
20	<i>Ophiopetra? oertlii</i> HESS, 1966	4	-	
ASTEROIDS		Material		
		Sm	Sa	
21	<i>Pentasteria longispina</i> HESS, 1968	10	1	

Fig. 7. Echinoderm remains contained in alpheid burrows; Upper Oolite Member at Malogoszcz

Comatulid crinoids: CC – calyx, CD – centrodorsal, R – radial; Echinoids: Tc – complete test, Tf – test fragment, Sp – spine; Stalked crinoids: Sf – stem fragment, Co – columnal, H – holdfast; Ophiuroids: Bv – vertebra, Ba – arm plate; Asteroids: Sm – marginal ossicle, Sa – ambulacral ossicle

traces *Gnathichnus pentax* BROMLEY, 1975, from another, hardgrounded ooid bed of the Upper Oolite Member, was presented earlier (RADWAŃSKA 1999, pp. 355-356 and fig. 11.1-1a). All remains of these massively stemmed crinoids (*Angulocrinus*, *Liliocrinus*, *Apiocrinites*) are thought to have originated by storm destruction of specimens that lived nearby having been cemented presumably to the hardgrounded portions of oolitic banks. Stronger agitation caused not only breakage of some specimens into columnar parts, but also tearing-out ('uprooting') of their holdfasts (see Text-fig. 8.9), which all were finally swept into the alpheid burrows.

Ophiuroids. Isolated plates of ophiuroids comprise numerous vertebrae and various arm plates. Of these, only some may be recognized taxonomically (see Text-fig. 8.2-3), to represent the two species established by HESS (1966): *Ophioderma? spectabilis* HESS, and *Ophiopetra? oertlii* HESS. All ophiuroid ossicles, relatively well preserved, are presumably remains of specimens (live or dead) swept into burrows where their bodies/skeletons decomposed.

To note, this is the first occurrence site of identifiable Late Jurassic ophiuroids in Poland (see RADWAŃSKA 2004b, pp. 127-128). In other countries, notable is a mass occurrence of ophiuroid isolated ossicles in some Oxfordian strata of Switzerland (see HESS 1975b).

Asteroids. Isolated plates of asteroids, largely marginals (see Text-fig. 8.1a-1b) and ambulacral plates (see RADWAŃSKA 2004b, pl. 2, fig. 8) are assigned to *Pentasteria longispina* HESS, 1968, a species whose complete skeletons are recorded from Oxfordian strata of Switzerland (see HESS 1968, 1975a; C.A. MEYER 1984). More or less complete skeletons of this species have recently been also found in oolite beds beyond the alpheid burrows at Małogoszcz (RADWAŃSKA, *unpublished*). Because of the larger size of live specimens of this species it is thought that their ossicles were swept into the burrows after the disarticulation of the skeletons somewhere nearby.

