

Oyster life positions and shell beds from the Upper Jurassic of Poland

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Machalski, M. 1998. Oyster life positions and shell beds from the Upper Jurassic of Poland. — *Acta Palaeontologica Polonica* 43, 4, 609–634.

Life positions of three oyster species, *Actinostreon gregareum* (J. Sowerby, 1816), *Deltoideum delta* (Smith, 1817), and *Nanogyra virgula* (Defrance, 1820) from the Polish Upper Jurassic (Kimmeridgian and Volgian) sequences, mainly from the parautochthonous shell beds, are reconstructed. The oysters reveal variation in morphology and/or settling behaviour, which is interpreted in terms of ecophenotypic response to the fluctuations in sedimentation rate and the softness of substrate. Both *A. gregareum* and *D. delta* could 'choose' between a mud-sticking and reclining mode of life. The latter strategy is manifested e.g., by a cup-shaped, *Gryphaea*-like morphotype documented for the first time in *D. delta*. *N. virgula* was previously regarded as a cup-shaped recliner, but the collected material suggests that many specimens could live in a lateral position or form clusters composed of mutually attached specimens. Sedimentation rates during the oyster life cycles can be inferred from the reconstructed oyster life positions and ranged from approximately 7–13 cm in the case of largest mud-sticking specimens to nil in flat, fan-shaped recliners. The oyster life habits can thus provide valuable insights into sedimentary and ecologic dynamics of oyster shell beds. The *Actinostreon* beds originated under dynamic bypassing conditions, whereas *Deltoideum* beds in a regime of starvation or total bypassing of sediment. In the case of the *Nanogyra virgula* beds, the evidence is ambiguous due to difficulties in reconstructing the life attitude of many specimens of this species.

Key words: Oysters, life positions, mud-stickers, recliners, ecophenotypy, shell beds, palaeoecology, sedimentology, Upper Jurassic, Poland.

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Introduction

After an initial phase of encrustation, many oysters lift their commissure off the hard substrate and develop morphologies, which reflect ecophenotypic (*sensu* Mayr 1966) or evolutionary response to the soft-bottom conditions (Stenzel 1971; Seilacher 1984,

1985). According to Seilacher (1984), they belong to 'secondary soft-bottom dwellers', which changed from rocky substrates to soft, muddy bottom. This group may be divided into two categories, corresponding to different life habits: (1) recliners which rest on the soft substrate (often partially sunk in it), and (2) mud-stickers passively stabilized by the surrounding sediment in vertical position with the umbones directed downwards.

Life positions of fossil oysters and oyster-like bivalves may be reconstructed based on: (1) functional morphology of the shells, a paradigm approach (Seilacher 1984: fig. 4; Fürsich & Oschmann 1986a, b; Lewy 1996); (2) comparison with Recent relatives (Chinzei *et al.* 1982); (3) growth relations of successive oyster generations cemented together (Seilacher *et al.* 1985; Machalski 1989); (4) distribution and orientation of epizoans and borings (Bayer *et al.* 1985); (5) imprints of the bioimmured (*sensu* Taylor 1990) substrate on the left, and the corresponding xenomorphic (*sensu* Stenzel 1971) sculpture on the right, valve (Machalski 1989); and (6) field observations of *in situ* preserved specimens (Hecker *et al.* 1962: p. 66; Fürsich 1980; Chinzei 1986).

Oysters belonging to the 'secondary soft-bottom dwellers' group often form spectacular shell beds in the fossil record (e.g., Hecker *et al.* 1962; Hudson & Palmer 1976; Flatt 1976; Seilacher 1984; Littlewood & Donovan 1988; Kidwell 1990). With some notable exceptions where specimens are still preserved in life position (e.g., Littlewood & Donovan 1988; Jimenez *et al.* 1991; Demarcq & Demarcq 1992), oysters in shell beds have usually been reoriented due to reworking by hydrodynamic agents. Reconstructed life positions of such displaced oysters provide a valuable information for deciphering the sedimentary and ecologic dynamics of oyster beds (Seilacher *et al.* 1985; Seilacher 1989; Fürsich & Oschmann 1986a, b; Machalski 1989). This, in turn, may help in the placement of oyster beds within the more general environmental framework, e.g., within that of sequence stratigraphy (Brett 1995).

In the present study I attempt to reconstruct life positions of some Late Jurassic (Kimmeridgian and Volgian) 'soft-bottom' oysters from Poland and discuss their significance for the recognition of ecologic and sedimentary dynamics of oyster shell beds. In this context I will also touch the problems of discrimination between ecophenotypic and evolutionary characters in fossil oysters.

The Jurassic oysters from Poland were described by Pugaczewska (1971). Some ecologic and sedimentologic aspects of the Kimmeridgian oyster shell beds were discussed by Kutek (1969), Dzik (1979), Seilacher *et al.* (1985), Machalski (1989), and Kutek *et al.* (1992). The present study is based on a part of an unpublished Ph.D. dissertation on the lower Kimmeridgian oyster shell beds (Machalski 1993). The oyster material described here (collected by myself, J. Dzik and the late H. Pugaczewska) is housed in the Institute of Palaeobiology, Polish Academy of Sciences, Warsaw (abbreviated ZPAL).

Geologic background

Most of the material under discussion comes from the lower Kimmeridgian deposits cropping out in the so-called Mesozoic Border of the Holy Cross Mountains, central

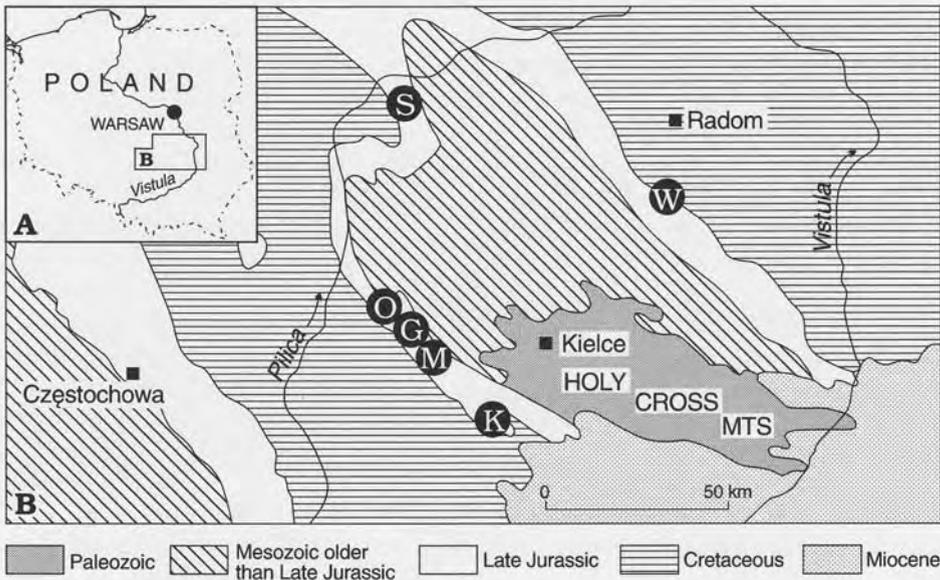


Fig. 1. Geographic and geologic setting of the Upper Jurassic oyster-bearing localities. A. Location map with the study area indicated. B. Geologic map of the study area to show the oyster-bearing localities. Explanations: K – Korytnica, M – Małogoszcz, G – Gruszczyn, O – Oleszno, S – Sławno, W – Wierzbica (modified after Kutek, Matyja & Wierzbowski 1992).

Poland, and representing the lower part of the Coquina Formation (Kutek 1994b). These deposits belong to the Hypselocyclum and Divisum zones in the standard biostratigraphic scheme (Kutek 1994b; Gutowski 1998). The material was collected in the huge cement plant quarries at Małogoszcz and Wierzbica, and in smaller outcrops at Gruszczyn, Oleszno and Korytnica (Fig. 1; for detailed geology and locality details see Kutek 1968, 1969; Seilacher *et al.* 1985; Gutowski 1998).

The Coquina Formation is a transgressive-regressive unit that consists of diverse oyster coquinas alternating with micritic and biomicritic limestones, marls and clays (Kutek 1994b). The base of the Formation is in many places a prominent hardground (Kaźmierczak & Pszczółkowski 1968), that caps the deposits formed in a restricted, probably oxygen-poor environment (Gutowski 1990; Kutek 1994b; Radwański 1995; Machalski 1993, 1996). Spectacular *Actinostreon* shell beds (Fig. 2A; = *Lopha* beds, *Alectryonia* beds of previous authors) from 0.3 to 10 m in thickness are widespread near the base of the Formation, occurring over the whole area around the Holy Cross Mountains. It is assumed that originally, prior to the post-Laramide erosion that removed Jurassic rocks from the present-day area of the Holy Cross Mountains, these shell beds covered an area of at least 10,000 sq. kilometres (Seilacher *et al.* 1985). Higher in the Coquina Formation, the proportion of clay and marl increases and *Actinostreon* is replaced by *Nanogyra nana* and *N. virgula*, that form diverse accumulations (Fig. 2B; Machalski 1993). The Małogoszcz quarry provides the best exposed section (Fig. 3) of the lower part of the Coquina Formation, known as Skorków Lumachelle (Kutek 1968; Seilacher *et al.* 1985).

