

The foraminifer *Elphidium excavatum* (Terquem) and its variant forms

ABSTRACT

The author agrees with Haake and Lutze in considering *Elphidium clavatum* Cushman and *Elphidium selseyense* (Heron-Allen and Earland) to be conspecific and in using the name *Elphidium excavatum* (Terquem) for this highly variable species. He believes, however, that certain varieties, or forms, of this species are associated with certain environments, and for this reason he considers it of importance to distinguish these forms taxonomically. The following names are suggested for these forms and the forms are described: *Elphidium excavatum* (Terquem) *forma clavata* Cushman, mainly arctic, *E. excavatum* (Terquem) *forma alba*, new name, mainly subarctic-boreal, *E. excavatum* (Terquem) *forma selseyensis* (Heron-Allen and Earland), mainly boreal, and *E. excavatum* (Terquem) *forma lidoensis* Cushman, mainly Lusitanian.

INTRODUCTION

Cushman (1930, pp. 18–19, pl. 7, figs. 8–9) described and figured a white, opaque *Elphidium*, which he referred to *Elphidium incertum* (Williamson). In the same paper (1930, p. 20, pl. 7, fig. 10), and in many others, he described and figured a translucent, yellowish-brown variety, which he named *Elphidium incertum* var. *clavatum*. These forms were recognized in arctic and subarctic waters of the Atlantic and the Pacific by several authors, and Boltovskoy (1954, p. 275, pl. 24, fig. 7) recorded the variety *clavatum* from the Southern Hemisphere. They were also recorded from Quaternary deposits, from the oldest (van Voorthuysen, 1949; Matoba, 1967), the middle (Gudina, 1966, 1969), and the youngest (Feyling-Hanssen, 1964; Michelsen, 1967; Jørgensen, 1971; Knudsen, 1971). Feyling-Hanssen (1964) found that a unit of his zonation of the marine Quaternary of the Oslo Fjord region in Norway, the early Holocene zone E, is characterized by frequent occurrence of Cushman's white, opaque *Elphidium incertum*, whereas the late glacial strata, zones A–D, contain an abundance of the yellowish-brown, translucent *E. incertum* var. *clavatum*.

Cushman (1944) and other authors found that there is a great amount of variation in these forms, and Parker (1952a) wrote that it was impossible, in the area investigated by her, to separate his *E. incertum* from the variety *clavatum*. In 1953, Loeblich and Tappan raised the variety to specific rank as *Elphidium clavatum* Cushman, and showed that the *Elphidium incertum* of Cushman is quite distinct from Williamson's *Polystomella umbilicatulula* var. *incerta* of 1858. This view was, in a convincing way, supported by Buzas (1966), who by statistical analysis and also by wall structure investigation proved that *E. clavatum* and the *E. incertum* of Cushman's concept can not be separated, and that *E. incertum* (Williamson), in addition to other differences, has a granulate wall structure instead of a radial wall structure. Thus the *E. incertum* of Cushman's concept has become a variety or simply a synonym of the original variety *E. clavatum*. Brodniewicz (1965) reached the same conclusion from investigation of these forms in material from the Baltic.

We will not consider *E. incertum* (Williamson) further, except to express doubt of the propriety of retaining the species in the genus *Elphidium* on account of the asserted difference in wall structure.

ARCTIC ENVIRONMENT

Elphidium clavatum Cushman is a characteristic element in benthonic faunas from moderate depths in arctic and subarctic waters of the present

day. In general, it accounts for a considerable percentage of such faunas, often constituting more than 50% of the specimens (cf. Phleger, 1952; Parker, 1952a, 1952b; Loeblich and Tappan, 1953; Cushman, 1944, 1948; Saidova, 1961; Cooper, 1964; Nagy, 1965; Leslie, MS.; Todd and Low, 1967; Vilks, 1969; Sen Gupta, 1971). A similar number of authors has encountered this taxon in marine deposits of the later ice ages of the Quaternary. The taxon is particularly dominant in Weichselian (Würm-Wisconsin) proglacial, interstadial and late glacial deposits (cf. Madsen, 1895; Cushman and Cole, 1930; Macfadyen, 1932; Brotzen, 1951; Weiss, 1954; Wagner, 1970; Feyling-Hanssen *et al.*, 1971). It may account for up to 100% of the assemblage in such deposits.

Elphidium clavatum is thus associated with an arctic environment, and, as a fossil, particularly when occurring in abundance, it is a reliable indicator of an ancient arctic environment.

BOREAL ENVIRONMENT

There are also many records of *Elphidium clavatum* in Recent faunas of lower latitudes. Van Voorthuysen (1951) found it in the vicinity of the Frisian Islands off the North Sea coast of the Netherlands, Jarke (1961) referred many specimens of *Elphidium* from stations in the North Sea to *clavatum*, Kureshy (1969) recorded it from The Wash in England, Haake (1962) found it off the German North Sea coast, and Brodniewicz (1965) and Lutze (1965, 1968) discovered it in the Baltic. As a fossil, it occurs in the Postglacial Warm Interval deposits in the Oslo Fjord area in Norway (Feyling-Hanssen, 1964), in Vendsyssel in northern Jutland (Knudsen, 1971) and in Holsteinian (Hoxnian) deposits (Buch, 1955; Wosizdlo, 1962; Fisher, Funnell and West, 1969).

The occurrence of *E. clavatum* in boreal as well as arctic waters and, as a fossil, in warm-water interglacial deposits reduces its value as a low-temperature indicator. However, as this type of occurrence is only scattered, it would not seem to be of any great importance. It is the high frequency of the species which is characteristic of arctic assemblages. However, Hansen (1965) found that *E. clavatum* was the most frequent species among the living foraminifera in the Øresund between Sweden and Denmark. In some samples it constituted more than 80% of the foraminiferal assemblage, which is a percentage expected only in arctic waters of the present day and in Late Pleistocene and very early Holocene marine sediments.

In this case, *Elphidium clavatum* is most probably confused with *Elphidium selseyense* (Heron-Allen and

Earland, 1909, 1911), which was originally described from the shore sands of Selsey Bill on the coast of southeast England and has later been recorded from many localities in the boreal region. Brand (1941), who found this species in Jade Bay, German North Sea coast, published an emended description of it. He emphasized that its test is planispiral with 7–9 (very seldom more than 9) chambers in the last-formed whorl, that its periphery is moderately lobulate, that the sutures are distinct, depressed, and, together with the umbilical region, contain granular material, and that the sutural bridges are poorly developed. Brand (1941, p. 66) designated figures 2a and 2c of plate 21 in Heron-Allen and Earland's paper of 1909 as lectotype, excluding figure 2b.

Such specimens occur in abundance in Aarhus Bay, Denmark; Kiel Bay, Baltic coast of West Germany (Richter, 1964); the Dollart-Eems estuary on the German-Netherlands border (van Voorthuysen, 1960); Langeoog Watt, German North Sea coast (Haake, 1962); the west coast of Denmark, and, as recorded by Hansen (1965), in the Øresund, if it is assumed that his *Elphidium clavatum* includes *E. selseyense*.

TAXONOMIC PROBLEMS

Hansen thus demonstrated the difficulty attached to the separation of *Elphidium clavatum* and *E. selseyense*. Haake (1962, p. 49) earlier arrived at the conclusion that the two belong to the same species. As a name for this taxon Haake used *Elphidium selseyense* (Heron-Allen and Earland), considering *E. clavatum* to be a junior synonym. In view of the great variation of the species, he thought that Heron-Allen and Earland's figure 2b, which had been excluded by Brand (1941) in his emendation, should also be regarded as a true *E. selseyense*.

Haake was followed by Wosizdlo (1962), who described *E. selseyense* from Holsteinian (Hoxnian) deposits in northwest Germany, and by Lutze (1965), who described the same form from the Baltic. Atkinson (1969, 1971) recorded it from Cardigan Bay, Wales. Lutze assumed that an older name must exist for such a common species and found one, after having studied topotype material, in *Polystomella excavata*, described by Terquem in 1876 from Dunkirk on the French North Sea coast, at the eastern entrance to the English Channel. Lutze transferred this species to the genus *Cribronion* Thalmann, and entered both *E. selseyense* and *E. clavatum* in the synonymy of *Cribronion excavatum* (Terquem). Lutze (1968) suggested that *Elphidium excavatum* in Cushman's concept be referred to *Elphidium articulatum* (d'Orbigny, 1839).

