BIOIMMURING LATE CRETACEOUS AND RECENT OYSTERS: 'A VIEW FROM WITHIN'

John W.M. JAGT[1], Christian NEUMANN[2] & Anne S. SCHULP[1]

(2 figures)

1. *Natuurhistorisch Museum Maastricht, de Bosquetplein 6-7, NL-6211 KJ Maastricht, The Netherlands; E-mail:* john.jagt@maastricht.nl*; anne.schulp@maastricht.nl*
2. *Museum für Naturkunde der Humboldt-Universität Berlin, Invalidenstraße 43, D-10115 Berlin, Germany; E-mail: christian.neumann@museum.hu-berlin.de*

ABSTRACT. Being obligate cementers, oysters (Ostreoidea), both fossil and Recent, often yield valuable information on their substrates, whether biotic/abiotic, perishable or inert. By a process called bioimmuration, oyster shells may preserve lightly or non-calcified sessile organisms already present on the same substrates, and occasionally replicate external features of such substrates on their unattached right valves (xenomorphism). From Upper Cretaceous (Campanian-Maastrichtian) strata in northwest Europe, there are numerous records of oysters attached to calcitic and aragonitic substrates, such as echinoids, bivalves (including other oysters, either conspecific or not), ammonoid and coleoid cephalopods, sponges and scleractinian corals. These examples all illustrate 'a view from above', cementation having occurred on the external surface of the substrate. Here we present two comparatively rare instances of fossil bioimmuring oysters and a spectacular Recent example, documenting oyster growth on the inside of partially broken echinoid tests, thus providing 'a view from within'.

KEYWORDS: Cretaceous, Recent, echinoids, bioimmuration, xenomorphism.

1. Introduction

Amongst Late Cretaceous bivalves, at least three groups comprise obligate sessile forms. Post-larval cementation in these molluscs has been linked to predation pressure (Harper, 1991a, b); being permanently fixed to a substrate, this would obviously have increased predator resistance in conjunction with the development of heavy ribbing and/or spines. Cementation by the right valve occurs in spondylids (Müller, 1970; Carter, 1972; Dhondt & Dieni, 1990) and dimyids (Hodges, 1991). Of the latter group, small-sized forms such as *Atreta nilssoni* (von Hagenow, 1842) and *A. costata* (Grönwall, 1900) at times cover large surfaces of tests of some holasteroid echinoids, showing a peculiar pattern of growth which Schmid (1949) referred to as 'orientierte Anheftung' and 'Inkrustazionszentrum'. Numerous examples of such cemented dimyids are known from the Lixhe 1 Member (Gulpen Formation; lower Upper Maastrichtian; Jagt, 1999) of the Haccourt-Lixhe area (Liège, Belgium). Invariably, associated sessile forms there include craniid brachiopods, certain sabellid and serpulid polychaetes (Jäger, 2004), and monopleurid bivalves, as well as juveniles of pycnodonteine oysters. Pedunculate brachiopods are extremely rare on such substrates (Jagt & Simon, 2004).

The third group includes palaeolophid, gryphaeid and liostreid oysters (classification according to Malchus, 1990), in which cementation to a substrate is by the left valve. Depending on size and structure (e.g., curvature, surface features), oysters can fairly rapidly encrust their substrates and also bioimmure any other sessile organisms (epibionts) on the same substrate. The concept of bioimmuration has been discussed in detail by Taylor (1990a), and numerous fine examples of Jurassic and Late Cretaceous bioimmured bryozoans, thecate hydroids, verrucid barnacles, algae plus other soft-bodied organisms have already been recorded in the literature (Voigt, 1956, 1966, 1968, 1979, 1981; Taylor, 1988, 1990a, b; Jagt, 1989; Jagt & Collins, 1989; Rohr & Boucot, 1989; Taylor & Todd, 1990, 2003; Palmer *et al.*, 1993; Voigt & Hillmer, 1996; Evans & Todd, 1997).

What the cemented oysters described in the papers referred to above have in common is the fact that they document the external surface of their substrates, with or without bioimmured epibionts. Thus, they provide 'a view from above'. Examples of post-larval oyster settlement on the inside of biotic substrates, such as empty echinoid tests, are much rarer. Here we describe two examples from the Maastrichtian (Late Cretaceous) of northeast Belgium and northeast Germany, and a spectacular Recent example from a beach in Bretagne (France). These document 'a view from within'.