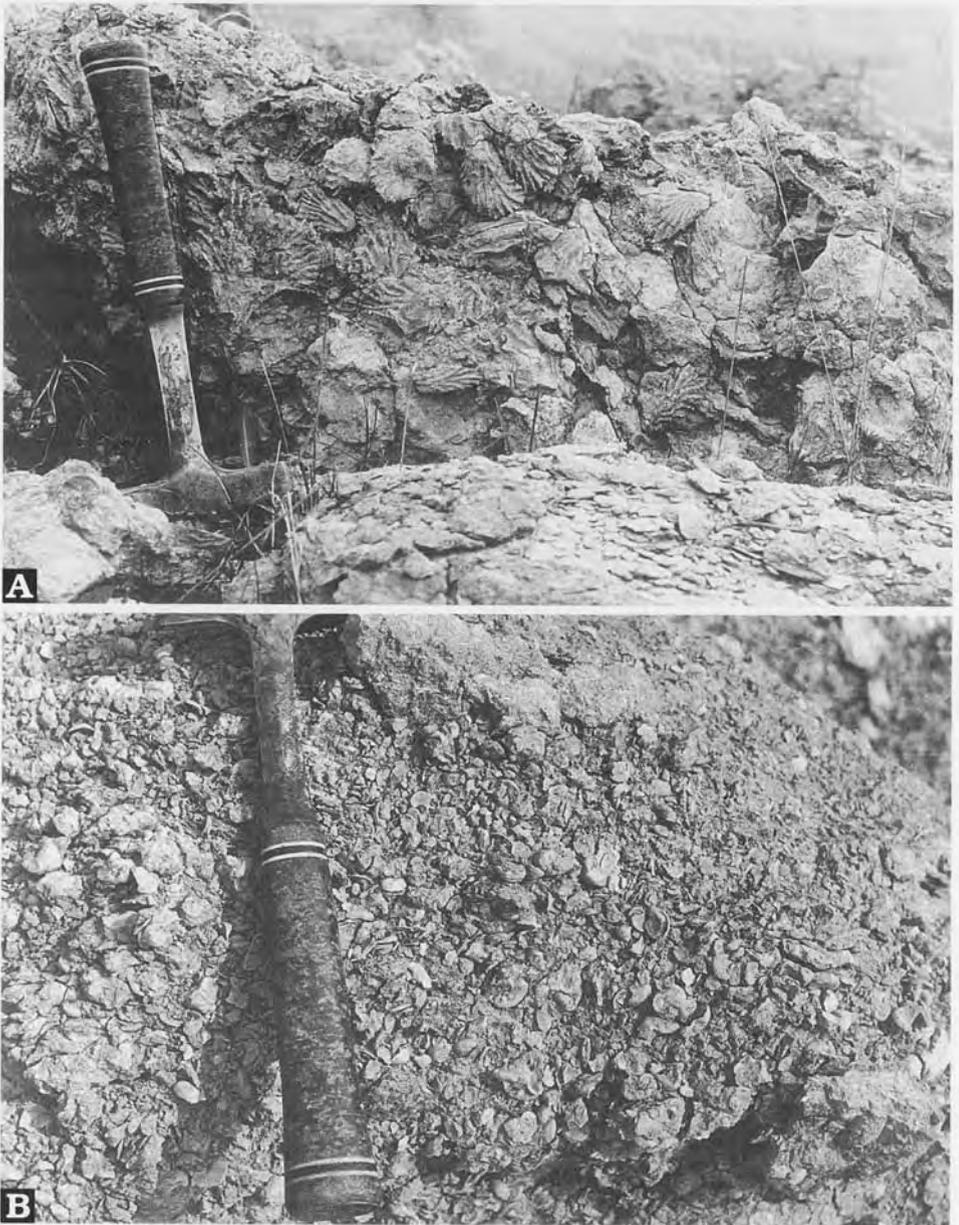


Fig. 2. Examples of the Upper Jurassic oyster shell beds of the Mesozoic border of the Holy Cross Mountains; Wierzbica quarry. **A.** *Actinostreon* shell bed. **B.** *Nanogyra virgula* shell bed. The hammer is 32 cm long.

Additional oyster materials come from a single outcrop of the middle Volgian limestones at Sławno in the same area (Fig. 1B). The limestones belong to the basal part of the Kcynia Formation and represent the Scythicus Zone (Kutek 1994a, b).

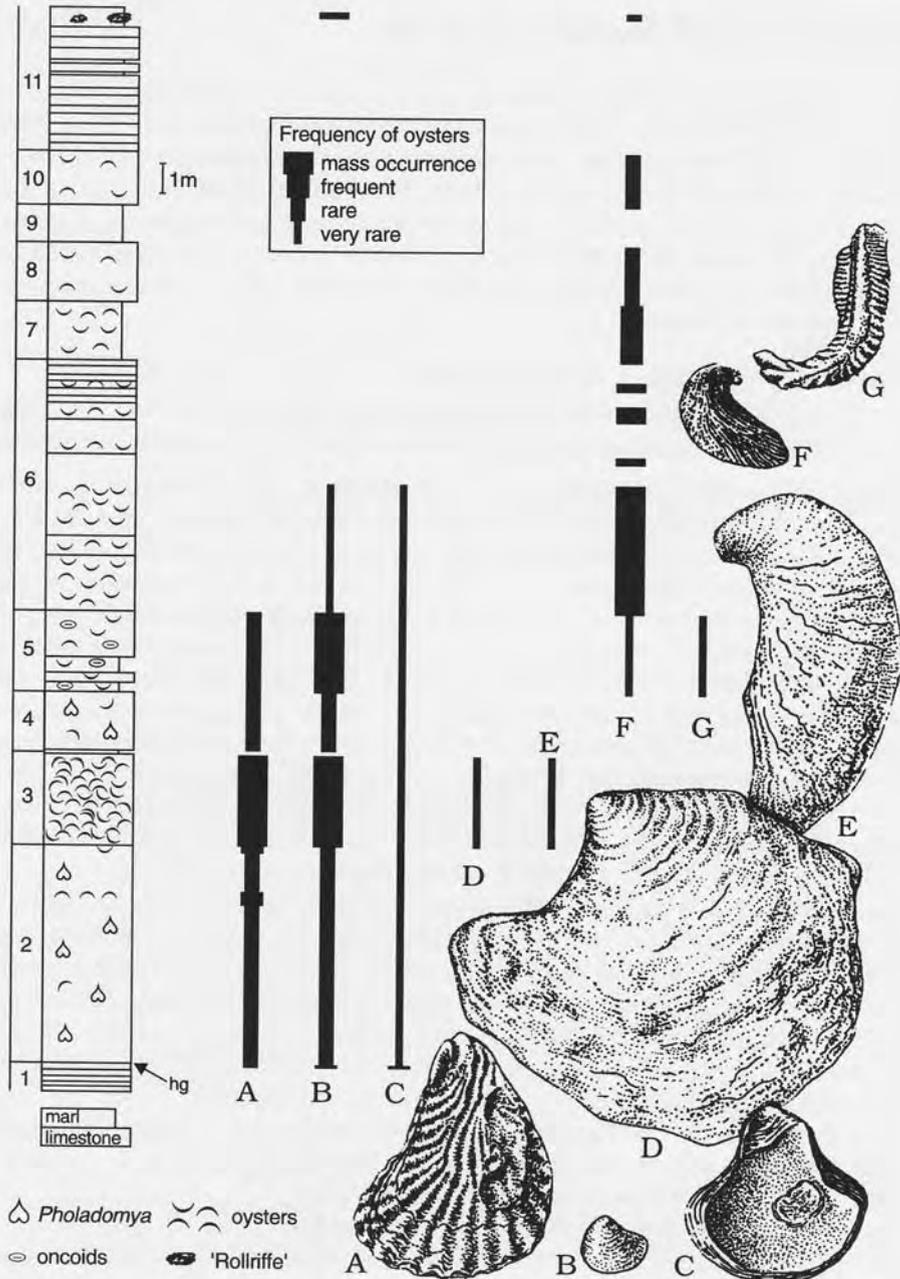


Fig. 3. Part of the Upper Jurassic section exposed in the Małogoszcz quarry to show the lithology of the Skorków Lumachelle (units 2–10) and distribution of oysters. Note *Actinostreon* shell bed (unit 3) sandwiched between *Pholadomya*-rich wackestones (units 2, 4). The illustrated profile starts with laminated mudstones capped by an intensively bored and encrusted hardground. The 'Rollriffe' have oyster/stromatolitic/serpulid framework (Machalski & Żywiecki in preparation). A – *Actinostreon gregareum*, B – *Nanogyra nana*, C – '*Liostrea*' spp., D – *Deltoideum delta*, E – *Gryphaea dilatata*, F – *Nanogyra virgula*, G – *Rastellum erucum*.

Life positions of Jurassic oysters

In the material from the Upper Jurassic deposits of the Holy Cross Mountains area, I have identified seven oyster species belonging to five genera (Machalski 1993). From the perspective of this study, the most interesting are the palaeolophid *Actinostreon gregareum* (J. Sowerby, 1816), and the gryphaeids *Nanogyra virgula* (Defrance, 1820) and *Deltoideum delta* (Smith, 1817) (the genus and family-level assignment of species follows that of Malchus 1990, except for *D. delta* which is now considered a member of Gryphaeidae, Malchus personal communication 1998). All these taxa occur abundantly in the studied deposits.

Actinostreon gregareum (J. Sowerby, 1816)

This plicate and generally equivalved oyster occurs in the lower part of the Coquina Formation, either forming geographically widespread shell beds (see above) or solitarily.

Shell bed recliners and mud-stickers. — The shell beds are exposed at the localities Małogoszcz, Wierzbica, Gruszczyn, Korytnica and Oleszno (Fig. 1B). They are composed mainly of densely packed oyster shells and their fragments (usually with a high proportion of articulated specimens; see Fig. 2A) set in the marly limestone matrix. The oysters are accompanied by skeletons of other epifaunal and semi-infaunal organisms such as serpulids, crustose bryozoans, terebratulid brachiopod *Epithyris subsella*, small thecideidid brachiopods, bivalves *Arcomytilus pectinatus*, *Falcimytilus* sp., *Trichites* sp., *Isognomon* sp., *Radulopecten* sp., *Gervillia*, and regular echinoids (isolated plates and spines). Chaotic orientation of the shells and their partial fragmentation both indicate that the shell bed formation was associated with high energy events (Kutek 1969; Seilacher *et al.* 1985; Machalski 1993). On the other hand, the high frequency of articulated specimens suggests that the shell beds are parautochthonous (*sensu* Kidwell *et al.* 1986) remnants of oyster banks (Machalski 1993).

