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Copepod-infested Bathonian (Middle Jurassic) echinoids from northern France

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ABSTRACT:

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New examples of Bathonian (Middle Jurassic) parasitic exocysts on acrosaleniid echinoid tests are recorded from northern France. These exocysts can be attributed to the life activity of copepod crustaceans and are considered to have been formed as a result of copepod larval settlement in these echinoids by way of the gonopores. Sexual dimorphism is recognised in copepod-infested *Acrosalenia spinosa* L. Agassiz, 1840, on the basis of size and position of gonopores, those in females being larger and wider apart, those in males smaller and situated subcentrally. The previous stratigraphic range of copepod cysts of this type (i.e., Middle Oxfordian to Middle Kimmeridgian) can now be extended down to the base of the Bathonian (*convergens* Subzone).

Key words: Parasitic cysts; Copepod crustaceans; Echinoids; Middle Jurassic; Bathonian; France.

INTRODUCTION

The present note adds new data to a recent monographic treatment of myzostomidan and copepod infestation of Jurassic echinoderms (Radwańska and Radwański 2005), by supplying information on two Middle Jurassic (Bathonian) echinoids of the family Acrosaleniidae Gregory, 1900, from northern France. These new data add significantly to previous records of such copepod-induced exocysts from members of the echinoid order Cidaroida Claus, 1880, and of the genus *Hemicidaris* L. Agassiz, 1838, all of Late Jurassic (Middle Oxfordian-Middle Kimmeridgian) age (see Radwańska and Radwański 2005, p. 115). We were inspired to write this note by Grygier (1988, p. 783), who noted that, "in order that potentially valuable specimens and new phenomena involving symbionts not be lost to zoology".

THE NATURE OF THE EXOCYSTS

The uniformitarian approach advocated by Radwańska and Radwański (2004, 2005), referred just in time by Boucot and Poinar, Jr. (2010, pp. 29–32 and figs 22–28), allows exocysts of this type to be ascribed to the life activity of copepods. As originally shown by Mehl *et al*. (1991), the structure of such cysts indicates that they were not formed by the copepods themselves, but by the echinoids which encapsulate the copepod by their own calcite skeleton. Subsequently, the copepods' link to the exterior is through a variable number of circular orifices, and there is no direct contact with the echinoid intestines. Consequently, Radwańska and Radwański (2005, p. 120) assumed that the copepod did not benefit from feeding on the echinoid body, but obtained nutrition from filtering passive water currents induced by the echinoid. As a result of such etho- and ecological adaptation, settling of cyst-inducing copepods on the echinoid test shows certain preferences (see below).

In addition to echinoids, several cysts of the same structure have been recorded from the stems of millericrinid crinoids from the Lower Jurassic of Germany (Weinfurtner 1989) and the Upper Jurassic (Oxfordian) of France (de Loriol 1886). Moreover, it should be noted that cysts of comparable shape and size in a range of extant echinoderms (e.g., ophiuroids, asteroids, and comatulid crinoids) may be formed by ascothoracican cirripedes of the genus *Parascothorax* Wagin, 1964. However, the illustrated examples in ophiuroids are all cutaneous (see Wagin 1964, figs 2–4; Grygier 1988, fig. 7), being composed of two peel-off layers (see Wagin 1964, fig. 4) and not impacting the ophiuroid's calcitic skeleton. This observation explains the absence of such cysts from the fossil record of any age, and their difference to those studied ones, too.

COPEPOD SETTLING

A preferred settling of copepods on echinoid tests can be distilled from the position of exocysts as illustrated in the literature. In cidaroids, such cysts have so far been recognised exclusively in either the peristomial or periproctal areas of the test. Infestation of the peristomial region was clearly illustrated by:

– Goldfuss (1829, pl. 34, fig. 8a), reillustrated by Mehl *et al*. (1991, pl. 5, fig. 6a), Radwańska and Radwański (2004, pl. 1, fig. 7; 2005, fig. 5.1) on an indeterminate cidaroid;
– Mehl *et al*. (1991, pl. 2, figs 2a-b), reillustrated by Radwańska and Radwański (2005, fig. 5–5a) on *Plegiocidaris coronata* (Goldfuss, 1829);
– Mehl *et al*. (1991, pl. 3, fig. 5a–b; pl. 4, fig. 5c–d) on *Paracidaris laeviscula* (L. Agassiz, 1840);
– Radwańska and Radwański (2004, pl. 1, fig. 8; 2005, fig. 6.3) on *Plegiocidaris monilifera* (Goldfuss, 1829).

