Megaspore assemblages from the Jurassic and lowermost Cretaceous of Bornholm, Denmark

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With 21 plates

Vignette:
Facsimile of figures 6.8, 6.1, 6.7, and 6.9 in Helge Gry's (1969) paper
on Jurassic megaspores from Bornholm

Helge Gry

This paper is dedicated to the late Dr. Helge Gry who, until a few years before his death in 1982, worked for the Geological Survey of Denmark in Copenhagen. He particularly enjoyed carrying out field work on Bornholm where he spent much time attempting to unravel the geological history of this tectonically complex area.

Contents

Abstract

There are more than 600 slides containing megaspores in "Helge Gry's collection", housed at the Geological Survey of Denmark in Copenhagen. The majority of the specimens are unnamed, all are from the Danish island of Bornholm in the Baltic Sea, and none has been described hitherto. The stratigraphic distribution of 22 of the taxa was, however, taken into account in a paper by Gry, published in 1969, and 16 of these were illustrated by small line drawings. He considered the lithology, areal extent and depositional history of what were thought at the time to be only Jurassic strata on Bornholm. The youngest part of the succession he discussed, the "Purbeck beds" (Rabekke and Robbedale Formations), are, however, now known to be mainly, if not entirely, of earliest Cretaceous age.

In the present paper Gry's megaspore records are brought up to date so that they can be used more effectively along with other microfossils in drawing biostratigraphical and palaeoenvironmental conclusions. All 22 taxa to which he referred are discussed and illustrated, mostly with scanning electron micrographs, and their nomenclature emended where necessary. Descriptions and figures of an additional 15 forms encountered in the collection are included. Three of these are new species of megaspores and one is a palynomorph of uncertain origin, named *Henrisporites bornholmensis*, *Paxillitriletes kristinae*, *P. rasmusii* and *Aneuletes discus* respectively.

Most, if not all, of the megaspores in Gry's collection are likely to have selaginellalean or isoetalean affinities. There is no evidence of the presence of heterosporous water ferns. The assemblages differ significantly in composition according to their relative ages, with several forms being of considerable biostratigraphic value. There is, however, still room for greater precision in determining local stratigraphic ranges, and also a need to apply occurrence data to palaeoenvironmental interpretations. This will require carefully documented collecting of new samples.

Introduction

More than 20 years ago Helge Gry (1969) gave an account of the lithology, areal extent, depositional history and megaspore content of Mesozoic deposits of the Danish island of Bornholm in the Baltic Sea (figs 1, 2). Emphasis was placed on the Lower and Middle Jurassic sections. The younger "Purbeck beds" were only briefly considered. At that time they were also thought to be Jurassic but are now considered to be largely if not entirely earliest Cretaceous, Berriasian (Gravesen et al., 1982). Discussion of the megaspores recovered from the deposits within several fault blocks on the southern and western parts of the island was restricted mainly to notes on the occurrence of previously described species and their stratigraphic significance. Of the 22 taxa recorded, 16 were illustrated by small line drawings.

Although the megaspores in Gry's paper have provided a useful basis for dating most of the members of the several Jurassic and earliest Cretaceous formations on Bornholm (Gravesen et al., 1982), the lack of descriptions and photographic illustrations of most of the taxa has rendered comparison with other mid-Mesozoic assemblages difficult. Only three species have been studied in some detail hitherto (Kempf, 1972). These

are *Margaritatisporites turbanaeformis* (referred to *Trileites candoris* herein), *Horstisporites kendallii* and *Istisporites murrayi* (*Trileites murrayi* herein), specimens of which were thin sectioned and examined under a transmission electron microscope (TEM). Gry did not provide the samples from which they were isolated. They had, instead, been collected from unspecified levels in the Hasle Klinkerfabrik clay pit (fig. 3) by two of Kempf's colleagues four years previously and were regarded as "Dogger in age" (Kempf, 1972, p. 152).

The main purpose of our paper is to bring Gry's work up to date so that its value can be better appreciated by others who attempt to use plant microfossils for resolving biostratigraphic problems and contributing to palaeoenvironmental interpretations within the Mesozoic. We describe and illustrate all of the species to which he referred, where necessary changing the nomenclature to bring it into line with current use. We also treat in a similar way other species in his slides which he did not mention so that our review of his megaspore collection is more comprehensive. The systematic descriptions are followed by a discussion of the botanical affinities of the plants represented, and of the biostratigraphic value and potential of the spores.

Geological setting

The exposed Mesozoic deposits of Bornholm range in age from Late Triassic to Late Cretaceous. Throughout their geographic extent the oldest beds unconformably overlie Lower Palaeozoic sedimentary rocks and Precambrian crystalline basement within a series of fault blocks situated at the southern end of the Fennoscandian Border Zone (Gravesen et al., 1982 and references cited therein). Outcrops are mainly restricted to low cliffs along the southern and western coasts (fig. 2). Inland exposures are limited to a few quarries, many of which are now disused, and as a result at least partly degraded by weathering and covered with vegetation. This applies particularly to the Jurassic and lowermost Cretaceous localities, the only good quarry exposure being of the Lower to Middle Jurassic Bagå Formation at its type locality, the Hasle Klinkerfabrik clay pit (fig. 3).

Much of the stratigraphic knowledge of the Triassic-Lower Cretaceous succession is attributable to the work of Gry (1956, 1960, 1968, 1969) but the nomenclature he used was mainly informal and applicable only locally within individual fault blocks. This approach is a reflection of the fact that most of the sediments accumulated in paralic environments. The facies change rapidly both vertically and laterally, and marine fossils are generally absent. Stratigraphic subdivision and correlation of sections throughout the area of outcrop was, however, hampered by Gry's descriptive, block-by-block approach but Gravesen et al. (1982) presented a new lithostratigraphic subdivision of the succession comprising two groups, three formations and ten members. Of these, only the Triassic Risebæk Member of the Kågeröd Formation and the Cretaceous Tornhøj and Rødbjerg Members of the Jydegård Formation are not considered further here. As shown on figure 4, significant periods of time are not, or may not be, represented in the Jurassic-Lower Cretaceous sedimentary succession. There are unconformities between the Bagå and Rabekke Formations, and perhaps also between the Hasle and Bagå Formations (see below). This is in contrast to the succession that has been interpreted, from shallow seismic investigations, to be present offshore in the eastern Rønne Graben, immediately to the west of Bornholm. Jensen & Hamann (1989) suggested on the basis of their geophysical data that sedimentation was continuous throughout the Jurassic and into the earliest Cretaceous (represented by the Berriasian Rabekke Formation) in this region, but they had no biostratigraphic data to support their con-

clusion. Both the Robbedale and Jydegård Formations are apparently absent from the graben.

Rønne Formation

Munkerup Member

Gry (1969) recovered megaspores from beds within what are now known as the Munkerup and Sose Bugt Members of the Rønne Formation (fig. 4). The areal extent of the first of these is very limited, both at outcrop and in the subsurface (Gry, 1969, pp. 73–75, figs 2,3; Gravesen et al., 1982, p. 14, figs 2,6,10), and it may be no more than 20m thick. The dominant lithology is grey to black clay. This commonly contains abundant particulate plant remains, occasionally forming coaly laminae one or two cm thick. Deposition in lacustrine conditions is indicated (Koppelhus, 1991). Harris (1937) recorded plants from it which he attributed to the *Thaumatopteris* flora of earliest Jurassic, Hettangian age. This dating has recently been confirmed on the basis of the composition of palynomorph assemblages recovered from the member by Koppelhus (1991) who referred them to the *Pinuspollenites-Trachysporites* Zone of Lund (1977).

Sose Bugt Member

Approximately 26m of the Sose Bugt Member is well exposed in the cliff at the type locality of Sose Bugt on the south coast, although the lower boundary with the Munkerup Member is not seen; indeed it is quite possible that the older member is absent from the area. The maximum thickness of the Sose Bugt Member has been estimated to be about 40m (Gravesen et al., 1982, p. 17). It extends a short distance inland from Sose Bugt and is thought to be also exposed on the coast further west near Rønne (east of Ormebæk; Gry, 1969, p.77, fig. 4; Gravesen et al., 1982, pp. 17,18, figs 6,7). The upper boundary with the Hasle Formation is poorly exposed west of Sose Odde (Surlyk & Noe-Nygaard, 1986).

Alternating beds of fine-grained, cross-laminated sand, often containing plant debris, and thin beds of grey laminated clay and interlaminated clays and silts dominate the succession. Concentrations of organic detritus forming thin coal seams, and rootlet-bearing paleosols are common (Arndorff, 1991). Some thick units of fine to medium-grained sand occur in the middle

part, and trace fossils are abundant at some levels in the middle and upper parts of the section.

Deposition on a partly vegetated lower delta plain traversed by sandy water courses is suggested for the lower Sose Bugt Member. The presence of marine trace fossils and other sedimentary characteristics of the upper part of the member indicate transgressive conditions at this time. A recent sequence stratigraphic analysis of the Sose Bugt Member (Surlyk et al., in prep.) has revealed a number of key surfaces within the succession, some of which may be tentatively correlated with surfaces identified by Haq et al. (1988) in their sea-level cycle chart.