Intraspecifically, Lutze (1965) separated from among his specimens of *Cribronion excavatum* in the Baltic a thicker form, which occurred in deeper and colder water and which compared closely with specimens of *Elphidium clavatum* from Alaska, and considered this to be a subspecies, *Cribronion excavatum clavatum*. This should be able to exist in the same area as the typical *C. excavatum excavatum* because salinity layering of the water provides a barrier between the two. Haake, who in 1967 in general followed the taxonomy of Lutze, demonstrated, however, by a study of the seasonal occurrences of populations of *Cribronion excavatum* that thick forms occur together with compressed ones in the same population and merely illustrate the great variability of the species.

The use of Terquem's specific name, *Elphidium*, or *Cribronion excavatum*, was adopted also by Lévy *et al.* (1969) and by Grabert (1971).

LUSITANIAN ENVIRONMENT

In his paper of 1962 (p. 49), Haake described and figured from the German North Sea coast some thick specimens with many irregular bosses in the central area, which he called form 1 of *Elphidium selseyense*. Lutze (1965, p. 97), discussing *Cribronion excavatum*, mentioned the same form from the Helgoland area and wrote that this development is emphasized in Mediterranean populations. Von Daniels (1970, p. 87) again recorded this form, as *C. excavatum*, from the Limski Channel, Istria, Yugoslavia, an inlet of the Adriatic. The present author has collected this multi-umbonate form in the Bay of Cremenach between Vannes and St. Nazaire in Brittany, France, where it occurred in abundance, and along the Danish coast, where it is less frequent. Buzas (1966, pl. 71, figs. 3–4) also figured this knobby form and considered it a variation of *Elphidium clavatum*. It is very close to *Elphidium lidoense* Cushman, 1936, and is by transitional forms connected with *Elphidium excavatum* (Terquem). Lutze (1965, p. 97) assumed that the multitude of umbilical knobs in the Mediterranean form was the result of the higher temperature of that environment.

ECOPHENOTYPES

According to the above observations, we deal with a highly variable species, *Elphidium excavatum* (Terquem), which comprises *Elphidium clavatum* Cushman, *E. incertum* Cushman (not Williamson), *E. selseyense* (Heron-Allen and Earland) and *E. lidoense* Cushman, and which is widely distributed in the shallower parts of Recent waters, as well as in marine deposits of Quaternary age. In all environments variations in shape and sculpture of this species occur, but a certain pattern in the distribution of different forms is recognizable. Thus,

in a pure arctic environment there is a clear predominance of the *Elphidium clavatum* form. In boreal environment, e.g., the North Sea region and the western Baltic, the typical *Elphidium excavatum*, i.e., the *E. selseyense* form, is dominant, whereas in Lusitanian regions, e.g., the west coasts of France and Portugal, the Mediterranean and the entrance to it, the *E. lidoense* form is most common. In transitional environments transitional forms are common, and different types intermingle.

This pattern must also be of palaeoecological significance, and for these reasons it must be considered of some importance to maintain a taxonomic separation between the major variations within the species. It is here suggested that this be done on a *forma* level, so that the earlier different "species" of the group are retained as forms of *Elphidium excavatum*. For the white form which Cushman misnamed *Elphidium incertum* and which occurs quite commonly in zone E of the early Holocene of the Oslo Fjord area, *forma alba* is suggested as an appropriate name.

A review of these forms is presented below. Some new information, obtained by the use of a scanning electron microscope, is included. Specimens from the Mediterranean, the west and north coasts of France, the Channel coast of England, the German North Sea coast, the West German Baltic coast, the Bay of Aarhus on the Danish Kattegat coast, the Danish North Sea coast, Spitsbergen and the east coast of Greenland have been studied, and, in addition, Quaternary material from Denmark, Sweden, Norway and Baffin Island has been at hand. Most of this material was collected by the author, some by other members of the Department of Micropalaeontology, University of Aarhus, Denmark, and some by colleagues from foreign institutes.

Elphidium excavatum (Terquem) *forma clavata* Cushman Plate 1, figures 1–9; plate 2, figures 1–9

Elphidium incertum (Williamson), var. *clavatum* CUSHMAN, 1930, p. 20, pl. 7, fig. 10. — CUSHMAN and COLE, 1930, p. 96, pl. 13, figs. 8–9. — CUSHMAN, 1939, p. 57, pl. 16, figs. 1–2. — CUSHMAN, 1948, p. 57, pl. 6, fig. 8. — VAN VOORTHUYSEN, 1949, p. 65, pl. 1, fig. 4. — PARKER, 1952, p. 412, pl. 5, fig. 11. *Elphidium incertum* (Williamson) and variants. — PARKER, 1952, p. 448, pl. 3, fig. 16. *Elphidium clavatum* Cushman. — LOEBLICH and TAPPAN, 1953, p. 98, pl. 19, figs. 8–10. *Elphidium incertum clavatum* Cushman. — FEYLING-HANSEN, 1954, p. 141, pl. 2, fig. 11. — BOLTOVSKOY, 1954, p. 275, pl. 24, fig. 7. *Elphidium clavatum* Cushman. — TODD and LOW, 1961, p. 18, pl. 2, fig. 1. *Elphidium incertum clavatum* Cushman. — FEYLING-HANSEN, 1964, p. 345, pl. 20, figs. 11–15. *Elphidium subclavatum* GUDINA, 1964, p. 69, pl. 1, figs. 4–10Q; text-fig. 1.

Elphidium clavatum Cushman. — BUZAS, 1965, p. 23, pl. 3, figs. 3–4.

Elphidium subclavatum Gudina. — GUDINA, 1966, p. 45, pl. 4, figs. 4–10; pl. 9, fig. 3; pl. 10, fig. 3.

Elphidium clavatum Cushman. — MICHELSEN, 1967, p. 236, pl. 4, fig. 6. — MATOBA, 1970, p. 51, pl. 6, fig. 11. — TODD and LOW, 1967, p. 33, pl. 4, fig. 17. — SEN GUPTA, 1971, p. 89, pl. 2, figs. 28–29. — KNUDSEN, 1971 (part), p. 273, pl. 11, figs. 12–13; pl. 20, figs. 7–8.

Description: Test planispiral, involute, biumbonate; central boss of clear shell material, large or small, even absent, or in a few cases subdivided; periphery rounded to subacute, slightly lobulate in the latest part of the test; chambers 8–13 (mostly 9) in the final whorl, gradually increasing in size as added; sutures depressed, backward-curved, with a single row of sutural pores and a few (2–7) short, usually distinct, sutural bridges; sutures usually closed before reaching umbilical region; surface pattern in central area, along sutures and around aperture, which was previously referred to as a granular or vesicular mass of shell material, appearing in scanning electron microscope to consist of separate papillae, which are generally uniform, low, conical, with circular base and rounded top, height 2μ – 5μ ; wall calcareous, thin, translucent, yellowish-brown, with radiate structure. Fragments from the chamber walls, as well as from the septa, produce black crosses in the polarizing microscope. Wall distinctly perforate; pores round; septa and apertural face with few pores; tendency towards developing fewer or no pores in central extensions of chamber walls than in other parts of chamber walls; aperture a single row of pores at base of apertural face.

Dimensions: Greatest diameter 0.23 to 0.70 mm. (Loeblich and Tappan, 1953, p. 98), 0.17 to 0.48 mm. (Feyling-Hanssen, 1964, p. 187, p. 345); microspheric form greatest diameter 0.27–0.48 mm., megalospheric form 0.19–0.34 mm. (Gudina, 1966, p. 46). A specimen from the Sandnes Interstadial had a greatest diameter of 0.36 mm., and a thickness of 0.18 mm.; another one from the same deposit had a diameter 0.38 mm. and a thickness of 0.18 mm. (Knudsen, 1971, p. 273).

Remarks: Gudina (1966, pp. 45–52) found that Loeblich and Tappan (1953, p. 98) included different forms under the name *Elphidium clavatum*, i.e., forms with an umbilical knob, forms without a knob and forms with a subdivided knob. In her material from the northern and far eastern seas of the USSR and from the Quaternary of Siberia, Gudina did not find a single specimen with a subdivided umbilical knob or with no umbilical knob, and to this purely arctic form she gave in 1964 the new name *Elphidium subclavatum*. She also observed and emphasized the fact that the sutural depressions in this

form are closed towards the umbilical area, i.e., do not reach the umbilical depression around the central knob. Gudina distinguished between a megalospheric form with $1\frac{1}{2}$ –2 whorls and 8–10 chambers in the last-formed whorl, and a microspheric form with $2\frac{1}{4}$ –3 whorls and 9–12 chambers in the last-formed whorl.