2. Bioimmuring oysters, fossil and Recent

It is widely known that oysters in particular may produce prime examples of xenomorphism, a term proposed by Stenzel (1971) to apply mainly to cemented bivalves in which the external configuration of the unattached shell closely imitates the substrate to which the cemented valve is attached. As discussed by Rohr & Boucot (1989),

xenomorphism is a special kind of bioimmuration, in which the animal attempts to compensate for any protusion/extension of the attached left valve by forming a corresponding bulge in the right, which thus mirrors the topography of the substrate. Obviously, in thin-shelled species, this mirrored image of the substrate on the right valve may be fairly detailed; in others, only contours are preserved and any ornament of the substrate is much subdued (Nestler, 1965; Carter, 1968; Abdel-Gawad, 1986; Freneix & Viaud, 1986; Darragh & Kendrick, 1991; Aqrabawi, 1993; Lehmann & Wippich, 1995; Kutscher, 1997; Cleevely & Morris, 2002; Reich & Frenzel, 2002).

At some levels, notably in the Upper Jurassic and Cretaceous, oyster cementation can also be of prime biostratigraphic importance when ammonites constitute the substrate used. During early diagenesis (Voigt, 1996), the aragonitic ammonite shells were often dissolved, leaving little or no trace except for the attachment areas of the left valves of oysters. The production of artificial casts of such bioimmured ammonites can often help in identifying the species, and thus assignment of the level that produced the specimen to a particular ammonite biozone (Lewy, 1972; Spaeth, 1985; Coquinot & Marchand, 2004; Taylor & Lewis, 2005).

As noted above, at certain levels in the Upper Cretaceous of northwest Europe, palaeolophid, gryphaeid and liostreid oysters cemented to 'secondary hardgrounds' are particularly common. The term 'secondary hardgrounds' refers to biotic/abiotic objects lying on the soft-bottom seafloor, and thus elevated above it; these are prime targets for settling larvae of many groups, including ostreoid bivalves. The pycnodonteine (gryphaeid) *Pycnodonte vesicularis* (Lamarck, 1806) was widely distributed, often covering more than 20-30 % of the available surface area of echinoid tests. By sheer weight increase during growth, such oysters occasionally caused the substrate to topple over and become available for additional encrustation by other organisms. Upper Cretaceous strata in the type area of the Maastrichtian Stage (northeast Belgium, southeast Netherlands) yield ample material of the ostreoid genera *Pycnodonte*, '*Hyotissa*', *Amphidonte*, *Gryphaeostrea*, *Rastellum*, *Agerostrea* and '*Acutostrea*'. Although much less common than '*Acutostrea*' in the Maastricht Formation, specimens assignable to *Pycnodonte* are amongst the largest of oysters in this unit. Cementation to echinoids, in particular to the large holasteroid *Hemipneustes striatoradiatus* (Leske, 1778), is common. Much rarer is attachment to other, non-ostreoid bivalves (pteriids) and scleractinian corals. All these examples illustrate external surfaces of substrates; internal features are rarely documented.

3. Selected examples

We have selected three examples of oyster cementation to the inside of echinoid tests, two of Late Cretaceous age and one from a Recent setting. Unfortunately, in both fossil examples only the left valves are preserved, so that the mirrored image of the encrusted substrate cannot be illustrated.
The Recent example, from the Natuurhistorisch Museum Maastricht collections (NHMM 2006 052) (see Fig. 1A-

C), is the most spectacular one. This is an isolated left valve of the common edible oyster, *Ostrea edulis* (von Linné, 1758), collected by Mr and Mrs Roelse (Vlissingen) from the low-tide line at La Grande Plage, St Cast (Bretagne, northwest France) in early August 2002. *Ostrea edulis* is widely distributed in the North Sea, the English Channel and the Atlantic Ocean (Stenzel, 1971; Lindner, 1977); although the present valve is not fresh, but slightly worn and of a whitish yellow colour, it does not present a fossil or subfossil. The specimen measures 33.5 mm in greatest length, and 35 mm in greatest width; the reniform muscle scar on the inside (see Fig. 1B) is 6.5 mm by 11.5 mm.

