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THE OCCURRENCE OF THE GENUS *KELLIELLA* (BIVALVIA, KELLIELLIDAE) IN SHALLOW-WATER, MIDDLE MIOCENE DEPOSITS OF POLAND

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Present-day representatives of the genus *Kelliella* are mostly confined to the abyssal zone (2000—6000 m), while paleontological data suggest shallower bathymetric requirements for their fossil congeners. The Late Eocene to Miocene records are from shallow-water (20—50 m) deposits; Pliocene and Pleistocene species come from deposits typical of bathyal zone (400—2000 m).

New species *Kelliella barbara* sp. n. is described from the Badenian (Middle Miocene) shallow-water sands in the southern slopes of the Holy Cross Mts.

Key words: Bivalvia, Kelliellidae, bathymetric conditions, Badenian, Poland.

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INTRODUCTION

The purpose of this paper is to describe a new species of the bivalve genus *Kelliella* M. Sars, 1870, which has been found in the Middle Miocene shallow-water deposits of Poland. This occurrence, along with other records of fossil Kelliellids, seems to suggest that the representatives of this genus have drastically changed their ecological requirements over the last 15 mln years. This may serve as a reminder that actualistic data should be taken with care when applied to paleoenvironmental reconstructions.

The occurrence of the genus *Kelliella* in the present-day marine environments is limited almost entirely to the abyssal zone (i.e. 2000—6000 m — see Knudsen 1970). Among the diversified bivale fauna living in the abyss [402 species after Clark (1962) or 263 species according to Knudsen (1979)], 8 species belong to the genus *Kelliella*. These are: *K. adamsi* (Smith, 1885), *K. atlantica* (Smith, 1885), *K. galatheae* Knudsen, 1970, *K. indica* Knudsen, 1970, *K. nitida* Verrill, 1885, *K. pacifica* (Smith, 1885), *K. tasmanensis* Knudsen, 1970, and *Kelliella* sp.

The species of the genus *Kelliella* are thus a minor element of the abyssal fauna, constituting merely 4% of its total species number (Knudsen 1970). Two abyssal species, *K. adamsi* (Smith), and *K. pacifica* (Smith), along with two other species of *Kelliella* reported from the hadal zone (i.e. deeper than 6000 m), i.e. *K. bruuni* (Filatova), and *K. sundanensis* Knudsen, belong to a group of 18 bivalve genera living at the depths greater than 5000 m (compared to the total number of 1717 Recent bivalve genera — see Vokes 1980).

The only species of *Kelliella* reported from depths shallower than the abyss is *K. miliaris* (Philippi, 1844). It is known to occur in the deeper parts of the sublittoral zone (i.e. 100—400 m) and within the bathyal zone (i.e. 400—2000 m). The species is relatively widespread in the Mediterranean Sea, along the Atlantic coast of North Africa, West Europe, and Norway (Clausen 1958), as well as in the North Atlantic and around Lofoten Islands (Nordsieck 1969). *K. miliaris* (Philippi) is among a few kelliellid species unknown from the abyssal zone (Knudsen 1960, Bouchet and Warén 1979). But the most interesting is that this is the only living species of the genus *Kelliella* known in the fossil state.

Fossil representatives of *K. miliaris* (Philippi) have previously been reported from the Pleistocene (Sicilian) of Sicily (Philippi 1844: 34—36, pl. 14: 15; Glibert and Van de Poel 1966: 21), and from the Lower to Middle Pleistocene of Rhodes (Sørensen 1984: 202—208, fig. 6A—D). In the present author's opinion, the specimens from the Late Badenian (Middle Miocene) sands of Monastyrz (Poland), housed in the Museum of the Earth, Warsaw, identified by Jakubowski (1977: 102—104, l. 11: 11—14, Text-pl. 7: 20—41, Text-fig. 4) as *Kelliella rotunda* (Sorgenfrei), belong to *K. miliaris* (Philippi). On the other hand, the specimens from the Badenian deposits of Kostej and Lapugy (Romania), and Vöslau (Austria), assigned by Kautsky (1939: 633, pl. 22: 27—28) to *K. miliaris* (Philippi), cannot be, according to the present author, attributed to that species.