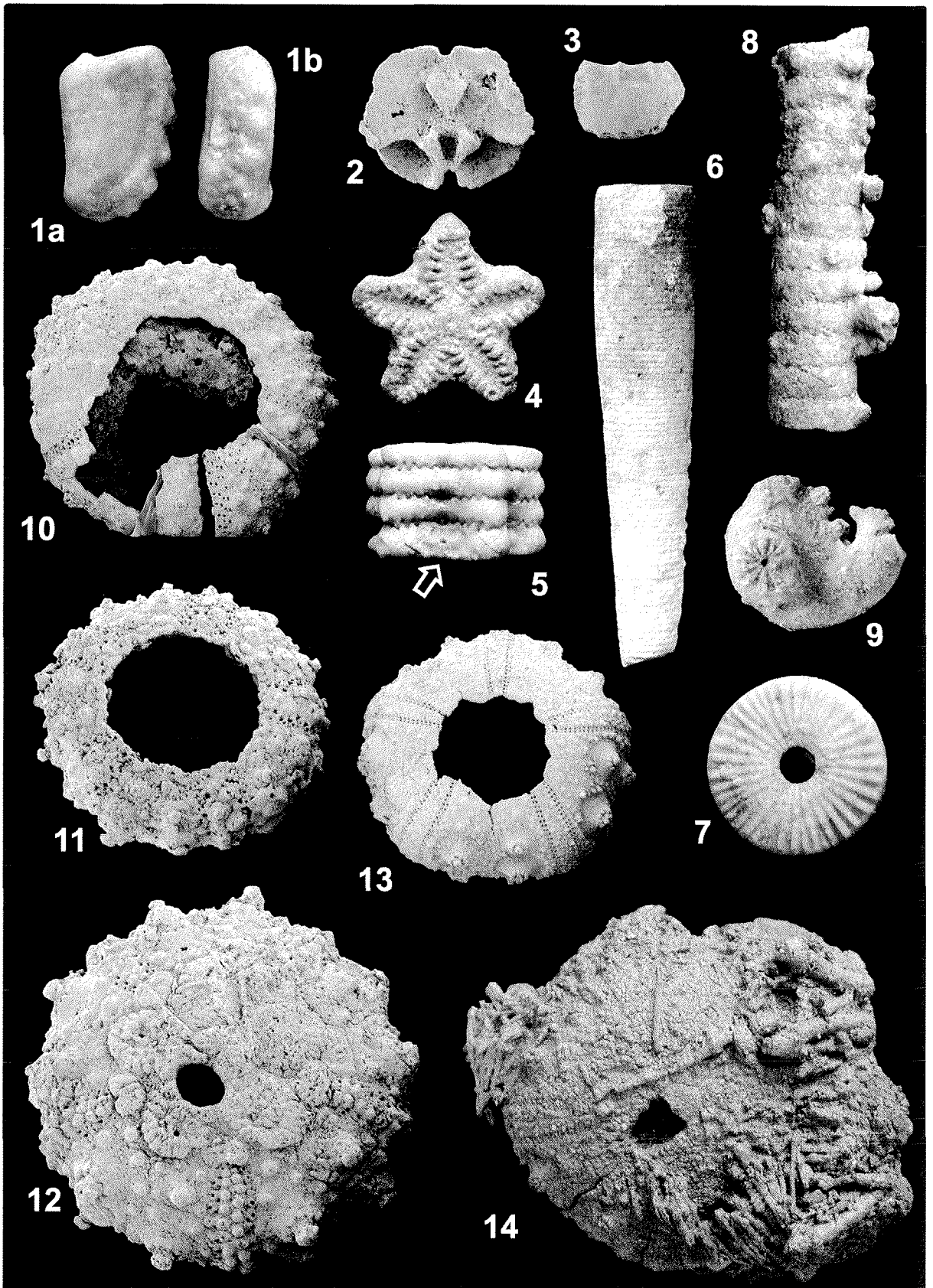
ENVIRONMENTAL CONCLUSIONS

The studied assemblage of comatulid crinoids from Małogoszcz and Karsy comprises 39 calyces and/or centrodorsals of seven taxa. Compared to these from modern habitats in the tropical Indo-Pacific the studied assemblage is very poor, both taxonomically and regarding the population density (see D.L. MEYER & MACURDA 1977: 26 species at a single locality at Lizard Island on the Great Barrier Reef; MACURDA & D.L. MEYER 1983: 14 species on a coral block from that Lizard Island; see also MESSING 1997, p. 4); densely populated are also the Red Sea habitats (see MAGNUS 1963: up to 700 specimens on 1m²). The studied assemblage is close to the values for the Caribbean (see HENDLER & *al.* 1995, p. 44: 8 species altogether). Nonetheless, the life habits and trophic requirements of the studied comatulids were probably similar to those domiciled in modern tropical/subtropical shallow waters, with bottom topography full of nooks and/or crevices favouring the development of cryptic refuges for comatulids which preferred a nocturnal mode of life.

In the Upper Oolite Member at Małogoszcz, alpheid burrows formed such refuges, lithified more or less early, and open at the sediment/water interface on extreme shallow-water and/or emergent oolitic shoals (comp. FÜRSICH & PALMER 1975). In these burrows, comatulids could hide at daytime, and they could live there as long as the burrows' openings remained free, not having been clogged by algae or sediment. Associated to comatulids were dwarf-sized gastropods, whose taxonomy remains as yet unclear (see RADWAŃSKA 2004b). The alpheid burrows discussed are thus interpreted as habitats for a selected crevice fauna (comp. PALMER & FÜRSICH 1974).

