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A pedunculate brachiopod population preserved *in situ* (Late Maastrichtian, NE Belgium)

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Abstract

The *in situ* preservation of a population of the pedunculate micromorphic brachiopod *Aemula inusitata* STEINICH, 1968 is highly exceptional. The substrate is a test of a holasteroid echinoid (*Echinocorys* gr. *conoidea*) from the Lixhe 1 Member (Gulpen Formation, Upper Maastrichtian) of Haccourt (Liège, NE Belgium), on which *Aemula* is associated with various adnate molluscan and bryozoan species. The palaeoecology of this population of *Aemula inusitata* is discussed.

Key-words: *Aemula*, brachiopod, Cretaceous, Maastrichtian, epifauna.

Résumé

La découverte *in situ* d'une population de brachiopodes pédicellés de l'espèce *Aemula inusitata* STEINICH, 1968 est un évènement exceptionnel. Le substrat est un test d'échinide holastéroide (*Echinocorys* gr. *conoidea*) récolté dans la Craie de Lixhe 1 (Formation de Gulpen, Maastrichtien Supérieur) sur lequel *Aemula* est associé à une épifaune comprenant diverses espèces de mollusques et de bryozoaires. La paléoécologie de cette population d'*Aemula inusitata* est discutée.

Mots-clefs: *Aemula*, brachiopode, Crétacé, Maastrichtien, épifaune.

Introduction

In situ preservation of pedunculate brachiopods is invariably rare in the fossil record. So far, only one example has been recorded from the Maastrichtian white chalk facies by SURLYK (1974), who described and illustrated four specimens of the platidiid *Aemula* sp. attached in living position to the test of an irregular echinoid (*Echinocorys* sp.) from the Maastrichtian white chalk of Hemmoor (northern Germany). Thus, the present material from Haccourt, which comprises an *in situ* population of eighteen individuals of *Aemula inusitata*, STEINICH, 1968, is of particular note.

The echinoid preserving the brachiopod population is housed in the collections of the Natuurhistorisch Museum Maastricht, under number NHMM GM 769 (G. Michels Colln).

Description and discussion

The echinoid test (Pl. 1, Fig. 1a-d), which measures 67.9 mm in height, 80.4 mm in length and 72.0 mm in width, is a typical representative of the group of *Echinocorys conoidea* (GOLDFUSS, 1829). As pointed out by JAGT (2000, p. 270, pl. 20, figs. 6, 7), there are two specimens (registration numbers 343a, b) in the GOLDFUSS type collection (Rheinische Friedrich-Wilhelms-Universität, Bonn). One is an internal flint mould; the other preserves the test and shows 'typical' Lixhe Member preservation. Characteristic of this form is the tall profile and comparatively coarse adapical tuberculation; it is this morphology that is common in the Lixhe 1 Member (Gulpen Formation) in the Haccourt/Lixhe and Maastricht areas. It may possibly extend downwards into the Vijlen Member (Interval 6) and upwards into the Lixhe 2 Member. The test shows a rich epifauna including, in addition to the brachiopods, several specimens of the bivalve *Atreta nilssoni* (VON HAGENOW, 1842), two of *Pycnodonte vesicularis* (LAMARCK, 1806) and a few cheilostome bryozoans. The occurrence of these adnate molluscs and bryozoans is not surprising, since almost all echinoid tests from the Lixhe 1 Member reveal such cementing species. However, the *in situ* preservation of a relatively large population of *Aemula* representatives is highly unusual. This small brachiopod is often found as loose shells when bulk samples of chalk are processed (SURLYK, 1970, 1972, 1982; JOHANSEN, 1987; SIMON, 1998; see also ŽÍTT *et al.*, 2002). A few loose specimens of *A. inusitata* from the white chalk facies of the Lixhe 1 Member in the Haccourt-Lixhe area are represented in the J.W.M. Jagt Collection (NHMM). The fact that the present specimens are preserved *in situ* on a test of *Echinocorys* is probably due to rapid burial, resulting from biotic or abiotic processes. Following burial, the echinoid must have remained undisturbed by burrowing animals for a prolonged period of time.