Examples of infestation of the periproctal region are:

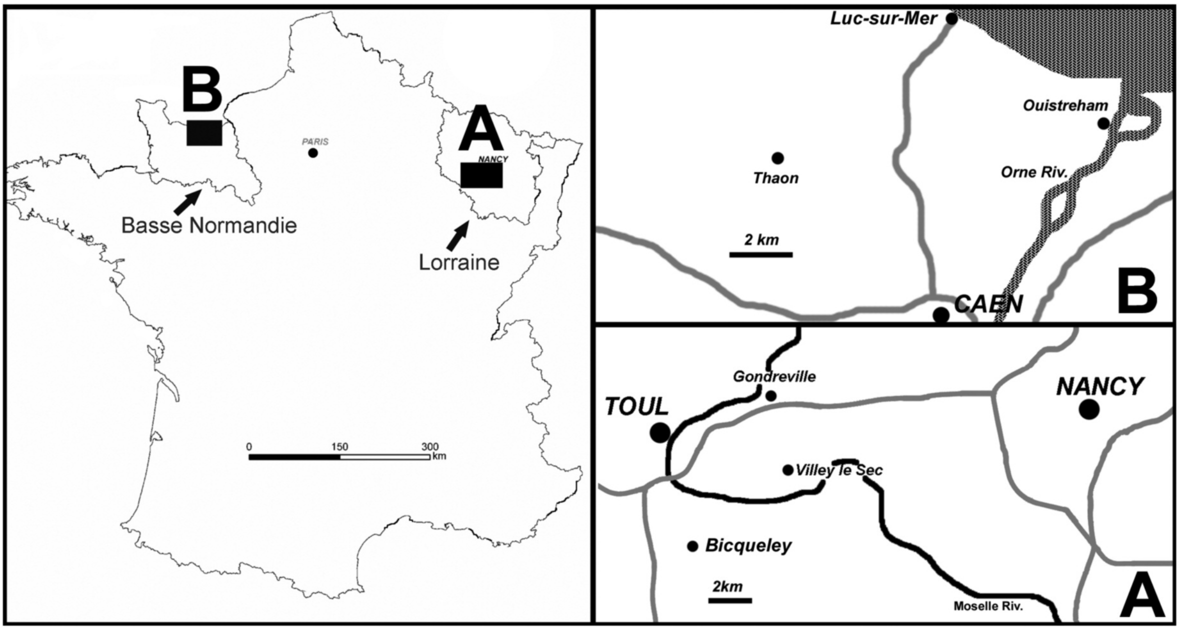
– Mehl *et al*. (1991, pl. 1, fig. 1a–c) on *Plegiocidaris coronata* and (their pl. 3, fig. 3) on *Paracidaris laeviscula*;
– Nicolleau and Vadet (1995), interpreted by Radwańska and Radwański (2005, fig. 5.3), on *Plegiocidaris crucifera* (L. Agassiz, 1840).

In species of *Hemicidaris*, three specimens, all from Chasseral-Kette (Switzerland) and illustrated by Mehl *et al*. (1991, pl. 5, figs 7–8; pl. 6, figs 9–12), have cysts also in the ambital part of ambulacral columns (see Radwańska and Radwański 2005, p. 115).