Specimens from the shell beds (Fig. 4A–D, G, H, J, L, M) range from straight and elongated to fan-shaped. In terms of functional morphology, the elongated shape (e.g., Fig. 4G, H) can be regarded as indicative either of the mud-sticking habit or of competition for space between specimens growing close to each other. Because no traces of contact with adjacent individuals are present in discussed material, I regard the elongated specimens as stick-shaped mud-stickers (Seilacher 1984). As concerns the fan-shaped individuals (e.g., Fig. 4M), their shape is more ambiguous in functional terms – they could be either spoon-shaped mud-stickers or fan-shaped recliners in Seilacher's (1984) scheme. Fortunately, criteria other than morphology are available for reconstructing the life positions of these oysters.

The majority of the *Actinostreon* specimens are attached to their congeners, forming sometimes what could be called bunches (or bouquets in terminology of rudist workers, see Skelton & Gili 1991) (Fig. 4H, L). At Małogoszcz a few actinostreons are attached to another bivalve *Gervillia* sp., which is preserved as bioimmured fragments on left valves, and as xenomorphic replicas on the right valves of the oysters (Fig. 4A, B). Among 326 *Actinostreon* specimens counted in a loose block of the coquina from Małogoszcz, 19 were colonizing *Gervillia* sp. In one case two individuals were found attached to a single specimen of *Gervillia* sp. Very few *Actinostreon* from the shell beds are attached to other shelly substrates (e.g., terebratulids, *Nanogyra nana*, and echinoid spines).

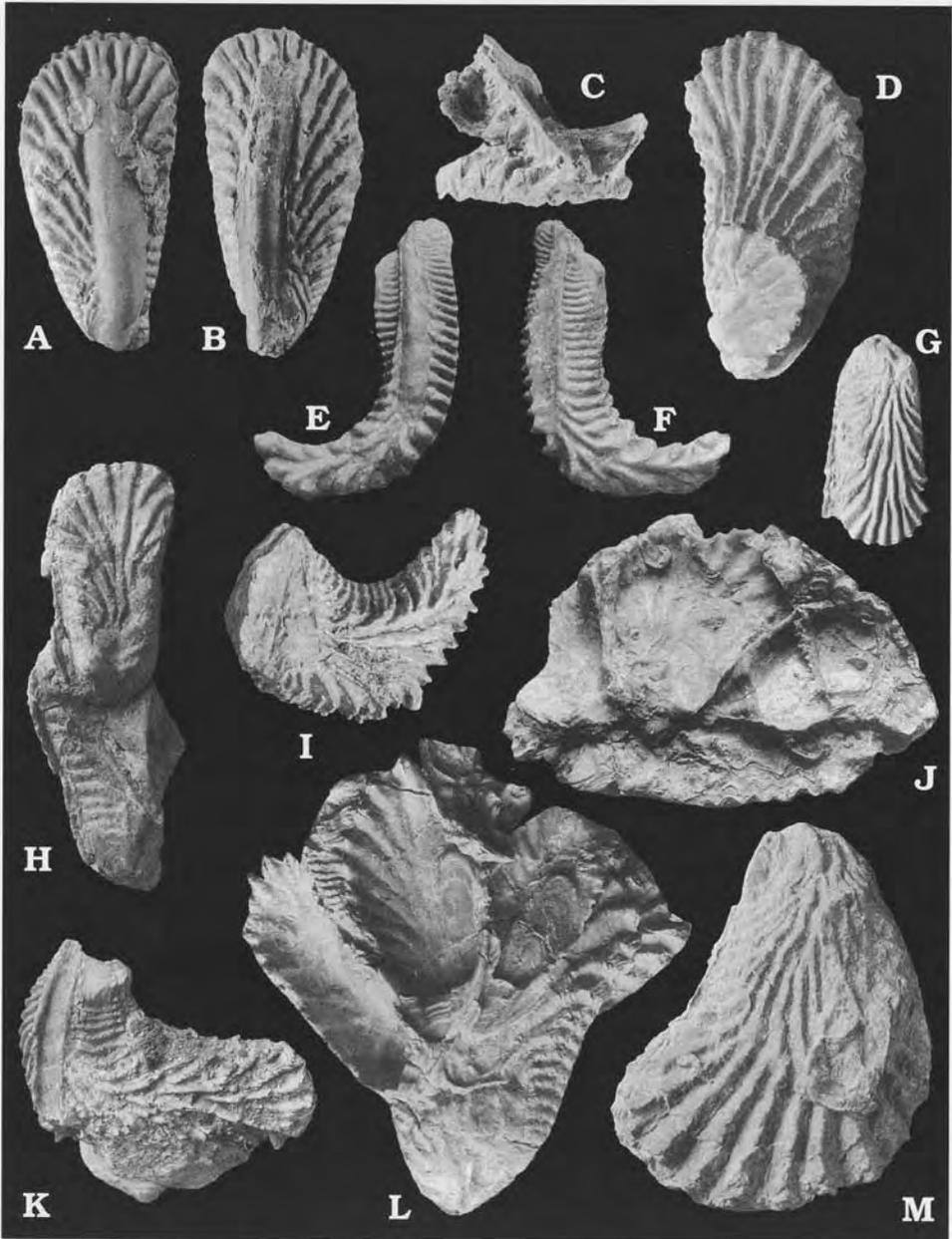


Fig. 4. *Actinostreon gregareum* (A–D, G–M) and *Rastellum erucum* (E, F) from lower Kimmeridgian of Korytnica (E, F, I, K), Oleszno (C, J) and Matogoszcz (A, B, D, G, H, L, M). Specimens A, B, E, F, I, K attached to *Gervillia* sp., the remaining specimens attached to their congeners. A, B. ZPAL L.V/ 74, RV (right valve, A) with a xenomorphic replica and LV (left valve, B) with bioimmured fragment of the host. C. ZPAL L.V/82. D. ZPAL L.V/75. E, F. ZPAL L.V/88, RV and LV view, respectively. G. ZPAL L.V/67, RV view. H. ZPAL L.V/78. I. ZPAL L.V/63. J. ZPAL L.V/83. K. ZPAL L.V/ 84, LV view. L. ZPAL L.V/81. M. ZPAL L.V/70. All specimens $\times 0.7$.

In most cases when the oysters are attached to their congeners, the growth directions of the successive generations are the same (Fig. 4D, H, L). The same is true for the majority of the *Actinostreon/Gervillia* pairs (Fig. 4A, B). According to Seilacher *et al.* (1985: fig. 6) this uniformity in growth directions points to a vertical life position, i.e. to a mud-sticking habit (Fig. 5A: 1, 2). This is supported by my field observations of the rare, vertically preserved *Actinostreon* bunches in the *Pholadomya*-rich wackestones that are interbedded with the shell beds. Within the shell beds themselves the presumed mud-stickers are reoriented, providing evidence of their reworked nature. The growth of particular bunches probably started on horizontal, reworked shells of former generations, as indicated by a single specimen from Oleszno (Fig. 4C). Recent *Crassostrea virginica* develops similar bunches of vertically growing specimens on muddy bottoms (Galtsoff 1964; Bahr & Lanier 1981).

Less frequent is the situation when the next-generation colonists show different growth orientation than their host (Fig. 4J). This suggests their horizontal life position as mud- or shell-supported recliners (Fig. 5B: 3; see also Seilacher *et al.* 1985).

Solitary recliners. — A distinct 'population' of *Actinostreon*, represented by scattered individuals, was found in Korytnica (Fig. 1B), in a marly oncolitic limestone layer overlying a thin *Actinostreon* bed, which forms the very base of the Coquina Formation there. The oncolitic layer also contains another palaeolophid *Rastellum erucum* (De-france, 1833) (Fig. 4E, F), numerous brachiopods, bivalves and, quite frequently, regular echinoids.

Specimens from Korytnica differ significantly in morphology from those from the shell beds, being strongly incurved posteroventrally (Fig. 4I, K). Moreover, the plicae are more densely spaced and have small funnel-shaped spines (see Carter 1968) on their crests, feature not observed in the specimens from the shell beds (Fig. 4I, K). The sickle shape of these oysters is well suited to the reclining mode of life (Fig. 5C: 4), representing the outriggered recliners category of Seilacher (1984). The same life position may be postulated for the similarly shaped, albeit narrower *R. erucum* from the same horizon (Fig. 5C: 5).

Approximately 80% of the 67 specimens from the oncolitic bed are attached to *Gervillia* and the growth directions of both the founder and its host are usually identical at their early growth stages (Fig. 4I, K). All *Rastellum* (26 specimens) from the same bed are attached to *Gervillia* too (Fig. 4E, F). This settlement preference is strange, considering that many other shelly substrates that should have been suitable for colonization were available in the original community. The uniformity in growth directions of *Gervillia* and palaeolophids at early growth stages also calls for an explanation. Were they 'incipient mud-stickers' that all failed to continue their vertical growth very early in the ontogeny (?reworking) and adjusted further growth in new life position? I am unable to answer this question.

Discussion. — In traditional, typologically oriented systematic palaeontology, several species could have been distinguished in the material from the *Actinostreon* shell beds. For example, the elongated morphotypes could have been determined as *A. rastellaris* (G. Münster, 1833), whereas the fan shaped ones as *A. solitarium* (J. de C. Sowerby, 1824). The presence of intermediate specimens between the extreme morphotypes

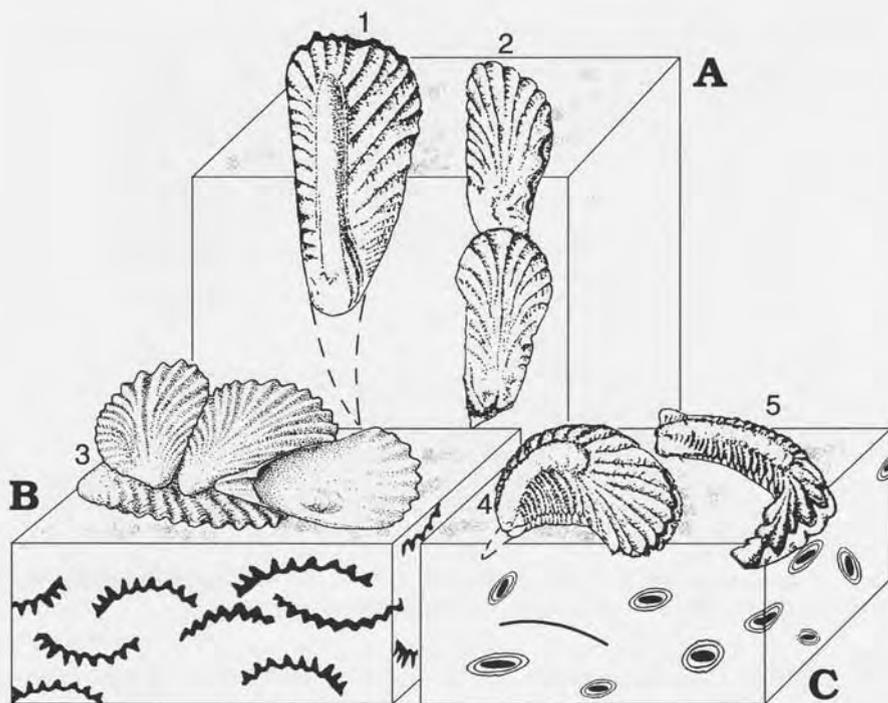


Fig. 5. Reconstruction of life positions of *Actinostreon gregareum* (A: 1, 2; B: 3; C: 4) and *Rastellum erucum* (C: 5). A. Mud-stickers. B, C. Recliners on shelly and oncolitic bottom, respectively. See text for further explanations.