Apart from *K. miliaris* (Philippi), following fossil species have previously been assigned to the genus *Kelliella*: *K. abyssicola* (Forbes, 1843) (Early Pliocene); *K. boettgeri* Meyer, 1886 (Late Eocene to Early Miocene); *K. patera* Sorgenfrei, 1958 and *K. rotunda* Sorgenfrei, 1958 (both from Middle Miocene). The latter species, according to Glibert and Van de Poel (1966: 21), represents the genus *Alveinus* Conrad, 1865. The present author is of the opinion that the material described by Rasmussen (1968: 55, pl. 2: 2) as *Kelliella rotunda* Soergenfrei, 1958, along with the specimens named by Nordsieck (1972: 32, pl. 7: 49) *Lutetia rotunda* (Sorgenfrei, 1958), should be attributed to the genus *Alveinus*.

Several specimens found in the Badenian sands in Nawodzice (Poland) belong also to the genus *Kelliella*. They differ, however, from the other representatives of *Kelliella* in their shell outline, shape and ornamentation

of lunule, and in hinge details. Therefore, they are distinguished as a new species, named *Kelliella barbara* sp. n.

The specimens from Nawodzice, described further in the text, are housed in the Museum of the Earth (Muzeum Ziemi, abbr. MZ).

SYSTEMATIC ACCOUNT

The suprageneric systematics is here applied according to Scarlato and Starobogatov (1979).

Subclass **Autobranchia** Grobben, 1984 [= **Mytiloida** Ferussac, 1822]
Order **Venerida** H. Adams and A. Adams, 1856
Suborder **Venerina** H. Adams and A. Adams, 1856 [= **Isocardiina** Dall, 1886]
Superfamily **Kellielloidea** Fischer, 1887
Family **Kelliellidae** Fischer, 1887
Genus *Kelliella* M. Sars, 1870

Type species: *Venus? miliaris* Philippi, 1844 [= *Kelliella abyssicola* M. Sars, 1870]

Kelliella barbara sp. n.
(pl. 31: 1—4; pl. 32: 1—2)

Holotype: Specimen MZ VIII Ml-2767/3; pl. 31: 3; pl. 32: 2.
Type horizon: Badenian.
Type locality: Nawodzice, 30 km SSW of Sandomierz, southern slopes of the Holy Cross Mts.
Derivation of the name: after the Greek word meaning strange, foreign, in this case strange to the shallow-water zone.

Diagnosis. — A *Kelliella* having rounded shell with a small umbo, sculptured with a fine, concentric striation, with the lunule only faintly demarcated.
Material. — 6 valves.

Dimensions (in mm):

	length	height
MZ VIII Ml-2767/$_1$	1.4	1.1
-2767/$_2$	1.3	1.0
-2767/$_3$	1.2	1.0
-2767/$_4$	1.2	0.9

Description. — Valve is very small, orbicular in outline, convex, inequilateral — the posterior part accounts for 65% of the valve length. Beak is very small, prosogyrate, slightly projecting above the dorsal margin, the anterior part of which is short and arcuate. Almost rectilinear, oblique posterodorsal margin connects angularly with weakly convex posterior margin. Regularly arcuate ventral margin gradually passes into the posterior margin, as well as into the strongly convex anterior margin.

Lunule is small, cordate, not depressed, delimited by a row of faint, indented dots.

Distinct, suborbicular pseudoprodissoconch is 0.20 mm high and shows smooth surface, while the dissoconch is ornamented with densely spaced, delicate concentric lines.

Growth stages are distinct.

External, opistodetic ligament is very short; nympha weakly delimited.

Hinge of the right valve consists of two teeth; lamelliform anterior tooth, more massive and projecting than the posterior one, is separated from the lunular margin with a deep socket; elongated, bent posterior tooth is divided into two parts by a gentle contraction: straight posterior part is wider and higher than the arched anterior one.

Hinge of the left valve consists of two teeth; weakly sinuate anterior tooth is placed at the ventral edge of thickened lunular margin, while posterior tooth, conforming to the lunular margin, is shorter and more prominent than the anterior one.

The anterior adductor muscle scar is oval in outline, indistinct. The posterior adductor muscle scar and the pallial line are not observable.

Ventral margin is smooth.