The mirrored image of the substrate of this oyster is remarkable, in this case the inside of a regular echinoid. Although details of ambulacral plating and pore zones are remarkably well preserved (Fig. 1A, C), a definitive identification of the echinoid called for a direct comparison. To this end, we used an unregistered test of *Paracentrotus lividus* (Lamarck, 1816) in the NHMM collections (from France, no detailed provenance data available), filled half of it with silicone rubber, broke it open, photographed it and placed it next to NHMM 2006 052 for direct comparison (Fig. 1D, E). In all details (e.g., 5-geminate ambulacral plating), there is correspondence between these two specimens, which also rules out the possibility that the echinoid mirrored could be fossil. In NHMM 2006 052, there are smaller outgrowths of the oyster shell on the right-hand side (Fig. 1B), which demonstrate that the echinoid test must have been broken at the ambitus. Moreover, the apical area (Fig. 1A) has irregular margins, suggesting that apical disc plating had already been lost and dispersed, and the test margin broken, either through predation, scavenging or wave action, prior to oyster cementation. The broken test lay on the seafloor for a certain period of time, which is clear from the occurrence of small spirorbid polychaetes which the oyster bioimmured. From personal observations (C.N.), we know that species of *Spirorbis* can settle within two to three days and reach diameters of nearly 3 mm in such a short timespan.

Paracentrotus lividus is widely distributed in depths between 0 and 30 m in the Atlantic (Ireland, England), the English Channel, and further south to Morocco, the Canary Islands and the Mediterranean (Mortensen, 1927[1977]; Hansson, 1999). With a diameter of *c*. 33 mm, the specimen to which the oyster attached was a fairly small test (compare Figs 1A and D).

The second example is a large-sized individual of the pycnodonteine *Pycnodonte vesicularis* (Fig. 2A-C) attached to a test fragment of *Hemipneustes striatoradiatus* (NHMM JJ 8805). This is from the lower Nekum Member (subunit IVe-1; Maastricht Formation) of late Maastrichtian age, as exposed at the CBR-Romontbos quarry, Eben Emael (Bassenge, Liège). *Hemipneustes striatoradiatus* is widely distributed in the type area of the Maastrichtian Stage and ranges from the Lanaye Member (Gulpen Formation) to the uppermost Meerssen Member (Maastricht Formation; Jagt, 2000), providing 'secondary substrates' *par excellence* throughout its range. In this particular case, the oyster larva settled on the inside of a broken test, near the anterior unpaired ambulacrum, and

extended growth laterally and posteriorly, closely following the broken margins of the test (Fig. 2B) and then becoming elevated. The shell did not protrude through the peristome (15.9 mm in width), as seen in Figure 2C. The oyster measures 65.5 mm in greatest height and 59.2 mm in greatest width; the muscle scar (Fig. 2A) is 16.0 by 17.2 mm, and the thickness of the echinoid test is 3.8 mm. Unfortunately, the right valve is not preserved; this would have shown a considerable upper bulge, and a flatter basal area to account for the concavity of the echinoid test overgrown. Attached to the external shell surface of the oyster are some serpulid polychaetes (Fig. 2B).