Gry (1969, fig. 7) dated the Sose Bugt section as Lias α. Koppelhus (1991) confirmed the age-range implied by this, i.e. Hettangian-early Sinemurian, on the basis of the miospores recovered. The assemblages from the lower part of the succession are similar to those from the Munkerup Member, hence placing it within the *Pinuspollenites-Trachysporites* Zone and dating it as Hettangian. The assemblages from the upper part contain fewer taxa. They correlate with the *Cerebropollenites macroverrucosus* Zone of Dybkjær (1991) which is thought to indicate a Sinemurian age.

Galgeløkke Member

The thickness of the Galgeløkke Member, which is known to be present only on the Rønne-Hasle Block (Gry, 1969, p. 77, fig. 4; Gravesen et al., 1982, pp. 18,19,22, fig. 7), seems to be quite variable, but it is considerably greater than that of the Sose Bugt Member. Gry (1969) suggested a range of between 150 and 210m. Very light coloured fine-grained sands together with heterolithic wavy and flaser-laminated sand and clay dominate the very variable lithology of the member. Thin coal seams overlying rootlet horizons and accumulations of carbonised plant detritus occur locally but particulate organic matter is widely dispersed. On the other hand, megaspores have not so far been recovered from any of these deposits.

The boundary between the Sose Bugt and Galgeløkke Members is approximately at the level of the horizons yielding the bivalve *Cardinia follini* Lundgren, which were interpreted by Gry (1969, p.77) to indicate a brackish-water incursion. The only other fossils to have been encountered are remains of the fossil plant *Dictyophyllum*, noted by Grönwall & Milthers (1916), rare agglutinating foraminifers (Sellwood, 1972), locally abundant trace fossils (Rolle, 1978) and miospores (Koppelhus, 1991).

The lack of megaspores and other age-diagnostic ossils meant that Gry (1969) had to date the Galgeløkke deposits solely on the basis of their stratigraphic position between the Sose Bugt and Hasle successions. Since the latter was determined to be of "Lias γ age"

(early Pliensbachian), the Galgeløkke Member was dated as Sinemurian. The miospore assemblages are similar in composition to those recovered from the upper part of the Sose Bugt Member, and all appear to correlate with the *Cerebropollenites macroverrucosus* Zone. There are fewer pollen grains in the Galgeløkke assemblages, and reworked Carboniferous spores seem to be more common than they are in the other two members (Koppelhus, 1991; Nielsen & Koppelhus, 1991). It is possible that the Galgeløkke Member was deposited at the same time as the upper Sose Bugt Member but in a different environment (Koppelhus, 1991). The overall composition of the palynological assemblages is consistent with a Sinemurian age but it does not provide unequivocal evidence for such a determination.

The Galgeløkke Member is thought to comprise a generally regressive tidal flat complex of sands and muds followed by a major tidal channel sequence with sandstones of sand-wave origin capped by marsh deposits (Sellwood, 1972; Rolle, 1978; Gravesen et al., 1982). Tyge (1990) interpreted the sedimentary succession at the type locality to comprise deposits of a delta front mouth bar and associated intertidal flats. Megaspores have rarely been found in either modern or ancient cross-bedded channel, shoal, bar and tidal flat sands. As pointed out by Gravesen et al. (1982), the member may well have accumulated during a regressive phase within a period of otherwise general transgression which ultimately led to the deposition of the overlying, fully marine Hasle Formation (Surlyk & Noe-Nygaard, 1986).

Hasle Formation

This consists of between 80 and 110m (Gry, 1969) of mainly moderately to well indurated coarse-grained siltstone and fine-grained limonitic sandstone (Gry, 1969). Gravels are present as thin laminae. Clay ironstones also occur. Hummocky cross-stratification is present in the siltstones and sandstones of the exposed part of the succession and is interpreted to reflect inner shelf deposition (Surlyk & Noe-Nygaard, 1986). Referred to as "marine Lias γ Beds" by Gry (1969), the formation has yielded an abundant marine invertebrate fauna (Gravesen et al., 1982, and references cited therein) which has dated it as early Pliensbachian (*Uptonia jamesoni* to *Prodactylioceras davoei* Zones). The lithologies of the formation at the type locality in low coastal cliffs to the south of Hasle and elsewhere are not suitable for the recovery of megaspores. They are also largely devoid of small spores and pollen grains; only a few, very impoverished assemblages have been recovered (Koppelhus, unpublished).
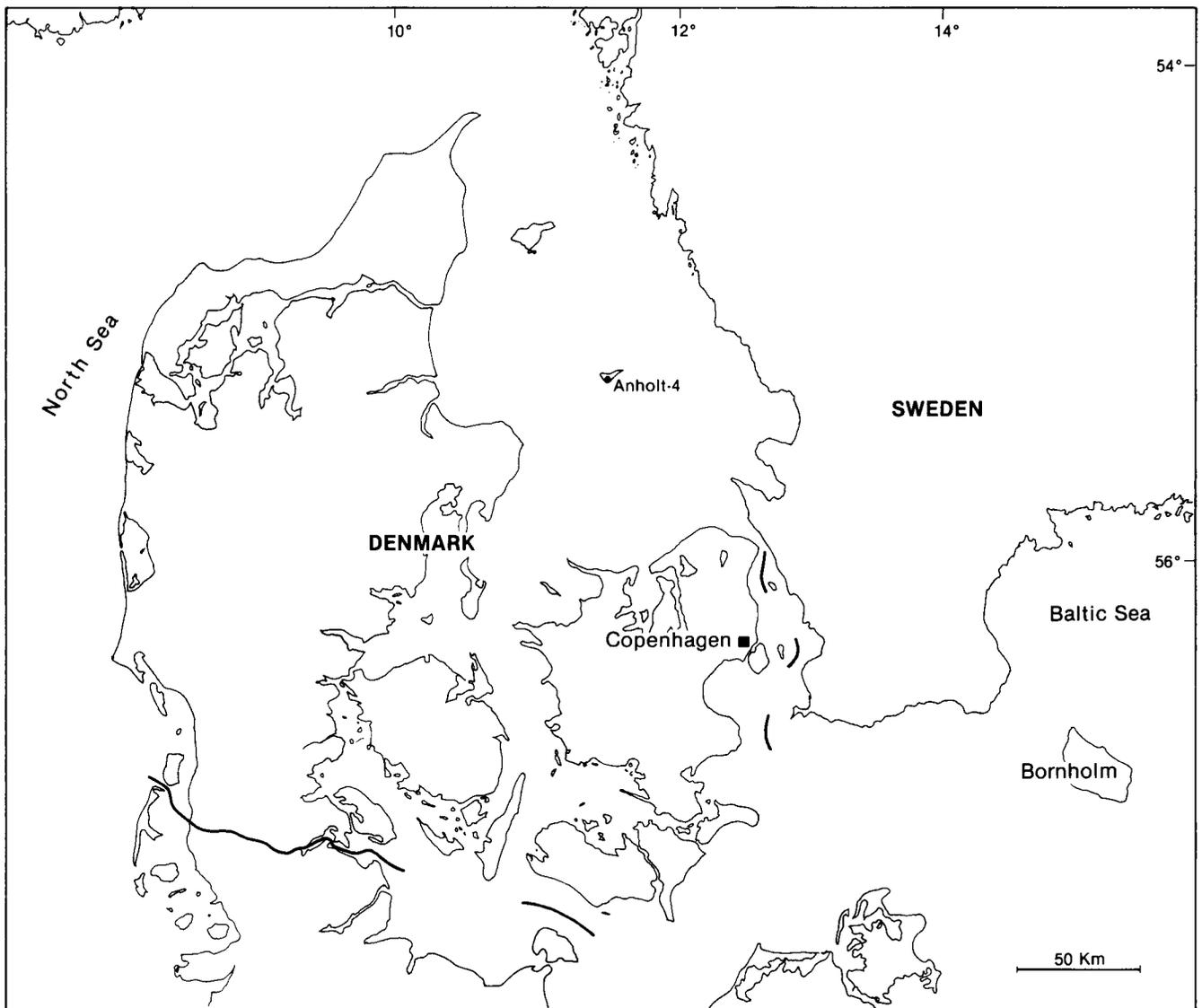
Fig. 1. Map showing the location of Bornholm in the southern Baltic Sea and of the Anholt-4 borehole to which reference is made in the text.

Bagå Formation

The Bagå Formation may conformably overlie, or rest disconformably on the Hasle Formation within the confines of the Rønne-Hasle Block. According to Gry (1969) it lies unconformably on Silurian shales within the Boderne outlier (fig. 2). Most of its more than 270m consists of sands, heteroliths, clays and coals typically in fining upwards cycles (Gry, 1960; Gravesen et al., 1982, pp. 26,27). At the type locality, the Hasle Klinkerfabrik clay pit (Gry, 1969, p. 80, fig. 5; Gravesen et al., 1982, fig. 20; Bagågraven clay pit in Hoelstad, 1985), the highest beds include conglomerates containing boulders of kaolinized granite (Gravesen et al., 1982, p. 27, fig. 25C,D).