(Fig. 6) strongly suggests, however, that only one biological species of *Actinostreon* is represented in the shell beds, as suggested earlier by Seilacher *et al.* (1985).

The morphology of *Actinostreon* from Korytnica corresponds well to that of *A. gregareum* (J. Sowerby, 1816) described from the English Corallian (see Arkell 1929–1937: pl. 22: 5–6; pl. 23: 1–4). The only difference lies in behaviour: in contrast to the Corallian specimens, which occur gregariously, forming clusters and even thin biostromes (Arkell 1929–1937; Fürsich 1977), the specimens from Korytnica occur solitarily.

The specimens from Korytnica may either be conspecific with those from the shell beds or may belong to a separate species. In the first case they would be only another ecophenotypic variant of the shell bed species. The problem is very difficult to resolve. The test proposed by Johnson (1981) for distinguishing the 'environmentally' controlled (ecophenotypic) variation from the 'genetically' controlled one, cannot be applied for the investigated oysters due to deformation of their early growth stages by bioimmuration and xenomorphism. I am convinced, however, that in both cases we are dealing with a single biological species *A. gregareum* (J. Sowerby, 1816). Such a conclusion seems to be reasonable in the light of the extreme ecophenotypic plasticity of Recent oysters documented by Thomson (1954), Galtsoff (1964), and Stenzel (1971).

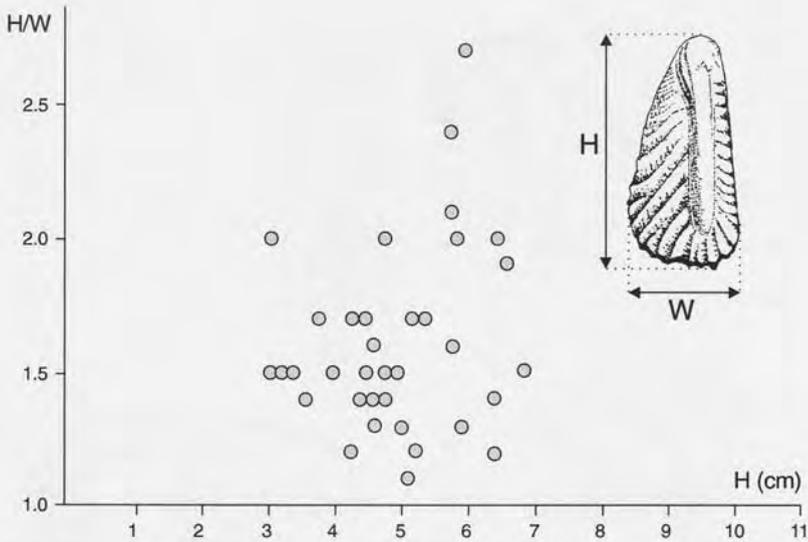


Fig. 6. Intrapopulation variability of *Actinostreon gregareum* from the shell bed at Małogoszcz, based on 36 specimens. Abbreviations: H – shell height, W – shell width.

Whatever the taxonomic position of the oysters, their distribution must have been strongly influenced by the sedimentation rate and the resulting type of the substrate. Vertical growth of mud-stickers is possible only when their shells are passively stabilized by surrounding sediment and must be tuned with its accumulation tempo. It seems reasonable to assume that at least the lower 50% of an animal must have been submerged in mud to allow its stabilisation in vertical position. Given that the maximum observed height of the *Actinostreon* shells from the shell beds is about 10 cm (Machalski 1993), the minimum rate of mud sedimentation may be suggested, although admittedly very roughly, as 5 cm during the life span of largest mud-sticking individuals (this, however, cannot be determined precisely in the investigated material). On the other hand, one may suggest that at least the upper 25% of the shell must have emerged above the sediment surface. This gives about 7 cm as a maximum value of sedimentation rate during the life span of largest mud-sticking oysters. In contrast, recliners, with their commissures close to the sea floor, could have grown only under conditions of a much lower, or even nil sedimentation rate (Fig. 5).

Deltoideum delta (Smith, 1817)

This is a large, generally flat oyster found in many outcrops of the Kimmeridgian Coquina Formation, mostly in the horizons well above the *Actinostreon* shell beds, and in the Volgian deposits at Sławno. Its shell is inequivalved, with a slight overlap of the left valve over the right one. The body cavity, usually very narrow in dorsal part and with a prominent branchitellum, acquires, during growth, a bottle or sickle shape. This shape is masked by prominent growth foliations flanking the anterodorsal and posterodorsal valve margins, so the specimens, in which the flanks are not broken off, are subtriangular in outline (see Arkell 1929–1937 and Stenzel 1971 for the detailed description and illustrations of the species).

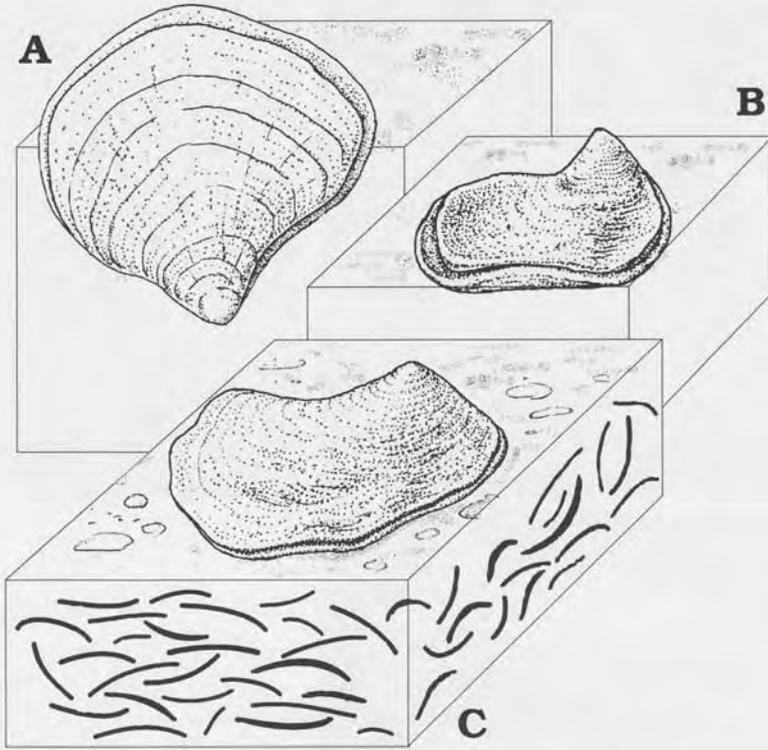


Fig. 7. Reconstruction of life positions of *Deltoideum delta*. A. Mud-sticker. B. *Gryphaea*-like recliner. C. Flat recliner on shelly bottom. See text for further explanations.

Kimmeridgian recliners and mud-stickers. — In the Kimmeridgian deposits the species occurs as scattered individuals or shell pavements and beds, up to 20 cm thick, which show evidence of reworking under high energy conditions (as indicated e.g., by overturned heavy shells of the associated *Gryphaea*). The high frequency of articulated specimens in many of these accumulations suggests their parautochthonous nature (Machalski 1993).

The life positions of the Kimmeridgian forms were discussed in Machalski (1989), based primarily on the material from the shell bed that occurs at the bottom of a clay unit at Wierzbica. The results may be summarized as follows:

1. Flat, fan-shaped specimens predominate. This morphology is ambiguous in functional terms, being indicative both of fan-shaped recliners and spoon-shaped mud-stickers in the scheme of Seilacher (1984).

2. A majority of the flat specimens reveal the traces of shelly substrates (imprints of the originally aragonitic shells and remnants of the calcitic ones) bioimmured throughout the whole surface of their left valve (Machalski 1989: figs 3, 5; for detailed treatment of the bioimmuration in *Deltoideum* see Todd 1993). This points to the reclining mode of life on shelly bottom with the left valve down (fan-shaped recliner, see Fig. 7C).

