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Myzostomid and copepod infestation of Jurassic echinoderms: A general approach, some new occurrences, and/or re-interpretation of previous reports

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ABSTRACT:

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A study of diverse cysts developed on fossil echinoderms from Poland results in the recognition that these on Late Jurassic crinoid stems are attributable to the life activity of myzostomidan polychaetes, and those on Middle and Late Jurassic echinoids, to the activity of copepod arthropods. A review of formerly reported cysts of coeval age from Europe and western Asia permits the distinguishing of several types that differ in shape and/or location on the echinoderm skeleton. Although the studied cysts qualify as trace fossils (which require a separate ichnotaxonomy), their ethological and ecological characteristics are presented in terms of interspecific parasite-host relationships. The classical interpretation of VON GRAFF (1885) is affirmed for myzostomidan endocysts in crinoid stems, whereas for echinoid tests a new interpretation is offered for large exocysts ('Halloween pumpkin-mask' type) as having been induced by copepods, comparable in their ethology to those on present-day biota (hydrocorals) other than echinoderms. A copepod attribution by MERCIER (1936) of cysts (*Castexia* type) on some Middle Jurassic collyritid echinoids from France is fully accepted. This is supplemented by some new finds in Poland, a re-study of the *Castexia* cysts from France, and a re-interpretation of former reports from the literature. Eco-ethological consequences of the location of copepods in the ambulacral and peristomial parts of cidaroid and hemicidaroid echinoids are discussed; larval settling apparently took place at the tubefeet pores and gonopores, through which the copepod larvae reached the echinoid's interior and began to parasitize it. Attribution of the discussed cysts to copepods yields, consequently, an extension of the stratigraphical range of the class Copepoda H. MILNE-EDWARDS, 1840, to the Early Jurassic.

In POSTSCRIPT, suggested is the bald-sea-urchin disease to have caused some lesions in the collyritid echinoids (Middle Jurassic: Callovian) from France.

Key words: Parasitic cysts, Myzostomidan polychaetes, Copepod arthropods, Crinoids, Echinoids, Ichnotaxa, Jurassic, France, Poland.

INTRODUCTION

The parasitic infestation recognisable in the fossil record has long attracted the serious interest of both zoologists and palaeontologists. In the mid-19th century, spectacular examples of nematodes infesting Tertiary insects (HEYDEN 1862, MENGE 1866) offered an impressive insight into the lesions of the infected insects (dipterans and beetles) and gains of the extremely well-grown nematodes stretching out of their victims (see Text-fig. 1; cf. also CONWAY MORRIS 1990). In general terms, parasitism has either been treated as a case of the pathology of a given host (MOODIE 1918, 1923; CLARKE 1921; ABEL 1935; TASNÁDI-KUBACSKA 1962; RADWAŃSKI 1972;

Jangoux 1984; Conway Morris 1981, 1990), or as one of the ecological categories of relationships between species (Ager 1963, Breimer & Lane 1978, Lane 1978, Grygier 1988, Boucot 1990, Ausich & Simms 1999). The majority of recognised examples have concerned destruction of, or structures in, the hard parts (skeletons) of the host's body. The most distinct are thus various holes, swellings, cysts, or galls induced by parasites. In soft parts of the body, only cysts encapsulating a parasite have a chance of surviving the taphonomic pathway. Their sometimes extraordinary preservation may be exemplified by a nematode cyst in a beetle's musculature, reported by Voigt (1957) from the Geiseltal browncoal of Eocene age.

The cited examples of nematodes show fossil parasites preserved in, or just projected off, the body of their hosts. All echinoderm cases studied concern, instead, the results of life activity of parasites that have markedly disturbed the host's skeleton, but have themselves been lost along the taphonomic pathway into the fossil record. Any interpretation of their nature may thus be regarded as controversial and provisional, as shown in the forthcoming reviews.

The parasitic infestation of echinoderms has long been of particular interest in the literature. This has concerned primarily crinoids, both present-day (von Graff 1884, 1887) and fossil (von Graff 1885; Moodie 1918; Clarke 1921; Yakovlev 1922, 1926; Mercier 1931), as well as the echinoids of the present-day (Koehler 1898, 1924; Hansen 1902; Stephensen 1933, 1935) and some fossil ones as well (Lambert 1927, Mercier 1936, Margara 1946, Roman 1952). Relatively little attention has been paid to the ophiuroids and asteroids (see e.g. Mortensen & Stephensen 1918; Stephensen 1918, 1933; further references in Humes & Hendler 1972, 1999, and Grygier 1988, 1991). The majority of indicated authors were dealing with parasitic myzostomes and copepods, and much less interest has been directed to other invertebrates, such as ascothoracidan crustaceans (see e.g. Brattström 1936, 1947; Wagin 1964; Madsen & Wolff 1965; Grygier 1988, 1991; Boucot 1990) and gastropods (see e.g. Koehler 1924, Tasnádi-Kubacska 1962, Lützen & Nielsen 1975, Breimer 1978, Kier 1981, Grygier 1988, Boucot 1990). To the present authors' knowledge, neither ascothoracidan nor gastropod parasitic damage has so far been recognised in Jurassic echinoderms of any kind.

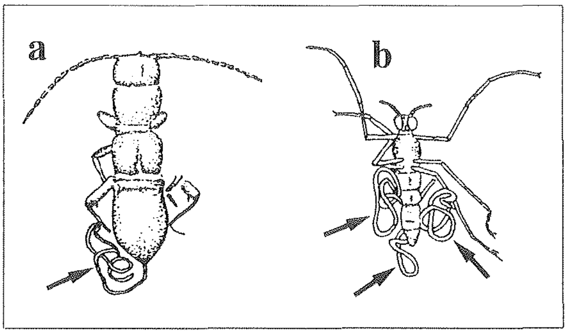

Fig. 1. The oldest, classical records of parasitic infestation: Tertiary insects parasitized by nematodes (arrowed) that appear to be expelled from the insect's body, either due to the lethal infection of the host, or its taphonomic squeezing; **a** – The beetle *Hesthesis immortua* von Heyden, 1862, with the parasitic nematode *Heydenius antiquus* (von Heyden, 1862) projecting from its anus (arrowed); Eocene/Oligocene browncoal of Germany (adapted from von Heyden 1862, pl. 10, fig. 36); × c.4. This is the original image, which was re-illustrated previously by Taylor (1935, fig. 6A), Howell (1962, fig. 85/7) [both with a *lapsus calami*: 'Heydonius'], and Conway Morris (1990, fig. 1A); **b** – A dipteran with the parasitic nematode *Heydenius matutinus* (Menge, 1866), three specimens of which (arrowed) are preserved; Baltic amber of Eocene age (adapted from Menge 1866, fig. 7); × c.8. This is the original image, which was re-illustrated previously by Taylor (1935, fig. 6B) and Conway Morris (1990, fig. 1B)

The scope of the present paper is to describe yet unknown cases, and/or to discuss previous reports of parasitised Middle and Late Jurassic crinoids and echinoids collected/referenced during systematic research on Mesozoic and Tertiary echinoderms from Poland and adjacent countries (Radwańska 1999a, 2003, 2004b; Radwański & Wysocka 2001, 2004; Radwański 2002; Radwańska & Radwański 2003, 2004). Some comparative material of Middle Jurassic age from France has also been taken into investigation.

The recognised examples of myzostomidan and copepod infestation in crinoids and echinoids, respectively, are treated in the present paper as two separate parts, following the locality data for the Polish specimens studied.

MATERIAL STUDIED

The newly presented specimens of crinoids infested by myzostomes, and echinoids infested by copepods, were yielded by several locations of the Middle to Late Jurassic carbonate succession in Poland, as follows.

Małogoszcz: Lower to low-Upper Kimmeridgian limestone/marly sequence of the Carbonate Platform Megafacies (see Matyja 1991) exposed in the Małogoszcz Quarry, western part of the Holy Cross Mountains, Central Poland (see Kutek & *al.* 1992, fig. 5; Radwański 1995, fig. 1). The studied myzostome cyst in a crinoid stem (Text-fig. 3.1a-1b) and 'Halloween pumpkin-mask' cysts in echinoids (Text-fig. 7) come from burrows of alpheid shrimps penetrating, and a residual lag capping, an omission surface of the oolite layer (see Radwańska & Radwański 2004) in the higher part of the Upper Oolite Member (arrowed in Text-fig. 1). This is the occurrence site of diverse crinoids, asteroids, ophiuroids, and echinoids (see Radwańska 1999a, Radwańska & Radwański 2004), for which the burrows have become a taphonomic trap.

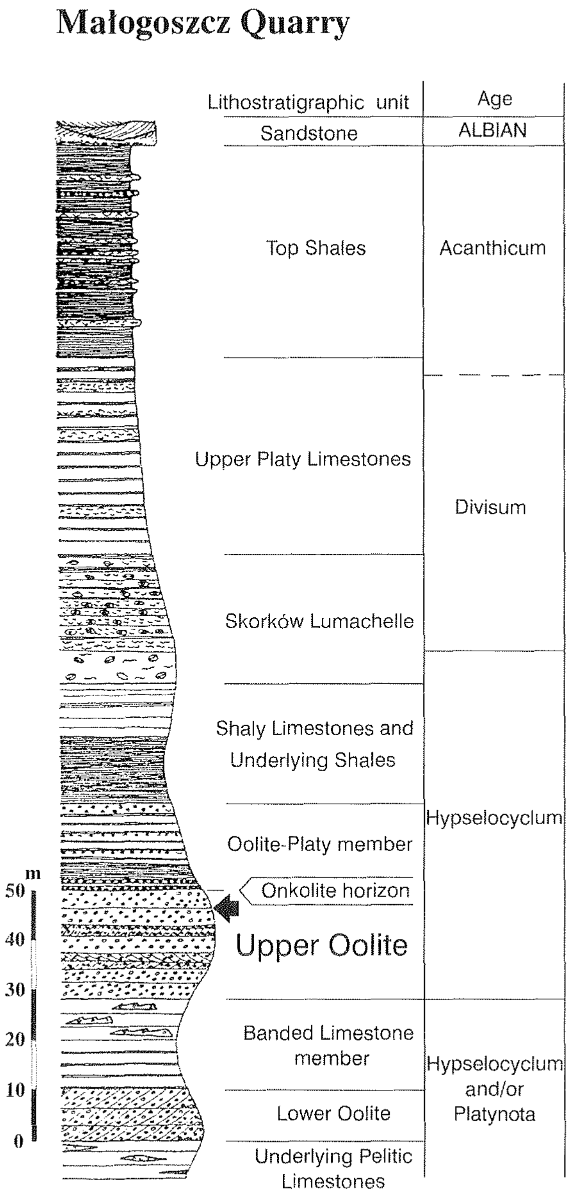

Fig. 2. Lower to low-Upper Kimmeridgian limestone/marly sequence exposed in the Małogoszcz Quarry (western part of the Holy Cross Mountains, Central Poland); adapted from Kutek & *al.* (1992, fig. 5; see also Radwański 1995, fig. 1), to show the position of the Upper Oolite Member and the occurrence site (arrowed) of myzostomid cysts in crinoid stems, and copepod cysts in echinoid tests (see Text-figs 3.1a-b and 7)

Wysprzenica: Upper Oxfordian sponge-cyanobacterial buildup of the biohermal type (see Matyja 1977, 1991) in the western part of the Holy Cross Mountains, Central Poland; exposed as the monadnock of Wysprzenica Hill near Bolmin (see Świdziński 1931, pp. 803-804). The myzostome-infested crinoid stem (Text-fig. 3.2) came from scree on the hill slopes.