Moreover, the alpheid burrows at Małogoszcz have also acted as preservational traps for other echinoderms, the assemblage of which comprises ten echinoid taxa, three stalked crinoids, two ophiuroids, and one asteroid (see Text-figs 7-8). Their diverse remains, in varying states of preservation (quite fresh, or heavily worn), indicate a multi-phase delivery into the burrows,

Fig. 8. Echinoderm associates of comatulid crinoids from alpheid burrows; Upper Oolite Member at Małogoszcz. Asteroids: *Pentasteria longispina* HESS, 1968: **1a** – Marginal ossicle in lateral view, **1b** – same, in outer view; both $\times 7$. Ophiuroids: **2** – *Ophiopetra? oertlii* HESS, 1966, vertebra in proximal view, $\times 10$; **3** – *Ophioderma? spectabilis* HESS, 1966, arm plate, $\times 10$. Stalked crinoids: *Isocrinus amblyscalaris* (THURMANN, 1861): **4** – Columnal (nodal), articular facet; **5** – Pluricolumnal composed of three internodals and one nodal (arrowed is a cirrus socket); both $\times 7$; *Liliocrinus* sp.: **6** – Longer fragment of column, nat. size; **7** – Columnal, articular facet, $\times 5$; *Angulocrinus echinatus* (SCHLOTHEIM, 1820): **8** – Longer fragment of column, with wart-like tubercles, **9** – Holdfast of a juvenile specimen, top view; both $\times 5$. Echinoids: **10** – *Phymosoma supracorallinum* (COTTEAU, 1865), test of a juvenile specimen, partially infilled with ooids, $\times 5$; *Pseudosalenia malogostiana* RADWAŃSKA, 1999: **11** – Juvenile specimen, oral view of empty test; **12** – Empty test of an adult specimen, aboral view; both $\times 10$; *Acrosalenia angularis* (L. AGASSIZ, 1840): **13** – Empty test of a juvenile specimen, aboral view; **14** – Test partially infilled, with spine canopy preserved, aboral view; both $\times 5$



most likely by storm-induced agitated water sweeping all its load into the burrows. The alpheid burrows were thus not only refuges for, but also preservational traps of, all echinoderms that inhabited oolitic shoals. This is especially true of the smaller-sized echinoids, some of which possess spine canopy in position, others having their tests empty, both cases indicative of rapid entombment of live specimens (see ASLIN 1968; SMITH 1984; RADWAŃSKA 1999, 2004b). If so, then the alpheid burrows were acting as mortal traps for still alive echinoids which could not escape from the burrows.

The alpheid burrows of the Upper Oolite Member at Małogoszcz have long acted as traps, both during the soft-bottom stage, and later, at hard bottom phase, when they became lithified and erosionally truncated. Even then, when the hardground was overgrown by massively-stalked crinoids *Apiocrinites*, the detrital material was still swept into the alpheid burrows. Comatulid crinoids studied are thought to have lived over the oolitic shoals successfully, to form local 'feather-star gardens'. Together with stalked crinoids, echinoids, ophiuroids, and asteroids they largely contributed to the formation of an 'echinoderm graveyard' (in German *Echinodermenlagerstätte*, see C.A. MEYER 1984).

Noteworthy is that in the whole section exposed at Małogoszcz Quarry the comatulids appear only at some intervals (see Text-fig. 1) which bear common burrows, and formed under extremely shallow-water conditions: oolitic shoals burrowed by alpheid shrimps (see RADWAŃSKA & RADWAŃSKI 2004b) and oyster shellbeds of supposedly storm-bar origin (see MACHALSKI 1996, RADWAŃSKA & RADWAŃSKI 2003). In both cases, an effective agent causing death and burial of comatulids was storm agitation. To this very agent some other Jurassic echinoderm lags/graveyards (*Echinodermenlagerstätten*) are, or should have been, ascribed (see ASLIN 1968, SMITH 1984, C.A. MEYER 1984, DONOVAN 1991).