The third and last example is more or less comparable, involving the same pycnodonteine species, but attachment was to a test fragment of a regular echinoid, a phymosomatid (Fig. 2D, E). The oyster is a particularly thick-shelled individual, which has a prominent older growth stage on account of having settled on a fairly narrow and strongly concave substrate. Unfortunately, the right valve is not preserved; this would have shown a convex umbonal portion, possibly with a subdued image of the ambulacral/interambulacral plating of the echinoid. The oyster measures 52.1 mm in greatest width and 90.7 mm in greatest height, the muscle scar being obscured by a flint nodule. From what is visible of the fragmentary
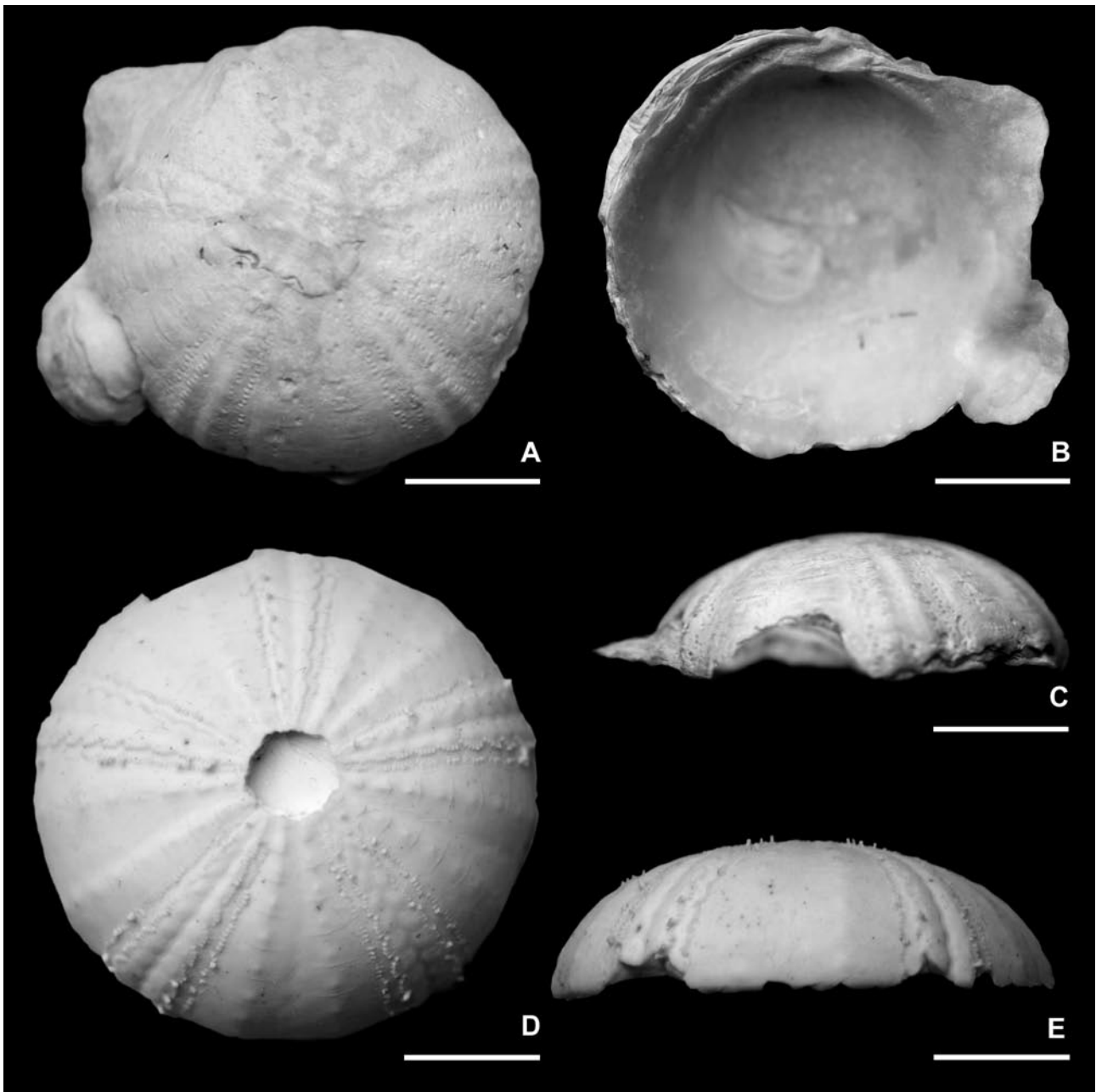