Bielawy: Oxfordian sequence of the salt-dome cored Zalesie Anticline, north-western Central Poland, exposed in the Bielawy Quarry (see Matyja & Wierzbowski 2002). The cyst-bearing echinoid (Text-fig. 6) came from the highest part of the section, which yielded some echinoids (see Radwańska 2003) and peculiar tube-dwelling polychaetes (see Radwańska 2004a, fig. 1: the same occurrence site, arrowed).

Częstochowa: Middle Oxfordian sequence of platy limestones with marly interbeds in the Polish Jura, southern Poland (see Radwańska 2003, fig. 2); precise location of the copepod-infested echinoid spine (Text-fig. 9e) unknown.

Wrzosowa at the city of Częstochowa, **Pierzchno** near Kłobuck, **Zawiercie**: localities of the Middle Jurassic (Callovian, for the most part) so-called 'Knobby Layer' (see Szulczewski 1968, Radwańska & Radwański 2003) in the Polish Jura, southern Poland; The 'Knobby Layer', being a residual lag of abundant reworked fossils, yielded worn specimens (see Text-fig. 13) of the echinoid *Collyrites ellipticus* (Lamarck, 1816) bearing copepod cysts of the ichnogenus *Castexia.*

MYZOSTOMIDAN INFESTATION

The infestation of fossil crinoids by the Myzostomida, which are a group of probably polychaetes of unclear affinity (see Grygier 1988, p. 780; Eeckhaut 1998, p. 96), or worms as previously treated (Howell 1962), was recognised first by von Graff (1885), whose monographs of the present-day myzostomidans (von Graff 1877, 1884, 1887) have remained basic and monumental till now. Ludwig von Graff, an eminent zoologist, then the Professor of zoology and comparative anatomy at the University of Graz (Austria), collected and/or had access to a relatively very small collection indeed (5 specimens altogether), but the largest ever reported, of infested crinoids from Late Jurassic sequences of Germany and Switzerland. Von Graff (1885) was aware of the fact that his myzostomidan interpretation of infested fossil crinoids concerned the structures solely of stems, instead of arms or pinnules infected by present-day myzostomes (see also FRANZÉN 1974, AUSICH & SIMMS 1999).

All specimens studied by VON GRAFF (1885) represented swellings of the crinoid stem, containing a kind of chamber ('cyst') inside the swelling and being provided with one or two external apertures on the swollen part of the stem. A picture of one such crinoid stem containing a myzostome cyst, presented by VON GRAFF (1885, pl. 16, fig. 4; see Text-fig. 3.1c herein), has been repeatedly reproduced in many monographic accounts and academic textbooks to demonstrate a fossil case of myzostomidan activity (e.g. STROMER V. REICHENBACH 1909, p. 109; ABEL

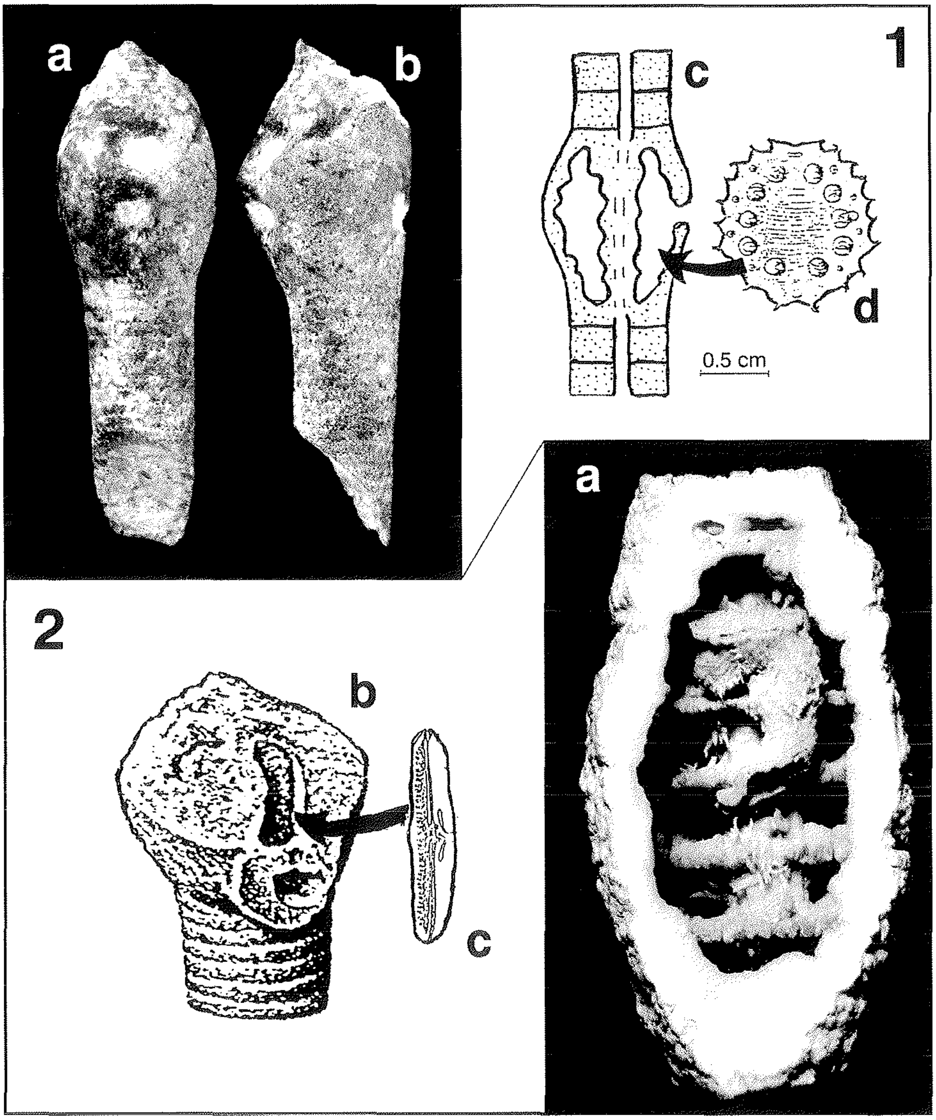

Fig. 3. Myzostomid infestation of crinoid stems. **1** – Disk-shaped myzostomid infestation producing a gall-like swelling in the stem of *Millericrinus* sp. from the Lower Kimmeridgian (Upper Oolite Member) of Małogoszcz (Holy Cross Mountains, Central Poland): a – Front view, to show two apertures of the myzostomid cyst (compare VON GRAFF 1885, pl. 16, fig. 5), b – Side view, to show the extent of the gall-like swelling, both × 1.5; c – Schematic section (based on: VON GRAFF 1885, pl. 16, fig. 4), to show the myzostomid cyst chamber and its suggested producer, whose morphology is exemplified (d) by the present-day 'free-living' *Myzostoma* sp. figured by MÜLLER (1963, fig. 520 = 1980, fig. 529). **2** – Worm-shaped myzostomid infestation producing a tunnel and gall-like swelling in the stem of *Millericrinus* sp. from the Upper Oxfordian of Wysprzenica near Bolmin (Holy Cross Mountains, Central Poland): a – Section of silicified gall-like swelling (crinoidal calcite completely removed), to expose the preserved wall of the myzostomid tunnel; visible are also silicified intercolumnal junctions and fibres spreading out from the intercolumnal faces; taken × 3; b – Schematic section of gall-like swelling (VON GRAFF 1885, pl. 16, fig. 13), to show the myzostomid tunnel and its suggested producer, whose morphology is exemplified (c) by the present-day 'free-living' *Mesomyzostoma reichenspergei* figured by GRABDA (1985, fig. 40E)

1920, fig. 117B; 1924, fig. 117B; DACQUÉ, 1921, fig. 228B; TASNÁDI-KUBACSKA 1962, fig. 108b; MÜLLER 1963, fig. 530 (middle); 1980, fig. 521 (left bottom); ZIEGLER 1972, figs 18 and 207; 1998, fig. 43H; RADWAŃSKA 1999b, fig. 13/1b).

Since VON GRAFF's (1885) time, only two cases of similarly infested crinoid stems of *Millericrinus* sp. have subsequently been reported, from the Late Jurassic sequence of Ernstbrunn in Austria (ABEL 1920, fig. 117*C* = 1924, fig. 117*C*; BACHMAYER 1964, fig. 136 = 1969, fig. 153). One of the specimens herein studied (see Text-fig. 3.1a-b) corresponds to this very type of myzostome infestation.

The second specimen studied (see Text-fig. 3.2a) corresponds to one of the worm-shaped myzostome cysts presented by VON GRAFF (1885, pl. 16, figs 11-13).

In connection with VON GRAFF's (1885) discovery, noteworthy are two reports by ROMAN (1952, 1953), who described large cysts, of an irregular shape, embedded in tests of the Neogene echinoid *Clypeaster* from Morocco and Turkey, respectively, and which he ascribed to the activity of parasitic myzostomidans. The shape of these cysts (see ROMAN 1952, fig. 2) was compared by him to that of the present-day species *Myzostoma pentacrini* VON GRAFF, 1884. To the present authors' knowledge, these reports remain the only ones on purported myzostomidan cysts in fossil echinoderms and/or other invertebrates besides crinoids.

Problem of *Myzostomites*

Nomenclatural aspects of myzostomidan cysts in crinoid stems remain open to discussion. Traditionally, all such cysts have long been classified as *Myzostomites*, a name introduced by CLARKE (1921, p. 58) for deep pits in a Carboniferous crinoid stem. In the *Treatise on Invertebrate Paleontology*, this genus name is treated twice, having been regarded by HOWELL (1962, p. *W*167) as pertaining to a *body fossil* of a worm, but as a *trace fossil* (*boring*) by HÄNTZSCHEL (1975, p. *W*129). These two authors used the same original figure of CLARKE (1921, fig. 46) as the type (sic!), classified by them as new at the species level, *Myzostomites clarkei* HOWELL, 1962, and reproduced the figure either in its original attitude (HÄNTZSCHEL 1975, fig. 79/3), or upside-down (HOWELL 1962, fig. 108/14).

More important is the fact that CLARKE's (1921) name has been used widely for various structures in crinoid stems, of Palaeozoic age in particular, which have nothing in common with those presented by VON GRAFF (1885) on Late Jurassic crinoids. When checking the literature to date, and comparing the illustrations with our collected specimens, it became apparent to us that any myzostomidan attribution of Palaeozoic forms remains just a surmise, or even 'a wishful guess'.