In the *Actinostreon/Nanogyra* shellbeds at Małogoszcz, comatulid remains (a single calyx only) and associated ophiuroid vertebrae evidently underwent a longer transport, having been thereby deposited far from their original habitats. The same taphonomic pathway concerns the handful of specimens collected at Karsy.

FINAL REMARKS

The frequency of comatulid crinoids in the Lower Kimmeridgian site of alpheid burrows at Małogoszcz is relatively high, when compared to other Late Jurassic records from Germany (GOLDFUSS 1829, GISLÉN 1924, SIEVERTS-DORECK 1958), Switzerland (THURMANN & ETALLON 1861, DE LORIO 1879, HESS 1975a), France

(DE LORIO 1889, GISLÉN 1924, SIEVERTS-DORECK 1958), and Portugal (DE LORIO 1880, 1891). These rather scarce occurrences of Jurassic comatulid crinoids are thus in their frequency clearly different from those ageing Late Cretaceous (see WIENBERG RASMUSSEN 1978, JAGT 1999) or Neogene (SIEVERTS-DORECK 1960; RADWAŃSKA 1987, 2003b). This evidences generally a phyletic radiation and adaptive plasticity of comatulids to colonise effectively shallow-marine post-Triassic habitats left by other crinoids that since the Late Cretaceous till Early Palaeogene have migrated to greater depths (see D.L. MEYER & MACURDA 1977, D.L. MEYER & OJI 1993, MESSING 1997).

Acknowledgements

Dr. Marcin MACHALSKI (Institute of Palaeobiology, Polish Academy of Sciences, Warsaw) and Adrian KIN, M.Sc. (Department of Palaeontology, University of Warsaw) are thanked for kind donation of some specimens to this study.

Dr. Hans HESS (Binningen, Switzerland) critically reviewed the manuscript and suggested some alterations which improved content of the text. Dr. John W.M. JAGT (*Natuurhistorisch Museum Maastricht*, The Netherlands) not only reviewed an early draft, but also trimmed the language considerably.

The Project has been supported financially by the Polish State Committee for Scientific Research (KBN), Grant No. 3 P04D 01925).

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Manuscript submitted: 10th October 2004

Revised version accepted: 20th March 2005

PLATES 1-4

PLATE 1

- 1 – *Comatulina* cf. *beltremieuxi* (DE LORIO, 1889); 1a – Aboral view of centrodorsal; 1b – Lateral view of centrodorsal; both $\times 7$; CKm/004; 1c – Radial plate, articular facet; CKm/005; $\times 10$
- 2-4 – *Comatulina peroni* (DE LORIO, 1889); 2 – Lateral view of calyx; CKm/006; 3a – Oblique-lateral view of calyx, 3b – Aboral view of centrodorsal; CKm/007; 4a – Lateral view of calyx, to show basal plate; 4b – Lateral view of calyx, to show radial plate; CKm/008; all $\times 7$
- 5 – *Palaeocomaster* sp., CKm/010; 5a – Adoral view of centrodorsal, 5b – Lateral view of centrodorsal; both $\times 7$