Figure 1A-C. Outer, inner and lateral views of a xenomorphic oyster (*Ostrea edulis* Linné, 1758; left valve, NHMM 2006 052, leg. Roelse), respectively, from low-tide line at La Grande Plage (St Cast, Bretagne, France). **D, E.** Silicone rubber infill of an average-sized test of a Recent *Paracentrotus lividus* (Lamarck, 1816), NHMM 2006 053, from an unspecified locality in France. Scale bars equal 10 mm. Note the close match in proportions, ambulacral/interambulacral shadowing and pore arrangement (5-geminate).
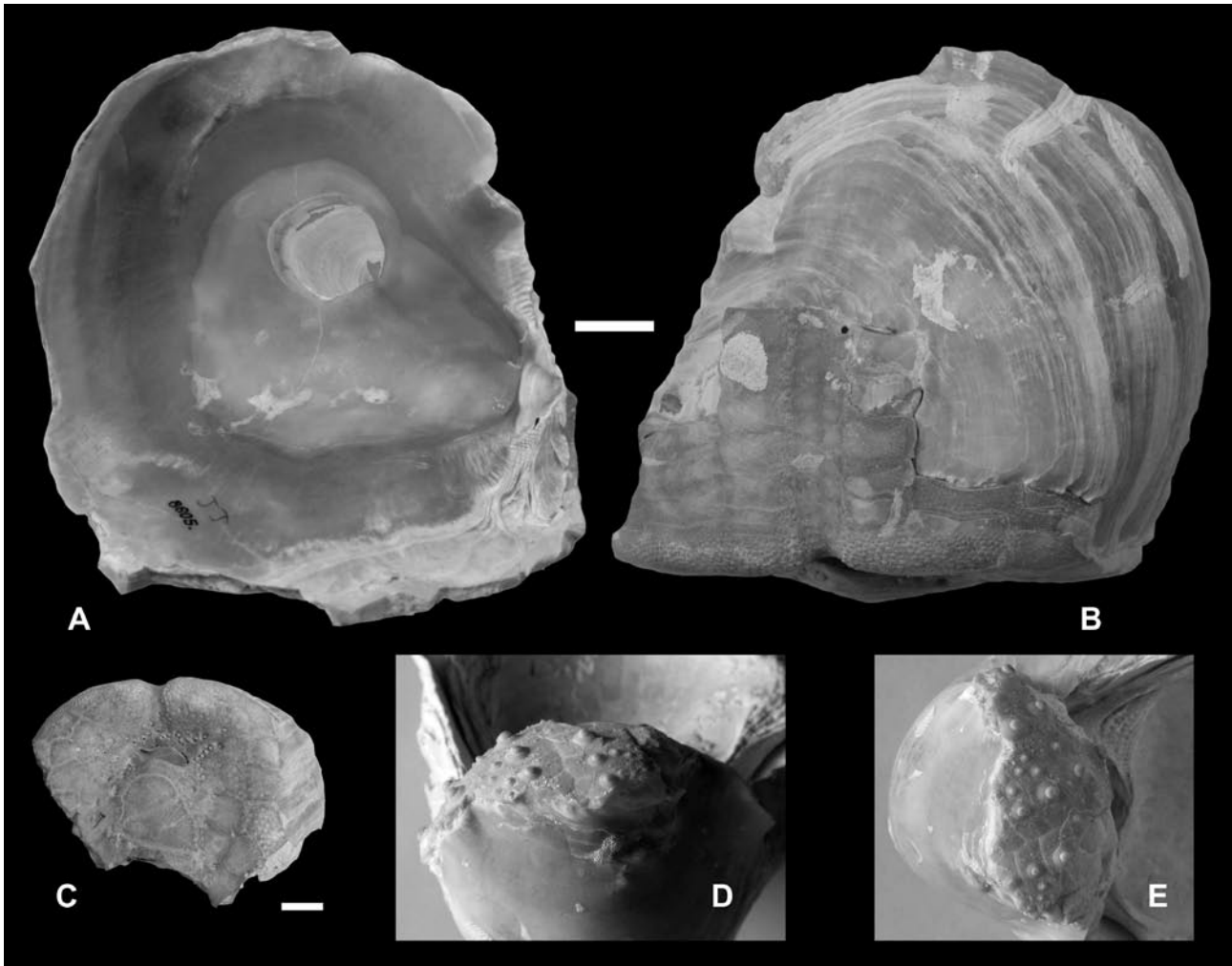
Figure 2A-C. Large-sized pycnodonteine oyster (*Pycnodonte vesicularis* (Lamarck, 1806)) following closely the rim of a broken test of *Hemipneustes striatoradiatus* (Leske, 1778), NHMM JJ 8805, from the CBR-Romontbos quarry, Eben Emael (Bassenge, Liège), Maastricht Formation, lower Nekum Member (subunit IVe-1). **A.** inside of valve; note muscle scar in centre; **B**. external view; **C**. lower view of test, with oyster sealing off peristome of echinoid, but not protruding from it. **D, E.** Large-sized and thick-shelled individual of *P. vesicularis* from the lower Maastrichtian of Rügen (northeast Germany), attached to a test fragment of the phymosomatid echinoid, *Rachiosoma granulosa* (*sensu* Kutscher, 2003 = *Gauthieria middletoni sensu* Smith & Jeffery, 2000). Private collection of Thomas Rößner (Berlin). Scale bars equal 10 mm.

test, the echinoid can be identified as *Rachiosoma granulosa sensu* Kutscher, 2003 (= *Gauthieria middletoni sensu* Smith & Jeffery, 2000); the test diameter is estimated to have been approximately 30 mm.