Gry (1969, pp. 78–84) described the succession under the local names Levka, Sorthat, and Bagå beds. These were not precisely correlated because of tectonic complications and rapid vertical and lateral variations in facies. On the basis of the megaspores recovered, he considered the Levka and Sorthat beds to be roughly contemporaneous whereas he thought the Bagå beds accumulated slightly later. He also placed the coal-bearing deposits at Korsodde and Onsbæk, and the conglomerate-bearing succession at Boderne, in the Bagå series or beds. He dated the Bagå Formation as a whole as Bajocian-Bathonian. The palynomorphs recovered from it, however, suggest that the lower part is at least as old as latest Toarcian (Hoelstad, 1985) and may well be older (Koppelhus & Nielsen, in prep.); hence the question marks through the "no stratigraphic record" interval between the Hasle and Bagå Formations on figure 4.

Any unconformable relationships between the base of the Bagå Formation and the underlying Lower Jurassic or older rocks may reflect early Middle Jurassic erosion of late Pliensbachian and younger Early Jurassic deposits, as suggested by Gravesen et al. (1982). The fining upward units of the Bagå Formation were deposited in a complex of meandering channels, levées and backswamps, and brackish interdistributary bays (Gravesen et al., 1982).
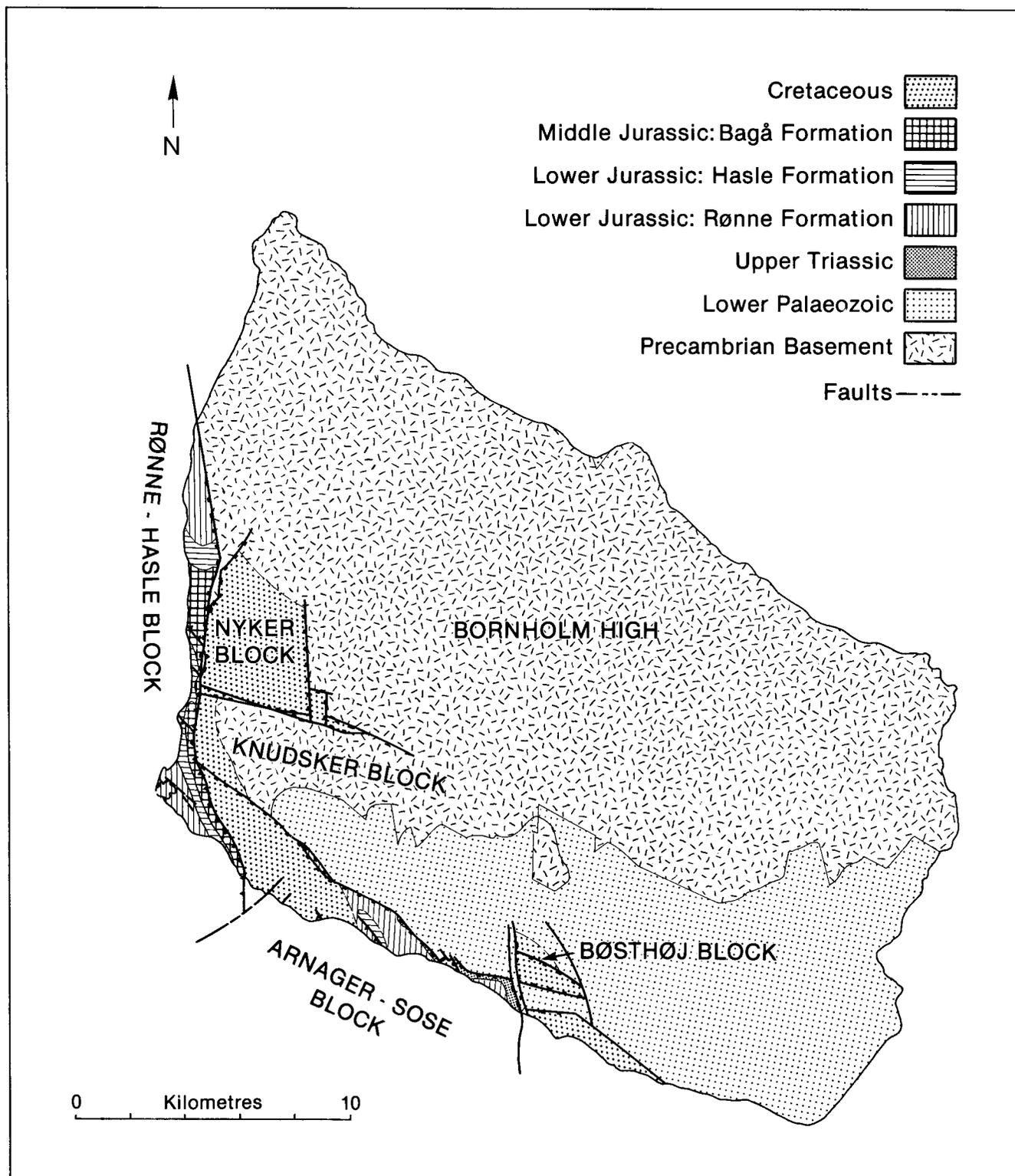
Fig. 2. Geological map of Bornholm, adapted from fig. 2 in Gravesen et al. (1982).

Rabekke Formation

The much younger Rabekke Formation of the Nyker Group overlies the Galgeløkke Member on the Arnager-Sose Block, and Palaeozoic or Precambrian kaolinized basement rocks on five other fault blocks (Gravesen et al., 1982, p. 28, figs 26,27). It consists of varying thicknesses of fluvial sandstone, sand and clay followed by supratidal-intertidal swamp clay, lignite

and sand. These comprise the Homandshald and Skyttegård Members respectively, and are equivalent to the "basal sequence" and "lower clay sequence" of Gry (1956). At the type locality in Arnager Bugt, the former is between 20 and 30m thick (Gry, 1956; Gravesen, 1982). The predominant medium- to coarse-grained and poorly sorted sands, sandstones and pebble beds are devoid of fossils apart from some rootlets and comminuted plant debris in the upper part of the member.

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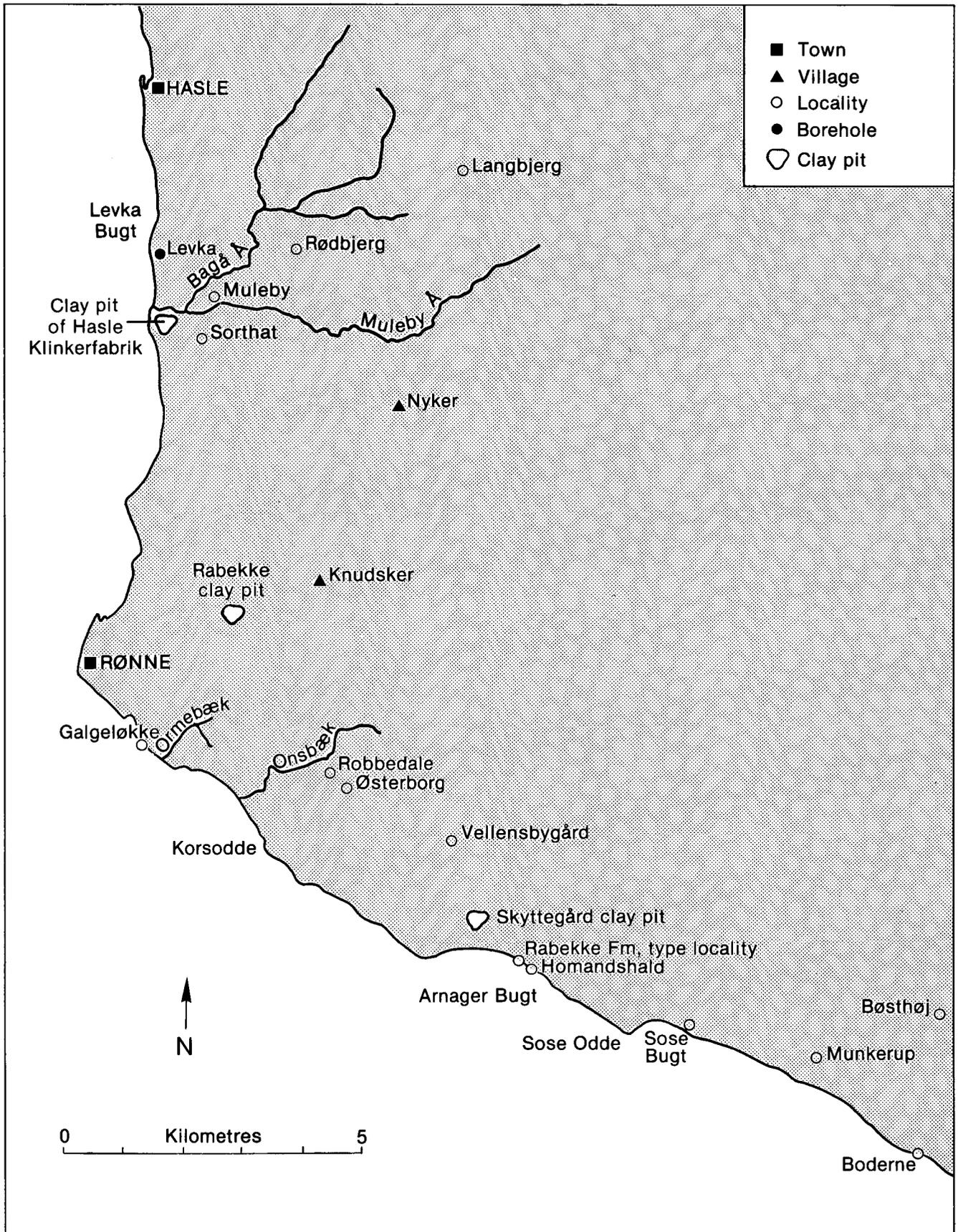
Fig. 3. Map showing coastline of part of southern and western Bornholm and location of all places on the island mentioned in the text apart from Sosevig. This is an alternative name for Sose Bugt. Gry (1969) referred to Vellengsby and Vellengsbygård whereas the spelling of the latter on the currently available topographic map is Vellensbygård.