Occurrence: With these characteristics in mind, specimens from Recent arctic waters can without hesitation be referred to *Elphidium excavatum* (Terquem) *forma clavata* Cushman. Specimens both from the east coast and from the west coast of Spitsbergen, examined by the present author, are all of indisputable *clavata* form. This is also the case with specimens from late glacial deposits in Norway, Sweden and Denmark. Particularly well-developed and numerous *clavata* forms occur in the so-called Younger Yoldia Clay of Vendsyssel in Denmark. They are yellowish-brown, translucent to hyaline, and very often with a small umbilical knob. In Mid-Weichselian (Würmian) Interstadial deposits from Vendsyssel and southwestern Norway (Feyling-Hanssen *et al.*, 1971) they are often thicker and possess a larger, clear, glassy, flat umbilical plug. Saidova (1961, p. 107) recorded *E. clavatum* from the Pacific, the Bering Sea, the Okhotsk Sea and the Japan Sea, and Gudina (1966, p. 21) classified it as arctic. She found it in abundance in the Obsk complex of the Middle Pleistocene of Siberia. Van Voorthuysen (1949) recorded *E. clavatum* from the Icenian of the Netherlands, but usually lower Quaternary specimens are of *E. selseyense* form there (Toering, personal communication).

***Elphidium excavatum* (Terquem) *forma alba* Feyling-Hanssen, n. form**

Plate 3, figures 1–9

Polystomella striatopunctata (Fichtel and Moll). — BRADY, 1884, p. 733, pl. 109, fig. 23.

Elphidium incertum (Williamson). — CUSHMAN, 1930, p. 18, pl. 7, figs. 5–9 (not *Polystomella umbilicatus*, var. *incerta* Williamson, 1858). — CUSHMAN, 1939, p. 57, pl. 15, figs. 22–24. — TEN DAM and REINHOLD, 1941, p. 54, pl. 3, fig. 8. — CUSHMAN, 1944, p. 25, pl. 3, figs. 28–31.

Elphidium incertum (Williamson) and variants. — PARKER, 1952 (part), p. 448.

Elphidium incertum incertum (Williamson). — FEYLING-HANSEN, 1954, p. 141, pl. 2, fig. 10.

Elphidium incertum (Williamson)? — BARKER, 1960, p. 226, pl. 109, fig. 23.

Elphidium incertum incertum (Williamson). — FEYLING-HANSEN, 1964, p. 344, pl. 19, figs. 16–17; pl. 20, figs. 9–10.

Elphidium clavatum Cushman, *sensu lato*. — BRODNIEWICZ (part), 1965, p. 210.

Elphidium incertum cf. Cushman form. — BUZAS, 1966, pl. 71, figs. 5–8.

Elphidium clavatum Cushman. — TODD and LOW (part), 1967, p. 33.

Description: This form differs from *forma clavata* by being white and opaque, by having a broadly rounded periphery and by very often not having an umbilical knob. The sutural bridges are usually broader than in *clavata* and the wall is thicker.

Dimensions: Usually the same as for *forma clavata*.

Remarks: On breaking the white, opaque chambers of the latest whorl of *forma alba*, the yellowish-brown test of *forma clavata* very often appears. Parker (1952b, p. 448) removed the outer whorls by treatment with acid and thus revealed a young form "apparently identical with the simpler, typical form of the *clavatum* variant." She discovered that the heavy-shelled variant, i.e., *forma alba*, constituted a large percentage of the fauna of facies 2, found in Long Island Sound, Gardiners Bay and Buzzards Bay, with temperatures varying from 1°C to 21°C and salinities from 28 to 30‰. Cushman (1939, p. 57) considered this form to be a cold-water species occurring along the continental shelf from Cape Hatteras northwards to Cape Cod. It occurs along the coast of Norway as far as North Cape. It has been recorded from Iceland and Alaska. Nørvang (1945, p. 31) considered its main distribution to be restricted to the arctic and temperate zones. Its distribution may be more southerly than that of *forma clavata*.

Very often *forma alba* occurs together with *forma clavata*, and numerous transition forms bridge the differences between the two, but in some cases, particularly in Weichselian deposits, they occur separated or nearly so. Thus, *forma clavata* dominates in glacial or late glacial deposits, whereas *forma alba* occurs in deposits of less severe environment. In the late Quaternary of the Oslo Fjord area, the early Holocene zone E is characterized by high frequency of *Elphidium excavatum forma alba*.

***Elphidium excavatum* (Terquem) *forma selseyensis* (Heron-Allen and Earland)**

Plate 4, figs. 1–7; plate 5, figs. 1–7

Polystomella excavata TERQUEM, 1876, p. 429, pl. 2, fig. 2a–d.
Polystomella striatopunctata (Fichtel and Moll) var., HERON-ALLEN and EARLAND, 1909, p. 695, pl. 21, fig. 2.

Polystomella striatopunctata (Fichtel and Moll) var. *selseyensis* HERON-ALLEN and EARLAND, 1911, p. 448.

Elphidium (*Polystomella*) *excavatum* (Terquem). – HERON-ALLEN and EARLAND, 1932, p. 439, pl. 16, figs. 22–23.

Elphidium incertum selseyensis (Heron-Allen and Earland). – BRAND, 1941, pp. 65–66.

Elphidium incertum (Williamson). – CUSHMAN, 1949, p. 28, pl. 5, fig. 9.

Elphidium excavatum (Terquem). – PARKER, 1952, p. 412, pl. 5, fig. 8.

Elphidium excavatum Terquem. – ROTTGARDT, 1952, pp. 182, 225.

Elphidium selseyensis (Heron-Allen and Earland). – VAN VOORTHUYSEN, 1957, p. 31, pl. 23, fig. 9. – VAN VOORTHUYSEN, 1960, p. 256.

Elphidium selseyense (Heron-Allen and Earland). – HAAKE, 1962, p. 49, pl. 5, fig. 15; pl. 6, figs. 1–5.

Elphidium selseyense. – RICHTER, 1964, pp. 343–351, text-figs. 5–6.

Elphidium clavatum Cushman. – BRODNIEWICZ, 1965 (part), p. 210, pl. 10, fig. 32. – HANSEN, 1965, p. 325, text-figs. 5–6.

Cribrononion excavatum (Terquem). – LUTZE, 1965, p. 96, pl. 15, figs. 39–41. – HAAKE, 1967, p. 14, fig. 2, pl. 1, figs. 1–14. – LEVY *et al.*, 1969, p. 93, pl. 1, figs. 1–2, 4.

?*Cribrononion miyakoense* UJIIÉ and KUSUKAWA, 1969, p. 766, pl. 1, fig. 4.

Elphidium clavatum Cushman. – KNUDSEN (part), 1971, p. 273, pl. 20, figs. 5–6.

Elphidium excavatum (Terquem). – MURRAY, 1971, p. 159, pl. 66, figs. 1–7.

Elphidium sp. MURRAY, 1971, p. 167, pl. 70, figs. 1–7.

Description: Test planispiral, involute, more or less compressed, usually biumbilicate; umbilical region of some specimens occupied by one or more small bosses; periphery rounded; peripheral outline more or less, but always moderately, lobulate; chambers usually 7–9 in the last-formed whorl, seldom more than 9, gradually increasing in size as added; sutures distinct, depressed, usually broadening and opening into umbilical area; sutural bridges generally poorly developed; sutural pores often developed as a continuous rift which opens into umbilicus; sutures, as well as umbilical area, occupied by numerous papillae of different sizes, each with a subcircular base and a rounded top. In addition to these primary papillae, there may occur smaller, pointed, secondary papillae, which may be rooted on the primary ones. Wall calcareous, thin, translucent, yellowish-brown to grey, with radiate structure, distinctly and densely perforate with round pores, the perforation continuing over the central extensions of the lateral chamber walls, the densely perforated wall conveying a hazy appearance to this form; aperture a single row of pores at the base of the apertural face.

Dimensions: Terquem (1876, p. 429) reported the greatest diameter of three specimens from Dunkirk as 0.35 mm., 0.48 mm. and 0.55 mm. Lutze (1965, text-fig. 8) recorded specimens from the western Baltic and from Langeoog Watt with diameters from 0.25 mm. to 0.64 mm. Haake (1967, text-fig. 18) measured specimens with diameters from 0.1 mm. to 0.4 mm. from North Sea tidal flats and 0.1 mm. to 0.55 mm. from Kiel Bay. Murray (1971, p. 159) reported 0.3 mm. as the average greatest diameter of British specimens.