Remarks. — The species *Kelliella barbara* sp. n. differs from *K. miliaris* (Philippi), the type species of *Kelliella*, in its outline, shape of lunule and hinge construction. The shell of *K. miliaris* (Philippi) is oval-shaped, transversally elongated, with arched posterodorsal margin, while the shell of *K. barbara* sp. n. is orbicular in shape, with straight posterodorsal margin. Both *K. miliaris* (Philippi) and *K. barbara* sp. n. are ornamented with concentric lines that are weaker and less densely spaced in the latter species than in the former (cf. M. Sars 1870: 201—209, pl. 12: 11—15; pl. 13: 16—26; Sørensen 1984; 203, text-fig. 6A—D). Lunule is large, cordate and delimited by a distinct groove in *K. miliaris* (Philippi), while it is small, cordate and delimited by a row of faint, indented dots in *K. barbara* sp. n. A similar kind of lunule is observed also in *K. bruuni* (Filatova, 1969), which lives in Kermadec Trench at the depth range 5900—9200 m, in the temperature 1.2°—1.5°C (Filatova 1969: 44—50, Knudsen 1970: 107—109).

K. barbara sp. n. differs from *K. miliaris* (Philippi) also in its hinge details (see pl. 2: 1—4) [1]. The lamelliform posterior tooth of the right valve is in both species

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[1] The teeth formula is used in the present paper neither in description nor in remarks. This decision is due to the absence of an unequivocal concept of the evolutionary origin of particular hinge details.

Philippi (1844) noted three teeth in the right and two teeth in the left valve of *K. miliaris*. M. Sars (1870) and G. O. Sars (1878) reported two cardinal teeth in each valve, while according to Fischer (1887), there is one cardinal tooth and two anterior lateral teeth in each valve. Gliber and Van de Poel (1966), in turn, treated cardinal parts of the hinge in *Kelliella* and *Miocardiopsis* (Glossidae) as being analogous to each other. Hence, they claimed, the Kelliellidae do not possess true lateral teeth. In this regard, Glibert and Van de Poel (1966) followed Harris (1920) to state that the margin of one valve in *Kelliella* merely overlaps the margin of the opposite valve.

Keen (1969) envisaged two cardinal teeth in the right valve of *K. miliaris* (Philippi) and one cardinal tooth and one lateral tooth in the left valve.

While describing four new species of *Kelliella*, Knudsen (1970) unfortunately did not specify the origin of their teeth.

Davies (1971) noted the anterior lateral tooth AI close to the cardinal 1, and a residual tooth 3b in the right valve, while he observed the deeply divided tooth 2 along with 4b in the left valve.

According to Jakubowski (1977), there are two cardinals 3a and 3b in the right valve converging at the angle 45°, and the horizontal lateral anterior tooth AIII. Similarly, two cardinals 2 and 4b and one horizontal lateral anterior tooth AII are present in the left valve.

The collection gathered by the present author is insufficient to undertake a study of the hinge development during ontogeny.

divided into two parts equal in length but in *K. miliaris* both these parts are also equal in strength and form the right angle with the apex situated just beneath the beak. The difference between the left valvs of the two species under comparison is more conspicuous. The anterior, lamelliform tooth in *K. miliaris* (Philippi) is sinuate, its posterior part being longer and more projecting than the anterior one, and the posterior tooth is very short. On the other hand, both the teeth are lamelliform in *K. barbara* sp. n., the anterior one being slightly longer, while the posterior more projecting.

Distribution. — The species *Kelliella barbara* sp. n. occurs only in its type locality at Nawodzice.

DISCUSSION

The majority of the present-day species of the genus *Kelliella* inhabit deep ocean basins within the abyssal and hadal zones. Only one species, *K. miliaris* (Philippi), can be found in the sublittoral zone. The individuals of *K. miliaris* (Philippi) live most commonly on sandy-clayey bottom within the depth range 100—400 m, but they range to even 700 m in depth (Nordsieck 1969).

In contrast, paleontological findings suggest other environmental requirements for fossil representatives of *Kelliella*. For example, shells of *K. boettgeri* Meyer are quite frequent in the Jackson Beds, a sedimentary unit within the Yazoo Clay (Mississippi and Alabama, USA). The age of the Yazoo Clay is determined as Late Eocene (NP18 to NP19 coccolith zones; cf. Frederiksen 1980), and the depth they have accumulated as ranging from 30 to 100 m. The bathymetric data concern, however, the eastern, deeper part of the sedimentary basin, while the locality of Jackson is closer to the ancient shoreline, where there was more terrigenous influx (Cheetham 1963). It seems, therefore, that *K. boettgeri* Meyer inhabited the shallower part of the basin, probably close to the upper limit of the postulated depth range.