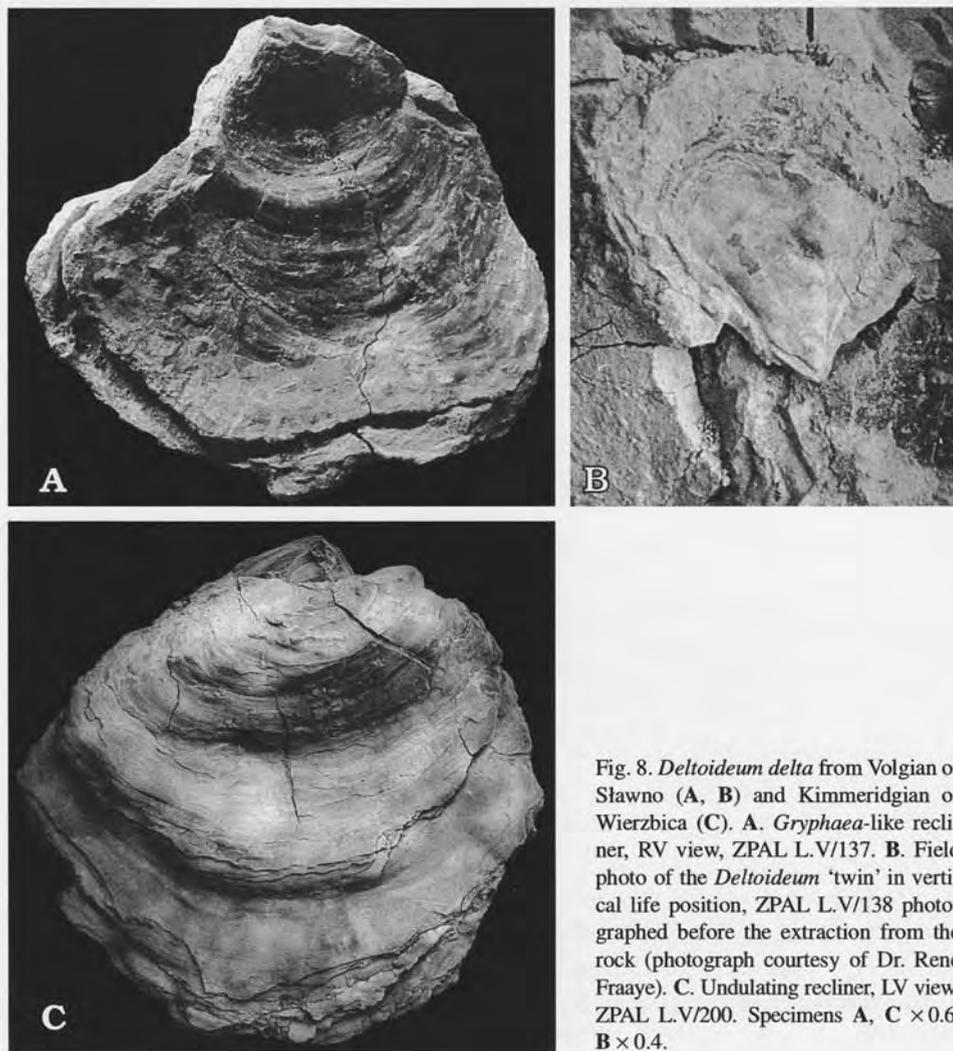


Fig. 8. *Deltoideum delta* from Volgian of Slawno (A, B) and Kimmeridgian of Wierzbica (C). A. *Gryphaea*-like recliner, RV view, ZPAL L.V/137. B. Field photo of the *Deltoideum* 'twin' in vertical life position, ZPAL L.V/138 photographed before the extraction from the rock (photograph courtesy of Dr. Rene Fraaye). C. Undulating recliner, LV view, ZPAL L.V/200. Specimens A, C $\times 0.6$, B $\times 0.4$.

3. A few specimens have their left valve slightly concave whereas their right valve is convex outwards (Machalski 1989: fig. 4). Traces of the substrate (small pieces of shells) are confined to peripheral zone of the concave left valve. These are also recliners, shaped and living like the Recent anomiid *Placuna* (i.e. in the convex-up position) and touching the bottom covered with shelly particles only with some parts of their left valve. The advantage of the convex-up shell form is that it allows for stability and prevents fouling on the relatively firm bottom, as convincingly suggested for many concavo-convex brachiopods by Lescinsky (1995).

4. Some other individuals are mutually cemented in pairs, in which both members, often articulated, show the same growth orientation (Machalski 1989: fig. 6). These 'twins' can be interpreted as mud-stickers, growing in parallel and almost simultaneously (one individual is always slightly smaller than the other) in the soft sediment.

A mud-sticking habit (Fig. 7A) can also be suggested for some rare solitary specimens that are extremely flat and lack any substrate traces, other than a minute attachment scar at the umbo. The vertical life position of the Kimmeridgian representatives of *Deltoideum* could not be confirmed by field evidence, as all the presumed mud-stickers in the shell beds are reoriented.

5. A unique specimen (Machalski 1989: fig. 7) lacks substrate traces at the part of the left valve corresponding to the early growth stage (with exception of a minute attachment trace at the tip of the umbo). The more adult part is irregular and patterned by the substrate imprints. This specimen may be interpreted as a mud-sticker which, after growing some time in vertical position, became eroded from the soft sediment and continued life in a horizontal position.

It may be added here that the latter specimen has a more than anecdotal significance, documenting that the 'choice' between a mud-sticking and a reclining mode of life depended only on environmental factors. Consequently, this specimen may be regarded as a 'natural experiment' proving that in the discussed material we are dealing with a single species rather than with morphologically similar but behaviourally different species.

Volgian mud-stickers and cup-shaped recliners. — At Sławno the oyster occurs as scattered individuals in pure micritic limestones, together with abundant other bivalves, dominated by *Pinna* sp. preserved usually in vertical life position.

Although the majority of *D. delta* occur here in a horizontal position, a few 'twins' identical to those occurring within the Kimmeridgian shell beds were also observed in a vertical position (Fig. 8B), thus confirming the mud-sticking habit of such associations. Among the horizontally preserved specimens, many reveal a morphology not encountered in the Kimmeridgian material. Their left valve is irregularly convex outwards, whereas the right one – consequently – is concave (Fig. 8A). The attachment scar in these specimens is small, and restricted to the umbonal part of the shell only. The resulted morphology approximates, though in a very imperfect way, that of *Gryphaea* (Hallam 1968; Seilacher 1984) or of the productid brachiopods (Każmierczak 1967; Brunton 1985; Lescinsky 1995). It also probably had the same functional task of stabilising the shell on the soft seafloor (cup-shaped recliners of Seilacher 1984).

Discussion. — The question arises whether the *Gryphaea*-like morphotypes from Volgian deposits are conspecific with *D. delta* from the Kimmeridgian. As concerns their internal morphology they show a similar dorsal narrowing of the body cavity as the Kimmeridgian material, so the difference is only in the external shape of the shell. A specimen newly collected at Wierzbica allows one to answer this question. Its surface bears prominent undulations, which are co-shaped with growth lines (Fig. 8C). These undulations indicate that the valve edge could change its growth direction during the life of one individual (probably as a result of fluctuating sedimentation rate). It is thus reasonable to conclude that the cup-like morphotype from Sławno is but an ecophenotypic variant of *D. delta*, formed in response to the soft bottom conditions (which are indicated independently by the micritic nature of the host sediment).

Like in the case of *Actinostreon*, the 'choice' between the mud-sticking and reclining habit of *D. delta* seems to be a response to the rate of the background sedimentation during the life of particular animals (Fig. 7). The vertically growing

specimens surely needed a relatively high tempo of the sediment accumulation to stabilize their shells. As the maximum height of *D. delta* shells is 17 cm, the sedimentation rate during their life span can be evaluated as at least around 7 cm and not more than around 13 cm (compare discussion on p. 618). In contrast, the flat reclining forms with their commissures just at the sediment-water interface surely could not survive any significant sediment input and the sedimentation rate during their life must have thus been very low to nil. The tempo of the sediment accumulation during the growth of *Gryphaea*-like individuals should have been intermediate between those of recliners and mud-stickers (Fig. 7).

Nanogyra virgula (Defrance, 1820)

The exogyrine oyster *Nanogyra virgula* (Fig. 9A–I) occurs in masses in the Coquina Formation in the same levels as *D. delta*, forming various shell beds (Fig. 2B). It is a small, helicospirally coiled oyster, with the overall shape varying from arcuate to bilobate. The left valve, covered with minute radial riblets, is invariably convex, and the right one – is flat or slightly concave. A rounded ridge runs dorso-ventrally along the left valve, dividing it into two fields – anterior and posterior. The angle between these fields, as seen in dorso-ventral section across the valve, ranges from obtuse to acute, depending on the specimen. The attachment scar at the umbonal region is usually very small (Fig. 9A), even when the available substrate is considerably larger (for the more detailed description of the species see Pugaczewska 1971; Gautret 1982; Fürsich & Oschmann 1986a, b).

Lateral recliners. — These were found in the basal *Deltoideum* shell bed of the clay unit exposed at Wierzbica (Machalski 1989). Some specimens from this bed reveal, besides the usual minute attachment scar at the umbo, also additional imprints of the bioimmured shell particles, which are restricted to the posterior field of the left valve (Fig. 9B). On the other hand, the serpulids colonizing the shells of some other *N. virgula* apparently during the life of the oysters (which is suggested by the uniformity of growth direction of the serpulids in respect to the valve margin of the oyster) are restricted to the anterior field of the left valve (Fig. 9D, E). Such a distribution of substrate imprints and serpulids indicates that these specimens reclined in a lateral position, touching the bottom only with the posterior field of the left valve (Fig. 10A: 1–2).

In all the specimens interpreted here as resting laterally on the bottom, the angle between the anterior and posterior fields of the left valve is normal or acute, but never obtuse. This would be expected from theoretical considerations, because the ‘obtuse’ valves would be unstable in the lateral position. On the contrary, they would be well suited for resting in the convex-down position.

