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REDESCRIPTION OF A DANIAN OYSTER *PYCNODONTE SIMILE*
(PUSCH, 1837) FROM POLAND

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Pycnodonte simile (Pusch, 1837) is revised and redescribed on the basis of a new material from the type horizon and area, i.e., Danian deposits of Puławy region, Middle Vistula Valley, Central Poland. Neotype of the species is designated. Variability and relations of *Pycnodonte simile* to other pycnodont oysters, especially to *Pycnodonte vesiculare* (Lamarck, 1806), are considered.

Key words: oysters, taxonomy, shell structure, Tertiary, Danian, Central Poland.

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INTRODUCTION

Relatively simple morphology of the shell and significant variability of the oysters assigned to *Pycnodonte* Fischer de Waldheim, 1835 result in the diagnoses of a particular species given by various authors often differing significantly from one another. The aim of this paper is to show the range of variability and to revise the taxonomy of *Pycnodonte simile* (Pusch, 1837) on the basis of the materials from the type horizon and area, i.e., the Danian deposits of the Puławy region, Middle Vistula Valley, Central Poland.

In the vicinity of Puławy (fig. 1) the uppermost Maastrichtian and Paleocene deposits crop out which were described recently by Abdel-Gawad (1986) and Machalski and Walaszczyk (1987). The Paleocene part of the profile is formed by a 50m thick sequence of marly gaizes with limestone intercalations. These deposits, called Siwak, have been assigned to the Upper Danian (Machalski and Walaszczyk 1987). Siwak crops out between Nasiłów and Góra Puławska on the left bank of the Vistula river, and between Kazimierz and Puławy on the right bank (fig. 1B).

The examined specimens of *Pycnodonte simile* come from Siwak deposits. The species is particularly abundant in a valley south of Par-

chatka and in another one situated in the middle of the village. Some rare specimens of *Pycnodonte simile* come also from other Siwak outcrops, i.e., from Bochatnica, Góra Puławska and Nasiłów.

The faunistic assemblage from the Siwak of Parchatka is dominated by *Pycnodonte simile* and another oyster *Gryphaeostrea* sp., which are accompanied by other bivalves, gastropods, and echinoids. The dominance of *Gryphaea*-shaped oysters in this assemblage is worth noting as this type of assemblages is rare in the Tertiary (Jablonski and Bottjer 1983).