The species *K. patera* Sorgenfrei, a component of *Leda pygmaea* — *Nassa cimbrica* assemblage, has been found in the micaceous sands within the Middle Miocene Arnum Formation, Denmark (Sorgenfrei 1958). While characterizing the bathymetric conditions in the basin, Sorgenfrei (1958: 414) stated, that "... the high frequencies of the shallow-water species and the evidence provided by the sediments are sufficient for assuming relatively shallow water, not deeper than 20 to 50 m..."

The specimens of *Kelliella barbara* sp. n. have been derived from fine-grained, unstratified, fossiliferous quartz sands, constituting the basal part of the Badenian (Middle Miocene) profile in Nawodzice (cf. Studencka 1986). Both the composition and the trophic structure of the molluscan assemblage from Nawodzice (known as *Circomphalus* assemblage — cf. Hoffman and Szubzda 1976) are very similar to those of some modern shallow-water benthic communities. In fact, the *Circomphalus* assemblage,

which includes the species *K. barbara* sp. n., is very close to the sublitoral community living in the Indian Ocean at the depth range of 20—30 m (Taylor 1971). The shallow-water character of the deposits from Nawodzice is also confirmed by the remaining, non-molluscan fossils (Bałuk and Radwański 1968).

The sedimentation of the fine-grained, quartz-glauconitic, Late Badenian sands from Monastyrz and Długi Goraj (Roztocze Region), where *Kelliella miliaris* (Philippi) is quite common, also took place under shallow-water conditions (ca 30 m), as stated by Jakubowski (1977), on the basis of the ecological requirements of the most abundant species.

The representatives of *Kelliella* in geologically younger strata (Pliocene and Pleistocene) are confined to deposits typical of greater depths. *K. abyssicola* (Forbes) for example, was found in the Early Pliocene (Tabianian — zones MPL1 and MPL2 of Cicha 1975) pelagic clays in Western Liguria, Italy (Robba 1981). The depth range they accumulated is estimated at 500—600 m, which corresponds to the shallow part of the bathyal zone.

The individuals of *K. miliaris* (Philippi) from the Early to Middle Pleistocene muds of Rhodes, also inhabited the bathyal zone, as reported by Sørensen (1984).

CONCLUSIONS

No deep-water representatives of *Kelliella* have been found in the Eocene through Miocene strata, whereas such forms predominate among modern kelliellids. Shallow-water Kelliellids, however, are well known in the fossil record; for example *Kelliella barbara* sp. n. from the Middle Miocene of Poland. Given the usual care at about ultimate inconclusiveness of negative evidence, one may then conclude that the paleontological data indicate a relatively rapid shift in depth requirements of the representatives of genus *Kelliella*, involving the change in optimal temperature, pressure, and other factors controlled by depth. Although it had inhabited shallow waters in the Eocene and Miocene, the genus *Kelliella* immigrated into the bathyal zone during the Pliocene to spread subsequently over both the abyssal and hadal zones where it now prefers to live. It is interesting, however, that this drastic change in habitat has not been followed by any change in the animal-sediment relation, as it is evidenced by the shell shape. Both fossil and Recent individuals have a strongly convex, subsphaerical shell that suggests sedentary or sluggish burrowing life just beneath the sediment-water interface (Stanley 1970). Such shell provides maximum buoyancy in soft, unconsolidated sediment.

It may be, therefore, concluded that particular living genera, and to a greater extent, particular living species are morely uncertain indicators

of ancient ecological conditions, even in the case of relatively young, Miocene environments; in older geological settings the situation is even farther removed from the actualistic data.