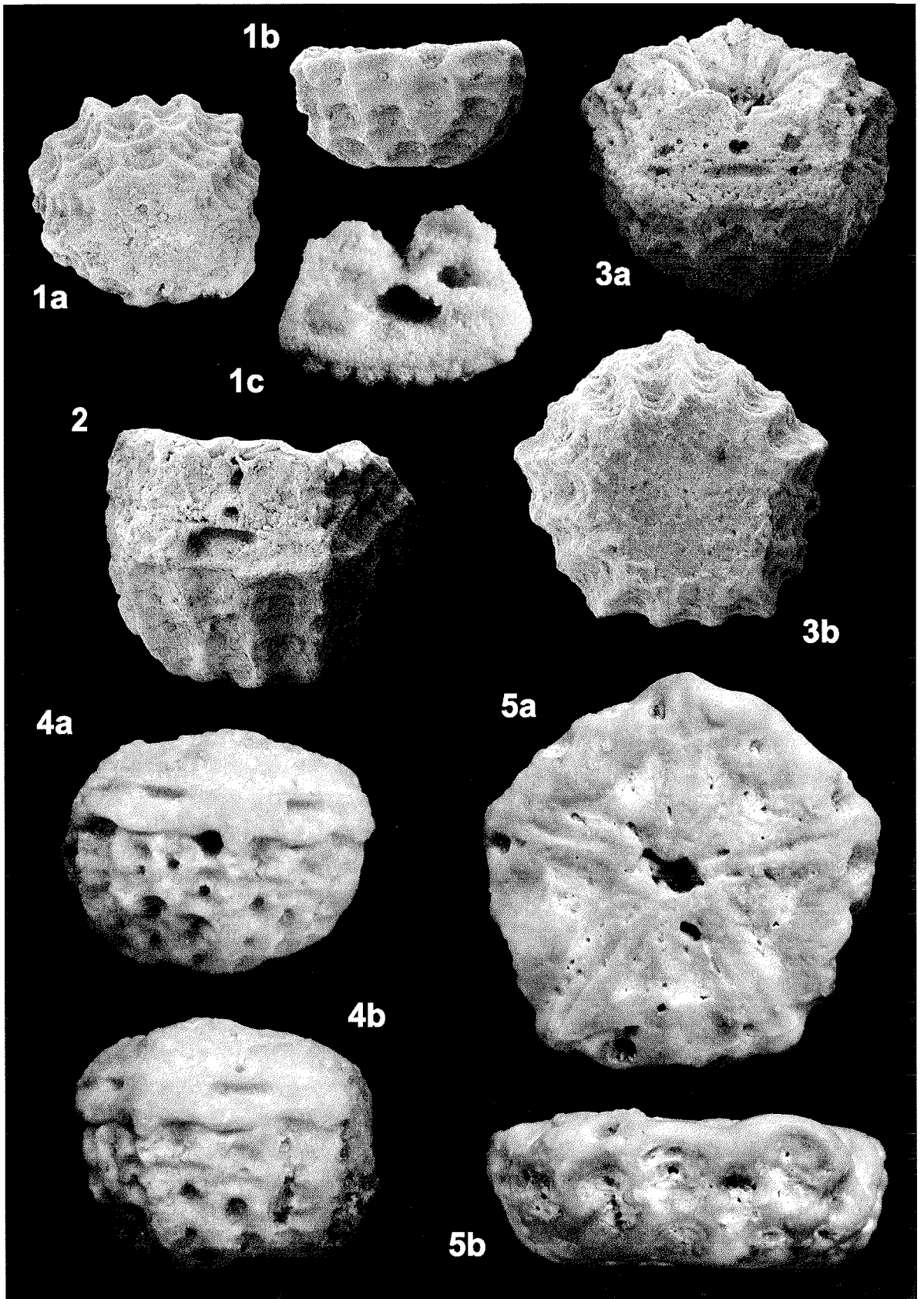


PLATE 2

Comatulina malogostiana sp.nov.

- 1-2** – Paratypes: 1a – Lateral view of centrodorsal, 1b – Aboral view of centrodorsal; CKm/003; 2a – Lateral view of calyx, to show radial plate; 2b – Lateral view of calyx, to show basal plate; 2c – Aboral view of centrodorsal; 2d – Adoral view of calyx; CKm/002; all $\times 7$
- 3** – Holotype: 3a – Adoral view of calyx, 3b – Lateral view of calyx, to show basal plate; 3c – Lateral view calyx, to show radial plate; 3d – Aboral view of centrodorsal; CKm/001; all $\times 7$