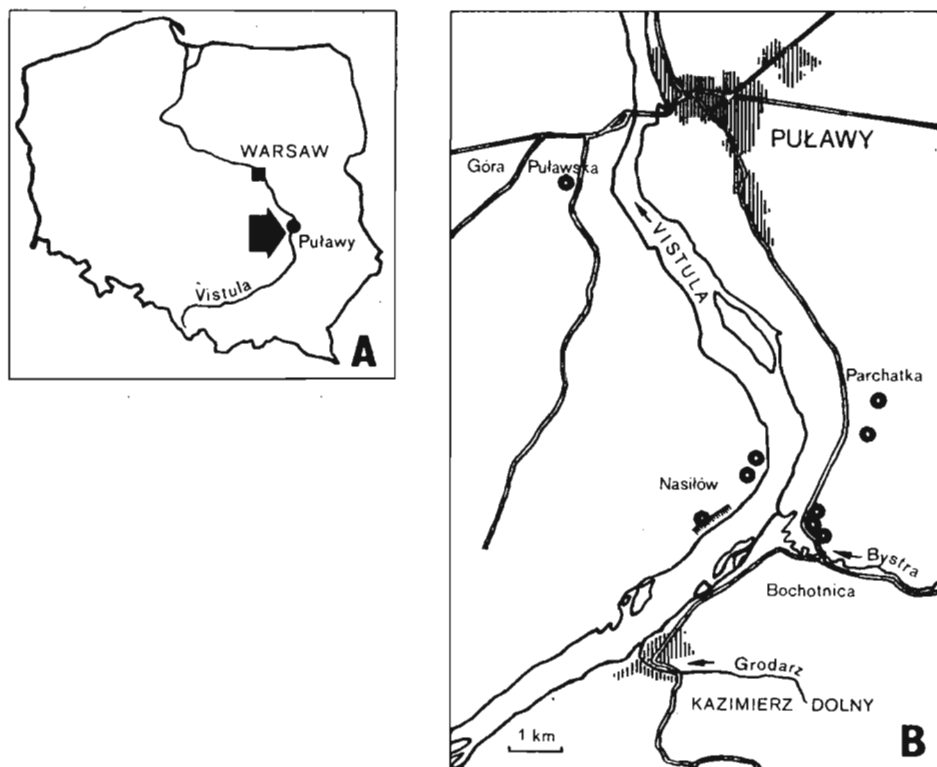


Fig. 1. Location of *Pycnodonte simile* (Pusch, 1837) sites on the territory of Poland (A) and in the Puławy region (B). Circles denote the outcrops of the Siwak.

The material described is housed at the Institute of Paleobiology, Polish Academy of Sciences, Warszawa (abbreviated ZPAL) and in the Museum of the Earth of the Polish Academy of Sciences (abbreviated MZ).

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The drawings have been made by Mrs. Gutkowska-Leszak and the photos by Mr. Dziewiński.

DESCRIPTION

Family *Gryphaeidae* Vyalov, 1936Subfamily *Pycnodonteinae* Stenzel, 1959Genus *Pycnodonte* Fischer de Waldheim, 1835*Pycnodonte simile* (Pusch, 1837)

(pl. 21, 22; fig. 3A—D, 4D—F)

1837. *Gryphaea similis* Pusch: 34, pl. 4: 12.
 ?1938. *Pycnodonta frauscheri* Traub: 50, pl. 3: 1a—d.
 1969. *Gryphaella similis* (Pusch); Cheltsova: 62, pl. 5: 1—5.
 1974. *Pycnodonta similis* (Pusch); Panteleev: 89, pl. 8: 3—7, pl. 9: 1—5, pl. 10: 1—5, pl. 11: 1—4.
 1974. *Pycnodonta frauscheri* Traub; Panteleev: 90, pl. 11: 5—8, pl. 12: 1—4, pl. 13: 1, 2.
 1977. *Pycnodonte (Phygraea) bechkochensis* (Weber); Pugaczewska: 192, pl. 11: 1, 2.
 ?1977. *Pycnodonte simile* (Pusch); Sobetski: 149, pl. 13: 1.
 1981. *Gryphaea antiqua* Schwetsov; Krach: 33, pl. 3: 5.
 1981. *Liostrea reussi* (Netschaev); Krach: 33, pl. 2: 11, 12.
 1981. *Amphidonta eversa* (Melleville); Krach: 34, pl. 3: 4 (non 1—3).
 1984. *Pycnodonta kalugini* Dmitriev: 43, pl. 2: 1, 2.
 1984. *Pycnodonta schwetsovi* Dmitriev: 45, pl. 2: 3, 4.
 ?1985. *Gryphaea similis* Pusch; Epitashvili: 29, pl. 3: 1—4.

Holotype: Specimen figured by Pusch (1837), pl. 4: fig. 12; redrawn here as fig. 3: A, B.

Neotype: Specimen ZPAL L II/27; fig. 3: C, D.

Type locality: Parchatka near Puławy, Middle Vistula Valley, Central Poland.

Type horizon: Middle part of the Siwak, Upper Danian.

Diagnosis.—Height of the shell usually exceeding its length, chomata-bearing parts of the commissural shelf well developed, chomata strongly marked and numerous; shell built of foliated material with minor contribution of vacuolar layers; right valve smooth.

Material.—132 mostly well preserved specimens (ZPAL L II/1—101, MZ VIII M1 1751/1—3, 1815/1—4, 1816/1—2, 1817—1820, 1822/1—2, 1824/1—2, 2806/1—13, 2807), mostly from Parchatka.