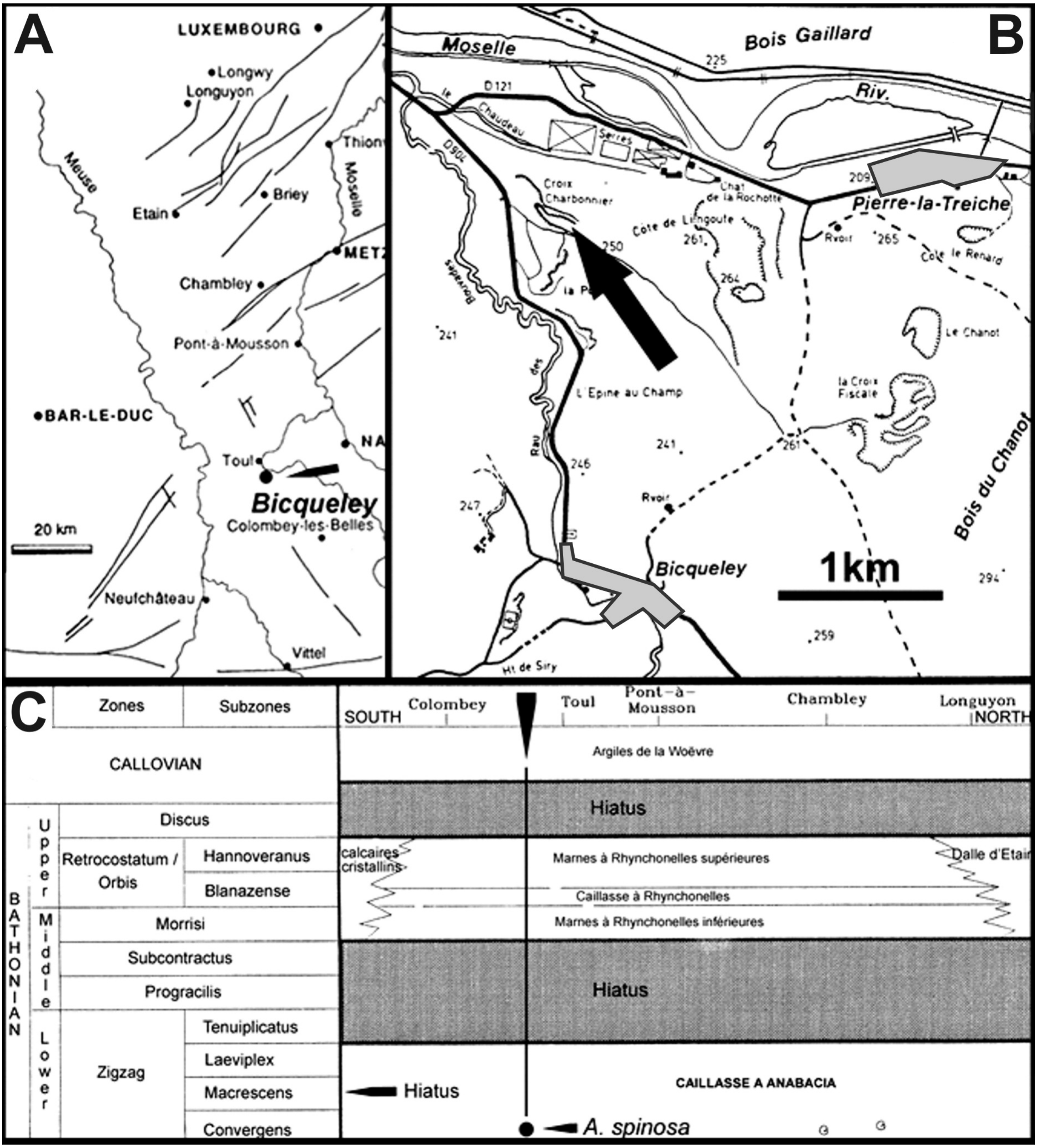
THE NEW MATERIAL

Provenance

The present material of *Acrosalenia spinosa* originates from Middle Jurassic strata in Lorraine and Basse-



Text-fig. 1. Location of Bathonian sequences in northern France which yielded the cyst-bearing echinoids: **A** – Bicqueley, Lorraine (see Text-fig. 2), **B** – Luc-sur-Mer, Basse-Normandie (see Text-fig. 3)