System	Stage		Group	Formation	Member
CRETACEOUS	LOWER	Berriasian — UPPER / LOWER	Nyker	Robbedale	Langbjerg
					Østerborg
				Rabekke	Skyttegård
					Homandshald
JURASSIC	UPPER	Tithonian	Bornholm	Bagå	
		Kimmeridgian			
		Oxfordian			
	MIDDLE	Callovian			
		Bathonian			
		Bajocian			
		Aalenian			
	LOWER	Toarcian			
		Pliensbachian U/L		Hasle	
		Sinemurian U/L		Rønne	Galgeløkke
		Hettangian U/L			Sose Bugt
					Munkerup

Fig. 4. Stratigraphy of the Jurassic and part of the Lower Cretaceous succession on Bornholm, modified from fig. 4 in Gravesen et al. (1982).

Hence its age can only be suggested on indirect evidence. The Skyttegård Member rests conformably on it, and has yielded ostracod assemblages which correlate with those from the German Oberer Münder Mergel and Serpulit (Christensen, 1963, 1966, 1974). These have been dated on the basis of ammonites (Casey, 1973), palynomorphs (Dörhöfer & Norris, 1977; Herngreen et al., 1980) and other evidence (Allen & Wimbledon, 1991) as early-?late Berriasian, although this differs from the Berriasian to early Valanginian determination proposed by Pelzer & Wilde (1987, fig. 2). Hence, the Homandshald Member is probably also Berriasian, but the possibility that it was deposited during the latest Jurassic (Tithonian/Portlandian) cannot be ruled out.

Skyttegård Member

The Skyttegård Member consists of variously coloured, but mainly dark grey, sandy structureless clay containing abundant particulate plant detritus, with subordi-nate silt, sand and lignite-bearing deposits. Rootlets and paleosols (red and yellow weathered horizons) also occur. It is from this part of the Rabekke Formation that Gry recovered a comparatively large number of megaspores which he noted were closely comparable to those described previously from the Wealden succession of southern England (Hughes, 1955, 1958) and coeval deposits in the Netherlands (Dijkstra, 1951). He nevertheless considered both the Rabekke and Robbedale Formations to be a Late Jurassic "Purbeck sequence" (Gry, 1969, pp. 85,86).

The absence of Upper Jurassic sediments on Bornholm has been attributed to erosion during the latest Jurassic (Gravesen et al., 1982). Deposition of the Nyker Group thus began with the coarse grained basal sediments of the possible earliest Cretaceous Homandshald Member. These are interpreted as fluviatile, valley-fill accumulations which pass rapidly upwards into lacustrine and swamp sands and clays of the Skyttegård Member, a few thin horizons of which indicate deposition in marginal marine conditions (Gravesen et al., 1982).

Robbedale Formation

The overlying Robbedale Formation is well exposed in several sand pits on the Arnager-Sose Block but it is also found on the Nyker, Knudsker and Bøsthøj Blocks (Gravesen et al., 1982, p. 32, figs 7, 27). It consists of 8–40 m of mainly fine- to coarse-grained sands (Noe-Nygaard & Surlyk, 1988). Trace fossils are common and evidence of bioturbation is abundant. Rootlets and plant debris occur at a number of levels, mainly in the Østerborg Member. This lower unit of the Robbedale Formation is generally finer grained than the overlying Langbjerg Member. It commences in bioturbated and *Ophiomorpha*-burrowed muddy, and clean, fine-grained sand (Jux & Strauch, 1968). These are regarded as shoreface (including beach, tidal flat and lagoonal) deposits that accumulated under the influence of tides and storms (Gravesen, 1977, 1982; Noe-Nygaard & Surlyk, 1988; Surlyk & Noe-Nygaard, 1988, fig. 14). The Langbjerg Member consists of medium to coarse pebbly, upper shoreface, foreshore and backshore sandwave and barrier-beach sands (Gravesen, 1977, 1982; Noe-Nygaard & Surlyk, 1988).

No age-diagnostic fossils have so far been found in either member, but since the basal part of the formation rests conformably on the mainly early Berriasian Rabekke Formation, and the lower beds of the overlying Jydegård Formation have been dated as late Berriasian, it follows that the Robbedale Formation is probably also of late Berriasian age (Christensen, 1963, 1974; Surlyk, 1980; Piasecki, 1984; Allen & Wimbledon, 1991).

Material and methods

Gry's collection of megaspores comprises more than 600 micropalaeontological cell-slides in which all specimens are stored dry and unmounted. Any notes on his laboratory processing methods that he may have made have not been found. It is, however, likely that the spores were isolated from both outcrop and borehole samples simply by washing in water and sieving the generally poorly consolidated sediments. The fact that mineral detritus remains attached to many specimens suggests that little or no attempt was made to clean them using chemicals (e.g. hydrofluoric acid).

The species he identified are referred to in his paper in the course of discussing the ages of different exposures and borehole sections, and their occurrences in the Lower and Middle Jurassic are tabulated (Gry, 1969). The form of presentation is not, however, conducive to readily determining the stratigraphic origins of the assemblages. Since the nomenclature of both the sedimentary units and some of the megaspore species is also out of date, the records of occurrences in his paper are presented again here using current terminology as follows:

Munkerup clay [Munkerup Member of the Rønne Formation]
Horstisporites areolatus, H. harrisii, Nathorstisporites hopliticus, Verrutriletes franconicus

Sosevig beds [Sose Bugt Member of the Rønne Formation]
Horstisporites areolatus, H. harrisii, Nathorstisporites hopliticus, Trileites turbanaeformis [now *T. candoris*], *Verrutriletes franconicus*

Vellengsby (Vellensby) clay [Sose Bugt Member]
Nathorstisporites hopliticus, Verrutriletes franconicus

Rønne area, white clay at Ormebæk [Sose Bugt Member]
Nathorstisporites hopliticus

Rønne area, below the marine (Lias γ; Hasle Formation) beds [Sose Bugt and ?Galgeløkke Members of the Rønne Formation]
Horstisporites areolatus, Trileites turbanaeformis

Rønne area, coal-bearing beds at Korsodde and Onsbæk [Bagå Formation]
Echitriletes russus [now *E. hispidus*], *Erlansonisporites sparassis, Maexisporites soldanellus, Thomsonia phyl-*
lica [now *Paxillitriletes phyllicus*], *Trileites murrayi, T. turbanaeformis*

Boderne beds [Bagå Formation]
Hughesisporites sp., *Thomsonia phyllica, Trileites murrayi, T. turbanaeformis*

Sorthat beds [Bagå Formation]
Erlansonisporites sparassis, Horstisporites areolatus, Minerisporites volucris, Thomsonia phyllica, Trileites turbanaeformis

Bagå beds [Bagå Formation]
Aneuletes patera, Bacutriletes clavatus, B. corynactis, Erlansonisporites sparassis, Horstisporites harrisii, Maexisporites soldanellus, Thomsonia phyllica, Trileites murrayi, T. turbanaeformis

Levka beds, coal-bearing succession [Bagå Formation]
Bacutriletes clavatus, B. corynactis, Erlansonisporites sparassis, Horstisporites areolatus, H. harrisii, Hughesisporites galericulatus, Minerisporites volucris, Thomsonia phyllica, T. cf. *pseudotenella* [now *Paxillitriletes* cf. *pseudotenellus*], *Trileites turbanaeformis*

Levka beds, deposits overlying coal-bearing succession [Bagå Formation]
Echisporites (sic.) *russus* in text, *Echitriletes russus* on fig. 7 in Gry, 1969), *Erlansonisporites sparassis, Horstisporites harrisii, Minerisporites volucris, Thomsonia phyllica, Trileites murrayi, T. turbanaeformis*

Purbeck beds [Rabekke and Robbedale Formations]
Echitriletes lanatus, Hughesisporites galericulatus, Minerisporites marginatus, Striatriletes sulcatus, Thomsonia cf. *pseudotenella, T. reticulata* [now *Paxillitriletes reticulatus*], *T.* spp., *Verrutriletes carbunculus* [now *Cabochonicus carbunculus*]

In order to describe Gry's material satisfactorily some of the specimens in the slides were removed so that they could be examined under a scanning electron microscope (SEM), an essential requirement of any modern analysis of the morphology of megaspores. Since the structure of the spore wall is of taxonomic significance, broken specimens and fragments considered likely to provide good cross-sections were also picked out for this purpose. All of the material selected was mounted on small, circular coverslips that had previously been glued to SEM stubs. Nail varnish was used

as the adhesive for both fixing the coverslips to the stubs and for mounting the spores. The specimens were coated with gold or gold-palladium prior to being examined under a Phillips 515 SEM housed in the Geological Institute, Copenhagen University and/or a Jeol JSM 840 SEM in the Department of Biological Sciences, University of Wales, Aberystwyth. The slide collection continues to be retained in the biostratigraphic collections of the Geological Survey of Denmark along with the SEM stubs bearing the specimens illustrated in this paper.