All such Palaeozoic forms, comprehensively reviewed by FRANZÉN (1974) and BRETT (1978), comprise more or less circular pits funnelling into the stem, some of which may even reach the lumen (central canal); they are distributed abundantly along longer portions of the crinoid stem. Numerous accounts (see reviews by FRANZÉN 1974, BRETT 1978) have enriched considerably our data on the age and geographic distribution of the infested crinoids, but they have borne little information on their nature.

Of special interest are the cyst-like, bulbous forms on arms of Carboniferous crinoids, which have been distinguished as *Schizoproboscina ivanovi* YAKOVLEV, 1939, the genus name of which was accepted in the *Treatise on Invertebrate Paleontology* (HOWELL 1962, p. *W*170 and fig. 108/12), as a worm body fossil. These peculiar, cyst-like structures from the Carboniferous of the Moscow region (see YAKOVLEV 1939; reprinted 1956) were comprehensively revised by ARENDT (1961), including YAKOVLEV's (1939) originals. The photographs (see ARENDT 1961, pl. 14, figs 1-12) clearly show that *Schizoproboscina* cysts, when removed or broken-off, display the pits typical of CLARKE's *Myzostomites* underneath (particularly, see ARENDT's pl. 14, figs 1a-1c); nonetheless, ARENDT called them *Schizoproboscina ivanovi* YAKOVLEV, 1939. If our inference is correct, then the genus name *Schizoproboscina* YAKOVLEV, 1939, is a junior synonym of *Myzostomites* CLARKE, 1921. This causes that the species name *ivanovi* YAKOVLEV, 1939, acquires priority over *clarkei* HOWELL, 1962. Consequently, *Myzostomites ivanovi* (YAKOVLEV, 1939) would then be the valid name for the type of CLARKE (1921) !

To stop progress of that taxonomical jungle, BRETT (1985, p. 628) proposed to replace the ichno-binomen *Myzostomites clarkei* HOWELL, 1962, by *Tremichnus cysticus* BRETT, 1985. This new binomen is obviously invalid according to the ICZN rules, both then (see ICZN, 3rd ed. 1985) and now (see ICZN, 4th ed. 1999), and cannot be thus regarded as available for further use.

To conclude, neither *Myzostomites*, *Schizoproboscina*, nor *Tremichnus* can be used to name the Late Jurassic forms studied here, or those of VON GRAFF (1885) and subsequent authors. All these call for a separate name!

It is also noteworthy that *Schizoproboscina*-like cysts have been reported recently by AUSICH & SIMMS (1999, fig. 69) on an Early Jurassic (Pliensbachian) crinoid stem from England. On the other hand, a myzostomidan attribution may be suggested of the cysts once reported by TÉTRY (1936) from the Early Jurassic ("Charmouthian") of France and ascribed by her to the activity of copepods (see below).

Enigmatic forms

Apart from the above cited or discussed forms, there are numerous reports of crinoid stems in which either one or several sequent columnals are heavily swollen into a cyst-like, almost spherical gall, provided with one large, circular (hole-like) opening. Such specimens have been noted from the Palaeozoic strata, ageing Ordovician (see WARN 1974, pl. 1, figs 1-29) to Carboniferous (see ARENDT 1961, pl. 14, fig. 10), as well as from Late Jurassic sequences, as noted by DE LORIOL (1886, pl. 65, figs 4-6 and 8-8a), HESS (1975, pl. 18, fig. 1 right), and KLIKUSHIN (1996, pl. 12, figs 5-6). Some of these structures have either been literally ascribed to the action of parasitic myzostomes, or simply called *Myzostomites* (e.g. WARN 1974, HESS 1975, CONWAY MORRIS 1981). None of them, however, bears analogies to those presented by VON GRAFF (1885). The same may be said of forms illustrated by MERCIER (1931, figs I-IV; all rough sketches), although one specimen – a gall-like swelling with a helicoidal tunnel exposed in section (see MERCIER 1931, p. 14 and fig. III) – is close to one newly described herein from Poland (Text-fig. 3.2a).

A spectrum of structures differing from those discussed by VON GRAFF (1885) and these described in the present paper is quite wide. It comprises bulbous cysts on a Late Carboniferous (Pennsylvanian) crinoid stem, reported by WELCH (1976, p. 224 and fig. 2) as probably true myzostomid, and re-illustrated repeatedly (LANE 1978, fig. 218/3; BOUCOT 1990, fig. 61; AUSICH & SIMMS 1999, fig. 67), as well as peculiar cyst-like swellings raised abundantly along longer stem fragments and interpreted as borings of unknown affinity by LANE (1978, fig. 218/1). Any genetic interpretation of all these structures remains as yet very vague.

As apparent from the referenced papers, probably no genetic connection to myzostomids is also held by the Ordovician-Permian enigmatic (ichno)fossil *Phosphannulus* preserved in some swellings of crinoid stems (see WARN 1974, WELCH 1976, LANE 1978, WERLE & *al.* 1984, BOUCOT 1990, EECKHAUT 1998, AUSICH & SIMMS 1999).

COPEPOD INFESTATION

Anomalies in ancient echinoids

Although an immense number of reports of various anomalies (deformations *vel* malformations) in tests of fossil echinoids have been published up to date, only a very minor part of them have discussed the possibility of parasite infestation. The majority of these are short reports (quite often published in very local journals) that deal with traumatic events, i.e. injuries caused usually by predatory attacks, as well as with regeneration of the injured tests. Surprisingly, many such reports concern, apart from sand-dollars, the heavily tested *Clypeaster* and its allies of Tertiary (Neogene) age (see, e.g., VADÁSZ 1914, 1915; TAVANI 1935; KOLOSVÁRY 1939; COMASCHI CARIA 1950; MITROVIĆ-PETROVIĆ 1964; ALI 1982; and reviews by ABEL 1935, TASNÁDI-KUBACSKA 1962, SMITH 1984). Anomalies in tests of Cretaceous echinoids have rarely been noted, but their attribution to the activity of parasites has been proposed (SAINT-SEINE 1951; KIER 1981; KIER *in* BOUCOT 1990, p. 70: fig. 53). Of such few reports, an important one by SMITH (1988, pp. 30-31 and pl. 40, figs 1-4) interpreted the bulbous swellings in the interambulacral columns as having been induced by endoparasites of the interradial gonads. All other test anomalies in echinoids, both present-day (see KOEHLER 1924) and fossil (see CAPEDER 1907, SMITH 1984), are evidently of pathogenic rather than the traumatic or parasitic nature. Such test anomalies have also been recognised in echinoids older than the Tertiary or Cretaceous, namely in Upper Jurassic (Lower Kimmeridgian) hemicidaroids from Poland (RADWAŃSKA 1999a, p. 312 and pls 16-18).

Anomalies of fossil echinoids examined in the present study are all cyst-like ones, external to the echinoid test. Of such anomalies, these reported by ROMAN (1952, 1953) and ascribed to the activity of myzostomes were discussed above. Cysts that are slightly elevated above the surface of the echinoid test, distinguished as *Castexia* by MERCIER (1936), are treated below under a separate heading. Middle Jurassic cysts assigned to this ichnogenus have been ascribed to the action of copepods by MERCIER

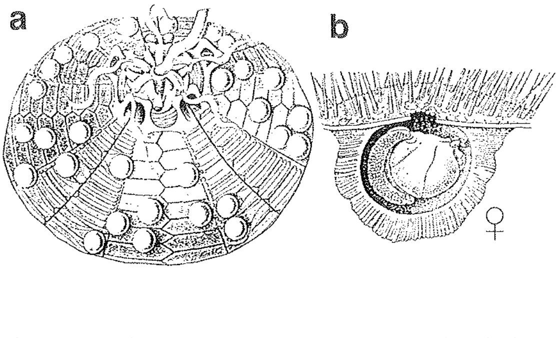

Fig. 4. Present-day case of copepod cysts on the inner side of echinoid tests; re-illustrated previously [with reference and/or drawing errors] by SOLOVYEV (1961, p. 118, fig. 3a-b) and BOUCOT (1990, p. 73, figs 59-60); **a** – Adoral side of the test of *Phormosoma uranus* WYVILLE THOMSON, 1877, with abundant cysts of the copepod *Pionodesmotes phormosomae* BONNIER, 1898; taken × c. 0.3; re-illustrated from KOEHLER (1898, pl. 9, fig. 50); **b** – Section of a cyst, to show the copepod *Pionodesmotes phormosomae* BONNIER, 1898, inside; taken × c. 3; re-illustrated from BONNIER (1898, pl. 10, fig. 1)

(1936), whose interpretation was inspired by the works of KOEHLER (1898) and BONNIER (1898) on present-day endocysts of echinoid tests (see Text-fig. 4).

Fossil endocysts that could qualify as counterparts of these latter ones (see Text-fig. 4) have never been found up to now. This certainly results simply from the fact that nobody has ever attempted to section a number of sediment-filled tests, which is the typical state of preservation of fossil echinoids. Empty or half-emptied echinoid tests that can easily be inspected are still taphonomic rarities in the fossil record (see ASLIN 1968; SMITH 1984; RADWAŃSKI & WYSOCKA 2001, p. 302).

Bulbous fossil exocysts, highly elevated upon echinoid tests to form gall-like structures of peculiar morphology (see Text-figs 5-7), have long escaped detailed attention, and have remained unnamed and/or overlooked in museum collections. All such records were concisely monographed by MEHL & *al.* (1991) who, after a thorough discussion, ascribed their origin to the action of trematodes. Our find of such very exocysts in Upper Jurassic cidaroid echinoids of Poland prompted the present study. Our reinterpretation, as having been induced by copepods, was inspired, however, not by KOEHLER's (1898) and BONNIER's (1898) works, but by those of ZIBROWIUS (1981) and STOCK (1981) who presented similar exocysts produced by copepods on present-day hydrocorals from Papua – New Guinea (see Text-fig. 8).

As concerns trematodes, invoked by MEHL & *al.* (1991) to produce the exocysts on echinoid tests, it is evident that the present-day forms build metacercarian cysts of distinctly smaller size (below 0.5 mm in diameter) solely in muscles, with a preference of masticate ones of the Aristotle's lantern (see TIMON-DAVID 1934, p. 3; JANGOUX 1984, p. 209).

'Halloween pumpkin-mask' cysts in echinoderms

Bulbous exocysts on echinoid tests and, rarely, on crinoid stems, that are provided with numerous, more or less circular orifices (see Text-figs 5-7), are reminiscent of a miniature pumpkin mask from a Halloween masquerade. The term *'Halloween pumpkin-mask' cysts* is thus coined herein for such cysts. All have hitherto been reported solely from the Jurassic (see Text-fig. 5), namely from Late Jurassic (Middle Oxfordian to Middle Kimmeridgian) echinoids, with the exception of some on crinoid stems reported from the Early Jurassic by WEINFURTNER (1989). The 'Halloween pumpkin-mask' cysts are the largest of all discussed in the present study, attaining a diameter up to about 1 cm on echinoid tests (see Text-fig. 6.3b), and up to 3 cm on crinoid stems (see Text-fig. 5.4a-4b).