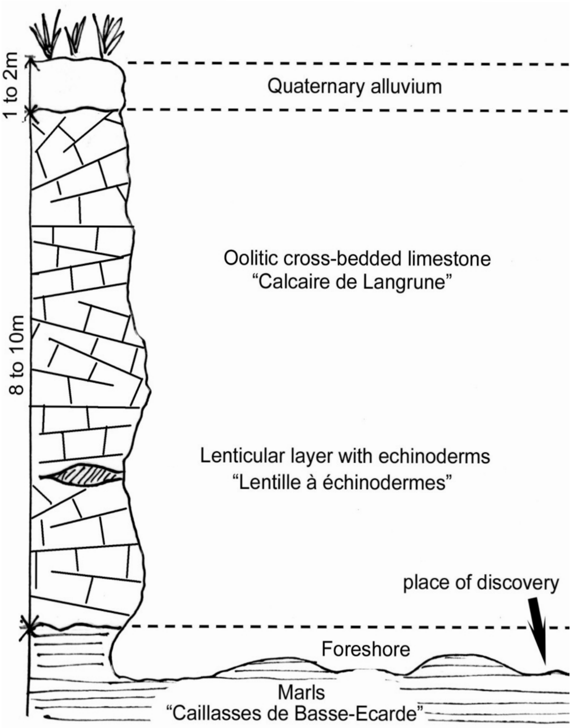
Text-fig. 2. Location of the Bathonian sequence which yielded the cyst-bearing echinoid from Lorraine (cf. Text-fig. 1A): **A** – Sketch-map of the region with lithofacies data (compare Mangold *et al*. 1994, fig. 1); **B** – the Bicqueley area, with provenance indicated (arrow); **C** – Lithofacies and stratigraphy; the specimen of *Acrosalenia spinosa* (see Text-fig. 4A-A') stems from the base of the 'Caillasse à Anabacia' (compare Mangold *et al*. 1994, fig. 2)

Normandie, France (see Text-figs 1–3). The test from Bicqueley (Lorraine) was collected from the base of the 'Caillasse à Anabacia', a unit attributable to the lower Bathonian *convergens* Subzone (see Text-fig. 2C; and Mangold *et al*. 1994). These strongly bioturbated strata yield mostly *Holectypus depressus* (Leske, 1778) and associated small cassiduloids ('*Echinobrissus*'), but *A. spinosa* had not previously been recorded. Amongst a dozen specimens of the latter species collected by one of us (E.P.), only a single reveals an exocyst (see Text-fig. 4).

The specimen from the cliffs at Luc-sur-Mer (Basse-Normandie) stems from a marly sequence ('Caillasses de Basse-Ecarde'), only exposed at ebb (see Text-fig. 3) and attributable to the upper Bathonian (see Mercier 1932; Dugue *et al*. 1997). Unlike Bicqueley, the Luc sequence yields abundant echinoids (see Cotteau 1884; Mercier 1932; Vadet 1993). Several specimens of *A. spinosa* have been collected by Jean-Philippe Dudziak; of these, the cyst-bearing one has been supplied to us for study (see Text-fig. 5).

The exocysts

The cysts in *Acrosalenia spinosa* studied here are, as far as their morphology and structure are concerned (see Text-figs 4-5), identical with those described from other Jurassic occurrences (Radwańska and Radwański 2005). They are hemispherical in shape and have a smooth outer surface composed of the echinoid's calcite. In lateral view, they are slightly bulbous and cover portions of the echinoid test surface to varying degrees (see Text-figs 4A' and 5A'). Excepted is a part close to the echinoid's periproct in one specimen, it which the cyst firmly adheres to the echinoid test (cf. Text-fig. 5A with 5A'). The orifices are distributed randomly (see Text-figs 4A and 5A), but are similar in number, i.e., twelve in the specimen from Bicqueley (Text-fig. 4) and eleven in that from Luc-sur-Mer (Text-fig. 5).



Text-fig. 3. Cliff section at Luc-sur-Mer (upper Bathonian), Basse-Normandie (cf. Text-fig. 1B), with provenance of *Acrosalenia spinosa* (see Text-fig. 5A–A') indicated (arrow); sketch of section based on notes supplied by Jean-Philippe Dudziak

The echinoid host

The echinoids studied best compare to *Acrosalenia spinosa*, whose taxonomic hierarchy and synonymy is briefly listed below.