Systematic palynology

Introduction

The spores that are described and illustrated below are grouped approximately according to overall morphology beginning with alete forms and those triradiate species that appear to have "smooth" exines when examined under a reflected light microscope. Weakly to strongly sculptured forms that are otherwise of "simple" overall appearance are then considered, followed by more complex species having prominent triradiate and/or equatorial flanges, long appendages on the proximal face and other characters. Such an informal organization enables probable natural relations to be taken into account more readily than if they are grouped according to Potonié's (1956 and later papers) widely-used formal system of morphological classification. This can be difficult to apply satisfactorily because of its hierarchical nature. It may artificially separate some taxa that are closely similar and bring together others that are better kept separate.

Systematics

* = taxon recorded by Gry (1969) although the nomenclature used is not necessarily the same.

ANEULETES Harris, 1961

Aneuletes discus sp. nov.

Pl. 1, figs 4–7; Pl. 2, fig. 1; Pl. 20, fig. 2

Diagnosis:
Spherical to subspherical bodies ranging from c. 240–460 μm in maximum diameter (50 specimens). In reflected light they appear as virtually featureless black discs that may be slightly swollen on one surface but lack any sign of a germinal feature. Their walls are so thick that they are rarely damaged in any way. Under the SEM the outer surface of these discs is roughened but lacks distinctive sculpture. The wall of sectioned specimens is seen to be remarkably homogeneous.

Derivation of name:
Gr. *discus*; after the typical shape of the palynomorph

Holotype:
Pl. 20, fig. 2; slide HGHol/1, Borehole 244.105, 37.50–42.12 m, Hasle Klinkerfabrik clay pit, Bagå Formation, Aalenian-Bathonian

Remarks:

Harris' (1961, p. 69) diagnosis of *Aneuletes* was intended for bodies "which resemble megaspores in size and structure, but have no furrows or cracks" (i.e. hollow sacs more than 200μm in diameter with thick walls and lacking germinal sutures or ridges). It is sufficiently broad-based to allow the inclusion of these forms in the genus. Their affinities are unknown; they may well not have anything to do with heterosporous plants.

Marcinkiewicz (1962, pl. 13, figs 6,7) illustrated two apparently disc-shaped microfossils in a paper devoted to Polish "Rhaeto-Liassic" megaspores. They were identified as questionable algae, but she did not discuss them. Kovach & Dilcher (1988, p. 106, pl. 5, figs 11,12) referred similar forms to the acritarch *Leiosphaeridia* sp. B and considered their occurrence to indicate marine conditions of deposition. It appears from notes in pencil on a couple of his slides that Gry also thought that these bodies might have an algal origin. There is as yet, however, no unequivocal evidence in his material, which comes from a number of beds within the Bagå Formation, to suggest that *A. discus* can be interpreted as a marine indicator.

There are some other apparently alete bodies in a few of Gry's slides, but these differ from *A. discus* in that they may be black or brown in colour in reflected light and appear to have somewhat thinner walls (recorded as only 6 μm on one specimen); as a result they tend to be preserved as slightly crumpled (deflated) sacs and may be partly broken. Under the SEM their outer surfaces are seen to be granular (Pl. 2, fig. 2). Their biological affinities are also unknown.

Occurrence on Bornholm:
Bagå Formation

*Aneuletes patera Harris, 1961

1961 *Aneuletes patera* Harris, p. 69, fig. 22A-F

Pl. 1, figs 1–3; Pl. 20, fig. 1

Remarks:
Harris' (1961) specimens of *A. patera* were described as being nearly spherical, but with a flat to slightly concave area of circular outline on one side. This extends to about 1/2–2/3 of the diameter of the spore, and within it are conspicuous swellings of rounded, elongate to slightly irregular outline which he considered to be local thickenings of the wall (hence verrucae and rugulae).

There are very few specimens of *A. patera* in Gry's

collection, and these comprise part of only one assemblage from the Bagå Formation. Our illustration of this species is confined to a reflected light photograph of a single specimen (Pl. 20, fig. 1) and some scanning electron micrographs of another specimen of probable Toarcian age from Anholt-4 borehole in the Kattegat to show the morphology of the taxon more clearly (Pl. 1, figs 1–3). Both compare closely in size and morphology to the type material from the Middle Jurassic of Yorkshire. The surface of the Anholt specimen is covered with granules and rugulae; the larger verrucate to rugulate swellings on the presumed proximal face are similarly sculptured.

Of the eight species of *Aneuletes* that have been documented to date (Batten & Kovach, 1990), six are of Triassic age (Kovach & Batten, 1989, p. 252) but only one of these, *A. rotundus* Fuglewicz, 1973, resembles *A. patera*. According to Fuglewicz (1973, p. 443), it is smaller, and lacks "knobs in concavity" and "small pits on spore surface". This latter character is unlikely to be of any significance in distinguishing species, and size is often an unreliable criterion (Harris, 1961 gives the size range for *A. patera* as 330–850 μm whereas that for *A. rotundus* is 220–450 μm; Fuglewicz, 1973). The presence of "elongated ridge-like swellings, irregularly undulate" in the "concavity" may be the chief character that differentiates *A. rotundus* from *A. patera*.

The only other species, *A. potoniei* (Danzé & Laveine, 1963) Candilier et al., 1982 is, in our opinion, doubtfully separated from *A. patera* on the basis of minor sculptural differences. The reported size range of *A. potoniei* (300–500 μm; Danzé & Laveine, op. cit., p. 87) almost entirely overlaps that for *A. patera*, and the possession of an exine which shows numerous perforations 2 μm in diameter (Candilier et al., op. cit., p. 2) is not of taxonomic significance, as noted above. Hence, although the specimen illustrated on Pl. 1, figs 1–3 herein, is similar to those identified as *A. potoniei* on pl. 1, figs 18, 23a and 23b in Candilier et al., we prefer to identify it as *A. patera* (see also figures of *A. patera* in Marcinkiewicz, 1988, pl.23, figs 8–10 and elsewhere).

Occurrence on Bornholm:
Bagå Formation (Bagå beds)

BACUTRILETES van der Hammen, 1955 ex Potonié, 1956 emend. Banerji et al., 1984

*Bacutriletes sp. cf. *B. clavatus* Marcinkiewicz, 1960

1960 *Bacutriletes clavatus* Marcinkiewicz, p. 719, pl. 3, figs 6,7

Pl. 2, figs 3–5; Pl. 20, fig. 3

Remarks:
Marcinkiewicz's (1960) original description of this species, at the time questionably referred to *Bacutriletes*,

was based on 6 specimens, all of which were damaged to varying degrees. She noted that the diameter of the spores, including the surface ornament, ranges between 350 and 400 μm, and that the sculptural elements are up to 65 μm in length, rounded in cross-section, and narrower basally than at their tips. The triradiate mark was noted as not being evident, and probably obscured by the sculpture. She compared it with *Verrutriletes litchii* (Harris) Potonié, 1956, from which it differs mainly in being smaller and in having larger projections.

The illustrations of *B. clavatus* in Marcinkiewicz (1960, pl. 3, figs 6,7; 1971, pl.8, figs 3–9; 1988, pl. 19, figs 2–4) do not suggest a close resemblance to most of the specimens that Gry referred to this species (e.g. Pl. 20, fig. 3 herein). The latter have shorter processes, seem to be closer to *Biharisporites scaber* Marcinkiewicz, 1960 and *Striatriletes excavatus* (Marcinkiewicz, 1962) Sweet, 1979, and may sometimes be difficult to distinguish from *Echitriletes hispidus*. The specimen illustrated on Pl. 2, figs 3–5 in this paper could even conceivably be a degraded *Bacutriletes corynactis* in which only the bases of the appendages are preserved. A specimen as strongly sculptured as that shown by Gry (1969, fig. 6.12) has not yet been found in his collection.

Almost all of the records of *B. clavatus* other than the few specimens recovered by Gry are Polish, documented principally by Marcinkiewicz from strata ranging in age from Pliensbachian to Bajocian (Batten & Kovach, 1990).

Occurrence on Bornholm:
Bagå Formation (Bagå beds; Levka beds, coal-bearing succession)

**Bacutriletes corynactis* (Harris, 1961) Marcinkiewicz, 1971

1961 *Triletes corynactis* Harris, p. 52, text fig. 15A-I
1971 *Bacutriletes corynactis* (Harris, 1961) Marcinkiewicz, p. 35, pl. 9, figs 4–7

Pl. 3, figs 1–5; Pl. 20, fig. 4

Remarks:
Gry (1969) referred this species to *Bacutriletes* but he failed to cite the basionym. The combination *B. corynactis* was, therefore, invalid according to the ICBN until 1971 when Marcinkiewicz correctly transferred the species from *Triletes* to *Bacutriletes*.

According to Marcinkiewicz, *B. spicatus* (Marcinkiewicz, 1962) Marcinkiewicz, 1971 differs in being smaller than *B. corynactis* (415–445 μm, as opposed to 585–616 μm in diameter; Marcinkiewicz, 1971, pp. 34,35) and in having more delicate appendages. Harris (1961) recorded the diameter of his specimens, *excluding* the appendages, as ranging from 310–480 μm. This suggests that the two species cannot be readily differ-

entiated on the grounds of size. The fact that the dimensions of the appendages supposedly differ according to Marcinkiewicz (1971, p. 57; 4–6 μm in mean diameter, 60–80 μm long in *B. spicatus*; 12–20 μm in mean diameter, 50–60 μm long in *B. corynactis*) may be sufficient to distinguish them, but our observations on the specimens Gry identified as *B. corynactis* suggest that their separation may be difficult to maintain.