Clusters. — A different growth strategy was followed by some individuals from another shell bed in Wierzbica (Fig. 2B), located a few metres below the clay unit. This shell bed, about 1 m thick and shell-supported, is composed of chaotically oriented, articulated and fragmented shells. The fossil assemblage consists of dominating *N. virgula*, associated with *D. delta*, other epifaunal or semi-infaunal bivalves such as *Isognomon*, *Camptonectes*, *Radulopecten* and *Stegoconcha*, brachiopods, cerithiid gastropods (preserved as substrate imprints on oysters), serpulids, bryozoans, and regular echinoids. Additionally, abundant echinoid grazing traces, representing the

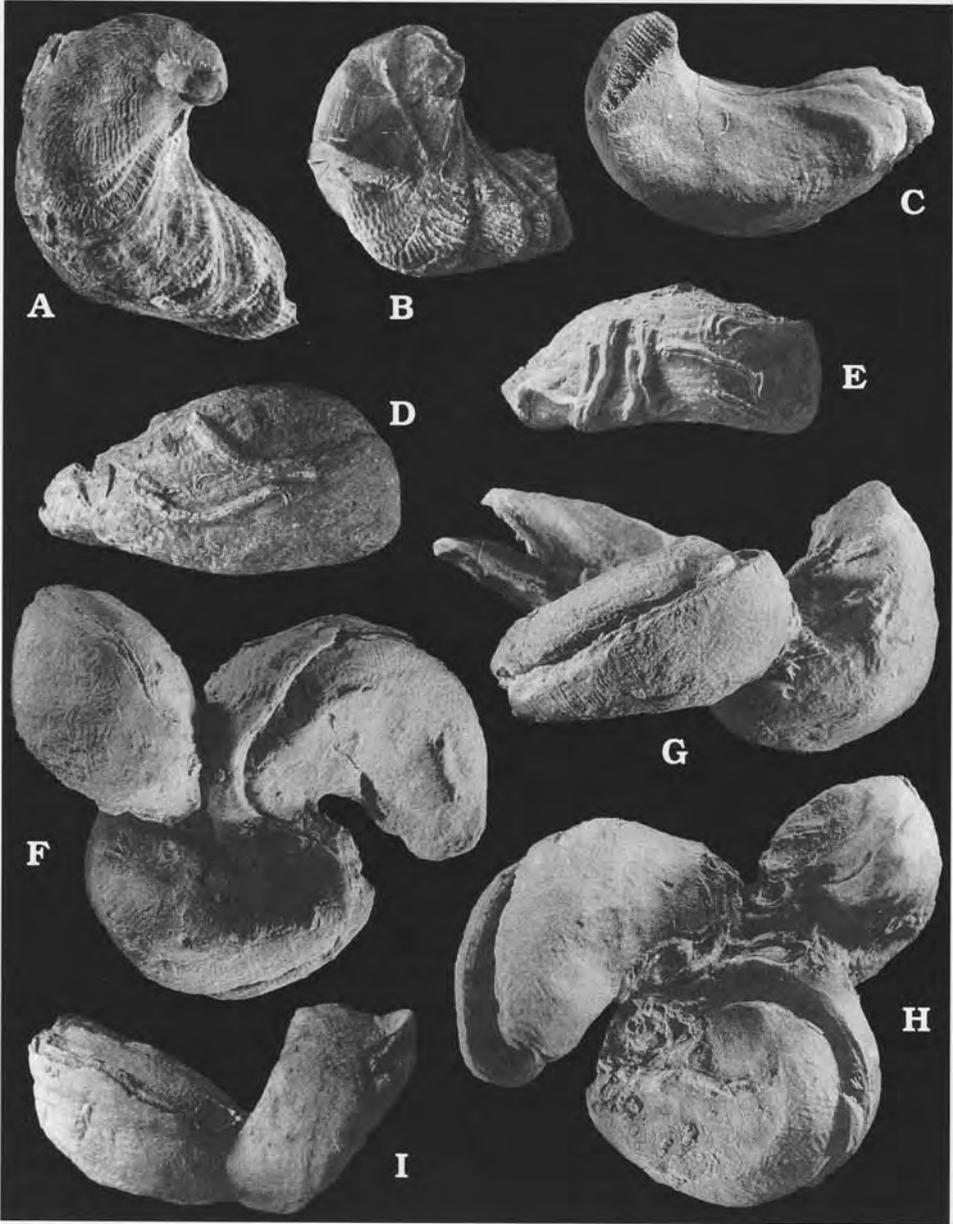


Fig. 9. *Nanogyra virgula* from lower Kimmeridgian of Wierzbica. A. ZPAL L.V/122. B. ZPAL L.V/123. C. ZPAL L.V/124. D. ZPAL L.V/125. E. ZPAL L.V/126. F–H. ZPAL L.V/128 with echinoid scratch marks obliterating the original sculpture of the shell. I. ZPAL L.V/127. All specimens $\times 2$. See text for further explanations.

ichnogenus *Gnathichnus* (see Bromley 1975), occur on a majority of the shells. The high frequency of articulated specimens suggests parautochthonous nature of the fossil assemblage.

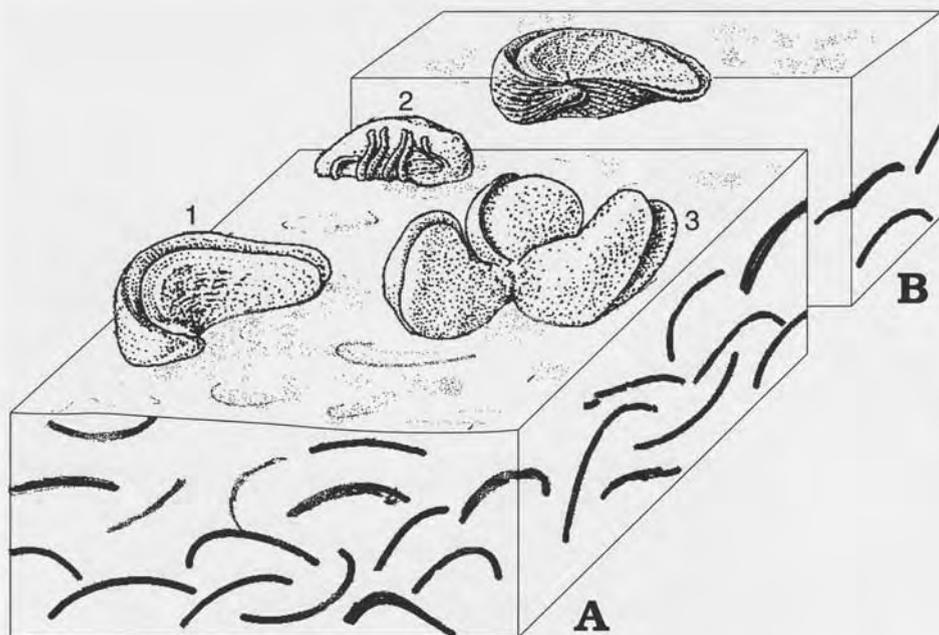


Fig. 10. Reconstruction of life positions of *Nanogyra virgula*. A: 1, 2. Lateral recliners. A: 3. Clustered recliners. B. Cup-shaped recliner. See text for further explanations.

The majority of the *N. virgula* specimens (61 of 96 examined individuals) from the shell bed are attached to other individuals of the same species, which usually are still preserved as fragments at the umbones of the colonists. Rare clusters of *N. virgula*, composed of 2 to 4 complete individuals cemented together and revealing different growth directions (Fig. 9F–I), also occur. Individual specimens in each cluster are almost of the same size. Their attachment sites, small as in other cases, are situated very close to each other. These facts convince me that the clusters represent life associations of individuals growing almost synchronously on the sea floor, in the position as suggested in Fig. 10A: 3.

Discussion. — The life position of *N. virgula* was discussed by Fürsich & Oschmann (1986a, b) based on material from the Kimmeridgian of France. These authors argued that the minute attachment scars, typical of *N. virgula*, were too small to support the fully grown individuals and that the gryphaeate, convex outwards shape of the left valve is an adaptation for living on the soft, soupy bottom (cup-shaped recliners in Seilacher's 1984 scheme). Accordingly, they reconstructed the oyster resting freely on the sea bottom in the convex-down position with the dorso-ventral ridge of the left valve sunken into the unconsolidated sediment (Fürsich & Oschmann 1986b: fig. 7, see Fig. 10B in this paper).

The specimens found in Poland suggest that individuals of *N. virgula* also adopted other life positions (see above). The statement that some specimens assumed a lateral life position and others lived in clusters does not contradict the conclusions of Fürsich

& Oschmann (1986a, b), who postulated a convex-down life attitude for many, but not all, individuals. The crucial point, however, is that the morphology of the clustered specimens does not differ in any respect from that of individuals which evidently lived solitarily, e.g., those attached to the minute conchs of cerithiid gastropods as evidenced by xenomorphic imprints on the oyster shells (Fig. 9C). Furthermore, the angle between the anterior and posterior fields of the left valve is obtuse in clustered specimens, as would be expected theoretically for those resting freely on the mud surface. Thus, when the shell that served as a substrate is a fragment, it is impossible to say whether we are dealing with a part of a cluster or with a solitary recliner, attached to the originally small substrate fragment. It is, therefore, impossible to demonstrate how many individuals in particular populations of *N. virgula* followed the clustered mode of life.

Similarly to the already discussed oysters, the 'choice' among potential life positions in *N. virgula* seems to be linked to the sedimentation rate and the type of substrate. It is conceivable that in the case of a relatively high sedimentation rate (a few mm in the life cycle of a single animal, otherwise this small oyster would be smothered by mud) and in the soft bottom conditions, the oysters followed the cup-shaped recliner strategy. In the case of a greatly reduced to nil rate of sedimentation, and probably on firm bottom, they acquired the lateral or clustered mode of life (Fig. 10).

Ecophenotypic versus evolutionary control of oyster shell morphology

It is well known that some characters of organisms are tightly constrained genetically and epigenetically, whereas other features are less constrained, allowing for ecophenotypic variation in their development (e.g., Johnson 1981; Trammer 1981; Seilacher 1985; Smith & Paul 1985; Gibson & Broadhead 1989). Following Waddington (1957) one may distinguish between 'developmentally canalised' characters (organisms), the development of which can proceed in only one direction regardless of the environment, and 'developmentally flexible' characters (organisms), the development of which can proceed in different ways under different environmental conditions.

The ecophenotypic effects are most easily recognizable in shells of *Deltoideum delta* which show the wide range of variation, being represented by flat, *Placuna*-like, and *Gryphaea*-like morphotypes. The slight overlap of the left valve over the right one is a feature found in many fossil oysters. According to Stenzel (1971) such an asymmetry of valves reflects the presence of an elastic conchiolin fringe on the right valve, reaching to the periphery of the left valve and providing a water-tight closure when the shell is shut. In the case of *Deltoideum* this feature additionally allowed for easy ecophenotypic modification of the shell into *Gryphaea*-like or *Placuna*-like shapes, depending on the nature of the bottom substrate (muddy in the first case and firm or shelly in the second one).