4. Discussion

Of prime importance in determining the attachment position of suspension-feeding animals, such as oysters, are physical-hydrodynamic parameters. In soft-bottom communities, such as the one represented at the sandy seashore of La Grande Plage (St Cast, Bretagne), secondary hardgrounds are frequently colonised since these are low in number (i.e., limited ecospace). In addition, there is fierce competition for such substrates, meaning that occasionally oyster larvae have to make do with what is available right there and then. The fact that the larva of *Ostrea edulis* settled on the inside of an echinoid test proves that this must have been broken around the peristome already and was positioned peristome

up. The fact that there is no adhering calcareous test material in NHMM 2006 052 is problematic; normally, oyster cementation to substrates is so tight that oyster and substrate are rarely separated. A possible explanation may be that there was still some organic material (film) present inside the echinoid test when the oyster larva settled, rapidly grew and thus filled the available space.

The examples above illustrate peculiar examples of oyster spat settling inside partially broken echinoid tests. Such occurrences may be expected to be commoner than recorded to date; collecting bias is strong in this case. Collectors tend to disregard broken echinoid tests and oysters are not amongst their favourites, either (Kutscher, 1997). In contrast to other biota, such as spirorbid and serpulid polychaetes as well as cheilostome bryozoans, oyster settlement and growth on the inside of whole echinoid tests appears to be extremely rare. 'Whole' is this case means unfragmented, but naturally without apical and peristomial plating. Judging from the occurrence of numerous juvenile specimens, the mortality rate

amongst attached oysters must have been high, and only a certain percentage of specimens reached maturity and attained large sizes. It may be that settlement inside whole echinoid tests severely restrained growth and thus led to premature death; only more examples of 'views from within' can determine this.

5. Acknowledgements

6. References

ABDEL-GAWAD, G.I., 1986. Maastrichtian non-cephalopod mollusks (Scaphopoda, Gastropoda and Bivalvia) of the Middle Vistula Valley, Central Poland. *Acta Geologica Polonica*, **36**: 69-224.

AQRABAWI, M., 1993. Oysters (Bivalvia-Pteriomorphia) of the Upper Cretaceous rocks of Jordan. Palaeontology, stratigraphy and comparison with the Upper Cretaceous oysters of northwest Europe. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, **75**: 1-135.

CARTER, R.M., 1968. Functional studies on the Cretaceous oyster *Arctostrea*. *Palaeontology*, **11**: 458-485.

CARTER, R.M., 1972. Adaptations of British Chalk Bivalvia. *Journal of Paleontology*, **46**: 325-340.

CLEEVELY, R.J. & MORRIS, N.J., 2002. Introduction to molluscs and bivalves. In: *Fossils of the Chalk* (2nd edition) (A.B. SMITH & D.J. BATTEN, eds). Palaeontological Association, Field Guides to Fossils, **2**: 99-160.

COQUINOT, Y. & MARCHAND, D., 2004. Xenomorphic growth in ostreids: an example from the middle Oxfordian of Burgundy (Dijon, France). *The Palaeontological Association, Newsletter*, **57**: 147-148.

DARRAGH, T.A. & KENDRICK, G.W., 1991. Maastrichtian Bivalvia (excluding Inoceramidae) from the Miria Formation, Carnarvon Basin, north western Australia. *Records of the Western Australian Museum* (Supplement), **36**: vi + 1-102.

DHONDT, A.V. & DIENI, I., 1990. Unusual inoceramid-spondylid association from the Cretaceous Scaglia Rossa of Passo del Brocon (Trento, N. Italy) and its palaeoecological significance. *Memorie di Scienze Geologiche*, **42**: 155-187.

EVANS, S. & TODD, J.A., 1997. Late Jurassic soft-bodied wood epibionts preserved by bioimmuration. *Lethaia*, **30**: 185-189.

FRENEIX, S. & VIAUD, J.-M., 1986. Huîtres du Crétacé supérieur du Bassin de Challans-Commequiers (Vendée). Biostratigraphie, taxinomie, paléobiologie. *Bulletin trimestriel de la Société géologique de Normandie et Amis du Muséum du Havre*, **73**: 13-79.

GRÖNWALL, K.A, 1900. Släktet *Dimyodon* in Danmarks krita. *Meddelelser fra Danske geologiske Forening*, **6**: 73-80.

HAGENOW, F. von, 1842. Monographie der Rügen'schen Kreideversteinerungen. III. Abtheilung: Mollusken. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*, **9**: 528-575.

HANSSON, H.G., 1999. *European Echinodermata check-list. A draft for the European register of marine species (part of 'Species 2000') compiled at TMBL (Tjärnö Marine Biological Laboratory)*, 83 pp. [http://www.tbml. gu.se/libdb/taxon/taxa.html]

HARPER, E.M., 1991a. Post-larval cementation in the Ostreidae and its implications for other cementing Bivalvia. *Journal of Molluscan Studies*, **58**: 37-47.