The specimens of *A. inusitata* studied fit the diagnosis given by STEINICH (1968, pp. 193, 194). The shell is

small, subcircular in outline with a flat dorsal valve and a slightly convex ventral valve, the external surface of the ventral valve being covered with numerous, small, regularly spaced tubercles. The beak is short and suberect, the foramen typically amphithyrid and irregular. Of some of the specimens, part of the shell was prepared away to reveal the brachidium. Dental plates are not developed; the hinge plates are fused and a median septal pillar is clearly visible on the dorsal valve floor. Two small processes may be seen at the ventral edge on top of the septal pillar. For a list of synonyms of *A. inusitata* STEINICH, 1968 reference is made to SIMON (1998, p. 206) who discovered a few loose specimens in the 'Craie phosphatée' at Ciply (*Belemnella obtusa* Zone, Lower Maastrichtian).

SURLYK (1974, p. 194) demonstrated that the lophohore of *A. inusitata* was a trocholophe in juvenile specimens (length < 1.0 mm), which evolved in the adult stage into a schizolophous type. *Aemula* did not reach the plectolophous stage seen in adult specimens of various species of the genus *Platidia* COSTA, 1852. The mode of life of *Aemula inusitata*, also studied by SURLYK (1974, pp. 192, 193), is very similar to that of related extant species of *Platidia*, as described in particular by ATKINS (1959a, b). In fact, amongst various brachiopod species homeomorphism has been observed. Representatives of *Platidia* COSTA 1852 (Platidiidae THOMSON, 1927), *Amphithyris* THOMSON 1918 (Platidiidae THOMSON, 1927), and *Megerlia* KING, 1850 (Kraussinidae DALL, 1870) exhibit a similar shell outline with a flat dorsal valve, an amphithyrid foramen and a slightly convex ventral valve. The dorsal valve is pressed against the substrate and often is irregular, whereas the ventral valve is more regular.

Shells of *Aemula inusitata* STEINICH, 1968 (Pl. 1, Fig. 3 and Pl. 2, Figs 1, 2) observed on the present echinoid test are of very different sizes (Fig. 1). The smallest specimen seen is 1.3 mm wide whereas the largest specimen is 4.7 mm wide. Size distribution (Fig. 1) does not exhibit distinct groups of individuals representing successive generations but appears to be a more or less continuous function. However, most of the specimens studied (11 in number) are adults with shell width exceeding 3.5 mm. Amongst these, eight individuals could be measured and these are represented in Fig. 1; three other large specimens could not be measured, as they are partially overgrown by shells of other cementing taxa. Five specimens may be considered as intermediate individuals (shell width > 1.5 mm, < 3.0 mm). Finally, two individuals represent juveniles (shell width < 1.5 mm). In summary, juvenile and young specimens are rare, and adults much better represented. The diagram in Fig. 2 illustrates this size-frequency distribution, with the specimens studied grouped into three size-frequency classes. This graph represents, at a small scale, a "negative view" of the right skewed distribution observed by SURLYK (1974,