Morphologic plasticity of *D. delta* invites speculations about the origin of the true *Gryphaea*. Assuming that the ancestors of the genus were flat, *Liostrea*-like oysters (Seilacher 1984, but see Stenzel 1971 for different view), one may imagine that the origin of the *Gryphaea* shape was preceded by the retarded calcification of the right

valve in its flat ancestors. The resulting overlap of the left valve over the calcified part of the right one may have served as a predisposition allowing the left valve of some specimens to grow into a cup in response to muddy bottom conditions. This feature, established firstly at the ecophenotypic level, could then become genetically fixed in some populations by the 'genetic assimilation' process (Waddington 1957; Rashootin & Thompson 1981).

Whatever the origin of *Gryphaea* might have been, the morphological evolution of *D. delta* proceeded in another direction. The prominent branchitellum of this species reflects the presence of long crescentiform gills (Stenzel 1971). Had the left valve grown into a true *Gryphaea* shape, the gills would have to be significantly shortened. The natural selection apparently operated towards the maintenance of long gills, or even towards their further elongation, thus preventing the species from transforming into the *Gryphaea* homeomorph. In Western Europe *D. delta* became extinct in the Kimmeridgian (Birkelund *et al.* 1983; Clausen & Wignall 1988), and in Poland it disappeared in the Volgian. In Siberia, the lineage survived at least up to the Early Cretaceous, culminating in Valanginian '*Liostrea*' *anabarensis*, whose lunate shape suggests extremely elongated gills (Carter 1968).

Actinostreon gregareum reveals a range of ecophenotypic plasticity comparable to that of *D. delta*, being able to produce elongated, fan-shaped, and incurved morphotypes. The notable difference, however, is the lack of morphotypes which would approximate the *Gryphaea*-shape in the 'populations' from the Kimmeridgian of the Holy Cross Mountains area, as noted previously by Seilacher *et al.* (1985). According to these authors, the absence of *Gryphaea*-like morphotypes in *A. gregareum* is caused by the lack of the commissural overlap in this species, in turn related to the presence of a zigzag commissure. This explanation seems to be correct at the ecophenotypic level. It is not true however, that the zigzag commissure and gryphaeate morphology are mutually exclusive as stated by Seilacher *et al.* (1985) because both characters co-occur in a plicate oyster, representing probably a new species of *Actinostreon*, from the Kimmeridgian of Czarnogłowy in Northern Poland (Fig. 11A-I).

Ecophenotypic effects in *Nanogyra virgula* are manifested by variation in shell outline and the angle between the anterior and posterior fields of the left valve. But the helicospiral growth pattern of its shell, lifting commissure off the substrate very early in ontogeny, seems to be tightly constrained genetically. The deeply convex, arcuate shape of the left valve and the minute size of the attachment scar are consequences of such a mode of growth. There is no reason to doubt that the morphology of *N. virgula* originated as an adaptation to life on soft muddy substrates, that are generally inhospitable to most epifaunal species due to scarcity of larger substrates available for colonisation, as postulated by Fürsich & Oschmann (1986a, b). The first appearance of the species (in the middle part of the early Kimmeridgian, see Gautret 1982; Birkelund *et al.* 1983) and its acme in the middle Kimmeridgian corresponds to the period of spreading of fine-grained deposits over the vast areas of epicontinental Europe ('virgulien' of French authors). But the helicospiral growth pattern of *N. virgula* became, probably very early in its evolution, tightly constrained genetically. As evidenced by the clusters described above, this growth pattern could not have been abandoned even in the case of the individuals which had larger substrates for their disposal. This feature differentiates *N. virgula*

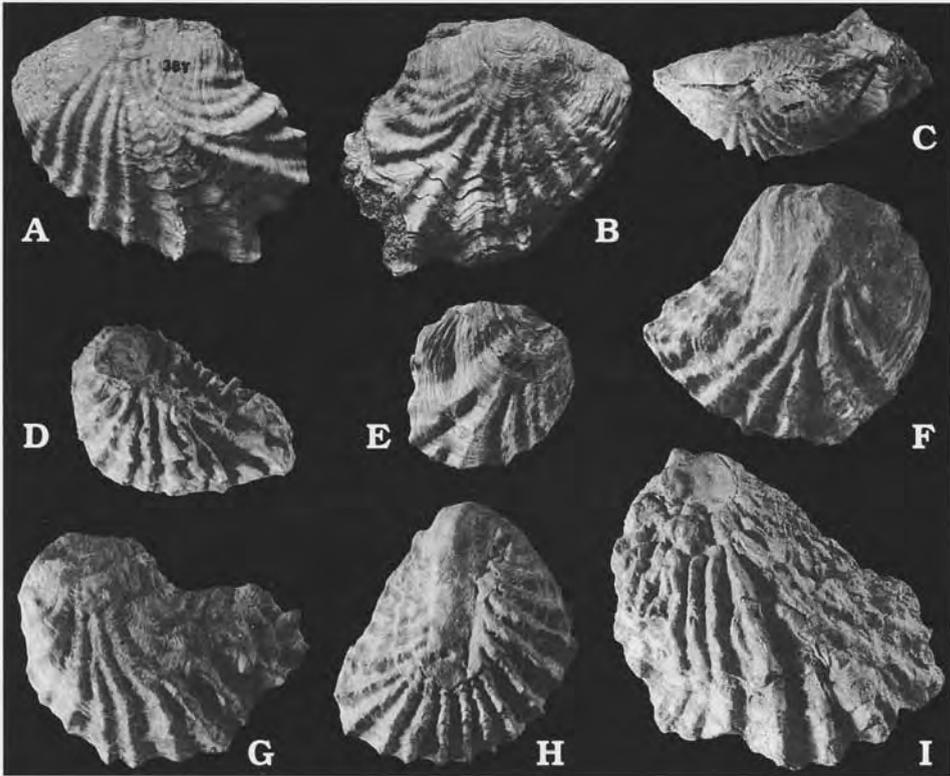


Fig. 11. *Actinostreon* sp. from lower Kimmeridgian of Czarnogłowy (Zarnclaff of German authors). A–C. Specimen 387 in Dzik's collection, LV view (A), RV view (B), umbonal view (C). D. ZPAL Mo.V/72, LV. E. ZPAL Mo.V/23, RV. F. ZPAL Mo.V/29, RV. G. ZPAL Mo.V/5, LV. H. ZPAL Mo.V/68, RV with a xenomorphic replica of an elongated object, probably the *Goniolina* stem (see Dzik 1979). I. ZPAL Mo.V/317, LV. All specimens $\times 1$.

from its ancestor *N. nana*, which could alternatively grow either in a planispiral or helicospiral manner, depending on substrate size (Fürsich & Oschmann 1986b). The morphological stability of the growth pattern in *N. virgula* along with its apparent behavioural flexibility may impose serious pitfalls in reconstructing the shell bed dynamics, as will be demonstrated in the next chapter.

Implications for reconstructing shell bed dynamics

The oyster shell beds from the Coquina Formation originated during the intervals of low net sedimentation rate when compared with the surrounding sediments. The shell beds consist of overpacked skeletons of many generations of essentially epibenthic (epifaunal to semiinfaunal) organisms while the associated sediments typically contain numerous infaunal bivalves in life positions which are indicative of much higher sedimentation rates (Seilacher *et al.* 1985; Machalski 1989, 1993).

The low net sedimentation rate in a given site may arise in several ways: from dynamic bypassing (sediment delivered to site but deposited only temporarily), total bypassing (sediment delivered to site but not deposited) or sediment starvation (failure of sediment delivery to site). The first two situations seem to be generally more typical of shallow environments and either occur during early transgressive or late regressive phases, whereas the latter is more characteristic of maximum transgression periods and more offshore settings (see Kidwell & Aigner 1985; Kidwell 1986, 1989, 1991; McGhee *et al.* 1991 for discussion of the ecologic and sedimentologic dynamics of shell beds and their environmental context).

The inferred oyster life positions may provide useful data for reconstructing the environment of the shell beds. The constituent 'soft bottom' oysters may be arranged in a sequence from mud-stickers to flat recliners, reflecting a decreasing rate of background sedimentation during their life cycles (Fig. 12A; see also fig. 5 in Seilacher *et al.* 1985). The shell beds exhibit features of reworking under high energy conditions and the contained oysters are usually displaced out of their life positions. One may postulate that the dominance of mud-stickers or cup-shaped recliners in such beds would indicate dynamic bypassing conditions during shell bed formation, whereas dominance of flat recliners would rather point to a starved or totally bypassed environment (Fig. 12B). However, the degree of accuracy in 'reading' the shell bed dynamics depends on that in reconstructing the life positions of the constituent oysters.

In the case of the *Actinostreon* and *Deltoideum* shell beds, the situation is straightforward as the life position of practically every specimen of these species can be readily reconstructed, based either on morphological analysis or on the growth relation of successive oyster generations (see above).

For example, the dominance of reoriented mud-stickers within the *Actinostreon* shell beds suggests that their sedimentary history consisted of: (1) relatively long periods of muddy background deposition, enabling the growth of specimens vertically embedded in sediment; (2) relatively rare winnowing events, most probably storms, leading to the removal of the fine grained sediment, its transport to the deeper parts of the basin, and an essentially *in situ* concentration of the 'rooted out' oysters. There must have also been some longer periods of non-deposition allowing for development of horizontally growing recliners. The multiple repetition of these processes and successive accumulation of the shells of dead oysters on the layers of former generations led to the origin of thick oyster shell beds. The growth of the next generation of mud-stickers and recliners started from reworked shells of former generations (taphonomic feedback; see Kidwell & Jablonski 1983; Kidwell 1991). To sum up, the *Actinostreon* shell beds were formed under a sedimentary regime dominated by dynamic bypassing conditions. Additional criteria are needed to answer the question of whether these conditions were associated with a transgressive or regressive environment. The wide geographic extent of the shell beds, their position near the base of the Coquina Formation, and the appearance of a new ammonite assemblage just above the first *Actinostreon* layer (Kutek 1994b), suggest their origin during early transgressive phases of the basin development.

In contrast, the *Deltoideum* beds and pavements are composed mainly of flat recliners indicating conditions of sediment starvation or total bypassing during shell bed formation.