Family Acrosaleniidae Gregory, 1900
Genus *Acrosalenia* L. Agassiz, 1840

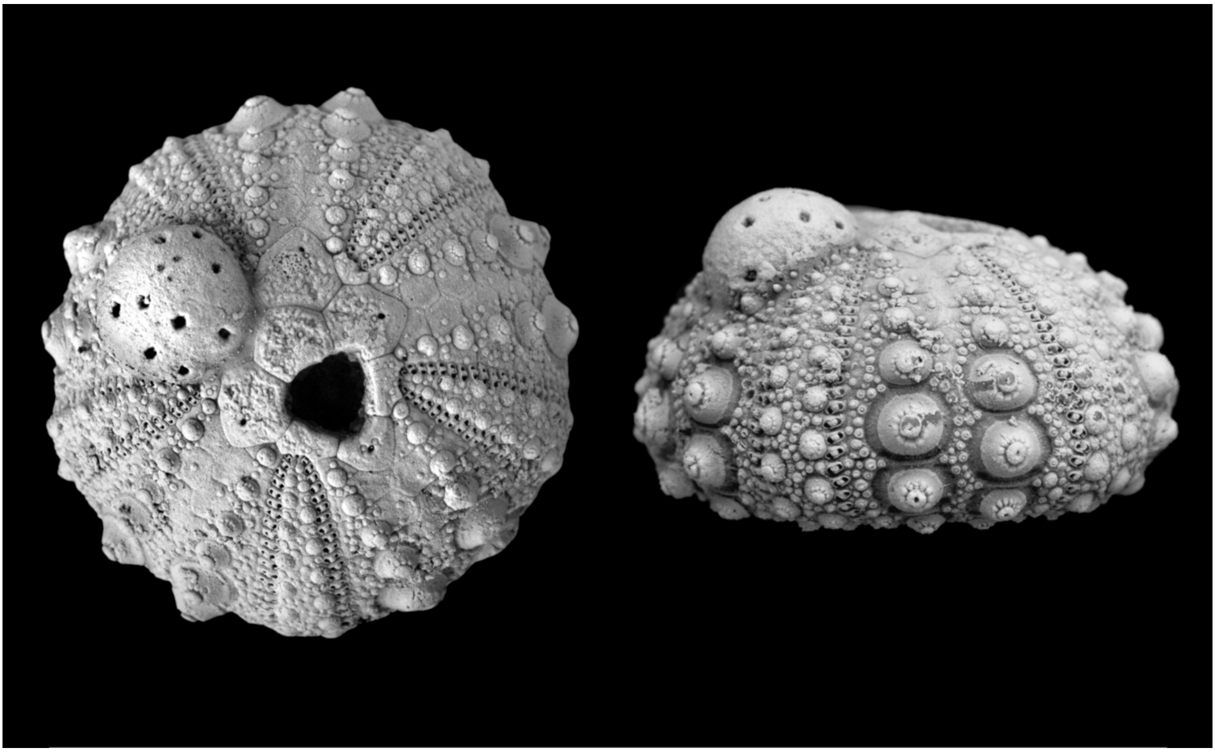
Acrosalenia spinosa L. Agassiz, 1840

1840. *Acrosalenia spinosa* Agassiz, pp. 39–40, pl. 18, figs 1–5.
1856. *Acrosalenia spinosa*; Desor, p. 140, pl. 20, figs 14–16.
1856. *Acrosalenia spinosa*, Agassiz; Wright, pp. 238–240, pl. 17, figs 3a–3f.
1871. *Acrosalenia spinosa*, Agassiz; Desor and de Loriol, pp. 248–250, pl. 40, figs 6–8.
1884. *Acrosalenia spinosa*, Agassiz, 1840; Cotteau, p. 823, pl. 497, figs 1–4.
1932. *Acrosalenia spinosa* Agassiz 1840; Mercier, pp. 173–174, pl. 5, figs 4a–4d.
1975. *Acrosalenia spinosa* Agassiz; Hess, p. 91, pl. 39, fig. 5.
1993. *Acrosalenia spinosa* Agassiz, 1840; Vadet, pp. 23–24, pl. 3, fig. 1.