A thorough study of the 'Halloween pumpkin-mask' cysts from German and Swiss collections was performed by MEHL & *al.* (1991), who regardless of their trematode interpretation, recognised that: (*i*) the cysts in cidaroid echinoids differ from those in hemicidaroids; (*ii*) all these cysts are emplaced in the interambulacral columns exclusively; (*iii*) the cyst is built by the echinoid, whose plates form the *"Schalen-Neubildung"*.

To follow the study by MEHL & *al.* (1991), new material from the Upper Jurassic (Upper Oxfordian to Lower Kimmeridgian) of Poland is presented (see Text-figs 6-7), and supplemented by the data of identical cysts (see Text-figs 5.3-4), identified in older (DE LORIOL 1886) or newer literature (NICOLLEAU & VADET 1995).

The recognitions presented by MEHL & *al.* (1991), of the two types of cysts (*i*), and of their location in interambulacral columns exclusively (*ii*), require comment, as follows.

Ad (*i*). The two types (*A* and *B*) of cysts distinguished by MEHL & *al.*, and regarded by them as strictly host-specific, evidently do not differ. Type *A* in the cidaroids *Plegiocidaris coronata* (GOLDFUSS, 1826) and *Paracidaris laeviscula* (L. AGASSIZ, 1840), from the Middle Oxfordian to Middle Kimmeridgian of Germany and Switzerland, are larger cysts, well developed and well preserved. Type *B* in the hemicidaroid *Hemicidaris intermedia* (FLEMING, 1828), from the Middle Oxfordian of one locality (Chasseral-Kette, Bern Jura) in Switzerland, is represented by three smaller cysts (see MEHL & *al.*, pl. 5, fig. 8 and pl. 6, figs 9-10a) of morphology identical to that of *A*, and several holes, interpreted as scars left after cysts had been damaged; the diameter of such holes is identical to that of *A*. The high host-specifity of these two types thus cannot be justified, and the smaller ones (of type *B*) should be interpreted as juveniles of type *A*.

Ad (*ii*). Cysts located in the interambulacral columns exclusively: At first insight, such is their general impression, especially of the larger cysts (type *A* of MEHL & *al.*). However, as ascertained from photos (MEHL & *al.*, pls 1-4), all these cysts either contact marginally, or partly overlap, the adjacent ambulacral column. The same is observed in smaller cysts (type *B* of MEHL & *al.*, pl. 5, fig. 8 and pl. 6, figs 9-10a), as well as in the specimen figured by GOLDFUSS (1829; see Text-fig. 5.1 herein) and re-illustrated by MEHL & *al.* (1991, pl. 5, fig. 6a).

Other comments on the features displayed by the cyst-bearing cidaroids and hemicidaroids described by MEHL & *al.* (1991) are presented below, after a description of the new material from Poland.

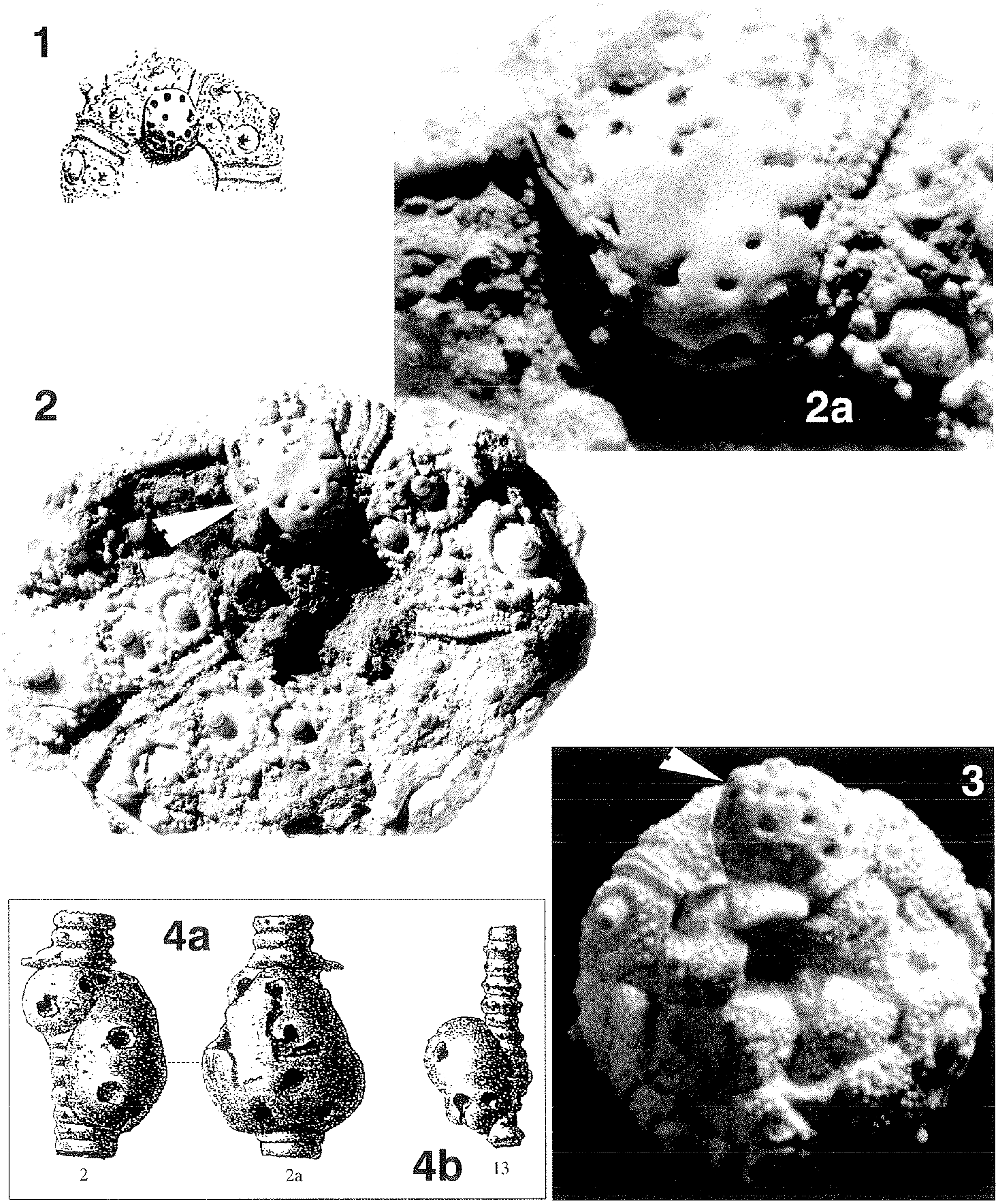

Fig. 5. Previous records of cysts in Late Jurassic echinoderms, interpreted herein as having been produced by copepods. **1** – GOLDFUSS (1829, pl. 34, fig. 8a): on a cidaroid, and classified by GOLDFUSS (1829, p. 94) as a juvenile sponge "*Manon Peziza* GOLDFUSS"; nat. size. **2-2a** – MEHL & *al.* (1991, pl. 2, figs 2a-2b): on *Plegiocidaris coronata* (GOLDFUSS, 1826), and classified by MEHL & *al.* as having been caused by a parasitic trematode; × 2, Fig. 2a × 5. **3** – NICOLLEAU & VADET (1995, cover photo): on *Plegiocidaris crucifera* (L. AGASSIZ, 1840), not commented (see NICOLLEAU & VADET 1995, p. 68 and pl. 33, fig. 1A); × 2. **4a-4b** – DE LORIOL (1886, pp. 423-424, pl. 80, figs 2-2a and 13, respectively): on stems of "*Millericrinus horridus*" [recte: *M. echinatus* (SCHLOTHEIM, 1820), see HESS 1975, p. 67], and classified by DE LORIOL as having been produced by unnamed parasites; nat. size