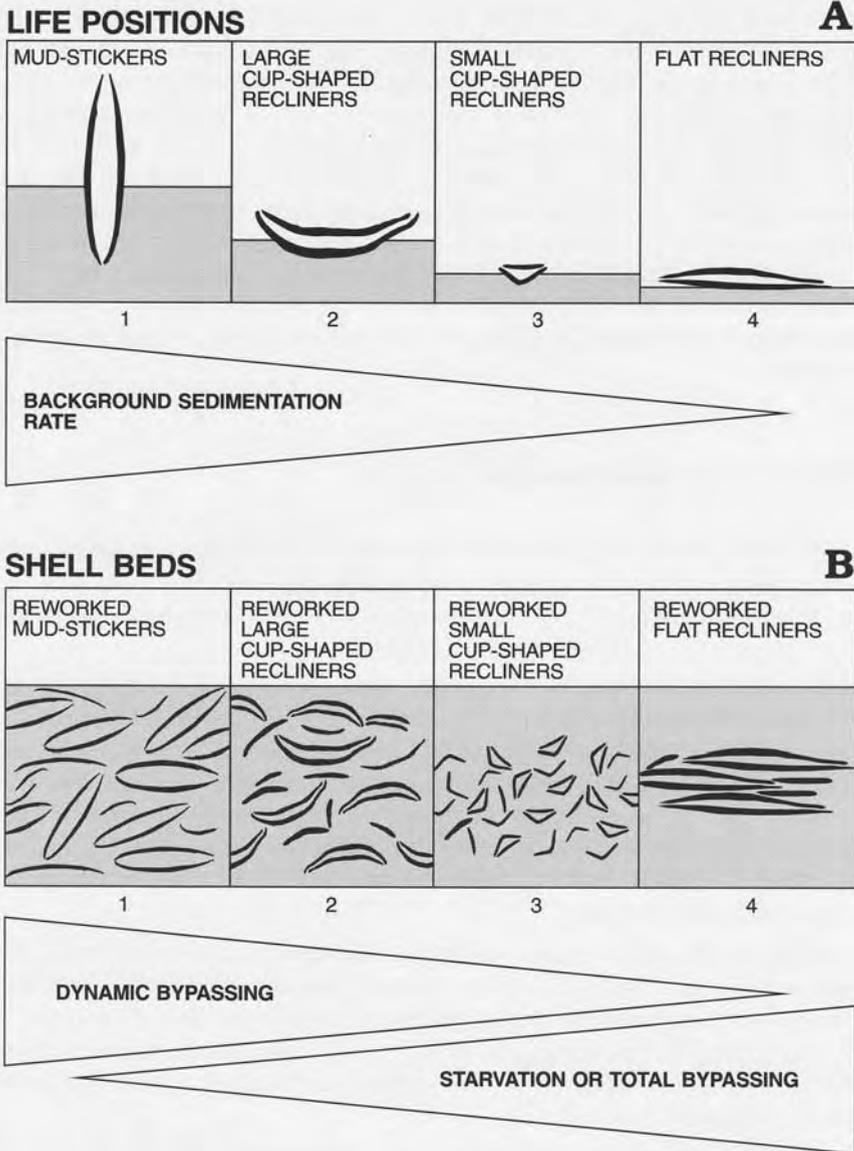


Fig. 12. **A.** Relationship between oyster life positions and rate of background sedimentation of fine sediment. **B.** The sedimentary regimes of shell beds composed of reworked oysters, which followed the life attitudes sketched in **A.** Explanations: **A:** 1 based on *Actinostreon gregareum* and *Deltoideum delta*, **A:** 2 based on *Gryphaea*-like specimens of *D. delta* from Sławno, **A:** 3 based on *Nanogyra virgula*, **A:** 4 based on *D. delta*. **B:** 1–4 idealized examples of the shell beds composed of those oysters. See text for further explanations.

The situation with the *Nanogyra virgula* beds is more complicated as the life attitude of many specimens of this oyster cannot be reconstructed unequivocally. If the oysters originally lived in the convex-down position on soft sediment, then the

shell beds they dominate would have been characterized by dynamic bypassing, although the amount of the bypassed sediment would be clearly lower than in the case of the *Actinostreon* beds, simply due to much smaller size of *Nanogyra*. Fürsich & Oschmann (1986a, b) postulated that most of the *N. virgula* accumulations originated through storm concentrations of the specimens, which were originally floating on the soft bottom. In the opposite case, if the *N. virgula* lived laterally or in clusters, a regime of sediment starvation or total bypassing would be indicated. The problem is not easy to resolve and additional information is needed. In the case of the above described shell bed from Wierzbica, such information may be provided e.g. by the intensive echinoid bioerosion of the shell material, which suggests total non-deposition on the bottom, resulting either from starvation or total bypassing of the sediment.

Summary and conclusions

- Several criteria can be employed in reconstructing life positions of fossil oysters. Among those criteria, oyster growth relationships and field observations of specimens preserved *in situ* give the most unequivocal results. The functional morphology, in turn, proves to be ambiguous in some cases.
- The life positions of three oyster species *Actinostreon gregareum* (J. Sowerby, 1816), *Deltoideum delta* (Smith, 1817), and *Nanogyra virgula* (Defrance, 1820) from the Kimmeridgian and Volgian strata of Poland are reconstructed and ascribed to different conditions of sedimentation rate and softness of substrate. The reconstruction of vertical life position of *D. delta*, previously based on indirect evidence, is proved by findings of vertically embedded specimens *in situ*. The *Gryphaea*-like mode of life in *D. delta*, and the lateral and clustered mode of life in *N. virgula* are documented for the first time.
- The problem of distinguishing between the ecophenotypic and evolutionary effects in morphology and behaviour of the oysters, may be successfully resolved by analyzing the specimens that combine different morphologies and/or life styles. This is exemplified by the 'undulating' individual of *D. delta* that shares the characters of the flat-shaped and the cup-shaped morphotypes that otherwise might have been regarded as separate species.
- Sedimentation rates can be inferred from the reconstructed oyster life positions. Together with the taphonomic data, this offers valuable insights into sedimentary dynamics of oyster shell beds, allowing to distinguish between different sedimentary regimes, e.g., between those of dynamic bypassing and starvation.

Acknowledgements

I am greatly indebted to Prof. J. Kaźmierczak (Institute of Palaeobiology, Polish Academy of Sciences) for supervising my Ph.D. thesis, part of which is presented here, and to Prof. A. Pszczółkowski (Institute of Geological Sciences, Polish Academy of Science) and Prof. A. Wierzbowski

(Geology Department of Warsaw University) for review of my thesis. Special thanks are due to Prof. S. Kidwell (Department of the Geophysical Sciences of the University of Chicago), Prof. F.T. Fürsich (Institut für Paläontologie der Universität Würzburg), Dr. N. Malchus (Departament de Geologia of the Universitat Autònoma de Barcelona), Dr. M. Kowalewski (Institute of Palaeobiology) for critical review of earlier draft of this paper. Dr. R. Fraaye (Geocenter Brabant, the Netherlands) kindly supplied a field photograph. M. Dziewiński is acknowledged for photographing, K. Sabath for drawing the specimens, J. Stolarski, and A. Kaim (all from the Institute of Palaeobiology) for computer processing of the line illustrations.

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Pozycje przyżyciowe ostryg i dynamika sedymentacyjna muszlowców ostrygowych z górnej jury Polski

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Streszczenie

W pracy zrekonstruowano pozycje przyżyciowe trzech gatunków ostryg z kimerydu i wołgu Polski, głównie z parautochtonicznych muszlowców kimerydu obrzeżenia mezozoicznego Gór Świętokrzyskich (odsłonięcia w Małogoszczy, Wierzbicy, Gruszczynie, Olesznie oraz Korytnicy). Gatunkami tymi są: *Actinostreon gregareum* (J. Sowerby, 1816), *Deltoideum delta* (Smith, 1817) oraz *Nanogyra virgula* (Defrance, 1820). Badane ostrygi należą do grupy wtórnych mieszkańców miękkiego dna (secondary soft-bottom dwellers). Wykazują one zróżnicowanie morfologii i behavioru zasiedlania podłoża, które można zinterpretować w kategoriach ekofenotypowej reakcji na zróżnicowanie tempa sedymentacji oraz stopnia zwięzłości osadu dennego. *A. gregareum* oraz *D. delta* mogły zarówno żyć w pozycji pionowej w osadzie (mud-stickers), jak i spoczywać na jego powierzchni (recliners). Ta druga strategia reprezentowana jest m.in. przez kubeczkowaty morfotyp *D. delta* (cup-shaped recliner) z wapieni wołgu w Sławnie, który przypomina kształtem *Gryphaea*. Morfotyp ten stwierdzono po raz pierwszy u *D. delta*. *N. virgula* była dotychczas uważana za formę spoczywającą wypukłością skorupy lewej na miękkim dnie. Zebrany materiał wskazuje, że ostryga ta mogła również żyć opierając się tylnym bokiem skorupy lewej na dnie (lateral recliner) lub też tworzyć kilkusobnikowe zrosty (clusters). Zrekonstruowane pozycje przyżyciowe ostryg zezwalają na odtworzenie tempa sedymentacji w czasie ich wzrostu, które wahało się od około 7–13 cm (w przypadku największych osobników żyjących pionowo w osadzie) do kilku milimetrów lub nawet zera (w przypadku płaskich morfotypów spoczywających na powierzchni osadu). Ustalenia te pozwalają z kolei odtworzyć dynamikę sedymentacyjną parautochtonicznych muszlowców ostrygowych. Wykazano, że muszlowce z *A. gregareum* tworzyły się przy przewadze warunków dynamicznego omijania dna przez osad (dynamic bypassing), podczas gdy muszlowce z *D. delta* w warunkach „zagłodzenia” dna (starvation) lub jego całkowitego omijania przez osad (total bypassing). Środowiska powstawania muszlowców z *N. virgula* nie sposób odtworzyć jedynie na podstawie trybu życia ostryg, gdyż nie może on być zrekonstruowany u wielu osobników tego gatunku.