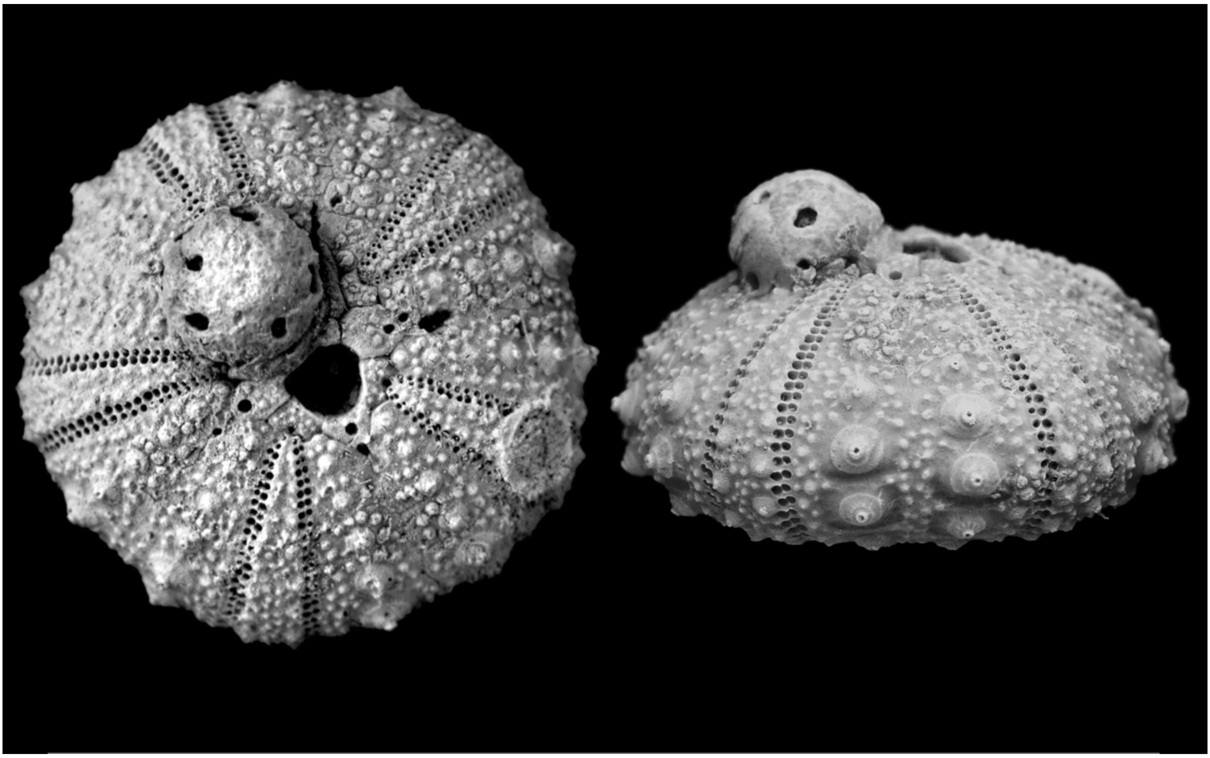
SEXUAL DIMORPHISM: The specimens studied show differences in gonopore size and position. In the Bicqueley test, these are smaller and situated subcentrally, while in the specimen from Luc-sur-Mer they are larger, with the first and fourth ones close to the outer margin of the plate (those of genital plates 2 and 3 are covered by the cyst; that of the fifth is much reduced). Such a pattern matches previous examples of expression of sexual dimorphism in echinoids (see Kier 1967, 1968, 1969; Smith 1984, pp. 84–85, fig. 3.39), in which larger, more widely spaced gonopores are typical of females.