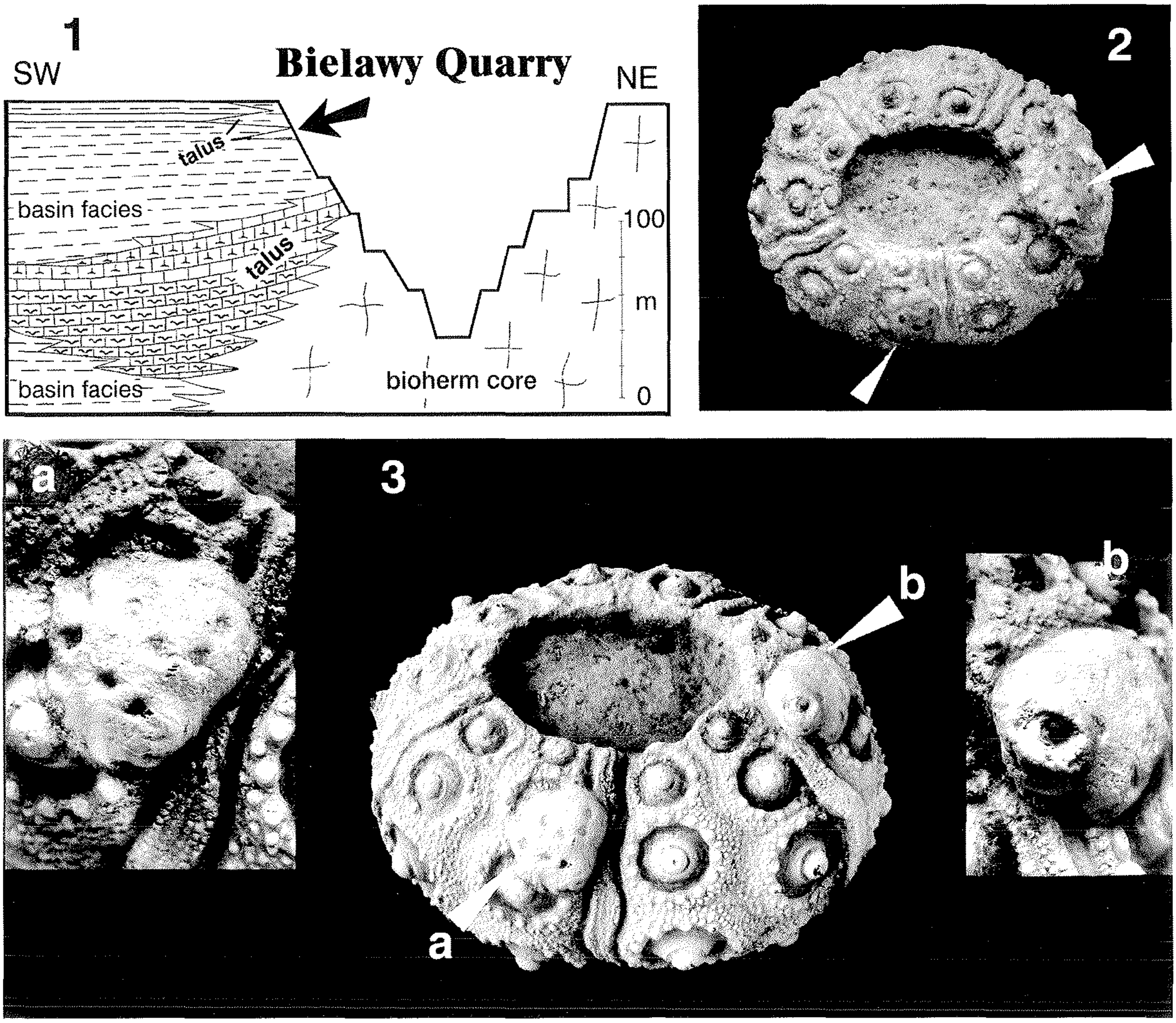

Fig. 6. Copepod cysts in an echinoid from Bielawy. **1** – Facies distribution of the Upper Oxfordian biohermal succession exposed in the Bielawy Quarry (Couiavia region, north-western Central Poland); adapted from MATYJA, MERTA & WIERZBOWSKI (1985, fig. 4) and RADWAŃSKA (2004a, fig. 2), to show the occurrence site (arrowed) of the cyst-bearing cidaroid. **2** – The cyst-bearing *Plegiocidaris monilifera* (GOLDFUSS, 1826) in oral view, as illustrated by RADWAŃSKA (2003, pl. 6, fig. 1c; nat. size), to show the position of the two barely discernible copepod cysts (arrowed) presented in Fig. 3. **3** – The same specimen of *Plegiocidaris monilifera* (GOLDFUSS, 1826) in oblique-oral view (taken × 1.5), to expose the two (**a**, **b**) copepod cysts, both shown × 3 in inserts; Specimen No. EOx/207. Note, the nearly adoral location of both cysts and their overlap of the ambulacral columns

New occurrences in Poland

The new material from Poland comprises larger cysts adhering to an echinoid test, as well as isolated smaller cysts, contained in echinoid detritus (Text-figs 6-7).

A showy specimen of the cidaroid, *Plegiocidaris monilifera* (GOLDFUSS, 1826), from the Upper Oxfordian of Bielawy in the Couiavia region, north-western Central Poland (see RADWAŃSKA 2003, pl. 6, figs 1a-1c), bears two cysts of the 'Halloween pumpkin-mask' type. The cysts (see Text-fig. 6.3) are located adorally on the cidaroid test, near its peristome, and they adhere to the ambulacral column, having been spread widely across the interambulacra. As far as we know, this is the first report of a fossil echinoid bearing two cysts preserved in position.

Five small cysts of the 'Halloween pumpkin-mask' type were found while sifting an echinoderm hash contained in alpheid burrows in the Upper Oolite Member, Lower Kimmeridgian in age, at Małogoszcz (see Text-fig. 2) in the Holy Cross Mountains, Central Poland. The alpheid burrows acted as a taphonomic trap on the highly turbulent sea bottom when the Upper Oolite Member was formed (see RADWAŃSKA & RADWAŃSKI 2004). These cysts, of a relatively smaller size than those mentioned above, are hemispherical and bulbous in shape, and thus more compact than the preceding ones. One of them adheres to ambulacral plates of an echinoid (Text-fig. 7.3a-3b). Of the echinoids recognised in this Member (see RADWAŃSKA 1999a), the species *Hemicidaris intermedia* (FLEMING, 1828) seems to be the most probable host of these cysts, the overall shape of which compares well to that of copepod cysts in present-day hydrocorals (see

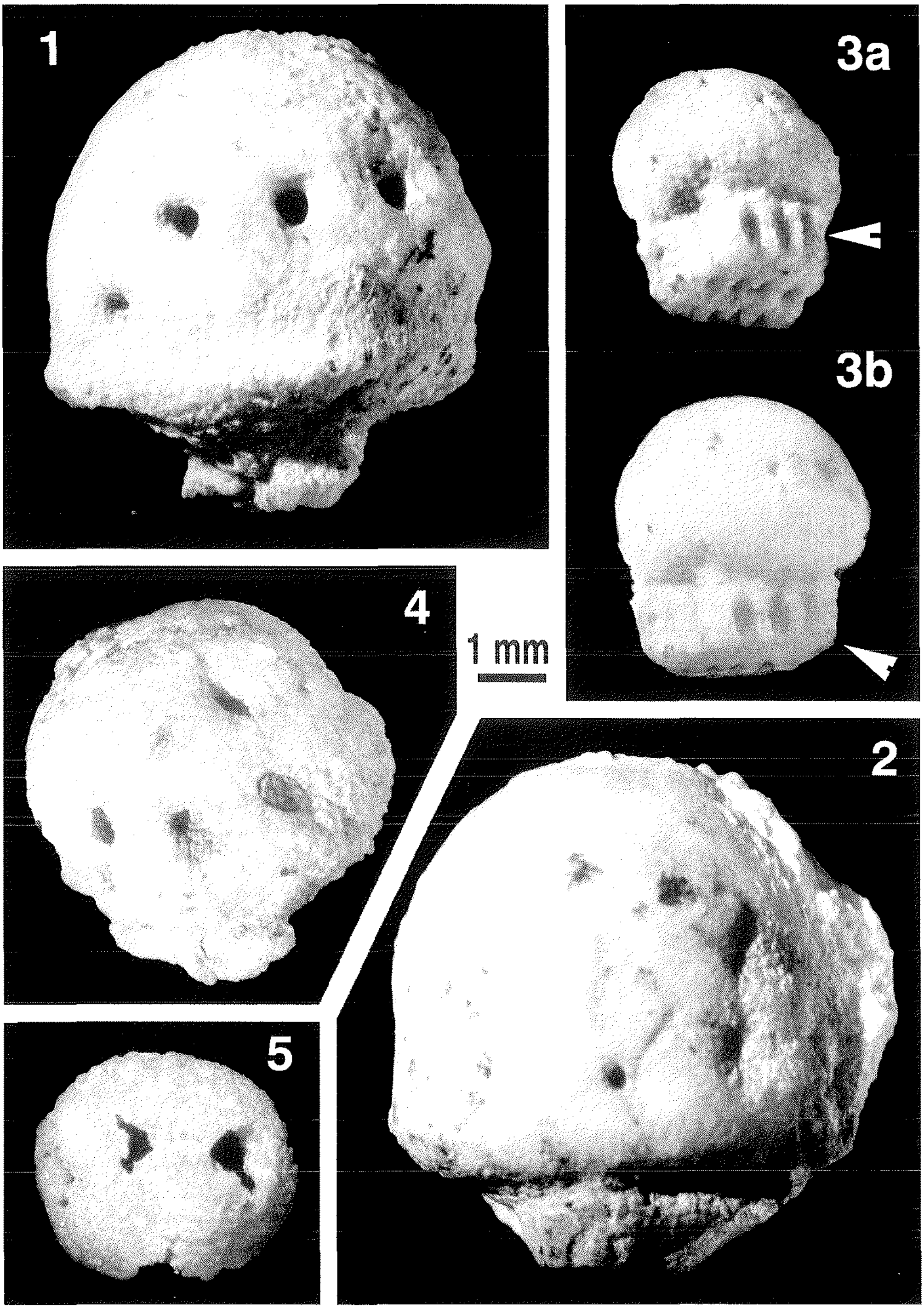

Fig. 7. 'Halloween pumpkin-mask' cysts on echinoid tests from the Lower Kimmeridgian (Upper Oolite Member) of Małogoszcz (Holy Cross Mountains, Central Poland), magn. × 10; comparable to those produced by the present-day copepod *Cystomyzom dimerum* STOCK, 1981, on hydrocorals (see Text-fig. 8). **1-2** – Side views of larger cysts of loaf-like shape; **3a-3b** – Oblique-lower and side views of a smaller cyst adhering to the ambulacral column of an echinoid test, to show ambulacral pores for tube feet (arrowed); **4-5** – Side views of smaller cysts of spherical shape

Text-fig. 8). The morphological resemblance of these cysts, as illustrated by ZIBROWIUS (1981; also Text-fig. 8 herein), has just inspired our copepod interpretation of all the 'Halloween pumpkin-mask' cysts discussed.