Description.—Shell small to medium sized (fig. 2A), strongly inequivalve, moderately inequilateral.

Left valve convex, ranging from high and short to low and elongated (pl. 21: 1—6, 8, fig. 2B, D), posteroventral lobe faintly developed. Outline very variable, mostly triangular, sometimes oval to circular. Posterior sulcus separating the lobe shallow to evanescent. Umbo anterior to nearly central, in most cases rising well above the hinge line. Attachment area variable in size, usually small (fig. 2C). In specimens with a very small attachment area, umbo high, strongly arcuate and overhanging the right valve (pl. 21: 5). Specimens with larger attachment area have a truncated umbo (pl. 21: 3). Hinge line short. Ligamental area triangular with relatively deep and wide resilifer bounded by narrow bourrelets. Chomata strongly marked, rarely single, most often dendroidal, sometimes strongly tangled (pl. 22: 7), usually restricted to the dorsal part of the commissural shelf. Occasionally, the chomata may encircle the whole valve (pl. 21: 4). Commissural shelf very well developed in the dorsal half of the valve, where it is separated from the shell cavity by a strong angulation. In the ventral half, the angulation is gentle to evanescent. Adductor muscle scar weakly marked. Ornamentation of the left valve consists of concentric,

irregularly spaced growth lines. Ontogenetic changes concern mainly the length/height ratio, which tends to decrease with age. On the valves of young individuals, the presence of posterior sulcus is manifested only by a bending of growth lines.

The right valve is smaller than the left; it is usually concave (pl. 21: 7) with its outline corresponding to that of the attached left valve. Umbo very small. Chomata developed along the posterodorsal and anterodorsal margins. Muscle scar strongly incised. Exterior surface marked by closely spaced growth lines.