Remarks: The density of pores varies from specimen to specimen both within *forma clavata* and within *forma selseyensis*, and within both forms it differs in different parts of the wall in the same specimen. Thus, in *forma*

selseyensis the apertural face shows few or no pores. In general, however, and considering at least approximately corresponding parts of the wall, the perforation is more dense in *forma selseyensis* than in *forma clavata*. This is observable with moderate magnification, because the more densely perforated wall of *forma selseyensis* gives this form a hazy appearance, whereas *forma clavata* appears more glassy. From twice to ten times more pores per square unit of wall surface occur in *forma selseyensis* than in *forma clavata*. As to the distribution of pores, there is a tendency in *forma clavata* to develop fewer or no pores in the central extensions of the lateral chamber walls than in other parts of the chamber walls, whereas *forma selseyensis* usually has chamber walls with normal perforation in their umbilical extensions.

The sutures are very often broader in *forma selseyensis* than in *forma clavata*, and, whereas they are usually closed or constricted before they reach the umbilical region in *forma clavata*, they are wide open towards the umbilicus in *forma selseyensis*.

The electron scanning microscope, as well as the light microscope, may reveal an elaborate pattern in the wall of *forma selseyensis*. The sinuous dividing lines of this pattern in most cases surround the pores of the test perforation, but they may also run across them. There may even be two or three pores within one such unit. This pattern illustrates the subdivision of the foraminiferal test wall into crystal units, as described for some other species by Towe and Cifelli (1967) and Hansen (1970). These units are also seen in *forma clavata*, particularly in etched specimens. In etched specimens of *forma selseyensis* a secondary subdivision is seen within the units of the primary pattern, i.e., the primary

units are subdivided into smaller units. This pattern may be also seen in some specimens of *forma clavata*, but it is more commonly demonstrated in *forma selseyensis*.

Occurrence: Terquem (1876) described *Polystomella excavata* from the beach of the Dunkirk area. Heron-Allen and Earland (1909, 1911) recorded *Polystomella striatopunctata* var. *selseyensis* from Selsey shore sand. *Forma selseyensis* is known from intertidal marshes of the Dovey estuary in Cardigan Bay (Atkinson, 1971), from the western Baltic, from the Danish coasts and from the German and English North Sea coasts (Brand, 1941; Haake, 1962; Lutze, 1965; Richter, 1964; Hansen, 1965; Brodniewicz, 1965). Kureshy (1969) recorded it, as *E. clavatum*, from The Wash on the English North Sea coast, and Lévy *et al.* (1969) and Murray (1970) reported it from the English Channel. Lees, Buller and Scott (1969) found it on the Connemara coast, western Ireland. Murray (1971) regarded this form as probably being a southern one. It seems to be mainly distributed in the southern part of the boreal and the northern part of the Lusitanian region of the European coasts, i.e., the North Sea, Skagerrak, Kattegat, western Baltic and English Channel coasts, the Irish Sea and the west coast of Ireland.

In samples from the Postglacial Warm Interval of the Oslo Fjord area (Feyling-Hanssen, 1964) and Vendsyssel in Denmark (Knudsen, 1971), *Elphidium clavatum* is recorded as quite common. The majority of these specimens belong to *forma selseyensis*. Lafrenz (1963) found it in the Eemian of Schleswig-Holstein, Konradi (in press) in the Eemian of Stensigmosse near Svendborg in Denmark, and Wosizdlo (1962) in the Holsteinian (Hoxnian) deposits of Schleswig-Holstein.

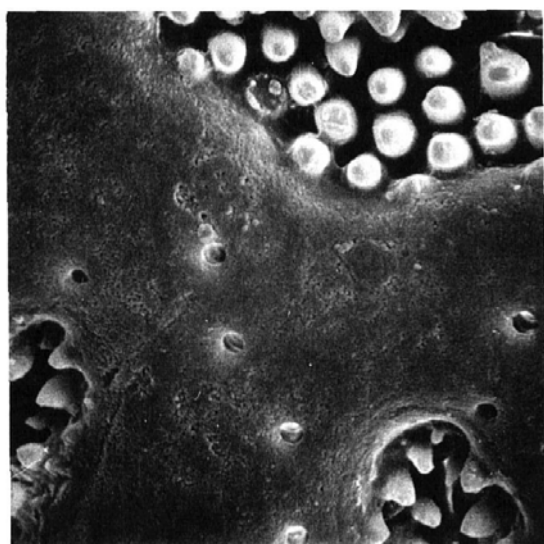
PLATE 1

1-9 *Elphidium excavatum* (Terquem) *forma clavata* Cushman

1-5, Recent specimen from Mygbugten (Mosquito Bay), East Greenland, taken at a depth of 10 m. 1, detail of central area with regular papillae, $\times 1700$. 2, side view of whole specimen, $\times 170$. 3, central area with sutures closed before they reach umbilicus, lateral extensions of chamber walls sparsely perforated, and poorly developed central knob, $\times 425$. 4, wall pores, $\times 1700$. 5, wall pores and etched surface, $\times 850$. Collector: Feyling-Hanssen, 1951.

6, side view of another Recent specimen from the same locality and depth, this one also having a poorly developed central knob, $\times 165$. Collector: Feyling-Hanssen, 1951.

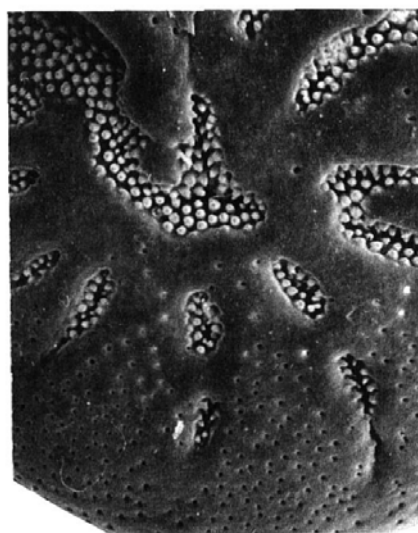
7-9, a specimen from the late Quaternary Lundergaard Clay, Denmark. 7, side view of a specimen with a well-developed central knob, $\times 160$. 8, central area with central knob, sutures closed before they reach the depression around the knob, no perforation of the test wall in the central area, and papillae poorly developed, $\times 710$. 9, edge view of the same specimen, $\times 200$. Collector: Knudsen, 1970.



1



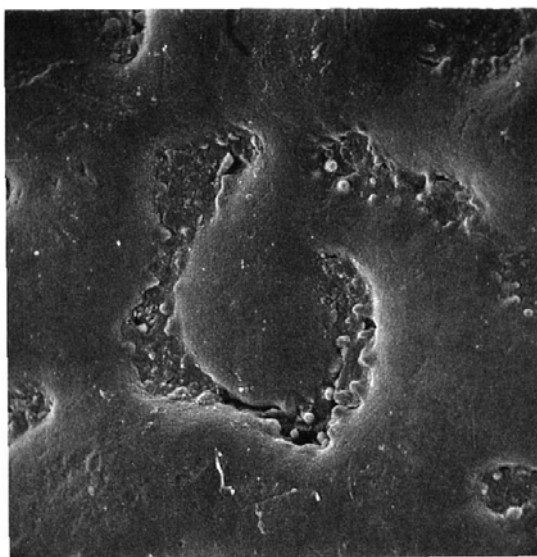
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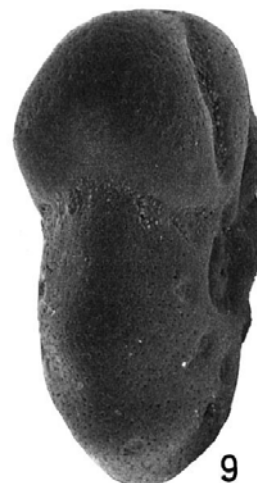
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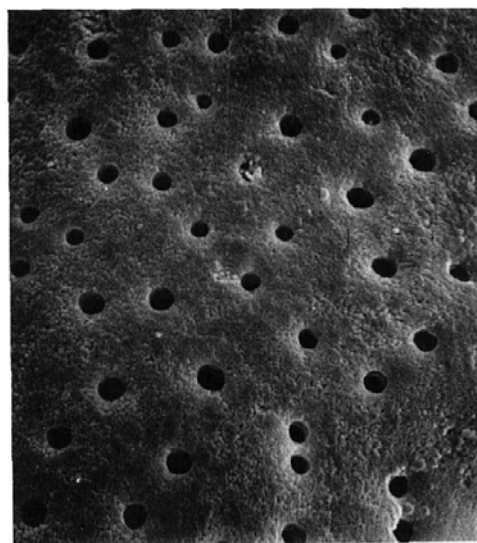
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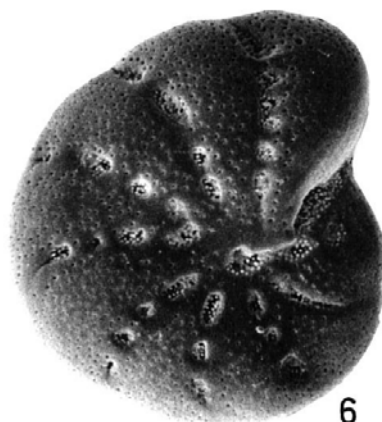
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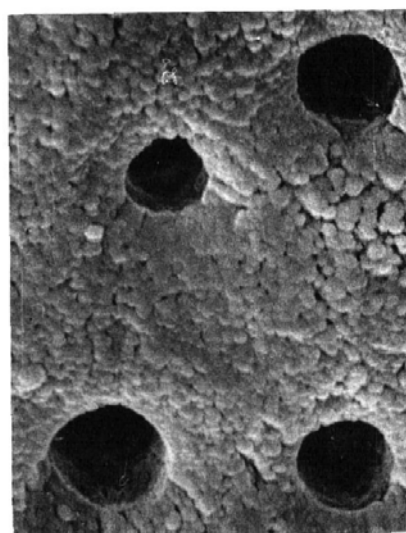
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4