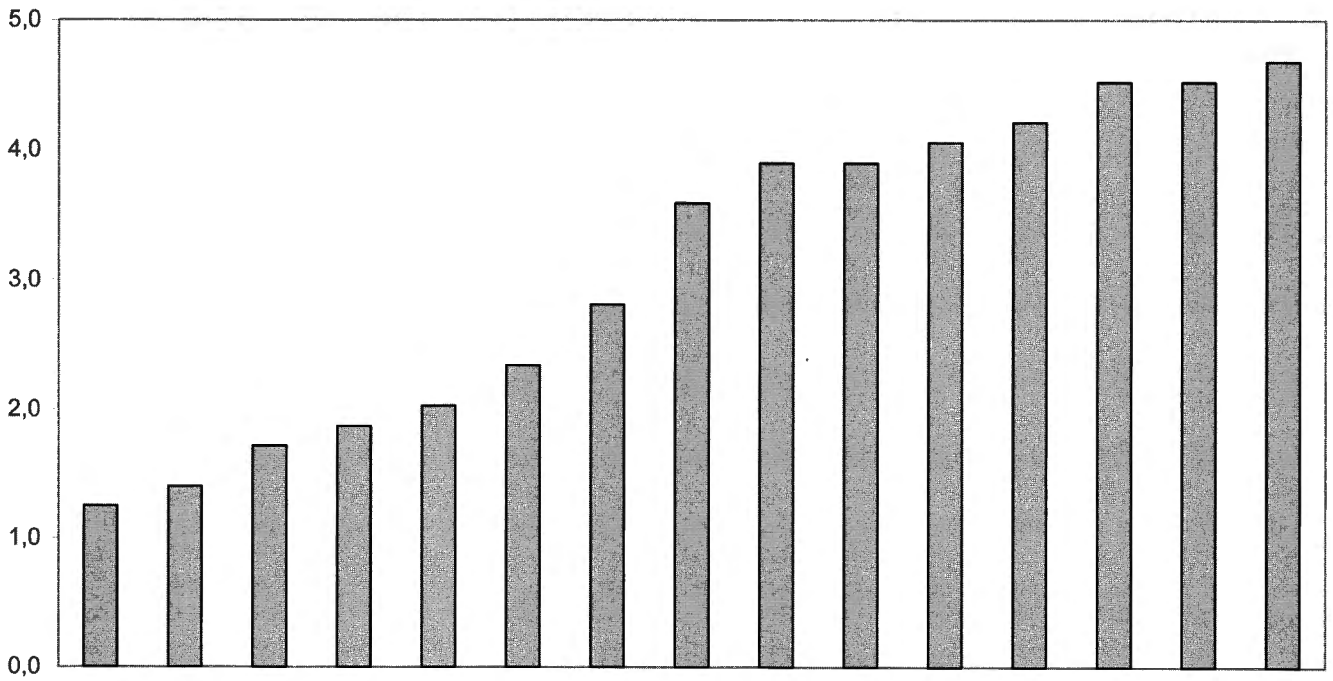

Fig. 1 — Measurements of specimens of *Aemula inusitata* STEINICH, 1968 preserved *in situ* on the test of the echinoid *Echinocorys* gr. *conoidea* (NHMM GM 769) from the Lixhe 1 Member (Gulpen Formation, Late Maastrichtian), CPL SA quarry, Haccourt (Liège, NE Belgium). The width (in mm) of fifteen specimens has been measured; three adult individuals (width > 3.5 mm) could not be measured as they are partially overgrown by an adjoining oyster (*Pycnodonte vesicularis*) or by a flint extension.

