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Oyster attachment scar preservation of the late Maastrichtian ammonite *Hoploscaphites constrictus*

JENS LEHMANN and MAX G.E. WIPPICH

Certain groups of gryphaeid oysters became secondarily adapted to soft-bottom conditions by developing heavy-weight cup-shaped shells resting loosely on the sediment. As larvae in nearly all species of oysters are unable to attach themselves successfully to mud-covered surfaces, even these taxa depend on particles which provide at least small-scale firm substrates (Stenzel 1971). Substrates usually available in soft bottom habitats are small clasts and are barely recognizable in the umbonal region of full-grown individuals. In some cases however, larvae happen to find larger objects, large portions of which are covered during growth and become moulded onto the attached valve as a negative imprint.

Ammonites show highly complex ornamentation and shell form, and moulding of ammonites by oysters provides the most spectacular examples. A number of such cases has been reported from Cretaceous strata. Kennedy (1971) mentioned oyster casts of ammonites in the Cenomanian Lower Chalk of Southern England. Lewy (1972) described *Protexanites* sp. and *Baculites* sp. preserved as attachment scars of *Pycnodonte (Phygraea) vesiculare* (Lamarck 1806) from the Coniacian and Campanian of Sinai. Stühmer *et al.* (1982) figured an ammonite from the Hauterivian of the Isle of Helgoland, Northern Germany, that is *Endemoceras* in our opinion, moulded by *Aetostreon latissimum* (Lamarck 1819). Kennedy (1993) reported ammonites being moulded by oyster overgrowth from the Late Campanian Craie de Trivières of the Mons basin, Belgium.

In the present paper we describe *Pycnodonte (Phygraea) vesiculare* from the Late Maastrichtian of Nasiłów, Poland moulding the ammonite *Hoploscaphites constrictus* (J. Sowerby 1817), that provides a 'text-book example' for moulding and xenomorphic growth in ostreids.

Material, locality, and stratigraphy. — The oyster described here was collected in 1983 by the late Jost Wiedmann. It was recently prepared by the authors and is now a part of the reference collection of the Geologisch-Paläontologisches Museum der Universität Tübingen (GPIT), under 1771.

The specimen is from the Nasiłów quarry, on the western banks of the river Vistula, about 100 km SE Warsaw, Poland. The section at Nasiłów exposes about 25 m of latest Maastrichtian (*Hoploscaphites constrictus crassus* Zone *sensu* Błaszkiewicz 1980) and Danian sediments (see Abdel-Gawad 1986: figs 4, 6). The specimen described herein was found in the siliceous limestones of late Maastrichtian age, about 40 cm below the hardground surface.

At Nasiłów *Pycnodonte (Ph.) vesiculare* is a characteristic component of the soft-bottom communities of the uppermost Maastrichtian, and is one of the most predominant bivalves at this locality (Abdel-Gawad 1986). Moulding of substrates is not uncommon in oysters from Nasiłów. Abdel-Gawad (1986: pl. 38: 5, 39: 6)