6



5

***Elphidium excavatum* (Terquem) forma *lidoensis* Cushman**
Plate 6, figures 1–7

? *Polystomella arctica* Parker and Jones. – TERQUEM, 1876, p. 428, pl. 2, fig. 1 (not Parker and Jones, 1865).

Elphidium lidoense CUSHMAN, 1936, p. 86, pl. 15, fig. 6. – CUSHMAN, 1939, p. 62, pl. 17, fig. 17. – ACCORDI and SOCIN, 1950, pp. 12, 15, pl. 1, fig. 8.

Elphidium incertum (Williamson) variants. PARKER, 1952, p. 448, pl. 4, figs. 1–2.

Elphidium selseyense (Heron-Allen and Earland), Extrem Form 1. – HAAKE, 1962, p. 49, pl. 5, figs. 12–14.

Elphidium clavatum Cushman, knobby form. – BUZAS, 1966, p. 590, pl. 71, figs. 3–4.

Elphidium (?) *lidoense* Cushman. – CITA and SILVA, 1967, pp. 35–36, 43, 47, pl. 2, figs. 1–2.

Cribrononion lidoense (Cushman). – LÉVY *et al.*, 1969, p. 94, pl. 1, fig. 9.

Cribrononion excavatum (Terquem); VON DANIELS, 1970, p. 87, pl. 7, fig. 11.

Description: *Forma lidoensis* differs from *forma selseyensis* in having many irregular bosses in the central area.

Dimensions: As for *forma selseyensis*.

Remarks: The papillae of the central area seem to have fused into a number of central knobs. Haake (1962, p. 49) described such specimens from the German North Sea coast. Lutze (1965, p. 97) mentioned their presence in Helgoland waters and observed that they are abundant in Mediterranean populations. He considered this strongly ornamented knobby form to be a temperature response of the species. Sometimes such forms may resemble *Elphidium gunteri* Cole, but they do not have the distinct, rectangular and often quite

numerous sutural bridges of this latter species. The umbilical part of the sutures is usually broader in *forma lidoensis* than in the other forms of *Elphidium excavatum*.

Occurrence: Scattered occurrences of this form are known from European boreal waters and also from the east coast of North America, but its main habitat is Lusitanian waters. The present author found it in abundance in the Morbihan Gulf and at Cremenach near Vannes on the west coast of France. Cushman (1936, p. 86) described it from Lido Beach, Venice, in the Adriatic, and Von Daniels (1970, p. 89) recorded it, as *Cribrononion excavatum*, from the Dalmatian coast.

The form described by Lentini (1968, p. 334) as *Protelphidium lidoense* (Cushman) seems to have a closer affinity to *Protelphidium anglicum* Murray than to the present form.

Parker (1958, p. 270) considered *Elphidium lidoense* Cushman from the Mediterranean conspecific with *E. granosum* (d'Orbigny) from the Miocene of the Vienna Basin. This might have some bearing upon an age relation between the forms dealt with, the *lidoensis* form probably having appeared in the pre-Quaternary and the *clavatum* form much later, during the cold climates of the Quaternary.

ACKNOWLEDGMENTS

This research was partly supported by the Danish National Research Council. I wish to thank Dr. F. W. Haake of Kiel, West Germany, for having provided me with material of Recent *Elphidium* from Langeoog.

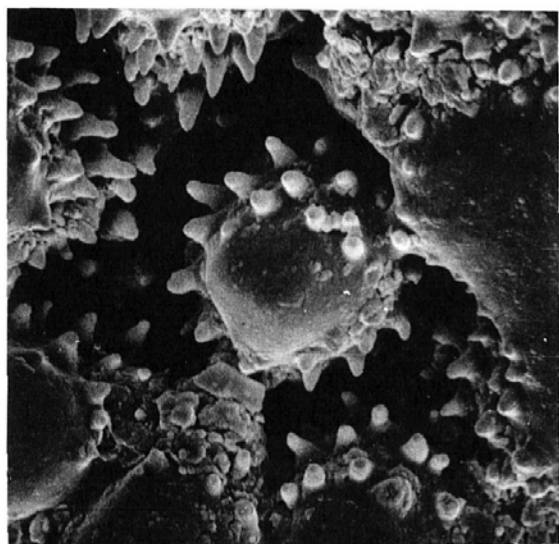
PLATE 2**1–9 *Elphidium excavatum* (Terquem) forma *clavata* Cushman**

1–3, a specimen from the early Holocene, zone D, Skaadalen, Oslo, Norway. 1, central area with umbilical knob and distinct, uniform papillae, $\times 1680$. 2, side view of whole specimen. The central extensions of the chamber walls are sparsely perforate, and the sutures are incompletely closed toward the umbilicus. $\times 170$. 3, pores of the test wall, $\times 1680$. Collector: Øyen (Pal. Mus., Oslo).

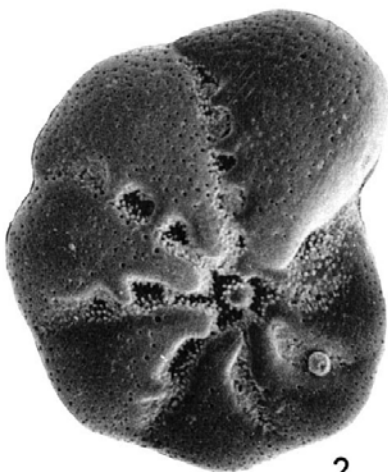
4–5, a specimen from the late Quaternary Lundergaard Clay, Lundergaard, Vendsyssel, Denmark. 4, side view showing very poorly developed sutural bridges, sutures which are closed towards the umbilical depression, and a poreless test wall in the central area, $\times 240$. 5, edge view of same specimen, thick but with subacute periphery, $\times 250$. Collector: Knudsen, 1969.

6, central area of a specimen from the late glacial of Løkken, Vendsyssel, Denmark, showing central knob, sutures closed towards umbilicus, and lack of wall perforation in central part of test, $\times 510$. Collector: Knudsen, 1968.

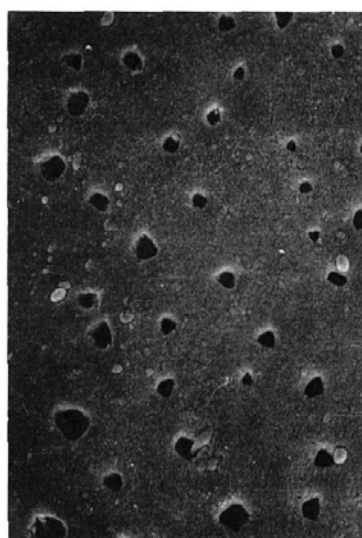
7–9, a specimen from the late glacial zone A_u at Fredrikstad, Oslo Fjord area, Norway. 7, large, flat central knob, $\times 425$. 8, side view of whole specimen, $\times 170$. 9, papillae of central area, worn and uniform, $\times 1400$. Collector: Feyling-Hanssen, 1962.