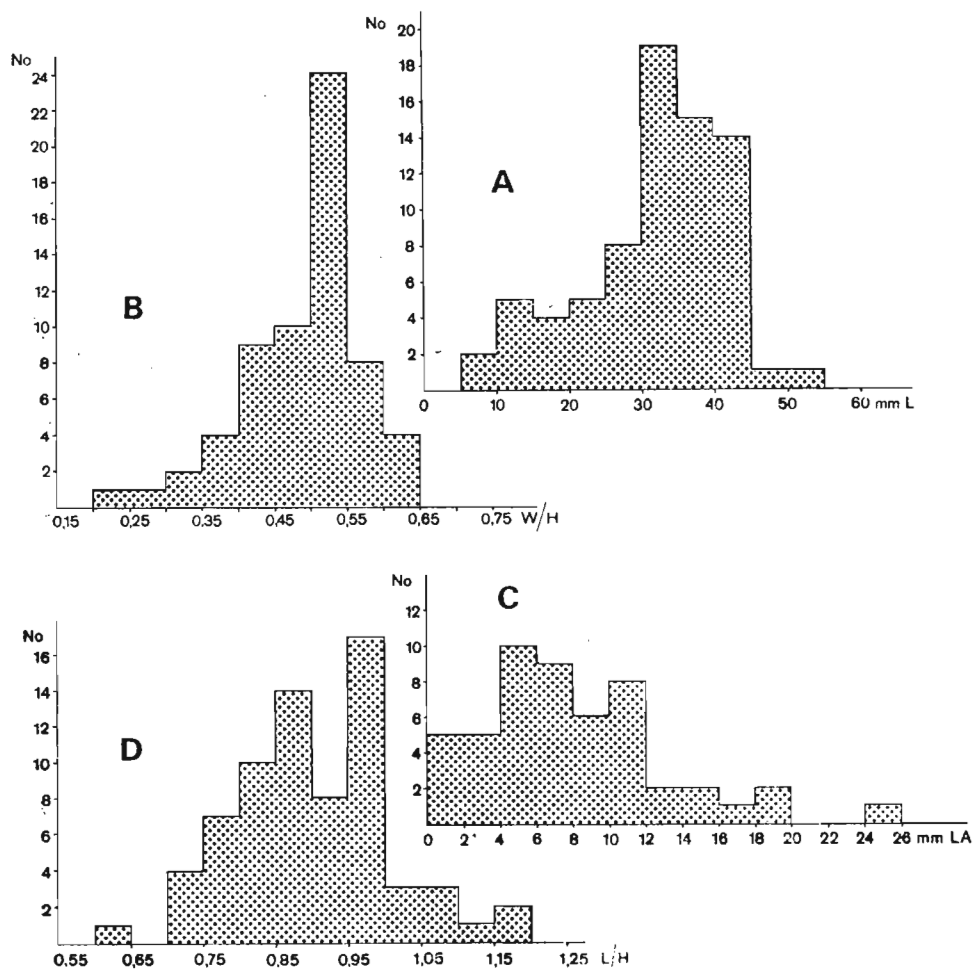


Fig. 2. Variability of *Pycnodonte simile* (Pusch, 1837) from the Danian of Puławy region. A Length-frequency histogram, $N = 74$. B width/height — frequency histogram, $N = 63$, $W/H = 0.49$. C size of attachment area (indicated by length of its longest diameter), $N = 51$. D length/height — frequency histogram, $N = 69$, $L/H = 0.91$.

Shell microstructure. — There occur two main types of microstructure: foliated and vacuolar (pl. 22: 1, 4–6). Very variable foliated structure dominates. It may vary within a single specimen (pl. 22: 4, 5) from regularly foliated to irregular complex crossed foliated structure (terminology after Carter 1980, see also Freneix 1982). Vacuolar structure is represented by rare intercalations within the foliated shell material (pl. 22: 1, 6).

Discussion.—Individual variability is very extensive in the investigated material from Siwak (pl. 21; fig. 2). It concerns the proportions and the outline of the shell, its curvature, the development of umbo, posteroventral lobe, and chomata. Some specimens are practically indistinguishable (fig. 3) from the holotype illustrated by Pusch (1837) and they are closely connected with the rest of the material by intermediate forms.

Stenzel (1971) assigned *Gryphaea similis* Pusch, 1837 to the genus *Pycnodonte* Fischer de Waldheim, 1835, subgenus *P. (Phygraea)* Vyalov, 1936. The subdivision of the genus by Stenzel, as based partially on ecologically controlled features, e.g., the shape of umbo, needs a revision, however, and is not followed by the present author.