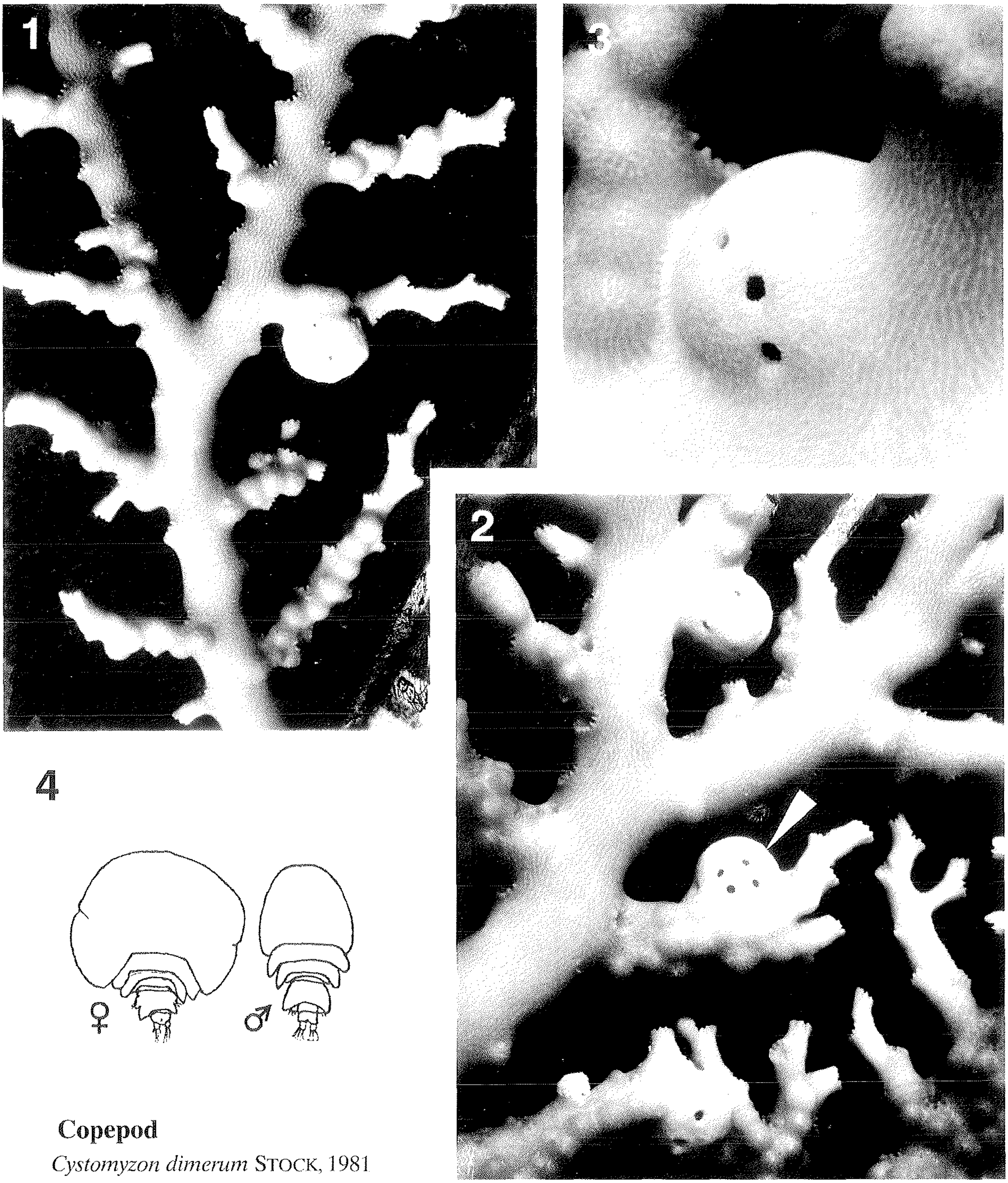

Fig. 8. Comparative present-day specimens of copepods and their cysts produced on hydrocorals. **1-3** – Cysts of the copepod *Cystomyzon dimerum* STOCK, 1981, on the hydrocoral *Stylaster papuensis* ZIBROWIUS, 1981; Figs 1-2 taken × 7.5, Fig. 3 × c.20; shore of Tagula Island, Louisiade Archipelago, Papua – New Guinea (see ZIBROWIUS 1981, pls 1-3); Original photos due to courtesy of Dr. Helmut ZIBROWIUS (Marseille, France); in Fig. 2 arrowed is the cyst illustrated by ZIBROWIUS (1981, pl. 1, fig. 8). **4** – Copepods *Cystomyzon dimerum* STOCK, 1981, taken × c. 40; the same location as above at Tagula Island, Papua – New Guinea (adapted from STOCK 1981, fig. 13a-b)

General comments

The 'Halloween pumpkin-mask' cysts, as evident from previously published data and our own material, tend to be located adorally on the host echinoid test, close to the peristome margin. Moreover, they are located very nearly an ambulacral column, either contacting it or spreading out from (see the above-given examples of GOLDFUSS 1829, MEHL & *al.* 1991, pls 1-2 and 4; also Text-figs 5-6 herein). One of the smallest cysts, and just interpreted by us as juvenile was growing upon the ambulacral plates (Text-fig. 7.3a-3b). This suggests that the tubefeet pores could be the place the copepod larva had settled preferentially. An alternative site for the copepod larva attachment is nearly at the margin of, or just upon, the apical disk of the echinoid. There are two such reports: one by MEHL & *al.* (1991, pl. 3, fig. 3: one cyst preserved, two lost); and the second by NICOLLEAU & VADET (1995; see Text-fig. 5.3 herein), in which the cyst partly overlaps the genital plate as far as the point where the gonopores are located in the adjacent plates.

From the above data, we suggest that both the tubefeet pores and gonopores are the places favoured by the copepod larvae to settle and develop. This ecological dependence has an ethological bearing, in that the tubefeet pores and gonopores may also have provided the routes through which the copepod larvae intruded into the echinoid's interior, to commence parasitism there. The echinoid would then have reacted against the intruder and begun to encapsulate it. The solid cyst-wall is evidently built by the echinoid, as was recognised by MEHL & *al.* (1991, fig. 1 and pl. 2, fig. 2c), and not by the copepod; the same is evidenced for the *Castexia*-type cysts (see below).

Consequently, it is assumed that the encapsulated copepod gradually lost any contact with the echinoid intestines, and could maintain contact with the exterior only through orifices it produced in the cyst part projecting over the echinoid test. At that point the adult copepod would have become a commensal rather than a true parasite to the echinoid host. As a commensal, it can be assumed to have benefited not directly from feeding on the echinoid body, but by passive water currents induced by the motion of the host's tubefeet and/or buccal organs to suck up food from the mucus streams flowing along the ambulacra, and directed to the peristome. This certainly can explain not only the favoured location, but also the further development of the copepods in close proximity to the ambulacral columns and peristome of the echinoids.

It is noteworthy that copepods that induce endocysts in present-day echinoids are also located adorally in the host's test (see KOEHLER 1898, 1924; and Text-fig. 4a herein). Moreover, the same location is preferred by some gastropods, like *Echineulima*, commonly regarded as parasitic (see LÜTZEN & NIELSEN 1975), but whose nature is more precisely predatory: their carnivorous behaviour does not differ from that of muricids or moon snails that drill the shell of their prey. The adoral side has also been reported as preferred by the bacteria that cause the bald-sea-urchin disease (see SCHWAMMER 1989, p. 102).

As concerns the cyst wall, MEHL & *al.* (1991) recognised that it was built by the echinoid, and not by the copepod. A photo of a sectioned specimen (MEHL & *al.*, pl. 2, fig. 2c) shows a solid plate of echinoid calcite (photo in ordinary light), which seems to be continuous, similarly to the case of *Castexia*-type cysts (see below: photo in polarised light, under crossed nicols, Text-fig. 11.3). The sketched interpretation of MEHL & *al.* (1991, fig. 1*C*), of a cyst wall composed of several additional echinoid plates, thus cannot be justified.

The 'Halloween pumpkin-mask' cysts on crinoid stems may reach a considerable size, up to 3 cm in diameter (see DE LORIOL 1886; and Text-fig. 5.4a herein). These have been recorded even from Early Jurassic sequences (WEINFURTNER 1989) distinctly older than those yielding cysts in echinoid tests. Futhermore, previous reports show that these cysts may appear 'gregariously': either two adjacent ones (DE LORIOL 1886, pl. 80, figs 2-2a; and Text-fig. 5.4a herein), or three or four on a small stem fragment (WEINFURTNER 1989, pp. 64-65: text and photo).

Large cysts on crinoid stems of Early Jurassic age have also been reported by TÉTRY (1936), who attributed them to copepods. However, her sketch-drawing (TÉTRY 1936, fig. 1) does show the cyst composed of a mosaic of minute ossicles, which apparently does not bear any similarity to the cysts discussed in the present paper and ascribed to the life activity of copepods. Suggested herein is its myzostomid provenance, comparable to the case reported from the stem of an extant crinoid by EECKHAUT (1998, fig. 1B).

Copepod cysts in echinoid spines

Copepod parasites in echinoid spines were discovered by H.J. HANSEN (1902) who had two spines at his disposal. Since then, very little has been supplemented (STEPHENSEN 1935; also 1933, p. 207) except for the work of STOCK (1968), who revised HANSEN's material and provided some new data.

All the above reports concern deep-water echinoids bearing relatively long but very thin spines. The copepod cysts in these spines, involving the distinct swellings, feature one apertural orifice each (see Text-fig. 9a-c).

A cidaroid spine with a comparable cyst, from the Middle Oxfordian of Poland (see Text-fig. 9e), is presumedly the first record of a copepod-infested echinoid spine in the geological past.

In the literature, only one case of a Miocene cidaroid spine, recognised by SIMONELLI (1889) from Italy (see Text-fig. 10), may be interpreted as having been induced by the parasites (see DACQUÉ, 1921, p. 476), but not unequivocally by copepods. Beyond comparison are present-day microlepadid cirripedes, which may slightly affect (?parasitically) the spines of diadematid echinoids they settle upon (see GRYGIER & NEWMAN 1991, p. 3 and fig. 1J), as well as Cretaceous-to-Recent 'cysticolous' gastropods domiciled in cidaroid spines, and modifying them to much greater extent (see KOEHLER 1924, p. 189; TASNÁDI-KUBACSKA 1962). Of the morphology almost identical to that shown by SIMONELLI (1889, pl. 4, figs 4-4a; Text-fig. 10 herein) are, instead, cystidiform swellings of arm pinnules, induced by a copepod in the present-day crinoid, as reported by GRYGIER (1988, fig. 8).

Copepod cysts *Castexia*

Copepod cysts of the ichnogenus *Castexia*, differing distinctly (see Text-figs 11-12) from those above discussed, were first reported from fossil echinoids by LAMBERT (1927), who interpreted them as scars left by juvenile *Antedon*, although he cited the personal opinion of Henri DOUVILLÉ, that they are structures produced by parasitic crustaceans. The copepod nature of these cysts, the first of such origin in the fossil record, was claimed by MERCIER (1936), who studied LAMBERT's specimen from Marolles (Sarthe), and two other from Courgeon (Orne), all in tests of the Upper Callovian echinoid *Collyrites dorsalis* D'ORBIGNY, 1851 [non L. AGASSIZ, 1840; name used by both LAMBERT and MERCIER].

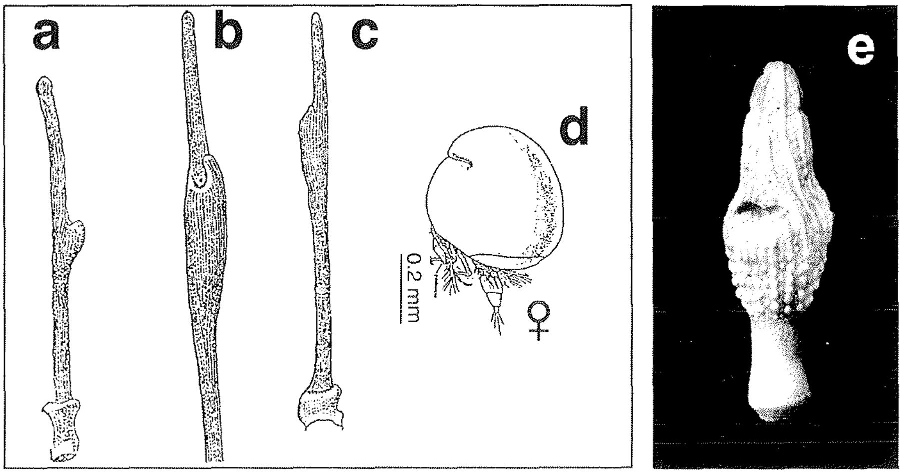

Fig. 9. Echinoid spines parasitized by copepods; **a-c** – Present-day specimens, re-illustrated from STOCK (1968, fig. 1): a – Spine of *Calveriosoma gracile* (A. AGASSIZ) with a cyst produced by *Calvocheres globosus* (H.J. HANSEN, 1902); **b-c** – Two spines of *Hygrosoma hoplacantha* (WYVILLE THOMSON, 1877) with cysts of *Calvocheres engeli* STOCK, 1968; **d** – The copepod *Calvocheres engeli* STOCK, 1968; re-illustrated from STOCK (1968, fig. 3a); **e** – Spine of *Plegiocidaris crucifera* (L. AGASSIZ, 1840) from the Middle Oxfordian exposed near Częstochowa, Polish Jura (southern Poland); magn. × 3

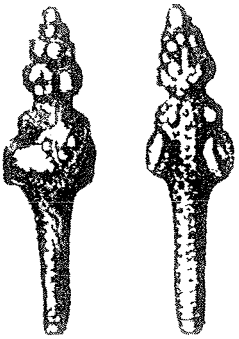

Fig. 10. Previous report of an anomalous fossil echinoid spine, distinguished as "*Phyllacanthus tirsiger* SIMONELLI, 1889" by SIMONELLI (1889, pl. 7, figs 4-4a; re-illustrated herein), and interpreted as possibly pathogenic by DACQUÉ, (1921, fig. 229)

MERCIER (1936) correctly recognised the encroaching of the echinoid test ornamentation upon the cyst (see MERCIER 1936, p. 150 and fig. II/1-2), but he incorrectly supposed the existence of a separate capsule produced by the parasitic copepod under the echinoid test (see MERCIER 1936, fig. II/3-4). All these cysts were classified by MERCIER within the category of trace fossils, and he called them *Castexia douvillei* MERCIER, 1936.