Scanning electron micrographs of the exoexine (*c.* 5–10 μm thick in the specimens examined) show it to be composed of a compact, comparatively robust, three-dimensional network of sporopollenin threads (Pl. 3, fig. 2). The surface of the appendages consists of a more open reticulum (Pl. 3, figs 2,5), but in cross-section the reticulation is less obvious (Pl. 3, fig. 3). The intexine is a membraneous, more homogeneous layer <1 μm thick (Pl. 3, fig. 4).

Occurrence on Bornholm:
Bagå Formation (Bagå beds; Levka beds, coal-bearing succession)

Bacutriletes onodios (Harris 1961) Hopkins & Sweet 1976

1961 *Triletes onodios* Harris, p. 53, figs 16I-L, 17A-E
1976 *Bacutriletes onodios* (Harris, 1961) Hopkins & Sweet, p. 57, pl. 11, figs 1–4

Remarks:
Gry (1969) did not mention *B. onodios* in his paper, but handwritten notes on a few of his slides indicate that he considered it to be present in his collection. We are not, however, convinced that any definitely belong in this species, preferring instead to place them in comparison as follows.

Bacutriletes sp. cf. *B. onodios* (Harris, 1961) Hopkins & Sweet, 1976

Pl. 2, fig. 6; Pl. 4, figs 1–5

Remarks:
The specimens in the collection that Gry identified as *B. onodios*, and which we compare with this species, are closest morphologically to that of the single "unusually small specimen" figured by Harris (1961, fig. 16L). Despite the degree of morphological variation allowed by Harris' circumscription, they may not, however, belong to this species. A few (e.g. that shown on Pl. 2, fig. 6) might be better placed in *Verrutriletes*. One of the forms illustrated (Pl. 4, figs 1,2) is closely similar to the specimen identified by Kovach & Dilcher (1988, pl. 1, figs 3–6) as *B. greenlandicus* (Miner, 1932) Potonié, 1956 and, to a lesser extent, to *Verrutriletes dasyplocoides* Schulz & Noll, 1987; both of these were described from Cretaceous deposits.

In common with a number of other verrucate to rugulate spores whose wall structure has been examined (e.g. *Verrutriletes compositipunctatus*, *V. dubius*

and *Striatriletes minimus* in Batten, 1988), the exoexine is seen to be spongiose and underlain by a thin, more homogeneous intexine (Pl. 4, figs 3–5).

Occurrence on Bornholm:
Bagå Formation

CABOCHONICUS Batten & Ferguson, 1967

Cabochonicus carbunculus (Dijkstra, 1949) Batten & Ferguson, 1987

1949 *Triletes carbunculus* Dijkstra, p. 22, pl. 1, fig. 12
1987 *Cabochonicus carbunculus* (Dijkstra, 1949) Batten & Ferguson, p. 72, pl. 1, figs 1–4; pl. 2, figs 2–8; pl. 3, figs 1–7; pl. 4, figs 1–6

Pl. 3, figs 6–8; Pl. 20, figs 5,6

Remarks:
This species was not illustrated by Gry (1969) but it was referred to in the text of his paper as *Verrutriletes carbunculus*. There are only a few fragments and even fewer complete specimens of this species in his collection. The morphology of the remains is closely comparable to that of the spores described by Dijkstra (1949, 1951) from Cretaceous deposits of the Netherlands and the UK (see Batten & Ferguson, 1987; Batten, 1988).

Occurrence on Bornholm:
Rabekke and Robbedale Formations (Purbeck beds).

ECHITRILETES van der Hammen, 1955 ex Potonié, 1956

Echitriletes hispidus Marcinkiewicz, 1960

1960 *Echitriletes hispidus* Marcinkiewicz, p. 719, pl. 4, fig. 1

Pl. 20, fig. 7

Remarks:
Marcinkiewicz's (1960) original description of this species was based on two specimens 530 and 575 μm in diameter. The spore was reported to be subcircular in outline with a low, slightly wavy triradiate ridge some 17 μm wide extending to about 1/2 the radius of the spore, and the proximal and distal surfaces to be covered by numerous hair-like projections about 25 μm long and 7 μm in basal width. An additional feature of the proximal face is the presence of "bumps" on the contact areas.

Gry (1969) appears to have found very few specimens of this species, insufficient to enable any to be examined under the SEM for this paper. He recorded them as *Echitriletes russus* Harris, 1961, but this species was shown by Marcinkiewicz (1971, p. 35) to be a junior synonym of *E. hispidus*. They appear to be closely similar in morphology to the specimens illustrated by Marcinkiewicz (1971, pl. 10, figs 3–6). The spore illustrated by Sweet (1979) has longer sculptural

elements than either Gry's specimens or those figured by Marcinkiewicz.

Occurrence on Bornholm:
Bagå Formation (Korsodde and Onsbæk, coal-bearing beds; Levka beds overlying coal-bearing succession)

Echitriletes lanatus (Dijkstra, 1951) Potonié, 1956

1951 *Triletes lanatus* Dijkstra, p. 11, pl. 2, fig. 22
1956 *Echitriletes lanatus* (Dijkstra, 1951) Potonié, pp. 36,37

Pl. 4, figs 6–8; Pl. 20, fig. 8

Remarks:
Gry (1969) mentioned this species in connection with the "Purbeck beds", but did not illustrate it. There are fewer than six specimens in his collection, and these are not only partly degraded but also appear to differ to some extent from the type material in being sculptured with shorter papillae (cf. for example, specimen of *E. lanatus* in Batten, 1975, pl. 13, fig. 4). Nevertheless, there is no reason to doubt their identification as *E. lanatus*. Scanning electron microscopy of the cross-section of a wall of a single fragment reveals an outer, spongiose exoexine underlain by a more homogeneous, membraneous intexine (Pl. 4, fig. 8).

Occurrence on Bornholm:
Rabekke and Robbedale Formations (Purbeck beds)

ERLANSONISPORITES Potonié, 1956

Erlansonisporites sparassis (Murray, 1939) Potonié, 1956

1939 *Triletes sparassis* Murray, pp. 480–482, figs 3,4
1956 *Erlansonisporites sparassis* (Murray, 1939) Potonié, p. 47
1961 *Triletes sparassis* Murray, 1939 emend. Harris, pp. 57–60, fig. 18A-D

Pl. 5, figs 1,2; Pl. 20, figs 9,10

Remarks:
In common with many identifications of megaspores, the morphology of the specimens that have been attributed by different authors to *E. sparassis* may sometimes appear to be at variance with the characters given in the original description. It is, in fact, a very variable form which is often difficult to identify with confidence. Harris (1961) found it necessary to emend the diagnosis to encompass a wider morphological range than was allowed for in Murray's description. Salient characters are a spore body that is nearly spherical, having a diameter that ranges from 300–850 µm, a triradiate ridge that is often rather sinuous and usually broad-based, but becoming membraneous upwards to a maximum height of about 75 µm, and a surface that is typically sculptured with a coarse network of irregular ridges up to 50 µm high. In some specimens the height

of the muri matches that of the triradiate ridge, rendering it rather difficult to distinguish, whereas in others the ridge is prominent (cf. Pl. 5, figs 1,2).

Occurrence on Bornholm:
Bagå Formation (Korsodde and Onsbæk, coal-bearing beds; Sorthat beds; Bagå beds; Levka beds, coal bearing succession; Levka beds above coal-bearing succession).

HENRISPORITES Potonié, 1956 emend. Binda & Srivastava, 1968

Henrisporites bornholmensis sp. nov.

Pl. 6, figs 1–8; Pl. 20, figs 19,20

Diagnosis:
Megaspore trilete, rounded triangular in equatorial outline; maximum diameter in polar view excluding zona 290–400 µm (50 specimens). Laesurae extend to equator of body, bordered by membraneous elevated lips 30–50 µm high which extend onto, and merge with zona. Width of zona 40–70 µm; outer margin continuous. Sculpture comprises spines that are evenly distributed over both proximal and distal surfaces, rounded in outline, and with rounded to pointed tips; up to 7 µm in basal width and 50 µm high. Triradiate flange and zona are of similar dimensions, and both have fairly smooth, continuous, margins.

Exoexine c. 10 µm thick, comprising a meshwork of sporopollenin threads orientated mainly subparallel to outer surface of spore. Alignment of threads is also evident on zona (Pl. 6, fig. 8) and triradiate flange where they are mainly parallel to surface of these structures. Intexine is a thin (c. 2 µm), more homogeneous membrane (Pl. 6, fig. 6).

Derivation of name:
After the island of Bornholm

Holotype:
Pl. 20, fig. 19; slide HGHol/2, Borehole 246.207, 26.00 m, Robbedale Formation, upper Berriasian

Remarks:
The spore body of species of *Henrisporites*, as emended by Binda & Srivastava (1968), is ornamented with granules, verrucae, rugulae, cones or spines, whereas most forms of *Minerisporites* are at least partly reticulate.