1



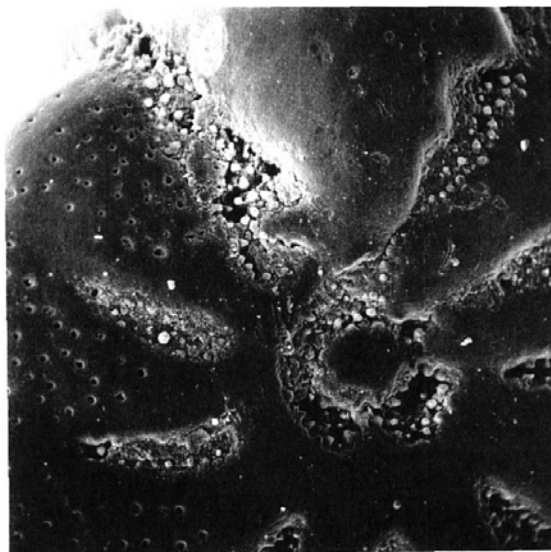
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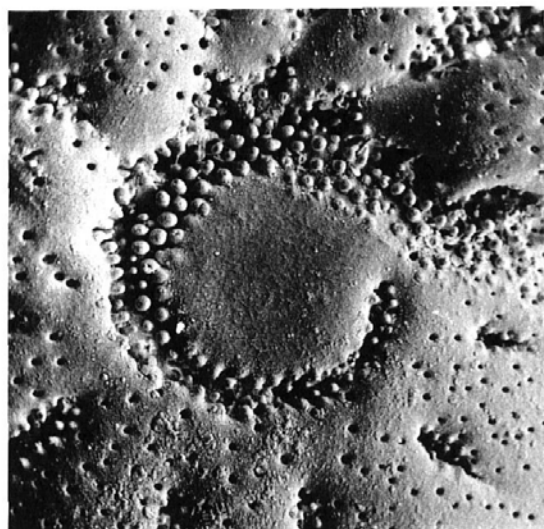
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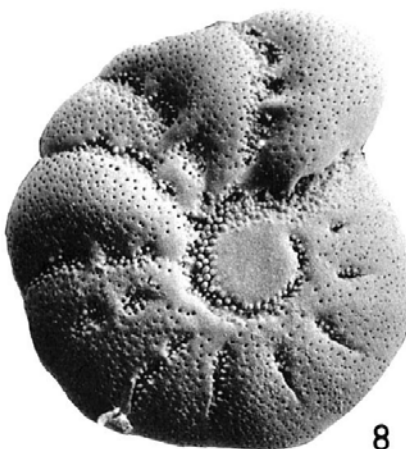
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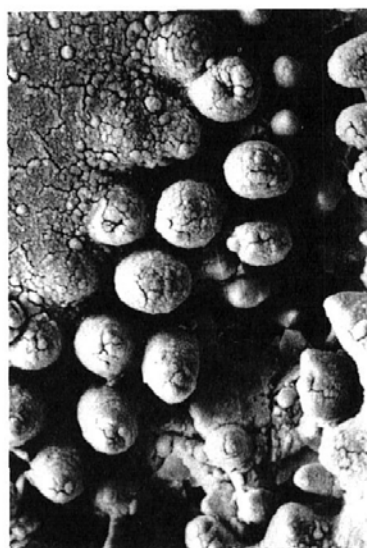
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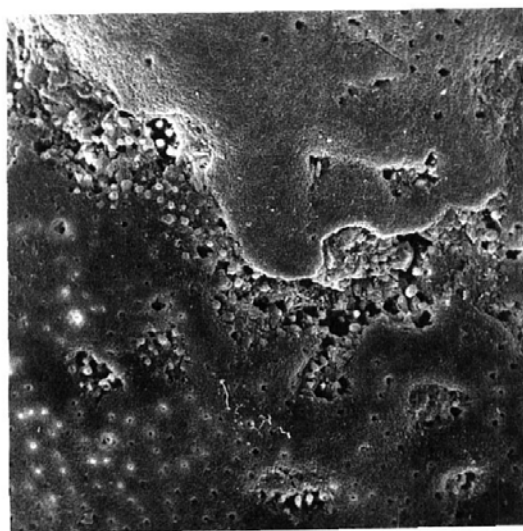
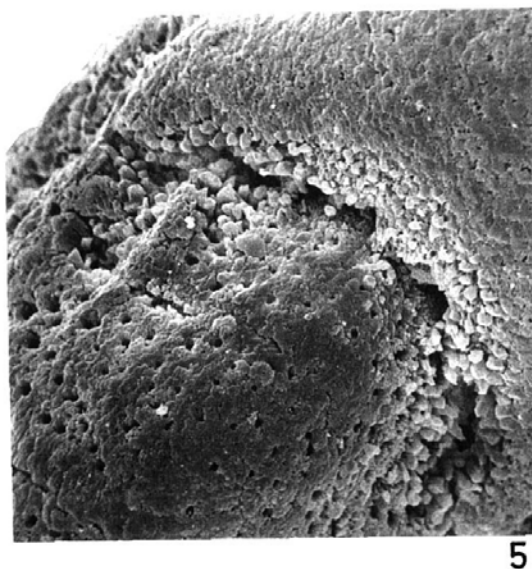
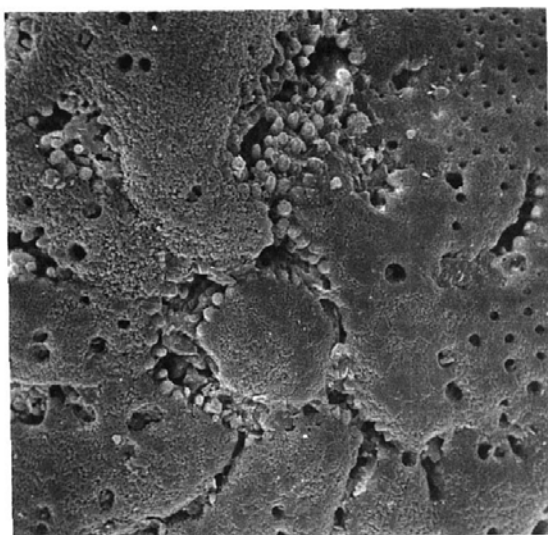
Watt and from Kieler Bucht; Dr. J. Haynes of Aberystwyth, Wales, for having sent me specimens of *Elphidium selseyense* from Selsey shore sand and from the Dovey estuary in Cardigan Bay; Mrs. K. L. Knudsen of Aarhus, Denmark, for giving me specimens of Recent and Quaternary *Elphidium* from Denmark; and Dr. G. Richter of Senckenberg, West Germany, for having provided me with material from the Jadegebiet. I am grateful to Dr. Haake, Mrs. Knudsen and Dr. G. Lutze, Kiel, for valuable discussions, and to Mrs. A.-L. Nørgaard of the Electron Microscope Centre in Copenhagen for her skilled operation of the scanning electron microscope. Mr. S. A. Meldgaard made the pictures for the plates, Mrs. L. Ø. Mogensen typed the manuscript, and Dr. J. R. Wilson corrected many of the mistakes in the English.