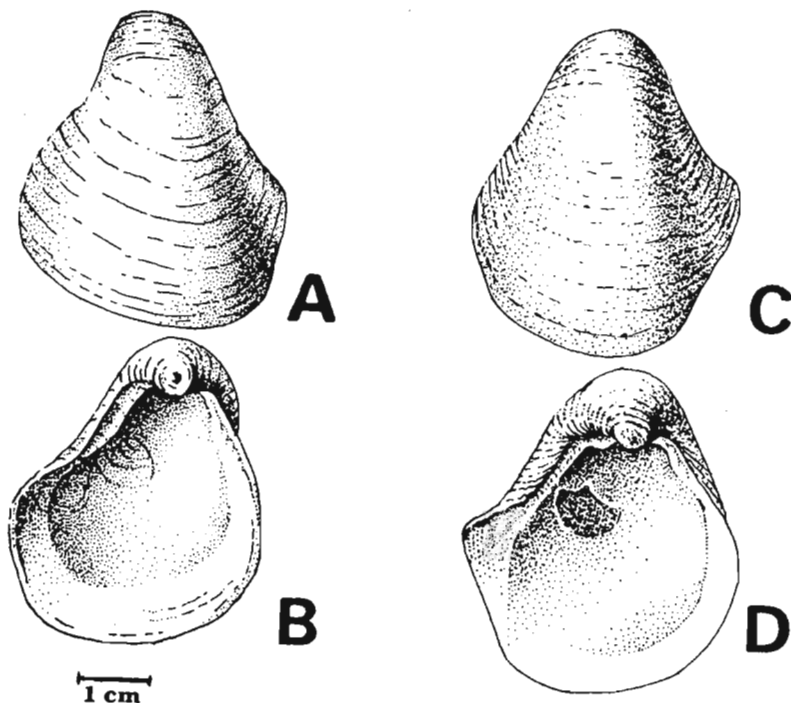


Fig. 3. *Pycnodonte simile* (Pusch, 1837). A, B holotype of the species (redrawn from Pusch, 1837, pl. 4: 12). C, D specimen from Parchatka designated as a neotype (ZPAL L II/27).

Pusch (1837) established *Gryphaea similis* on the material from the "Cretaceous marls of Kazimierz-on-Vistula". The stratigraphic position of the species given by Pusch and followed by many authors (e.g. Cheltsova 1969, Sobetski 1977) should be corrected, however, because until now Pusch's species has been reported only from Danian deposits of the region (Siemiradzki 1931, Matwiejewówna 1935) while it has never been found in the Cretaceous strata of the environs of Puławy (author's own observations and Abdel-Gawad 1986). Thus, the Danian Siwak is the type horizon and the Puławy region is the type area of the species. As Pusch's holotype located at the Warsaw University was lost during the World War Two, the neotype is here designated for *Pycnodonte simile*.

Some authors, e.g. Coquand (1869), Woods (1913) and Tzankov (1981), considered *P. simile* as conspecific with *Pycnodonte vesiculare* (Lamarck, 1806), widely reported

from Cretaceous and Danian strata of Europe, Asia, Africa and North America (Coquand 1869, Ravn 1902, Arkhangel'sky 1905, Woods 1913, Wade 1922, Cheltsova 1969, Müller 1970, Freneix 1972, Tzankov 1981). In the studied area, the latter species occurs in the uppermost Maastrichtian deposits (Pugaczewska 1977, Abdel-Gawad 1986). *P. simile*, however, differs from Lamarck's species in the following features:

- 1) the maximum size is nearly half that of *P. vesiculare*;
- 2) the posterior lobe is usually less strongly developed (fig. 4, 5); the mean value of the length/height index is 0.91 whereas it equals 1.13 in the population of *P. vesiculare* from the uppermost Maastrichtian siliceous limestones of Puławy region (fig. 5);
- 3) the parts of the commissural shelf containing chomata are well developed and distinct, whereas they are weakly marked and bear usually only few hardly recognizable chomata in *P. vesiculare* (fig. 4);
- 4) the right valve is smooth, whereas it is distinctly radially sculptured in *P. vesiculare*;

5) the shell is mainly foliated in structure with intercalations of thin vacuolar layers (pl. 2: 1, 4—6); in *P. vesiculare*, the shell consists of thick vacuolar layers separated from each other by thin layers of solid foliated material (pl. 2: 2, 3).

Some features that have been regarded in the literature as taxonomically valuable seem to be ecologically controlled. For example, according to Abdel-Gawad (1986), "*Gryphaea similis* Pusch differs from *P. vesiculare* in its gryphate left valve, a more curved elevated umbo, small xenomorphic area and also in number and position of chomata". Similarly, Cheltsova (1969), Sobetski (1977) and Epitashvili (1985) point to the curving of the umbo and the shape of the left valve as main features separating the two species. In the present author's opinion, only the character of chomata is of taxonomic value, whereas the other features depend upon the mode of attachment and size of available substrates (pl. 21). It has already been stated by Woods (1913) that the size of attachment area and the resulting shape of the umbo of pycnodont oysters depend on the size and shape of substrate.