The structure of the wall of *H. bornholmensis* is closely comparable to that of *Minerisporites marginatus* (cf. Batten, 1969, pl. 67, fig. 12; Kovach & Dilcher, 1988, pl. 3, fig. 10) and similar forms (e.g. *Minerisporites patagonicus* Archangelsky & Villar de Seoane, 1989, pl. 2, fig. 6).

With the exception of *H. delicatus* and *H. triassicus* (see below), all of the other species of *Henrisporites* that have been described have come from Barremian and younger Cretaceous rocks. Of these, *H. undulatus* (Dijkstra, 1951) Potonié, 1956 is closest morpholog-

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ically to *H. bornholmensis*, but its sculptural elements are more irregularly dispersed, variable in length, and mainly flattened rather than rounded in cross-section; the distal surface is also more densely sculptured. *Henrisporites affinis* (Dijkstra, 1951) Potonié, 1956 has shorter, more irregular sculptural elements which, on the proximal face, comprise rugulae in part; the margin of the zona is also spinose. *H. angustus* Tschudy, 1975 has a much narrower zona and a rather "wrinkled" distal surface. *H. rarus* Li & Batten in Li et al., 1987 differs in several ways, including in being significantly larger, in having a more triangular outline, and in bearing shorter and more widely scattered sculptural elements. The three species described by Binda & Srivastava (1968), *H. elkwaterensis*, *H. granulatus* and *H. sheilae*, have shorter spines and less pronounced triradiate flanges. Other Cretaceous species (*H. elegans* Gamerro, 1977; *H. heteracanthus* Gamerro, 1975; *H. musachioi* Gamerro, 1977; *H. ollerensis* Lachkar in Floquet & Lachkar, 1979) and the two Triassic forms (*H. delicatus* Marcinkiewicz, 1978 and *H. triassicus* Kozur, 1973) are also not closely comparable in morphology.

Occurrence on Bornholm:
Robbedale Formation (Purbeck beds)

Henrisporites undulatus (Dijkstra, 1951) Potonié, 1956

1951 *Triletes undulatus* Dijkstra, p. 13, pl. 2, figs 1,5
1956 *Henrisporites undulatus* (Dijkstra, 1951) Potonié, p. 68

Pl. 5, figs 3,4,6,8

Remarks:
Gry appears to have included this form in *Echitriletes hispidus*, but the presence of a zona and triradiate flange renders the determination inappropriate. Its sculpture is more regular than that of *H. affinis* (Dijkstra, 1951) Potonié, 1956. It differs from *H. bornholmensis* in that the triradiate flange is subtended by hair-like appendages, and both the zona and the sculptural elements generally have a more fibrous appearance.

Occurrence on Bornholm:
Robbedale Formation (Purbeck beds)

Henrisporites sp.

Pl. 5, figs 5,7

Remarks:
This species resembles *Henrisporites triassicus* Kozur, 1973 to some extent, but it may be rather closer to another Triassic form, *Narkisporites insignis* Fuglewicz, 1973. This has a similar appearance in polar view; indeed, apart from the fact that it is sculptured with rather more numerous spinose elements, the description given by Fuglewicz (1973, pp. 429,430) could also be applied to the specimen illustrated here.

Occurrence on Bornholm:
Rabekke and Robbedale Formations (Purbeck beds)

HORSTISPORITES Potonié, 1956

*Horstisporites areolatus (Harris, 1935) Potonié, 1956

1935 *Triletes areolatus* Harris, pp. 158,159, pl. 26, figs 3,10, text-fig. 51A-F
1956 *Horstisporites areolatus* (Harris, 1935) Potonié, 1956, p. 45.

Pl. 7, figs 1–8; Pl. 8, fig. 1; Pl. 20, figs 11,12

Description:
In polar view, spore circular to subcircular in equatorial outline. Triradiate ridges up to *c.* 20 μm high and 30 μm in basal width, extend to *c.* 3/4 of radius (Pl. 7, figs 1,3). Exine rather uniformly reticulate but becoming less pronounced adjacent to proximal pole; contact areas sometimes delineated by an alignment of muri (Pl. 7, figs 3,4). Size of most specimens falls within lower part of range for the species, many being *c.* 600 μm in diameter. In cross-section, muri are rounded to flat-topped or taper to a blunt tip (Pl.7, fig. 6), and are up to *c.* 6 μm wide and 15 μm high. Lumina are rounded to polygonal in outline, and up to 20 μm in maximum diameter.

Most specimens are proximo-distally compressed. Damaged spores and fragments reveal that exine is essentially two-layered. Exoexine is between 10 and 20 μm thick, excluding muri, and composed of compactly spongiose sporopollenin. Beneath is a thin (1–2 μm) intexine comprising a reticulate meshwork of sporopollenin threads orientated mainly parallel to inner surface of wall (Pl. 7, figs 5,7,8) giving it a laminated appearance.

Remarks:
It has not been possible so far to obtain any scanning electron micrographs at high magnifications that clearly show the construction of these wall layers. Assuming, however, that the close morphological resemblance of *H. kendallii* with *H. areolatus* means that they are also structurally similar, the electron micrographs of the wall of the former appear to confirm these observations, particularly with respect to the intexine (see description of *H. kendallii* below).

H. areolatus is very similar to *H. casses* and *H. kendallii*. According to Harris (1961) they are distinguished mainly on the basis of size, wall thickness and the "mesh size" of the reticulum, although he pointed out (Harris, 1961, p. 63) that the last of these may well be related to overall size. This does indeed seem to be the case. The only significant difference between *H. areolatus* and *H. kendallii* is their size, given as 600–1400 μm and 320–510 μm respectively by Harris. The 90

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μm difference between the smallest *H. areolatus* and the largest *H. kendallii* is not significant because specimens of intermediate dimensions may be found. *H. casses* is significantly larger than *H. kendallii*, the sculpture is proportionally more enlarged, and the exine considerably thicker. It overlaps *H. areolatus* in size to a considerable degree, its range being between 890 and 1900 μm according to Harris.

When present in large numbers in his samples from the Middle Jurassic of Yorkshire, Harris (1961) had no difficulty in identifying the species. The assemblages tended to be of rather uniform size and appearance, only one of the three types normally being present at a particular locality. This uniformity is also apparent in Gry's assemblages although few comprise more than 50 specimens. Most are comparatively small and either diminutive examples of *H. areolatus* or assignable to *H. kendallii*. In large assemblages, specimens ranging in size between 510 and 600 μm may be identified as one or other species depending on the mean diameter of the "population" as a whole, but when found as isolated individuals, the basis for a decision on the species to which they should be referred becomes arbitrary.

Occurrence on Bornholm:
Munkerup Member (Munkerup clay), Sose Bugt Member (Sosevig beds), ?Galgeløkke Member, Bagå Formation (Sorthat beds; Levka beds, coal-bearing succession)

Horstisporites casses (Harris, 1961) Marcinkiewicz, 1980

1961 *Triletes casses* Harris, pp. 60,61, fig. 19D,F
1980 *Horstisporites casses* (Harris, 1961) Marcinkiewicz, p. 51, pl. 5, figs 1–3; pl. 6, figs 1,2

Remarks:
Only one fragment of *H. casses* has been encountered in Gry's collection. As noted above, this species is similar to *H. areolatus* but much larger and sculptured with proportionally wider lumina and broader and higher muri.

Occurrence on Bornholm:
A single sample from the Bagå Formation

Horstisporites harrisii (Murray, 1939) Potonié, 1956

1939 *Triletes harrisii* Murray, p. 480, figs 1,2
1956 *Horstisporites harrisii* (Murray, 1939) Potonié, p. 45

Pl. 8, figs 2–8; Pl. 20, fig. 13

Remarks:
As pointed out by both Gry (1969) and Bertelsen & Michelsen (1970), Jung's (1960) criteria for separating *Horstisporites semireticulatus* Jung, 1960 from *H. harrisii* lost their significance when Harris (1961) emended the diagnosis of the latter. The specimens in Gry's

collection are rounded in equatorial outline and have a prominent triradiate ridge. They are sculptured with verrucae and ridges on the contact areas which give way to an irregularly reticulate wall equatorially and distally (e.g., Pl. 8, figs 6,8). This may be clearly developed or rather poorly defined. Curvaturae may be weakly developed, manifested mainly by a change to different ornamentation where the lumina, if any, are smallest and the muri are lowest. Harris (1961) noted that the proximal surface bears smaller tubercles than the distal face, but this is not necessarily so; occasionally the proximal sculpture can be more prominent.

H. harrisii can be difficult to separate from *Erlansonisporites sparassis*, as Harris (1961) also found; he presumed the most "difficult" specimens to be immature or unusual forms of other species. The spores that Gry labelled as *H. harrisii* show quite a variety of sculpture ranging from small verrucae (tubercles) to ridges forming a reticulum. The specimens figured as *H. harrisii* by Marcinkiewicz (1980, pl. 5, figs 4,5) are similar. The morphology of the mainly Cretaceous species *H. reticuliferus* (Dijkstra, 1951) Potonié, 1956 resembles that of *H. harrisii* but it does not bear verrucae on the proximal face.