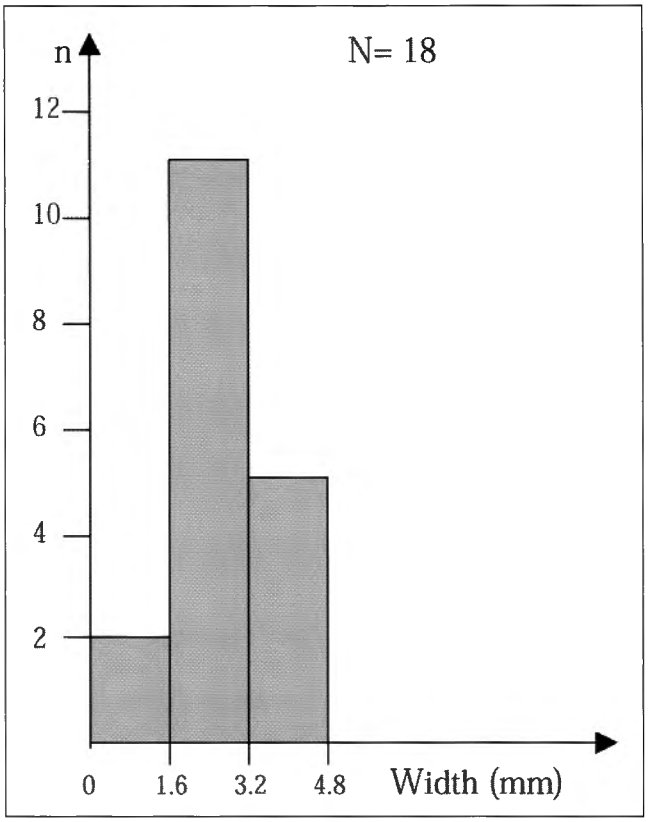

Fig. 2 — Size-frequency diagram for *Aemula inusitata*, preserved *in situ* on *Echinocorys* gr. *conoidea* (NHMM GM 769), from the Lixhe 1 Member (Gulpen Formation, Late Maastrichtian), CPL SA quarry, Haccourt (Lixhe, NE Belgium); N – total number of specimens studied; n – number of individuals in different size classes; abscissa – width (in mm) of individuals measured.

fig. 6, p. 200) for the size-frequency histogram of 101 isolated specimens of *Aemula inusitata* STEINICH, 1968 collected at Karlstrup (Denmark) which indicates a very high mortality for juveniles and young specimens. In view of the fact that the individuals attached to the echinoid test described here must be interpreted as 'living animals', a left-skewed distribution for the size-frequency was to be expected.

As already pointed out by SCHMID (1949) and demonstrated once more by SURLYK (1974, pp. 191, 192), epifauna did not attach to a substrate at random. On the contrary, species fixation is quite consistent. For instance, careful observation of specimens of *Atreta nilssoni* shows that the line through the centre and one 'ear' of this bivalve passes through only one point. This was named the "*Inkrustations-Zentrum*" by SCHMID (1949). This point is, in fact, the highest point on the *Echincorys* test when it lays on the seafloor. For the present specimen this pivotal point is close to the apex, suggesting this test to have been in a stable position, with flat base down, on the seafloor.

In contrast to the regular attachment pattern seen in *A. nilssoni*, shells of *A. inusitata* are not consistently oriented. This type of attachment has also been noted by SURLYK (1974, p. 192), who assumed that slight displacement might have occurred during final burial. Of the eighteen specimens discussed here, the ventral umbos appear to be positioned randomly, reflecting the position taken up by the larva at the moment of its fixation. If displacement of the brachiopod shells had resulted from burial conditions, one might have expected all shells attached close together on a restricted small portion of test surface to have undergone a similar vectorial displacement. If their umbos were regularly positioned, a vectorial displacement should affect the umbo positions in the same way. This is not observed here; in fact, six specimens of *A. inusitata* attached to a restricted surface not larger than 5 cm, present randomly directed umbos.

In the example described by SURLYK (1974), the four specimens of *Aemula* sp. were situated in the upper portion of the echinoid test, like the other epifaunal elements. This is obviously different to the epifaunal distribution seen in the present *Echinocorys* gr. *conoidea*. Large specimens of *Atreta nilssoni* are attached near the apex of the test and some medium-sized individuals occupy the upper half. The lower half of the test reveals no specimens of *Atreta nilssoni*. In contrast, all specimens of *Aemula inusitata* are situated exclusively in the lower test half; the one placed highest on the test is at a height of 34.4 mm, measured from the base of the echinoid. This suggests that fixation of the larval stage was impossible or very difficult in a higher position, probably because of high-energy hydrodynamic conditions. However, it is also possible that previously attached juveniles had been removed by wave surge during storms. Naturally, cemented species such as *Atreta nilssoni* could better withstand such stormy conditions and thus were able to colonise the upper part of the echinoid substrate.