In the case of populations of *P. simile* from Puławy region, the dominance of small attachment areas is most readily explained by a scarcity of sufficient objects which could be colonized by these oysters. Oysters encrusting large objects, e.g., nautiloid shells, have large attachment area and, in this respect, are indistinguishable from *P. vesiculare*. Specimens of *P. vesiculare* from the uppermost Maastrichtian of the same region have in general, large attachment areas, as the substrates they used were large sponges, gastropods, bivalves, ammonites and nautiloids common on the Maastrichtian sea-floor (Abdel-Gawad 1986: fig. 25, 26).

According to Cheltsova (1969), *P. simile* differs from *P. vesiculare* in having a subrhombic shell structure (a synonym of the irregular complex crossed foliated structure, Carter pers. communication). As in the author's materials such a structure, occurring only in some individuals, intergrades with the other structure types (like in Pectinacea see Carter 1980), it is most probable that it has no systematic value.

The specimens from Siwak described by Pugaczewska (1977) as *Pycnodonte (Phygraea) bechkochensis* (Weber, 1934) and by Krach (1981) as *Gryphaea antiqua* Schwetsov, 1929 belong clearly to *P. simile*. Pugaczewska's specimens lack the deep sulcus typical of *P. bechkochensis* (see Cheltsova 1969). Krach's specimen (MZ VIII M1 1820—1824) have no features typical of *P. antiqua*, which is diagnosed by its long hinge line, commissural shelf lacking chomata, and shell longer than high (Vyalov 1948, Karagyuleva 1964, Cheltsova 1969, Panteleev 1974). On the contrary, they are high shells with weakly marked sulcus and well developed dorsal parts of commissural shelf containing strongly marked chomata typical of *P. simile*.

All the specimens regarded by W. Krach (1981) as *Liostrea reussi* (Netschaeu, 1897), i.e. MZ VIII M1 1751/1—3, MZ VIII M1 1815—1818 are conspecific with *P. simi-*