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BARBARA STUDENCKA

WYSTĘPOWANIE RODZAJU *KELLIELLA* (BIVALVIA, KELLIELLIDAE) W PŁYTKOWODNYCH OSADACH BADENU POLSKI

Streszczenie

W pracy starałam się pokazać, że do rekonstrukcji paleośrodowisk nie zawsze możemy korzystać z danych aktualistycznych. Dobrym tego przykładem jest rodzaj

Kelliella M. Sars, którego przedstawiciele w ciągu ostatnich 15 mln lat radykalnie zmienili swoje wymagania ekologiczne. Najstarsze znaleziska tego rodzaju (*K. boettgeri*) pochodzą z płytkowodnych (ca 30 m) osadów późnoeoceńskiego basenu w stanie Mississippi (USA). Również z tą strefą głębokości (20—50 m) związane jest występowanie gatunków *K. barbara*, *K. miliaris* i *K. patera* w mioceńskich osadach na obszarze Danii i Polski, podczas gdy znaleziska przedstawicieli rodzaju *Kelliella* z pliocenu i plejstocenu Włoch i wyspy Rodos (*K. abyssicola*, *K. miliaris*) związane są z osadami tworzącymi się w strefie batialnej (400—2000 m). Natomiast współczesne występowanie rodzaju *Kelliella* jest niemal całkowicie ograniczone do strefy abysalnej (2000—6000 m). Wśród małżów tej strefy do rodzaju *Kelliella* należy 8 gatunków. Ponadto 2 gatunki zostały znalezione w strefie hadalnej oraz w głębszych częściach strefy sublitoranej i batialnej.

W pracy opisałam nowy gatunek *Kelliella barbara*, pochodzący z płytkowodnych, piaszczystych osadów badenu z Nawodzic koło Klimontowa. Okazy tego gatunku są przechowywane w Muzeum Ziemi PAN.

EXPLANATIONS OF PLATES 31 AND 32

Plate 31

Kelliella barbara sp. n.

1. Left valve, exterior. MZ VIII Ml-2767/4.
2. Left valve, interior. MZ VIII Ml-2767/2.
3. Holotype. Right valve, interior. MZ VIII Ml-2767/3.
4. Right valve, exterior. MZ VIII Ml-2767/1.

approx. ×45

Plate 32

Kelliella barbara sp. n.

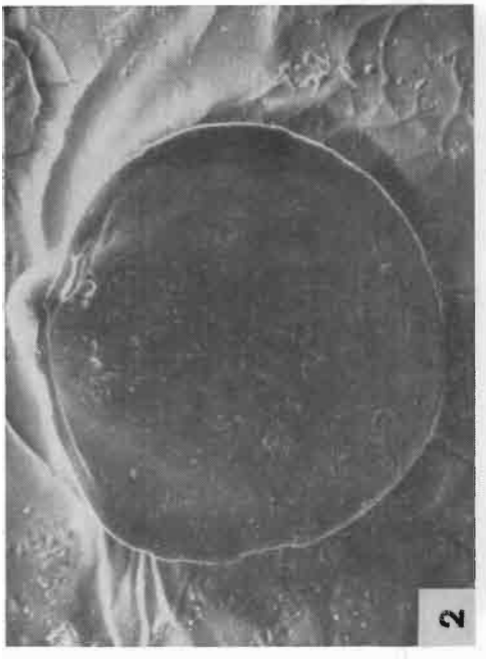
1. Hinge of the left valve. MZ VIII Ml-2767/2.
2. Holotype. Hinge of the right valve. MZ VIII Ml-2767/3.

Kelliella miliaris (Philippi, 1844)