HARPER, E.M., 1991b. The role of predation in the evolution of cementation in bivalves. *Palaeontology*, **34**: 455-460.

HODGES, P., 1991. The relationship of the Mesozoic bivalve *Atreta* to the Dimyidae. *Palaeontology*, **34**: 963-970.

JÄGER, M., 2004. Serpulidae and Spirorbidae (*Polychaeta sedentaria*) [*sic*] aus Campan und Maastricht von Norddeutschland, den Niederlanden, Belgien und angrenzenden Gebieten. *Geologisches Jahrbuch*, **A157**: 121-249.

JAGT, J.W.M., 1989. ..... And they never knew what hit them. *Correspondentieblad van de Nederlandse Malacologische Vereniging*, **248**: 538-541.

JAGT, J.W.M. & COLLINS, J.S.H., 1989. Upper Cretaceous cirripedes from N.E. Belgium. *Proceedings of the Geologists' Association*, **100**: 183-192.

JAGT, J.W.M., 1999. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium – Part 1: Introduction and stratigraphy. *Scripta Geologica*, **116**: 1-57.

JAGT, J.W.M., 2000. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium – Part 4: Echinoids. *Scripta Geologica*, **121**: 181-375.

JAGT, J.W.M. & SIMON, E., 2004. A pedunculate brachiopod population preserved *in situ* (Late Maastrichtian, NE Belgium). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **74**: 97-103.

KUTSCHER, M., 1997. Fossile Austern – mehr als nur ein 'Verzweiflungs'-Mitbringsel. *Arbeitskreis Paläontologie Hannover*, **25**: 49-60.

KUTSCHER, M., 2003. Bestimmungschlüssel der Seeigel (*Echinoidea*) [*sic*] der Weißen Schreibkreide (Kreide, Unter-Maastrichtium) von Rügen (Deutschland) und Møn (Dänemark). *Erratica*, **5**: 3-41.

LAMARCK, J.B.A.P.M. de, 1806. Mémoires sur les fossiles des environs de Paris, comprenant la détermination des espèces qui appartiennent aux animaux marins sans vertèbres, et dont la plupart sont figurés dans la collection des vélins du Muséum. *Annales du Muséum d'Histoire naturelle (Paris)*, **8**: 156-166.

LAMARCK, J.B.A.P.M. de, 1816. *Histoire naturelle des animaux sans vertèbres, 3. Les échinides*. Paris, Déterville & Verdière, 59 pp.

LEHMANN, J. & WIPPICH, M.G.E., 1995. Oyster attachment scar preservation of the late Maastrichtian ammonite *Hoploscaphites constrictus*. *Acta Palaeontologica Polonica*, **40**: 437-440.

LESKE, N.G., 1778. *Jacobi Theodori Klein Naturalis dispositio Echinodermatum, edita et descriptionibus novisque inventis et synonymis auctorum aucta*. Leipzig, G.E. Beer, xxii + 278 pp.

LEWY, Z., 1972. Xenomorphic growth in ostreids. *Lethaia*, **5**: 347-351.

LINDNER, G., 1977. *Elseviers gids van de zeeschelpen*. Amsterdam/Brussel, Elsevier, 256 pp.

LINNÉ, C. von, 1758. *Systema naturae, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata, 1(6). Regnum animale*. Holmiae, Laurentii Salvii, iv + 824 pp.

MALCHUS, N., 1990. Revision der Kreide-Austern (Bivalvia: Pteriomorphia) Ägyptens (Biostratigraphie, Systematik). *Berliner geowissenschaftliche Abhandlungen*, **A125**: 1-231.

MORTENSEN, T., 1927 [1977]. *Handbook of the echinoderms of the British Isles*. Oxford, Oxford University Press/Rotterdam, W. Backhuys, ix + 471 pp.

MÜLLER, A.H., 1970. Dysodonta (Lamellibranchiata) als bemerkenswerte Epizoen auf Porifera. *Monatsberichte der deutschen Akademie der Wissenschaften Berlin*, **12**: 621-631.

NESTLER, H., 1965. Die Rekonstruktion des Lebensraumes der Rügener Schreibkreide-Fauna (Unter-Maastricht) mit Hilfe der Paläoökologie und Paläobiologie. *Beiheft zur Zeitschrift Geologie*, **49**: 1-147.