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PLATE 3

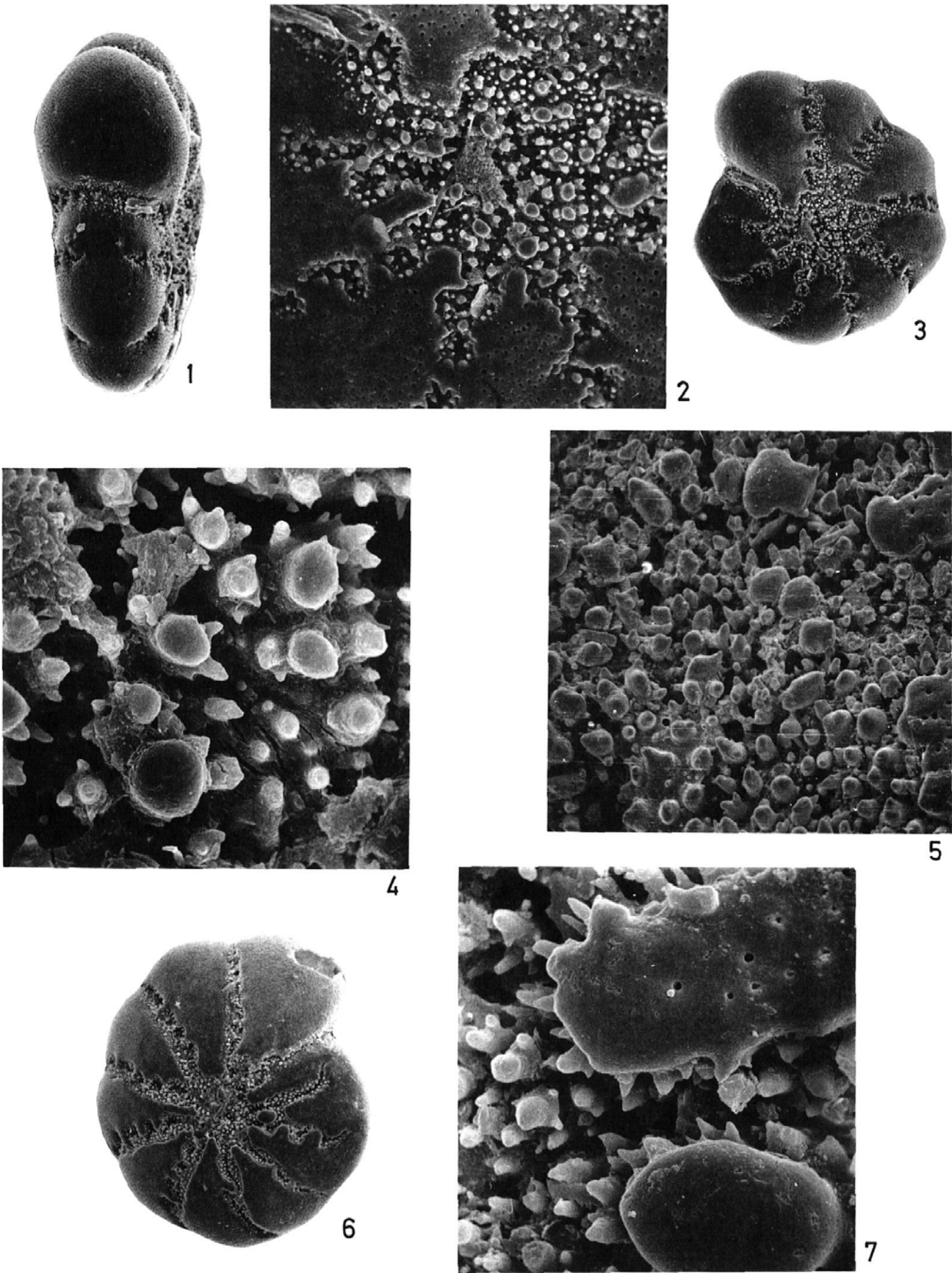
- 1–9 *Elphidium excavatum* (Terquem) *forma alba* Feyling-Hanssen, n. form
1–3, specimen from Hoxnian (Yarmouthian) deposits at Inner Silver Pit (sample 16) in the western North Sea. 1, side view illustrating the quite distinct sutural bridges and the umbilical knob, $\times 160$. 2, central area, $\times 520$. 3, edge view, illustrating thickness of specimen, $\times 240$. Collector: Funnell, 1964.
4–6, specimen from Holocene zone E of Oslo, Norway. Surface corrosion has taken place. 4, side view showing the poorly developed sutural bridges, lack of umbilical knob, and scarcity of wall pores, in the central part of the test, $\times 210$. 5, details of the aperture, which consists of a row of pores at the base of the apertural face. Crystal units are visible, particularly in the apertural face. $\times 570$. 6, edge view, $\times 230$. Collector: Feyling-Hanssen, 1962.
7–9, specimen from an Eemian? deposit at Fjøsanger near Bergen, Norway. 7, edge view, $\times 140$. 8, details of central part, which lacks an umbilical knob, $\times 390$. 9, side view, showing short, broad sutural bridges and lack of umbilical knob, $\times 160$. Collector: Mangerud, 1968.



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PLATE 4

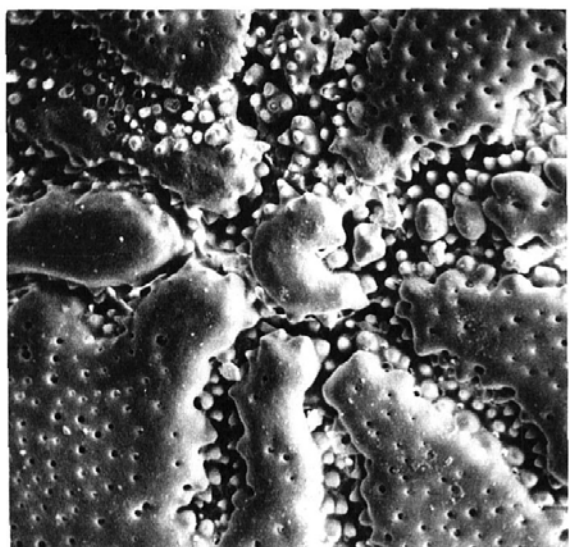
- 1–7 *Elphidium excavatum* (Terquem) *forma selseyensis* (Heron-Allen and Earland)
 1–4, specimen from the Lim Fjord, Denmark, taken at a depth of 4 m. 1, edge view, $\times 170$. 2, central area, showing sutures opening into umbilical area and different-sized papillae, $\times 390$. 3, side view of whole specimen, $\times 140$. 4, details of central area with secondary papillae projecting from primary ones, $\times 1380$. Collector: Bendtsen, 1969.
 5, central area of a specimen from the Jade Gebiet, German North Sea coast, showing different-sized papillae, $\times 425$. Collector: Richter, 1961.
 6–7, another specimen from the Lim Fjord, Denmark, taken at a depth of 4 m. 6, side view, $\times 140$. 7, details near central area, including primary and secondary, partly pointed, papillae, $\times 1330$. Collector: Bendtsen, 1969.



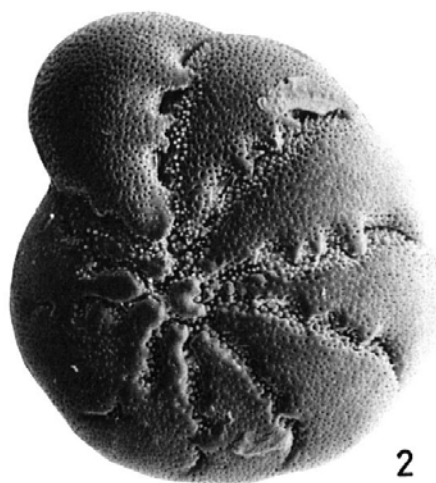
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PLATE 5

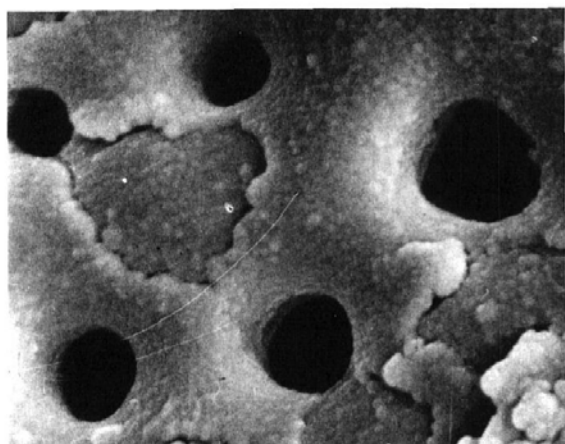
- 1–7 *Elphidium excavatum* (Terquem) *forma selseyensis* (Heron-Allen and Earland)
1–4, specimen from Kiel Bay, Baltic Sea. 1, central area showing sutures opening into the umbilical area and wall perforation in the central extensions of the chamber walls, $\times 430$. 2, side view showing dense perforation, $\times 170$. 3, details of wall with pores, $\times 8500$. 4, papillae, just above centre of test, $\times 1700$. Collector: Richter, 1961.
- 5–7, specimen from Selsey (Sussex) shore sand. 5, wall pores in corroded test surface, $\times 1700$. 6, details of test surface, showing crystal units, $\times 8500$. 7, central area with widely open sutures, $\times 425$. Collector: Haynes, 1965.