Other details appear to substantiate this observation on palaeoecology. *Aemula inusitata* is a brachiopod with a pustulate ventral valve; the numerous tubercles ornamenting the external surface of this valve are regularly spaced and they normally cover the whole surface. All specimens studied here exhibit a tuberculate ventral surface but the tubercles are never visible on the highest part of the shell surface; this is always attrite. The median and umbonal regions of the ventral valve represent the highest portion of the shell exposed to wave action. In contrast, tubercles are well preserved near the commissural zones which constitute the portion of the shell less extensively exposed to environmental conditions. Attrition of the tubercles confirms high-energy conditions. Moreover, this *Aemula* population is not evenly distributed low on the test. Indeed, eleven specimens are attached on the right-hand side of the test (and mostly posteriorly) whereas only five are placed on its left-hand side; two juveniles are situated anteriorly. This distribution pattern suggests that the right-hand side presented better living conditions, an observation substantiated by the fact that oldest and largest specimens, which were still alive when

buried, are all positioned on that side. On the left-hand side, only smaller and/or juveniles specimens are observed.

The grazing action of predators was perhaps an additional problem for specimens of *Aemula* fixed to the upper part of the echinoid test. It may be assumed that these small, pedunculate brachiopods attached in this zone were unable to offer resistance to grazers. Cemented molluscs such as *Atreta nilssoni* were much better adapted in this respect.

It may also be observed that a small specimen of *Pycnodonte vesicularis* attached to the substrate at the same time as individuals of *Atreta nilssoni*, reflecting a single "*Inkrustations-Zentrum*" near the apex of the test. The other, large specimen of *P. vesicularis* obviously settled later and during its growth grew over individuals of *Aemula*. This second oyster does not conform to the first "*Inkrustations-Zentrum*", suggesting that it developed after the echinoid had been displaced from its original position. Another explanation might be that this second *P. vesicularis* attached much later, when the test was partially exhumed, allowing a second phase of epifaunal colonisation.

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Explanation of Plates

PLATE 1

Fig. 1. — *Echinocorys* gr. *conoidea* (NHMM GM 769) from the Lixhe 1 Member (Gulpen Formation, Late Maastrichtian), CPL SA quarry, Haccourt (Liège, NE Belgium), exhibiting a rich epifauna, including the bivalves *Atreta nilssoni* and *Pycnodonte vesicularis*, various bryozoans and a population of eighteen individuals of *Aemula inusitata*, attached to the lower half of the echinoid test, mainly to the right-hand flank; a – left lateral, b – right lateral, c – aboral and d – posterior views, respectively. Magnification: x 0.80