PALMER, T.J., TAYLOR, P.D. & TODD, J.A., 1993. Epibiont shadowing: a hitherto unrecognized way of preserving soft-bodied fossils. *Terra Nova*, **5**: 568-572.

REICH, M. & FRENZEL, P., 2002. Die Fauna und Flora der Rügener Schreibkreide (Maastrichtium, Ostsee). *Archiv für Geschiebekunde*, **3**: 73-284.

ROHR, D.M. & BOUCOT, A.J., 1989. Xenomorphism, bioimmuration, and biologic substrates: an example from the Cretaceous of Brazil. *Lethaia*, **22**: 213-215.

SCHMID, F., 1949. Orientierte Anheftung von *Ostrea vesicularis* Lamarck, *Dimyodon nilssoni* Hagenow und *Crania parisiensis* Defrance. *Mitteilungen aus dem geologischen Staatsinstitut Hamburg*, **19**: 53-56.

SMITH, A.B. & JEFFERY, C.H., 2000. Maastrichtian and Palaeocene echinoids: a key to world faunas. *Special Papers in Palaeontology*, **63**: 1-406.

SPAETH, C., 1985. Aufwuchs und xenomorphe Skulptur bei *Aetostreon latissimum* (Lamarck) (Ostreidae) aus dem Hauterivium von Helgoland. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, **59**: 57-70.

STENZEL, H.B., 1971. Oysters. In: *Treatise on Invertebrate Paleontology*, Part N, Mollusca 6, Bivalvia 3 (R.C. Moore, ed.). Boulder, Geological Society of America/Lawrence, University of Kansas Press, N953-N1224.

TAYLOR, P.D., 1988. A probable thecate hydroid from the Upper Cretaceous of southern England preserved by bioimmuration. *Paläontologische Zeitschrift*, **62**: 167-174.

TAYLOR, P.D., 1990a. Preservation of soft-bodied and other organisms by bioimmuration – a review. *Palaeontology*, **33**: 1-17.

TAYLOR, P.D., 1990b. Bioimmured ctenostomes from the Jurassic and the origin of the cheilostome Bryozoa. *Palaeontology*, **33**: 19-34.

TAYLOR, P.D. & LEWIS, D.N., 2005. *Fossil Invertebrates*. London, The Natural History Museum, 208 pp.

TAYLOR, P.D. & TODD, J.A., 1990. Sandwiched fossils. *Geology Today*, **6**: 151-154.

TAYLOR, P.D. & TODD, J.A., 2003. Bioimmuration. In: *Palaeobiology II* (D.E.G. Briggs & P.R. Crowther, eds.). Oxford, Blackwell Publishing, 285-289.

VOIGT, E., 1956. Der Nachweis der Phytals durch Epizoen als Kriterium der Tiefe vorzeitlicher Meere. *Geologische Rundschau*, **45**: 97-119.

VOIGT, E., 1966. Die Erhaltung vergänglicher Organismen durch Abformung infolge Inkrustation durch sessile Tiere, unter besonderer Berücksichtigung einiger Bryozoen und Hydrozoen aus der Oberen Kreide. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **125**: 401-422.

VOIGT, E., 1968. Über Immuration bei fossilen Bryozoen dargestellt an neuen Funden aus der Oberen Kreide. *Nachrichte der Akademie der Wissenschaften zu Göttingen, II. Mathematisch-physikalische Klasse*, **4**: 47-63.

VOIGT, E., 1979. The preservation of slightly or non-calcified fossil Bryozoa (Ctenostomata and Cheilostomata) by bioimmuration. In: *Advances in bryozoology* (G.P. Larwood & M.B. Abbott, eds.). Systematic Association, Special Volume, **13**: 541-564.

VOIGT, E., 1981. Erster fossiler Nachweis des Algen-Genus *Fosliella* Howe, 1920 (Corallinaceae, Rhodophyceae) in der Maastrichter und Kunrader Kreide (Maastrichtium, Oberkreide). *Facies*, **5**: 265-282.

VOIGT, E., 1996. Submarine Aragonit-Lösung am Boden des Schreibkreide-Meeres. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, **77**: 577-601.

VOIGT, E. & HILLMER, G., 1996. Soft-tissue moulds preserved by bioimmuration in the new bryozoan genus *Kunradocella* (Cheilostomatida). In: *Bryozoans in space and time* (D.P. Gordon & J.A. Grant-Mackie, eds.). Wellington, New Zealand: 361-366.