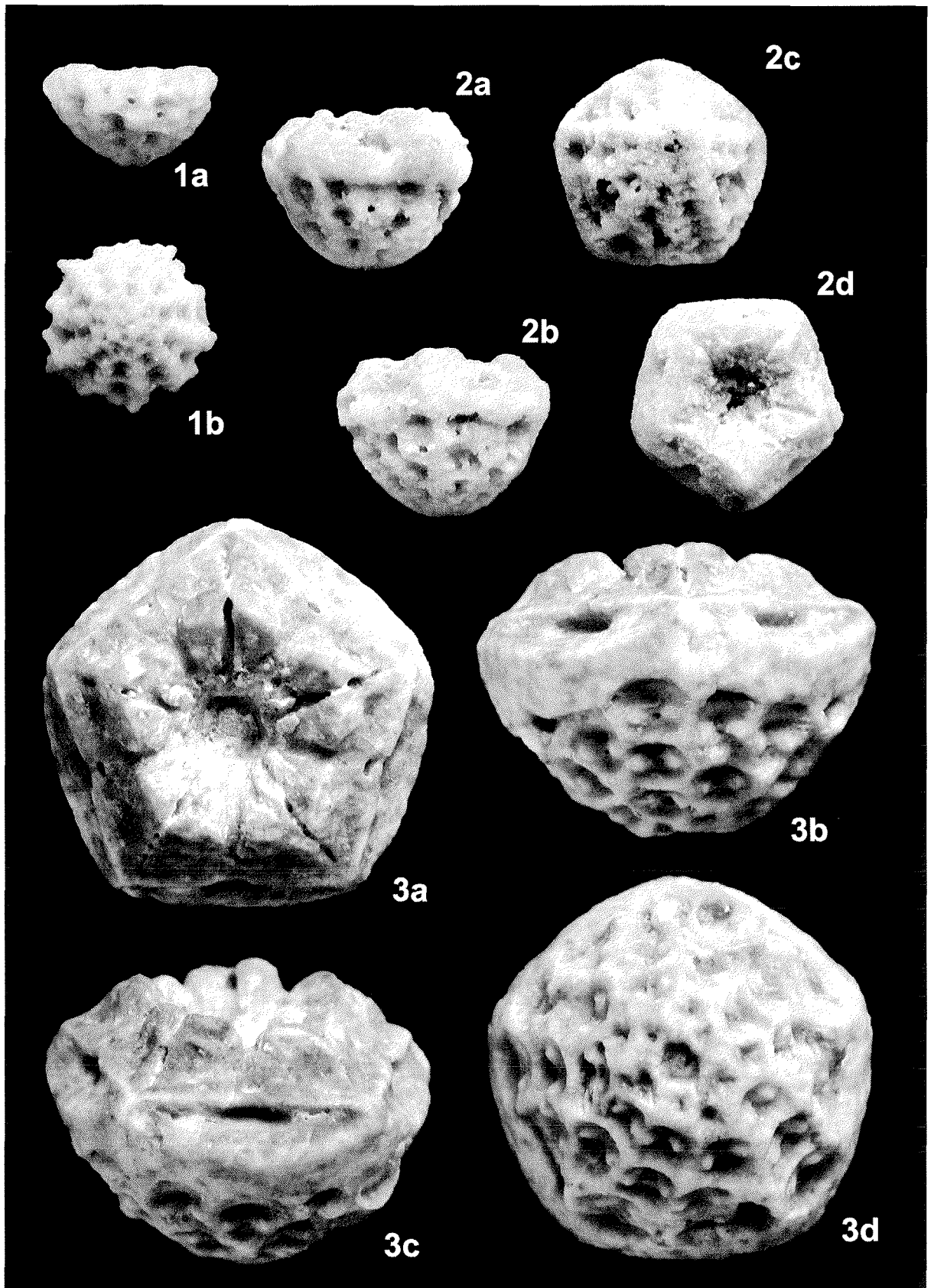


PLATE 3

- 1 – *Comatulina* sp., CKm/009; 1a – Lateral view of centrodorsal, 1b – Adoral view of centrodorsal; all $\times 7$
- 2 – *Palaeocomaster karsensis* sp.nov., CKm/011, holotype: 2a – Lateral view of calyx, to show not observable basal plate; 2b – Lateral view of calyx, to show radial plate; 2c – Oblique-lateral view of calyx, to show articular facet of radial plate; 2d – Adoral view of calyx; 2e – Aboral view of centrodorsal; all $\times 7$