New material from the Callovian of the region of Orne, collected by Mr. Philippe NICOLLEAU and donated to the present authors, comprises 10 specimens of *Collyrites*, but only five bear preserved cysts. The number of cysts in an echinoid test is one or two, always located on the aboral side of the test, regardless of its situation on the ambulacral (Text-fig. 11.1a) or interambulacral column (Text-fig. 11.1b).

Generally, the newly collected cysts display features concordant with those presented by Mercier (1936). All are convexly elevated upon the echinoid test (Text-fig. 11.1, 1a-1b and 12. 1-2), but their major part penetrates deeply into the test interior (Text-fig. 11.2-3). The smallest cyst (Text-fig. 11.1a) is interpreted as juvenile, while the others are adult. The number of tear-shaped orifices ranges from 5 in the juvenile, to 16 in an adult (Text-fig. 11.1b), but it varies quite a bit in specimens of similar size (see Text-fig. 12.1-2). In the juvenile cyst, the orifices tend to be located peripherally, near the cyst margin (Text-fig. 11.1a; see also Mercier 1936, fig. II/2). In the adult cysts, they may also appear at the cyst centre (Text-fig. 11.1b; cf. also Lambert's cyst *in* Mercier 1936, fig. II/1).

Sections of the cyst-bearing tests show clearly that echinoid calcite has built the copepod wall (see Text-fig. 11.2-3), contrary to the interpretation by Mercier (1936), but in agreement with the findings of Mehl & *al.* (1991) with respect to the above-discussed 'Halloween pumpkin-mask' cysts.

Some of the sectioned cysts are empty (Text-fig. 11.2), but the others are half-filled with the same sediment (calcareous siltstone) as the echinoid test (see Text-fig. 11.3). The partial infilling of such cysts indicates that they were broken in their basal part, located inside to the echinoid test, when the latter was filled with sediment.

If is notable that in the French material herein studied, some specimens of *Collyrites* and their cysts are abraded (syn-depositionally, or diagenetically) to variable extents. The echinoid sculpture upon the cysts is thereby preserved in some specimens only (see Text-figs 11.1b and 12.1-1a), but is more or less completely worn away in others (see Text-figs 11.1a and 12.2).

Identical cysts have been reported as common by Solovyev (1961) from the Middle Callovian of the Caucasus, Daghestan, and Turkmenia, all in tests of a collyritid classified as *Collyrites ellipticus* (Lamarck, 1816). With no reference to Mercier's (1936) report, Solovyev

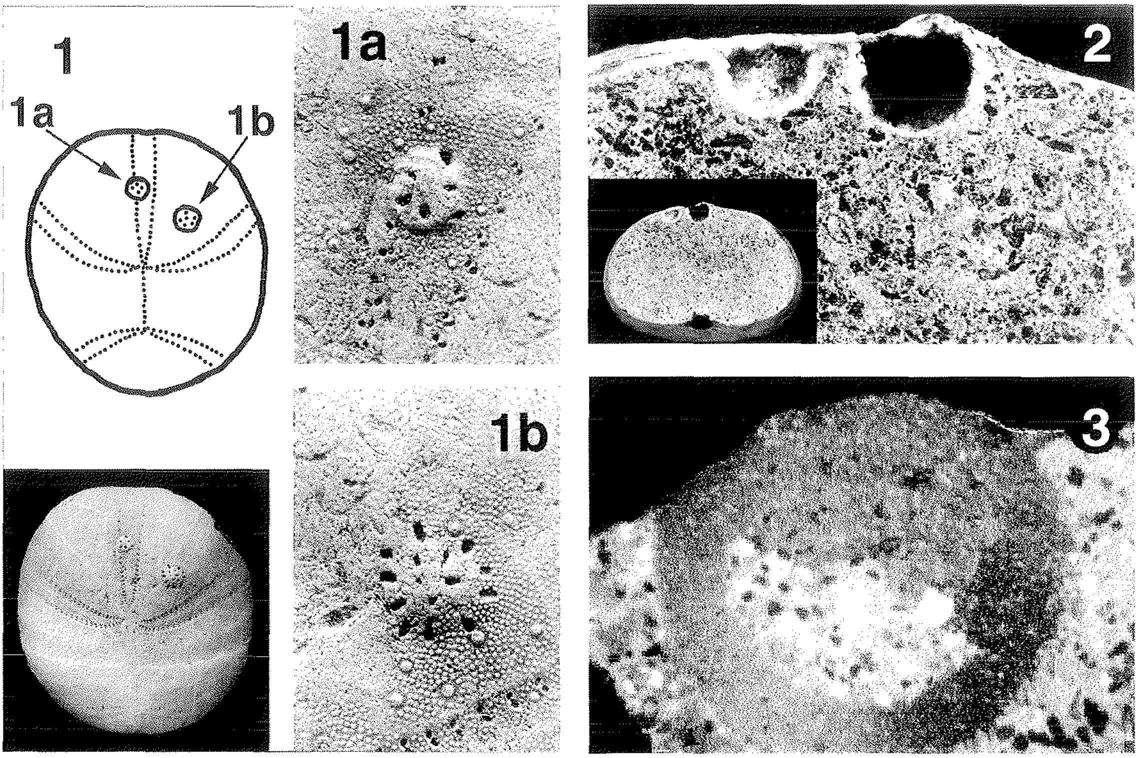

Fig. 11. Copepod cysts, *Castexia douvillei* Mercier, 1936, in *Collyrites dorsalis* d'Orbigny, 1851, from the Upper Callovian of Mortagne-au-Perche (Orne) in France; the specimens are identical to those studied by Lambert (1927) and Mercier (1936); they were collected and kindly donated by Mr. Philippe Nicolleau (Aiffres, France). **1** – General view of the cyst-bearing echinoid *Collyrites dorsalis* d'Orbigny, 1851, nat. size; sketch shows two cysts (a, b; arrowed), magnified × 5 in Figs 1a (juvenile cyst in ambulacral column) and 1b (adult cyst in interambulacral column). **2** – Section through two neighbouring cysts, to show their walls built of echinoid calcite (white in photo), × 5 (cf. insert in actual size). **3** – Close-up of another cyst (thin section × c.20), to show the light extinction (nicols crossed) of one calcite crystal composing both the echinoid test and the cyst wall

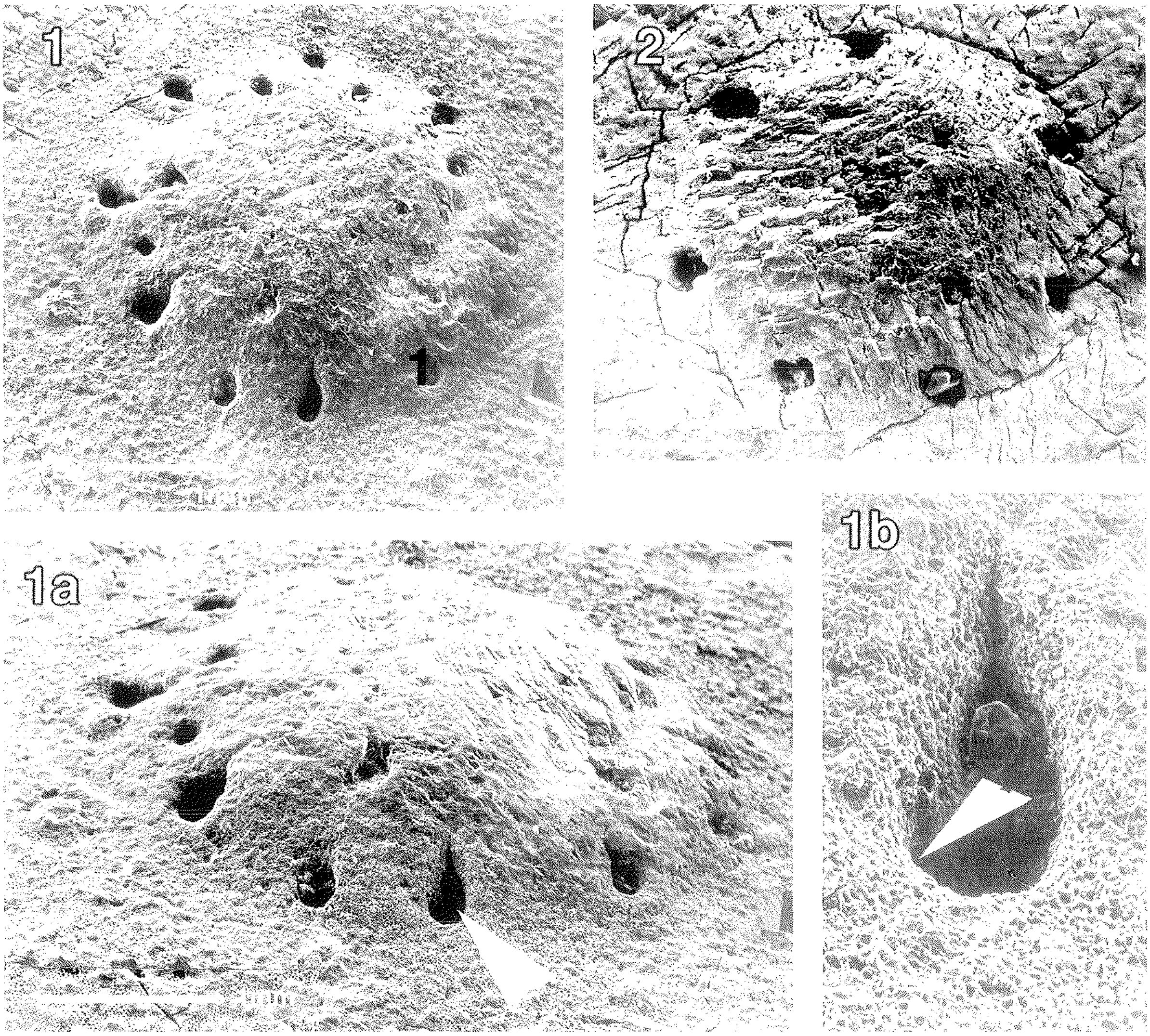

Fig. 12. Copepod cysts, *Castexia douvillei* Mercier, 1936; SEM images of those on specimens of *Collyrites dorsalis* d'Orbigny, 1851, other than that in Text-fig. 11; location, age, and donor data the same as for Text-fig. 11. **1** – Top view of a cyst; 1a – Oblique-side view of same cyst, to focus on echinoid sculpture (miliary tubercles) encroaching over the cyst; arrowed is one of the cyst orifices, shown magnified in Fig. 1b; 1b – Close-up of a cyst orifice (arrowed in Fig. 1a), showing the labyrinthic fabric of the echinoid stereom adjusting the cyst margin (arrowed), × c.100. **2** – An abraded cyst, top view, to show continuation of echinoid calcite composing the copepod cyst: visible are cleavage planes of calcite rhombohedron $\{10\bar{1}1\}$

(1961) noted the echinoid sculpture upon the cysts, and interprteted the cyst wall as separate from that of the echinoid test (see Solovyev 1961, fig. 2b; re-illustrated by Boucot 1990, fig. 58). Moreover, Solovyev recognised the location of the cysts (one or two on a given collyritid) solely in ambulacral columns, with a preference for the 3rd (median) ambulacrum (see Solovyev 1961, fig. 1a). While interpreting all these cysts as those of parasitic copepods (referring to Bonnier 1898), he named them in the category of trace fossils as a new ichnotaxon, *Canceripustula nocens* Solovyev, 1961. This binomen is clearly a junior synonym of *Castexia douvillei* Mercier 1936.