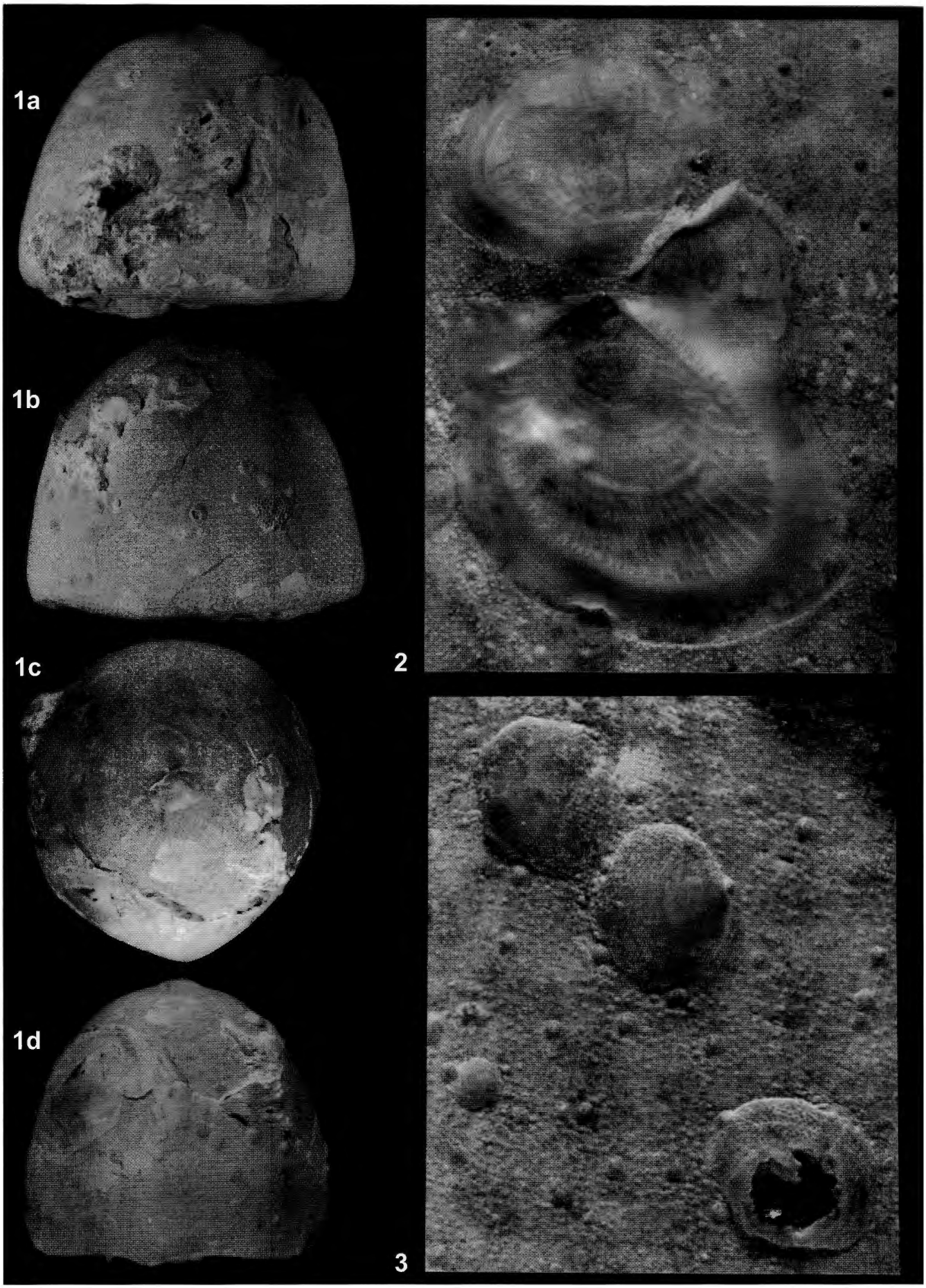
Fig. 2. — A well developed specimen of *Atreta nilssoni* and a single *Pycnodonte vesicularis* cemented to the apex of *Echinocorys* gr. *conoidea* (NHMM GM 769); representatives of *A. nilssoni* occur mostly on the upper half of the echinoid test. Magnification: x 5.5

Fig. 3. — Four specimens of *Aemula inusitata* in ventral view, preserved *in situ* on the test of *Echinocorys* gr. *conoidea* (posterior right-hand side). Note that the specimens are positioned at random; a juvenile individual is seen close to the left-hand margin of the photograph. The ventral shell surface is covered in regularly spaced tubercles; attrition of these tubercles occurred, since the highest portion of the valve near the ventral umbo appears smooth. Magnification: x 9.8

PLATE 2

Fig. 1. — Two specimens of *Aemula inusitata*, preserved *in situ* on *Echinocorys* gr. *conoidea* (NHMM GM 769), on right-hand flank of the test. These specimens show random attachment and attrition of the highest portion of the ventral valve. A cemented, cribromorph cheilostome bryozoan (P.D. Taylor, pers. comm.) is seen close by. Magnification: x 12

Fig. 2. — Three individuals of *Aemula inusitata*, preserved *in situ* on a test of *Echinocorys* gr. *conoidea* (right-hand flank). The adult specimen on the left-hand side covers a fracture in the echinoid test which took place before the moment of settlement and development of the brachiopod. On the right-hand side is seen a juvenile specimen of *A. inusitata.* Magnification: x 5.8