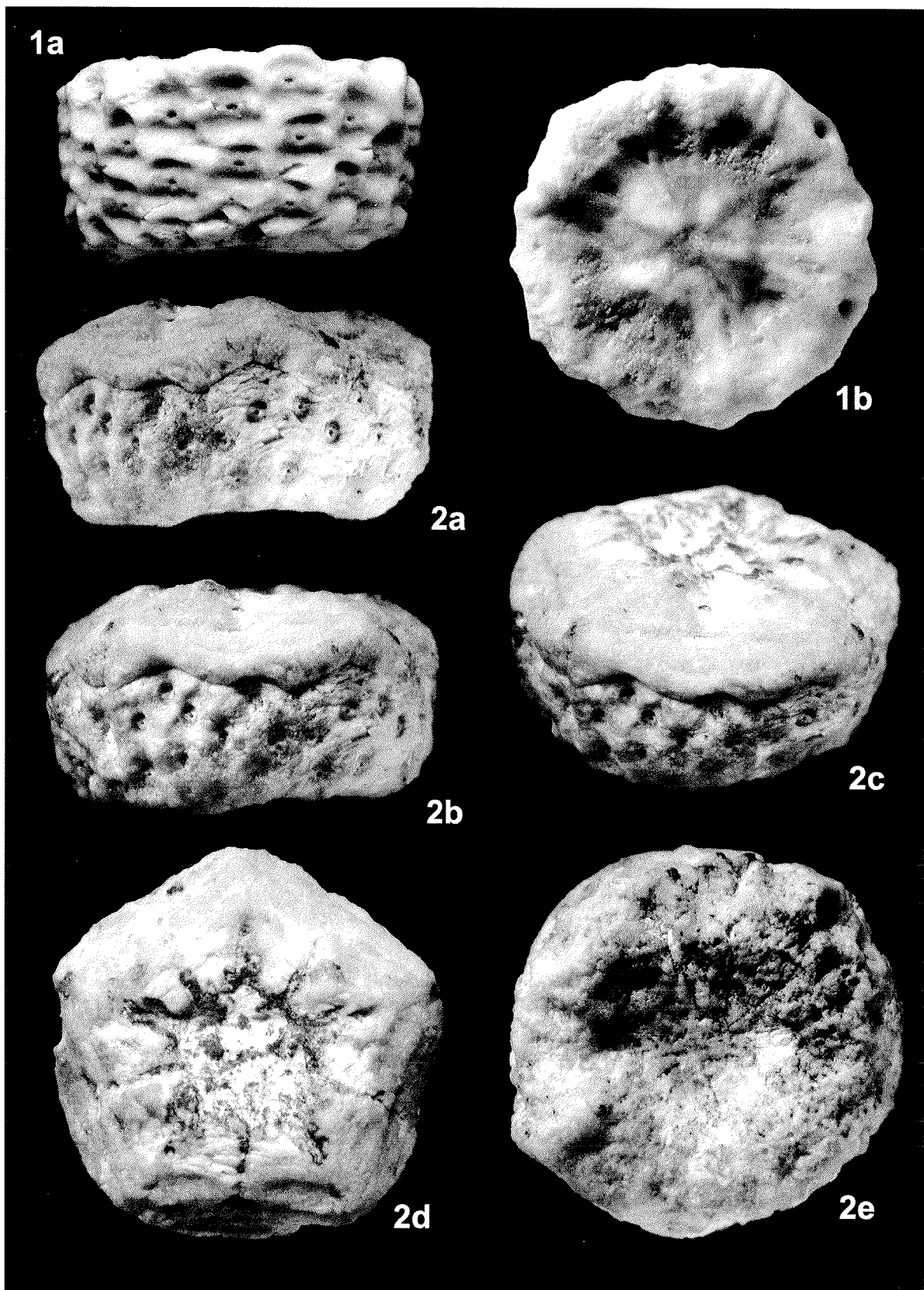


PLATE 4

Solanocrinites sanctacrucensis sp.nov.

- 1 – Holotype, CKm/012: 1a – Articular facet of radial plate; 1b – Lateral view of calyx, to show basal plate; 1c – Adoral view of calyx; 1d – Lateral view of calyx, to show the overhanging radial ring
- 2 – Paratype, CKm/013: 2a – Lateral view of calyx, to show radial plate; 2b – Lateral view of calyx, to show basal plate