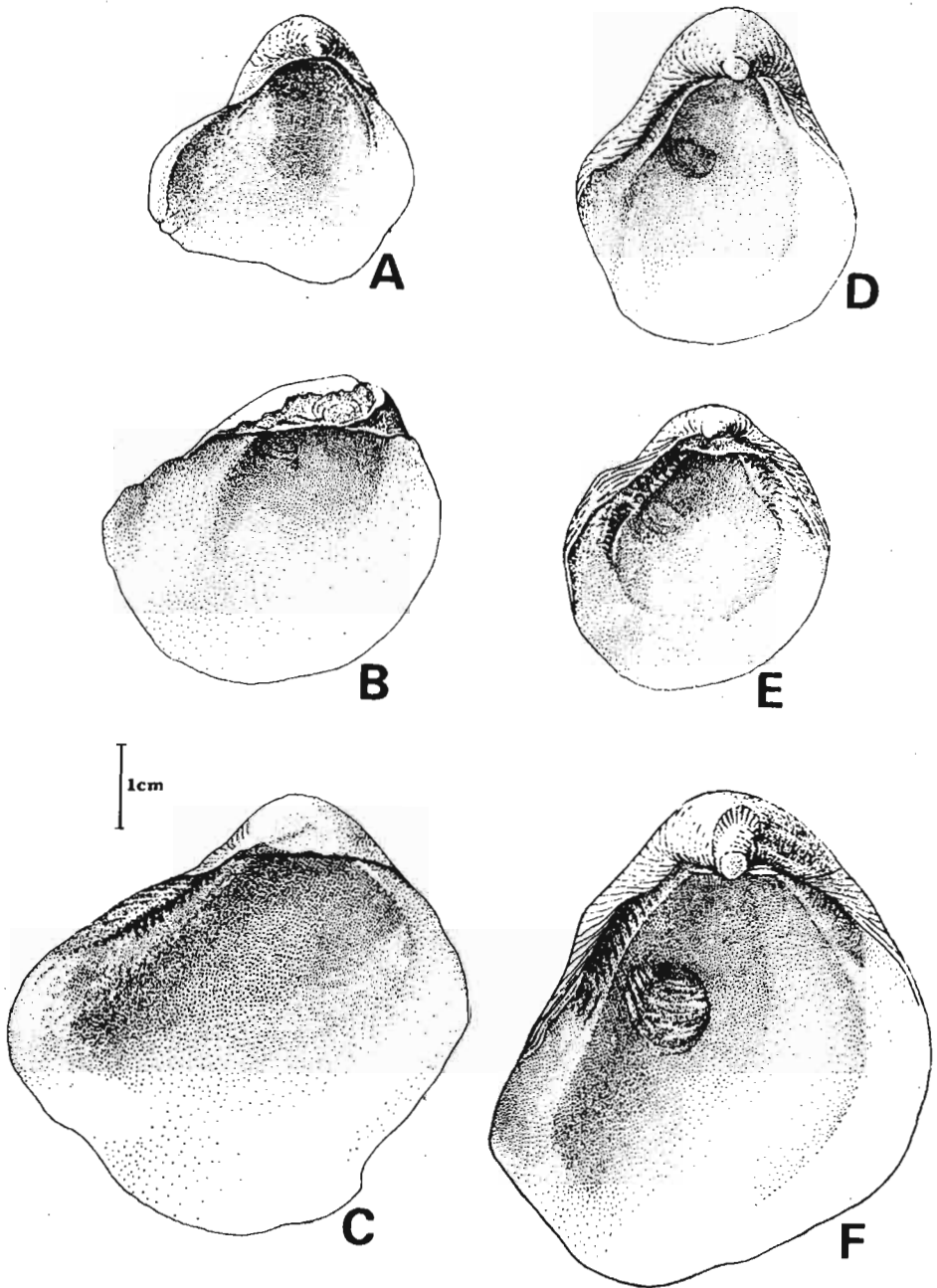


Fig. 4. A—C *Pycnodonte vesiculare* (Lamarck, 1806); A specimen ZPAL L II/102, from the uppermost Maastrichtian of Puławy region (Nasiłów quarry), B specimen ZPAL L II/103 from the Lower Campanian chalk of Mielnik on Bug, C specimen ZPAL L II/104, from the uppermost Maastrichtian of Puławy region (Nasiłów quarry). D—F *Pycnodonte simile* (Pusch, 1837), Danian of Parchatka, D—ZPAL L II/27, E—ZPAL L II/34 and F—ZPAL L II/70.

le. Most of them are small-sized juveniles identical to juvenile parts of adult shells as well as to juvenile shells of *P. simile* in the author's collection.

As to the poorly illustrated oysters determined by Traub (1938), Sobetski (1977) and Epitashvili (1985) as *P. simile*, they may as well represent other related species.

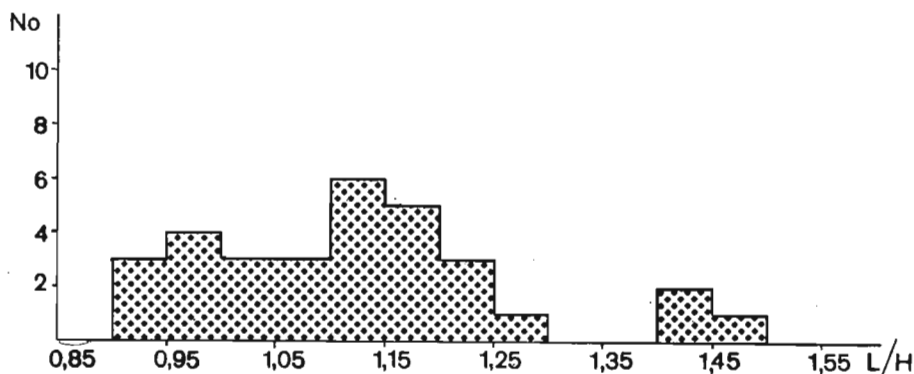


Fig. 5. Length/height—frequency histogram of *Pycnodonte vesiculare* (Lamarck, 1806) from uppermost Maastrichtian siliceous limestones of Puławy region (mainly Nasilów quarry), $N = 31$, $L/H = 1.13$.