This is the first record of sexual dimorphism expressed in gonopore size and position in any Jurassic echinoid. Formerly, such had been postulated by Lambert and Thiéry (1911, pl. 6, figs 22–27) and Kier (1969, p. 220), on the basis of prolongation of genital plates almost to the ambitus, for the Bathonian arbaciid *Acrosaster michaleti* Lambert. In other echinoids, sexual dimorphism does not appear to become commoner until the latter part of the Late Cretaceous (see Philip and Foster 1971; Smith 1984).

REMARKS: The two specimens studied display some morphological variables in the pronounceness of tubercles, in ambulacral column particularly, as well as in the proportion of the apical disc and periproct to the test



Text-fig. 4. Copepod exocyst in the gonopore of genital 3 of a male specimen of *Acrosalenia spinosa* from Bicqueley, Lorraine: **A –** Apical view, **A'** – Lateral view; both × 5 (Eric Poirot Collection)



Text-fig. 5. Copepod exocyst in the gonopore of genital 3 of a female specimen of *Acrosalenia spinosa* from Luc-sur-Mer, Basse-Normandie: **A** – Apical view, **A'** – Lateral view; both × 5. (Jean-Philippe Dudziak Collection) diameter. As revealed by specimens illustrated in the synonymy, such variables conform to the intraspecific variability recognized by previous authors. Nevertheless, all these cues may suggest a species revision to be needed, what remains now beyond the scope of the present paper.

It may be commented, however, that some differences may result from the typotypic (environmental) conditions of habitats the discussed echinoids lived in. Moreover, weathering conditions in the exposures should also be taken into account, as exemplified by the studied specimens: one coming from the quarried marly limestones (see Text-fig. 4), and the other (see Text-fig. 5) from the washable marls of the sea cliff, exposed at ebb.

Cotteau (1880a, pp. 298–299; 1884) correctly interpreted the stratigraphic range of *Acrosalenia spinosa* to be Bajocian to Bathonian, with a rare record from the locality May (Calvados area; Cotteau 1884, p. 823), probably of Bajocian age. Mercier (1932, p. 174) recorded the species to be abundant in the upper Bathonian of the entire Calvados region. It is also common in the Swiss Jura, where it is restricted to the Bathonian (see Hess 1975, p. 91), as well as in the English Cornbrash Formation (see Wright 1856, p. 240).

The species is unknown from Poland, where the sole member of the genus to have been recorded, *A. angularis* (L. Agassiz, 1840), occurs in the lower Kimmeridgian (see Radwańska 1999).

Ethology of the copepod

As noted above, Radwańska and Radwański (2005, p. 120) recently concluded cysts developed exclusively either along ambulacral pores (tube feet) or via gonopores of the host echinoid. The present material of *A. spinosa* conforms to this pattern in that in both tests these cysts are positioned in such a way that their centre covers precisely the place of the gonopore in the third interambulacrum. It may be thus assumed that these gonopores were the routes through which the copepod larvae settled. After having entered the test, the echinoid reacted by adding skeletal material around the growing copepod so as to encapsulate it externally.

FINAL REMARKS

The new finds of copepod-induced cysts of this type add to the list of previous records of such peculiar structures in echinoid tests. Overall, their number is so low that it currently is impossible to stipulate any general rules as to their occurrence. However, future research might consider the following. In general, all Middle and Late Jurassic echinoids infested by copepods represent vagile benthic animals, free-living and actively moving across the seafloor where access of copepod larvae would have been easy. The order Cidaroida, however, with records from Poland, Germany and France, comprises only representatives of two genera, *Plegiocidaris* Pomel, 1883, and *Paracidaris* Pomel, 1883, which would indicate some host specifity amongst copepods. The two examples of *Acrosalenia spinosa* described herein show an identical cyst position (over gonopore 3), which suggest a specialized ethology of the copepod involved. All tests of *Hemicidaris intermedia* (Fleming, 1828), collected at a single locality in Switzerland, suggest copepod infestation of the entire echinoid population spread over a restricted area. The resultant echinoid/copepod parasite relationship may thus be triggered by the ecology of echinoids, the ethology of copepods or by local environmental conditions.

The new material extends the range of copepod cysts down to the base of the Bathonian (*convergens* Subzone).

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