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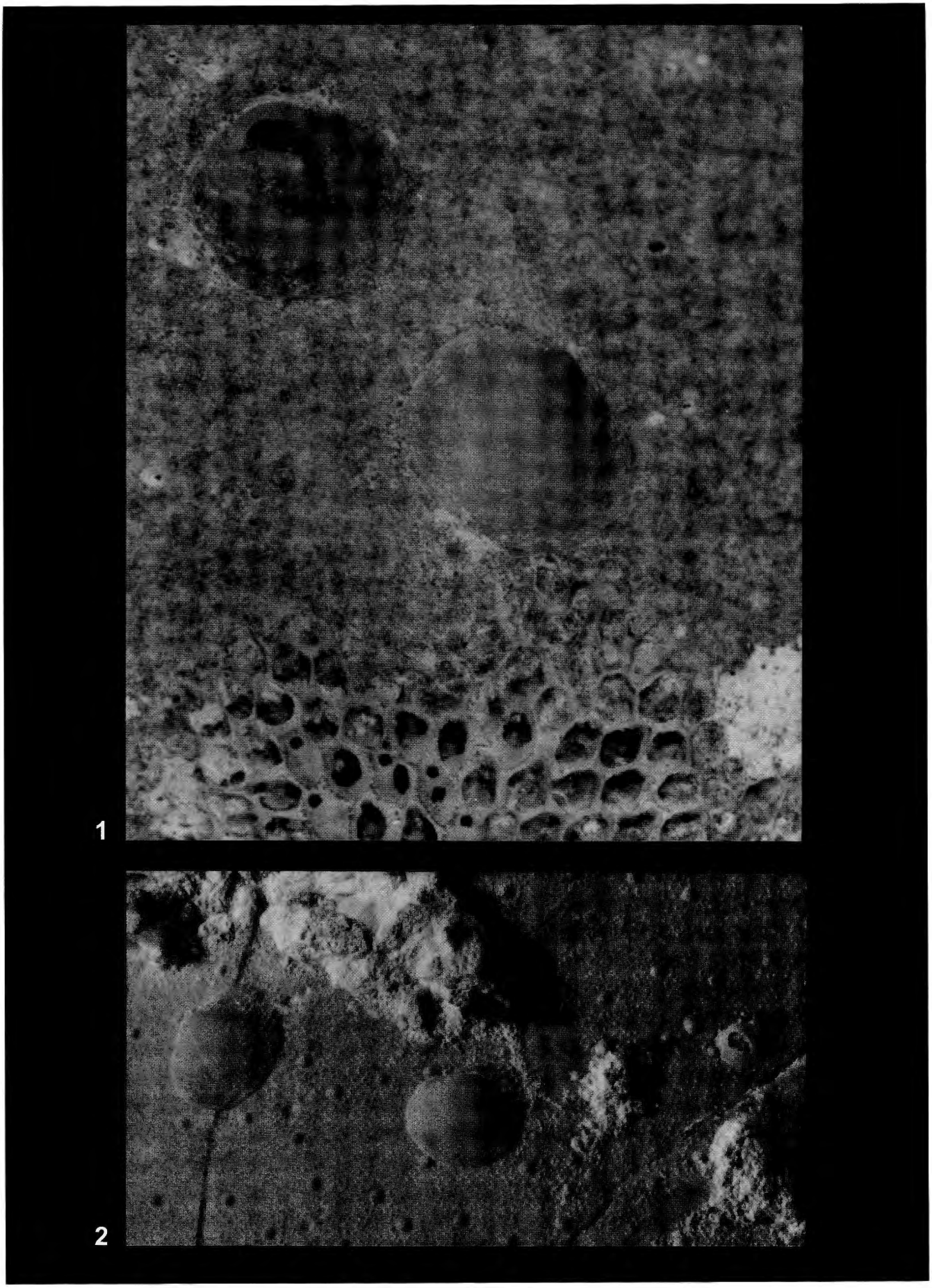

PLATE 2