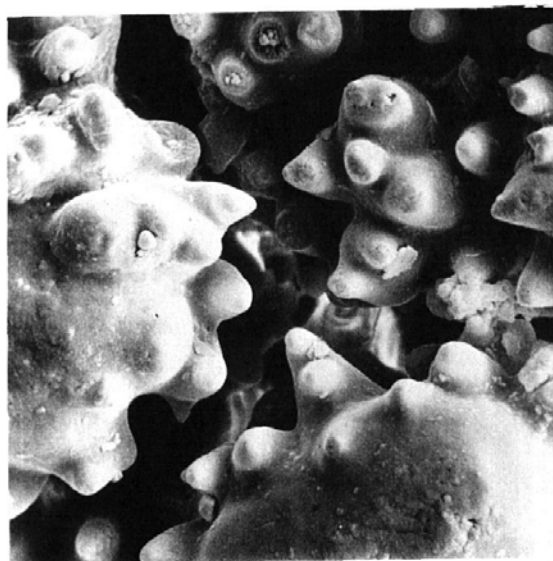
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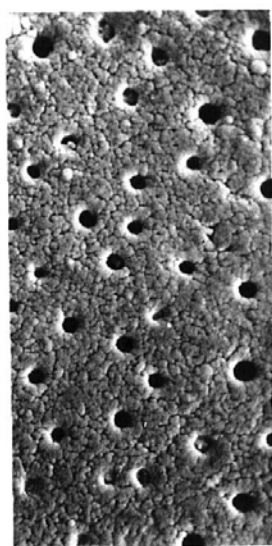
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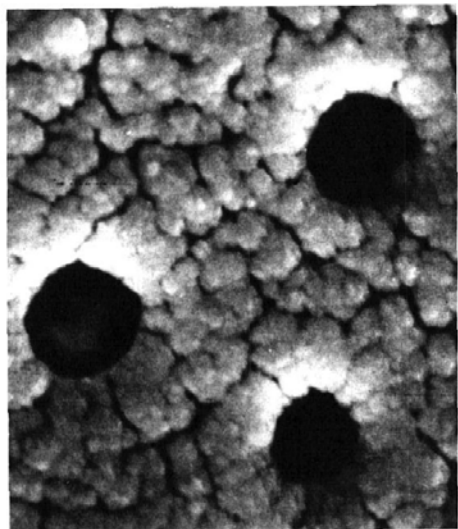
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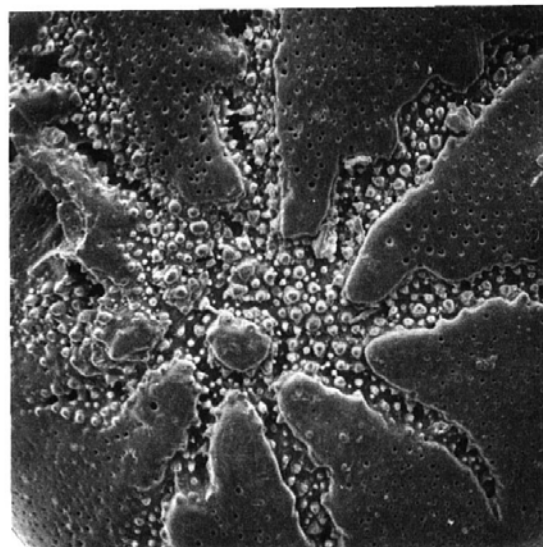
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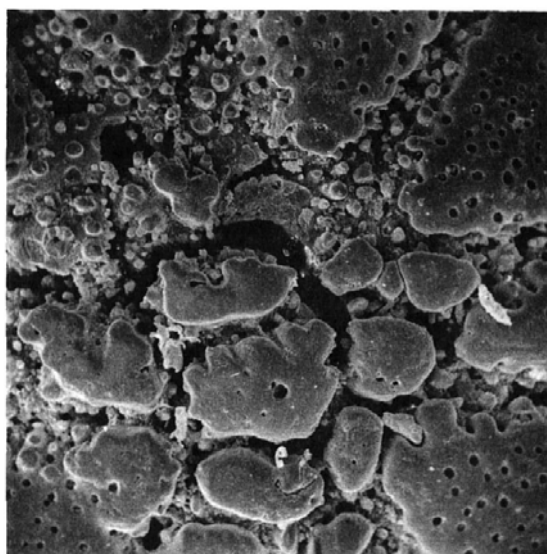
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PLATE 6

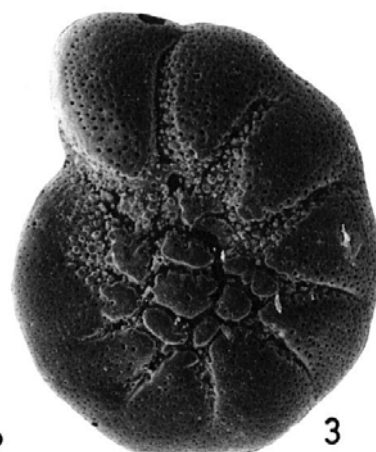
- 1–7 *Elphidium excavatum* (Terquem) *forma lidoensis* Cushman
1–4, specimen from the beach of Alberoni, Italy. 1, edge view, $\times 180$. 2, central area with many knobs, $\times 430$. 3, side view showing sutures widely opening into umbilical area, $\times 180$. 4, detail of latest suture with different-sized and partly pointed papillae, $\times 1730$. Collector: Bang, 1966.
5, central area of a specimen from the beach of the Morbihan Gulf, Brittany, France, showing knobs and papillae, $\times 670$. Collector: Feyling-Hanssen, 1969.
6–7, another specimen from the beach of Alberoni, Italy. 6, central area with knobs and papillae, $\times 820$. 7, side view of whole specimen, $\times 170$. Collector: Bang, 1966.



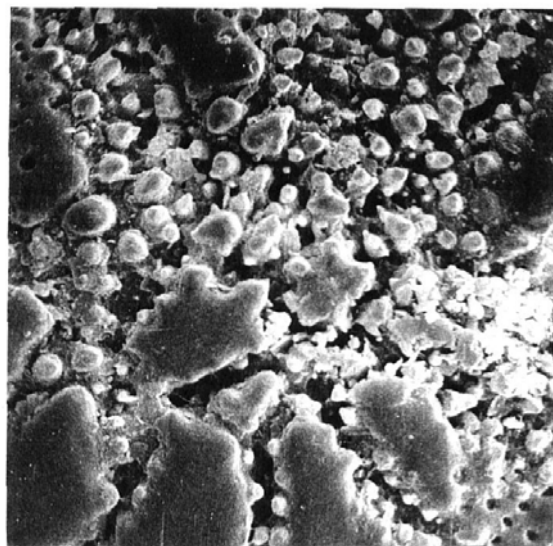
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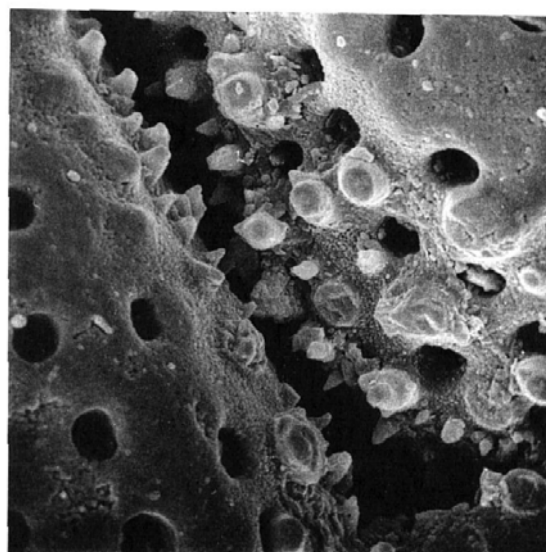
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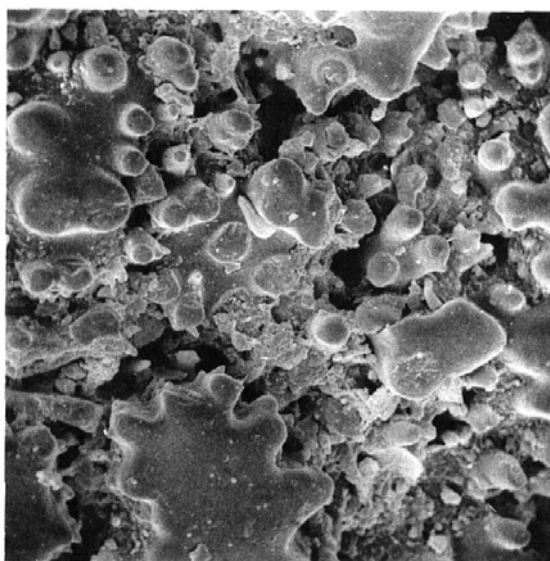
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