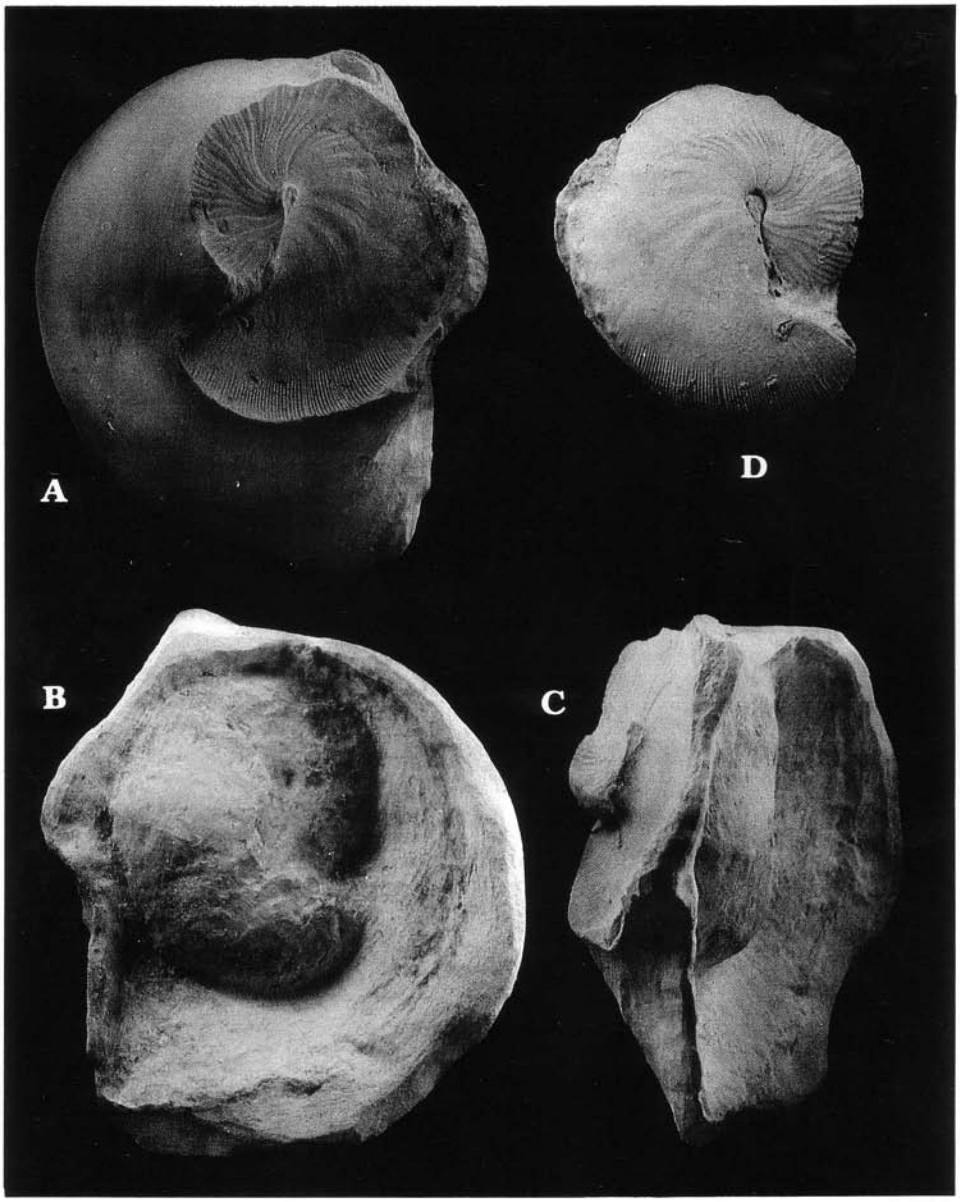

Fig. 1. *Pycnodonte (Phygraea) vesiculare* (Lamarck 1806), Upper Maastrichtian of Nasiłów, Poland (GPIT 1771/1). □A. Left valve with attachment area moulding a macroconch of *Hoploscaphites constrictus* (J. Sowerby 1817); its rubber cast shown by D. □B. Right valve with xenomorphic sculpture roughly reproducing the shape of the substrate. □C. Oblique view showing equivalence of concave attachment scar on the left valve (left) and convex xenomorphic sculpture on the right valve (right). All figures are in natural size.

figured two specimens of the species from this outcrop with broad attachment areas, one of them clearly moulding a sponge.

Description. — The oyster (GPIT 1771/1) appears to be fully grown, showing a maximum length of 75 mm. Its calcitic shell material is partly silicified. Greyish stains of silica acid are visible, particularly on the left valve. The two valves are articulated.

The left valve is conical and possesses a large attachment area which comprises about a quarter of the total valve surface. It shows a negative mould of a scaphitid ammonite. Nearly the entire right flank and part of the venter is moulded. Even very fine details of ornamentation are excellently preserved.

The right valve shows a convex xenomorphic area at its dorsal part that comprises nearly half of the complete valve. It roughly reproduces the form of the ammonite, and its body chamber hook and umbilical depression can be clearly seen. By contrast, the ventral half of the right valve is concave as usual, with the typical ornament of slight radial furrows common in gryphaeid oysters.

The ammonite-mould can be confidently referred to *Hoploscaphites constrictus*. Within the wide range of variability of this species the present specimen resembles best the lectotype as redefined by Kennedy (1986). It is a small macroconch with weak ribs on the flanks of the body chamber, and a row of small ventrolateral clavi that terminate 90° before the aperture. Remains of matrix on the dorsal part of the oyster show an imprint of the ammonite, indicating that the internal mould was originally present.

Moulding and xenomorphic growth in ostreids. — Ostreid growth, and thus shell form, is largely controlled by extrinsic factors, particularly shape of the substrate and mechanical properties of the shell material.

The attached left valve of *Pycnodonte (Ph.) vesiculare* undergoes a three-phase growth, as described by Nestler (1965). Shell development starts with an encrusting ('hippopodium') stage that posseses a flat and extremely thin shell. The surface of the substrate is reproduced as a negative imprint by simple passive moulding as the juvenile left valve grows across. According to Nestler (1965), the extension of the encrusting stage depends on the dimension of the substrate and its degree of convexity. In the present case, the great surface area and low convexity of the *Hoploscaphites* shell enabled the oyster to cover it almost completely and to reach a relatively large size before lifting itself off from the substrate.

When shifting to the second stage of growth the shell margin lifts off from the plane of attachment, and thus the shell attains a cup-shaped form.

Shell development ends with free growth, in which the anchorage function of the substrate is abandoned. Anchorage is now attained by internal thickening of the left valve in order to stabilize the position of the oyster resting on the sediment. In this third stage no significant growth of the shell margin occurs.

Shape and ornament of the right valve is mainly a response to mechanical stress during shell closure (Lewy 1976). In gryphaeid oysters the mineralized part of the right valve is considerably smaller than the left valve, the space left between the two is covered by a layer of flexible conchioline extending beyond the right valves rim (Stenzel 1971). Being originally flat, this conchioline sheet has to attain a concave shape when it is pressed into the concave interior of the left valve everytime the shell is closed. This is achieved by folding the conchioline sheet in order to shorten its external margin. During growth the calcified part of the right valve grows progressively across the inside of the conchioline sheet and the radial folds thereby become moulded onto the valve, producing a 'pseudoornament' (*sensu* Lewy 1976) of radial furrows.

Xenomorphic ornament of the right valve is formed in the incrusting 'hippopodium' stage. In order to maintain an equal distance between the valves to accomodate the soft parts, the right valve has to reproduce the shape of the substrate as well as the attached left valve (Stenzel 1971; Taylor 1990). The positive image on the right valve is generally more obscure, but it nevertheless shows some details as seen in the specimen described above.

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Jens Lehmann, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Sigwartstraße 10, 72076 Tübingen, Germany.

Max G.E. Wippich, Institut für Geologie, Ruhr-Universität, Universitätsstraße 150, 44801 Bochum, Germany.