In the new French material studied herein, the echinoid test sculpture (miliary tubercles) clearly continues up onto the cyst (cf. Mercier 1936, fig. II/1-2), with an identical stereom pattern throughout (see Text-figs 11.1b and 12.1a), corresponding to the *labyrinthic stereom fabrics* of Smith (1980, fig. 1; 1984, fig. 3.2). Moreover, the stereom trabeculae are adjusted precisely to outline the cyst orifices (see arrowed part in Text-figs 12.1a and 1b), which indicates that the orifices were in function when the stereom was formed. In abraded specimens, the cleavage planes of the calcite crystals composing each echinoid plate also continue up onto the cyst (see Text-fig. 12.2). These features are all firm evidence that the wall of the cyst, composed of calcite, was produced by the echinoid, not by the copepod, and that the cyst itself was developing simultaneously with the echinoid's growth. The copepod that induced and inhabited the cyst should thus be regarded as an ectoparasite of the echinoid, responsible for the deformation of its test, but having its orifices external to the test and, hence, supposedly not enabling contact of the copepod with the echinoid's intestines.

To conclude, the new material of *Castexia* from Mortagne-au-Perche (Orne) indicates (see Text-figs 11-12) that:

(*i*) The cysts were located both in ambulacral and interambulacral columns of the collyritid test;
(*ii*) The cyst wall was produced by the collyritid, and not by the parasitic copepod;
(*iii*) The cysts are exocysts, contrary to the endocysts of BONNIER (1898), which MERCIER (1936) and SOLOVYEV (1961) cited;
(*iv*) The cystose ichnotaxon *Castexia douvillei* MERCIER, 1936, has priority over *Canceripustula nocens* SOLOVYEV, 1961, which is herein recognised as a junior synonym;
(*v*) Taking into account the close relation of the species *Collyrites ellipticus* (LAMARCK, 1816) and *Collyrites dorsalis* D'ORBIGNY, 1851, and their suggested conspecifity (see COTTEAU 1867-1874), a high degree of host specifity of the copepod inducing the *Castexia* cysts may be postulated.

Castexia cysts in Poland

The collected material of *Castexia*-bearing echinoids from Poland is scanty and badly preserved. It comes from the peculiar, so-called 'Knobby Layer' of Callovian age, composed of often heavily jumbled fossils of various kinds and forming a thin layer (usually less than 20 cm thick) of residual lag capped by a stromatolitic layer (see SZULCZEWSKI 1968, RADWAŃSKA & RADWAŃSKI 2003). All the *Castexia* cysts occur on *Collyrites ellipticus* (LAMARCK, 1816), a species that bears these cysts in France, the Caucasus, and beyond. This tends to confirm the high host-specifity of the cyst-producing copepod over vast areas of Europe through to eastern Asia.

The collected specimens are more or less worn, thus having their echinoid sculpture much damaged. Such almost 'bald' cysts on the 'bald' collyritids (see Text-fig. 13) have appeared at Wrzosowa in the city of Częstochowa, and in the nearby localities Pierzchno near Kłobuck, and Zawiercie in the Polish Jura, southern Poland.

A general comment

The copepods inducing the *Castexia*-type cysts from France and Poland settled not only in the ambulacra of their host collyritid echinoids (as stated by SOLOVYEV 1961, BOUCOT 1990), but also in the interambulacral columns (see Text-figs 11.1b and 13a-b), and on the aboral, not adoral side of the test. In respect to this, and to the stratigraphical age of collyritid echinoids (Middle Jurassic: Callovian), it is inferred that a copepod stock ancestral to that producing the 'Halloween pumpkin-mask' cysts was involved, but with a somewhat different ethology.

FINAL CONCLUSIONS

The present report of myzostomidan and copepod cysts in Middle to Late Jurassic echinoderms, crinoids

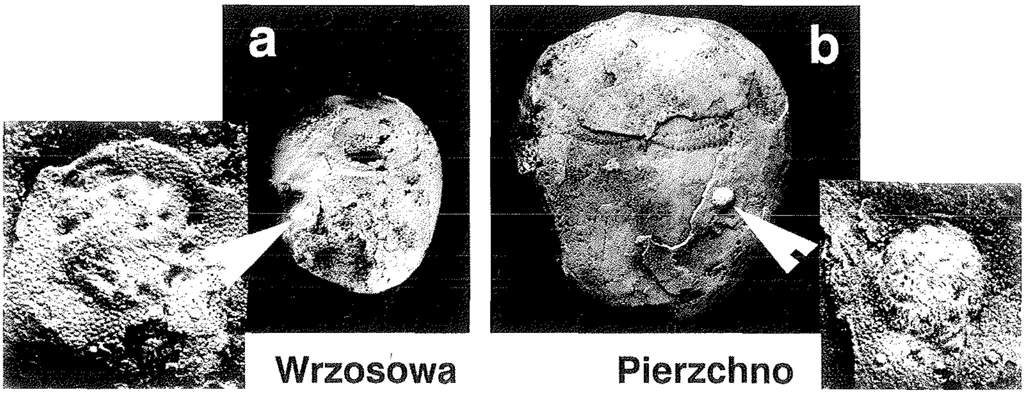

Fig. 13. Worn specimens of *Collyrites ellipticus* (LAMARCK, 1816) bearing *Castexia* cysts from the Callovian 'Knobby Layer' of the Polish Jura, southern Poland; nat. size for echinoids, close-up × 5 for cysts: **a** – Specimen from Wrzosowa, with a well preserved cyst, whereas the echinoid test is almost completely eroded; **b** – Specimen from Pierzchno near Kłobuck, with a smaller (juvenile) cyst

and echinoids respectively, allows us to conclude that such cysts should be treated as *trace fossils*, not *body fossils*.

The interpretation of cysts in crinoid stems as having been induced by the myzostomes is still somewhat uncertain, in agreement with the statements of some previous authors (CLARKE 1921; FRANZÉN 1974; HÄNTZSCHEL 1975; BRETT 1978, 1985; BOUCOT 1990). The new material from Poland enriches the spectrum of formerly known forms by the inclusion of one featured by a tubular canal (Text-fig. 3.2) that may be ascribed to the life activity of an elongate, worm-shaped myzostomid.

A more realistic interpretation of the exocysts on echinoid tests and spines, as well as on some crinoid stems, may be made based on their morphological similarity to present-day copepod cysts developed either in echinoid spines or in invertebrates other than echinoderms (see Text-figs 8-9). Unfortunately, there are no present-day echinoids that bear exocysts on their tests, to be directly comparable to cysts of the 'Halloween pumpkin-mask' type or the *Castexia* type (see Text-figs 5-7 and 11-13); these cysts may thus be regarded as having been induced by an extinct lineage of copepods.

Our interpretation of these cysts having been induced by copepods involves the assumption that copepods were already extant in the Jurassic. If so, then the stratigraphical range of the class **Copepoda** H. MILNE-EDWARDS, 1840, commonly regarded as Miocene to Recent (see PALMER 1960, p. *R*202), or Lower Cretaceous to Recent (CRESSEY & PATTERSON 1973; ZIEGLER 1998, fig. 84 and p. 185) must be extended back to the late Middle Jurassic (Callovian), as evidenced by the parasitized echinoids, or even Early Jurassic, as indicated (WEINFURTNER 1989) by some parasitized crinoids.

We are aware that the discussed copepod cysts fall into the category of trace fossils. Traces ascribed to the life activity of copepods thus evidently preceded the first record of copepod body fossils, documented by parasitic individuals in an Early Cretaceous fish from the Santana Formation, Brazil (CRESSEY & PATTERSON 1973; see also BOUCOT 1990, pp. 60-61).

To follow the coevolutionary trends or pathways promoted by BOUCOT (1990), it is thought that the copepod-echinoid parasitic relationship, so spectacular in the present-day biota (see Text-figs 4 and 9a-d), was established as early as the Middle Jurassic. The antiquity of the copepod-echinoid parasitic relationship thus seems to have developed some 150 my ago. The copepod-crinoid parasitic relationship (see WEINFURTNER 1989) appears to have originated even earlier, in Early Jurassic time.

POSTSCRIPT

In several French specimens of *Collyrites dorsalis* D'ORBIGNY, 1851, there occur irregular, variable in size and patchily distributed perforations (up to 4-5 per specimen); all tend to locate on the adoral side of the collyritid

Fig. 14. Supposed case of the first fossil record of bald-sea-urchin disease: **a** – *Collyrites dorsalis* D'ORBIGNY, 1851, from Mortagne-au-Perche, France (Middle Jurassic: Callovian), × 2; coll. P. NICOLLEAU (Affaires, France): there are three irregular lesions (arrowed) around the peristome but adjusted to the ambulacral columns, **b** – Present-day specimen of *Spatangus purpureus* (O.F. MÜLLER, 1776) from Krk offshore, Croatia; slightly reduced; Re-figured from SCHWAMMER (1989, fig. 3): numerous lesions located around the peristome and along the ambulacral columns, primarily the ambulacrum *V* (right of the plastron)

test, just around its peristome, alongwith the ambulacral columns (see Text-fig. 14a). Their variable shape, size, and mode of dispersal are identical with these of lesions caused by the bald-sea-urchin disease (see Jangoux 1984, Maes & Jangoux 1984), as exemplified in the present-day echinoids, both regular *Echinus* (see Maes & Jangoux 1984, fig. 10) and irregular *Spatangus* (see Schwammer 1989, fig. 3; and Text-fig. 14b herein). If such morphological convergence is not fortuitous, then the herein reported test damages (Text-fig. 14a) would be the first case of bald-sea-urchin disease in the fossil record. Under present-day conditions, as reported by Maes & Jangoux (1984, p. 221), test perforations caused by the bald-sea-urchin disease (see Maes & Jangoux 1984, figs 10 and 11E) are always lethal to infected echinoids.

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