3. Hinge of the left valve. MZ VIII Ml-2768/2.
4. Hinge of the right valve. MZ VIII Ml-2768/1.

3—4 Skagerrak Straits, Recent

approx. ×90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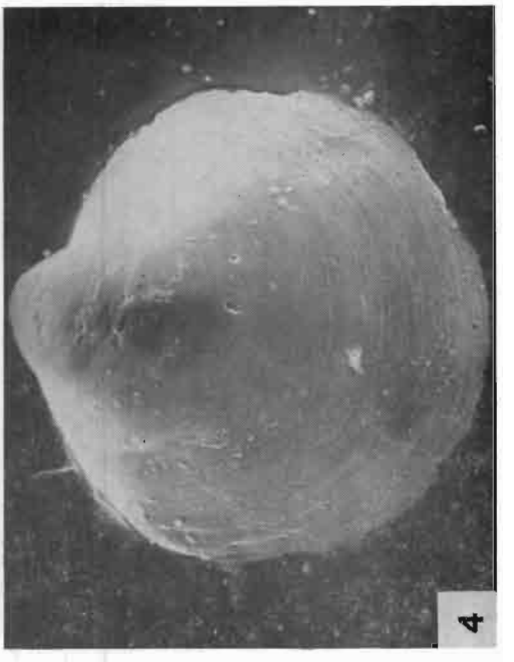
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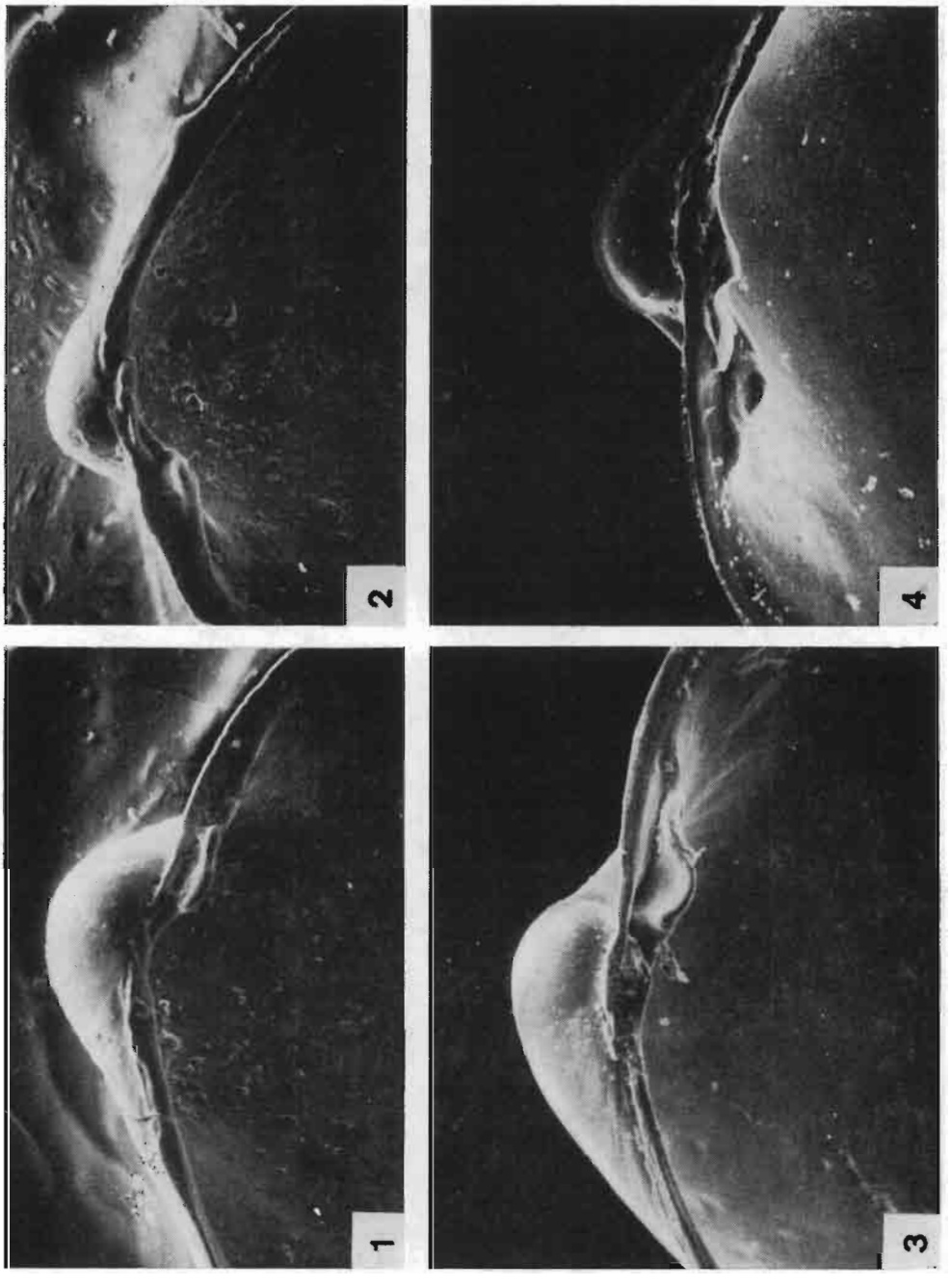
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