Stratigraphic and geographic distribution.—USSR: Maastrichtian of Crimea, Danian of Georgia, Maastrichtian, Danian and Thanetian of Mangyshlak; Poland: Upper Danian; ?Austria: Thanetian.

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TAKSONOMIA OSTRYGI *PYCNODONTE SIMILE* (PUSCH, 1837) Z DANU
OKOLIC PUŁAW

Streszczenie

W pracy opisano i zilustrowano (pl. 21, 22; fig. 2—4: D—F) morfologię i mikrostrukturę muszli, a także wyznaczono neotyp (okaz ZPAL L II/27; fig. 3: C, D). Zgodnie z wynikami ostatnich badań (Machalski i Walaszczyk 1987) siwak uznano za wieku dańskiego. Większość okazów pochodzi z okolic wsi Parchatka. Margliste gezy i wapienie środkowej części siwaka odsłaniające się w pobliżu tej wsi stanowią horyzont typowy gatunku.

W oparciu o zbadane cechy całej populacji przedyskutowano różnice między *P. simile* a *P. vesiculare* (Lamarck, 1806) (pl. 22: 2, 3; fig. 4: A—C, fig. 5). Stwierdzono, że *P. simile* różni się od *P. vesiculare* mniejszymi rozmiarami muszli, słabszym wykształceniem płatu tylnego, silniejszym wykształceniem półek z chomata, brakiem rzeźby na prawej skorupie oraz bardzo małym udziałem struktury pęcherzykowej w budowie ściany muszli. Wskazano, że takie cechy jak powierzchnia przyczepu i sposób wykształcenia wierzchołka nie mają znaczenia taksonomicznego gdyż zależą wyłącznie od wielkości i kształtu podłoża do jakiego przyczepiały się ostrygi.

W pracy wykazano także, że, w ostatnich latach, okazy należące do *P. simile* były błędnie oznaczane jako *P. bechkoehensis* przez Pugaczewską (1977) i jako *Gryphaea antiqua* i *Liostraea reussi* przez Kracha (1981).

Praca wykonana w ramach problemu MR II 6.

EXPLANATION OF PLATES 21 AND 22

Plate 21

Pycnodonte simile (Pusch, 1837), Danian, Parchatka near Puławy,
Central Poland

1. Left valve, ZPAL L II/41, external view, $\times 1.5$.
2. Left valve, ZPAL L II/58, external view, $\times 2$.
3. Left valve, ZPAL L II/19, external view, $\times 1.5$.
4. Left valve, ZPAL L II/35, internal view, $\times 1.5$.
5. Left valve, ZPAL L II/22, internal view, $\times 1.5$.
6. Left valve, ZPAL L II/28, internal view, $\times 2$.
7. Right valve, ZPAL L II/50, internal view, $\times 1.5$.
8. Left valve, ZPAL L II/52, internal view, $\times 2$.

Plate 22

1, 4—7 *Pycnodonte simile* (Pusch, 1837), Danian, Parchatka near Pulawy, 2, 3 *Pycnodonte vesiculare* (Lamarck, 1806) Lower Maastrichtian, Isle of Rügen, German Democratic Republic.

1. Thin section of shell (ZPAL L II/94) normal to hinge axis and commissural plane; foliated and vesicular (arrowed) structures are visible, $\times 5$.
2. Thin section (ZPAL L II/105) oriented as above to show intercalations of vacuolar and foliated structures, $\times 2$.
3. Umbonal region of the same specimen, $\times 5$.
4. Thin section of the articulated specimen ZPAL L II/95, $\times 2$.
5. Central part of the same specimen showing irregular complex crossed foliated (if) and regular foliated (rf) structures, $\times 5$.
6. Umbonal part of the same specimen showing vacuolar structure (arrowed), $\times 10$.
7. Fragment of commissural shelf of specimen ZPAL L II/5 to show chomata, $\times 3$.