Occurrence on Bornholm:
Munkerup Member (Munkerup clay), Sose Bugt Member (Sosevig beds), Bagå Formation (Bagå beds; Levka beds, coal-bearing succession; Levka beds, above coal-bearing succession)

Horstisporites kendallii (Harris, 1961) Kempf, 1972

1961 *Triletes kendallii* Harris, pp. 63,64, fig. 19A-C
1972 *Horstisporites kendallii* Kempf, p. 152, figs 14–17

Remarks:
The distinction of this species from morphologically similar *H. areolatus* and *H. casses* is discussed above (see *H. areolatus*). The single specimen from the Bagå Formation photographed under reflected light by Kempf (1972) is a little under 400 μm in diameter. The transmission electron micrographs of sections through the exine of this species show that it comprises a thick (10–15 μm, excluding sculpture) exoexine (= perine in Kempf, op. cit., p. 156), the outer part of which consists of more densely packed sporopollenin threads than the inner part. In addition, the direction of orientation of the threads is irregular to mainly normal to the surface in the outer zone, but parallel to it beneath, giving it a somewhat laminated (lamellate) appearance. The intexine (= exine in Kempf) is very thin (c. 0.5 μm). It is attached to, and structurally merges with, the inner zone of the outer wall, but the lamination is more pronounced.

H. kendallii has been reported previously from only a few localities (Batten & Kovach, 1990). Where the ages of the occurrences are known fairly accurately,

these are confined to the Middle Jurassic, Aalenian-Bajocian.

Occurrence on Bornholm:
Munkerup Member (Munkerup clay), Sose Bugt Member (Sosevig beds), ?Galgeløkke Member, Bagå Formation (Sorthat beds; Levka beds, coal-bearing succession)

Horstisporites planatus (Marcinkiewicz, 1960) Marcinkiewicz, 1971

1960 *Maexisporites planatus* Marcinkiewicz, p. 718, pl. 3, fig. 2
1971 *Horstisporites planatus* (Marcinkiewicz, 1960) Marcinkiewicz, pp. 36,57, pl. 12, figs 1–9

Pl. 9, figs 1–5; Pl. 20, figs 14–16

Remarks:
Marcinkiewicz's (1960, p. 718) original description of this species was based on "about 10 specimens in a very damaged state". The diameter of the spores was noted to range from 240–465 µm (mainly 368–400 µm). Other characters recorded were its subcircular outline, clearly defined triradiate suture up to 20 µm high (i.e. bordered by raised lips), and the presence of a subequatorial flange 10 µm wide. The surface of the spore was described as lightly granular (cf. Pl. 9, fig. 5 herein). Subsequent to maceration of various specimens at a later date and examination in transmitted light, Marcinkiewicz (1971) realised that the sculpture was finely reticulate rather than granulate. As a result, she decided that the species would be more appropriately placed in *Horstisporites*. At the same time she made several modifications and additions to her earlier description of the species as follows: a greater maximum diameter (490 µm); width of triradiate ridge, which may be slightly sinuous, 10–15 µm; arcuate ridges similarly developed, joining with the ends of the triradiate ridges where they occasionally form minute auriculae; exine 6–8 µm thick; reticulum consists of a network of muri *c*. 3 µm wide and up to 2–6 µm high surrounding lumina mainly 4–10, but up to 30 µm, in diameter.

Occurrence on Bornholm:
Sose Bugt Member

HUGHESISPORITES Potonié, 1956

Hughesisporites galericulatus (Dijkstra, 1951 emend. Hughes, 1955) Potonié, 1956

1951 *Triletes galericulatus* Dijkstra, p. 14, pl. 2, fig. 16; pl. 3, fig. 5
1955 *Triletes galericulatus* Dijkstra, 1951 emend. Hughes, pp. 212,213, pl.12, figs 1,2
1956 *Hughesisporites galericulatus* (Dijkstra, 1951 emend. Hughes, 1955) Potonié, p. 71

Pl. 9, figs 6–9; Pl. 10, figs 1,3; Pl. 20, fig. 18

Remarks:
Dijkstra (1951) described *H. galericulatus* as having a gula, in common with a number of Carboniferous megaspores, but Hughes (1955) showed that the construction of the proximal area differs from this in that it consists of triradiate ridges surrounded by pointed appendages; hence his emendation.

The morphology of the species is remarkably consistent even though specimens are seldom common in assemblages. Those in Gry's collection are entirely typical in being between 300 and 400µm in diameter, and in having a rounded to rounded-triangular equatorial outline, a prominent triradiate ridge, and a spinose contact face. The spines arch towards the ridge and may be discrete or connected along part or most of their length.

The exoexine is *c*. 18–20µm thick and composed of tightly packed sporopollenin threads that make the wall in cross-section look granular at magnifications of *c*. ×2000 (Pl. 10, fig. 3). At higher power the outer "smooth" surface appears foveolate. The intexine may be 1–2µm thick and of more homogeneous construction.

Occurrence on Bornholm:
Bagå Formation (Levka beds, coal-bearing succesion), Rabekke and Robbedale Formations (Purbeck beds)

Hughesisporites variabilis Dettmann, 1961

1961 *Hughesisporites variabilis* Dettmann, p. 76, pl. 1, figs 15–20, pl. 2, fig. 1.

Pl. 10, figs 2, 4–8; Pl. 20, fig. 17

Remarks:
Gry referred informally in his records to specimens of this species as "sourface" or "wrinkle face", and in his 1969 paper he noted it to be a new species of *Hughesisporites*. Reference to this genus is based on the appearance of the proximal face, the contact areas of which bear radially arranged, sinuous muri. Gry's specimens as viewed in reflected light and under the SEM are very similar to the Rhaetian material from Tasmania on which Dettmann (1961) based *H. variabilis*. They differ in having a gently undulating wall with a smooth surface equatorially and distally, although at high magnifications the surface is seen to be finely granular. They are also significantly larger, having a maximum diameter of between 620 and 700 µm as opposed to between 200 and 420 µm for dry, and 500 µm for "cleared" (translucent) Tasmanian specimens.

Hughesisporites ionthus Harris, 1935 is similar to *H. variabilis* but, according to Dettmann (1961), differs in having a ridge that delineates the lower margin of the contact faces. Dettmann also regarded the cavate exine of her species to distinguish it from *H. ionthus*. Gry's specimens are closer in size to those found by Harris, for which a diameter of 500–600 µm was documented

(Harris, 1935, p. 166), but they appear to differ in having a more delicate proximal sculpture and perhaps also a more sinuous triradiate ridge.

Hughesisporites pustulatus Marcinkiewicz, 1962 is also similar. This species was described from the Lower Jurassic (Lias γ) of Poland on the basis of a single specimen 300 µm in diameter. The triradiate ridge was noted to be c. 20 µm wide and to reach 3/4 of the spore radius in length. The surface of the contact area was described as being covered with small knobs (Marcinkiewicz, 1962, p. 493). Its size range was given as 300–400 µm in a later publication (Marcinkiewicz, 1981, p. 186). Hence, it is smaller than the species recorded here as *H. variabilis*, but whether only a single taxon is, in fact, involved is not clear.

Occurrence on Bornholm:
Bagå Formation (Boderne beds)

MAEXISPORITES Potonié, 1956

Maexisporites sp. cf. *M. misellus* Marcinkiewicz, 1962

1962 *Maexisporites misellus* Marcinkiewicz, pp. 473, 491, pl. 2, figs 6,7

Pl. 11, figs 1,2

Remarks:
Marcinkiewicz (1962, p. 491) described this species as having a "hardly discernible" tetrad scar and a "faintly granular" sculpture. The specimens she illustrated (1962, pl. 2, figs 6,7) suggest that the triradiate ridge is more prominent and the sculpture more strongly developed than is implied by her description, and this is confirmed by two further illustrations in a later paper (Marcinkiewicz, 1971, pl. 3, figs 2,3).

Hitherto, all records of *M. misellus* have been Rhaetian (Kovach & Batten, 1989), which means that by identifying the few specimens from the Bagå Formation here as this species, its stratigraphic range is immediately extended. On the other hand, the morphology of the species is not so distinctive, and its present apparently very restricted range may be misleading. In the circumstances, the most appropriate course of action seems to us to merely compare Gry's specimens with *M. misellus*.

Occurrence on Bornholm:
Bagå Formation

Maexisporites soldanellus (Dijkstra, 1951) Potonié, 1956

1951 *Triletes soldanellus* Dijkstra, p. 10, pl.2, fig. 17
1956 *Maexisporites soldanellus* (Dijkstra, 1951) Potonié, p. 25

Pl. 11, figs 3–8; Pl. 21, figs 1,2

Remarks:
Specimens of this species are very common in the Bagå

Formation. They are rather more strongly sculptured on the contact areas, and sometimes also elsewhere, than those on which the species is based (personal observation). Dijkstra (1951, p. 10) described the sculpture as "finely granulated, granules about 2 µ in diameter". Most seem, however, to be within what is reasonable to regard as an acceptable range of morphological variation for the species. Specimens sculptured with granules and/or small rugulate elements have, therefore, been included in *M. soldanellus*.

The exoexine is composed of a densely packed, comparatively robust network of sporopollenin (Pl. 11, fig. 5) which gives the surface of the spore a reticulate appearance at high magnification (Pl. 11, fig. 6).

Occurrence on Bornholm:
Bagå Formation (Korsodde and Onsbæk, coal-bearing beds; Bagå beds)

MINERISPORITES Potonié, 1956

Minerisporites marginatus (Dijkstra, 1951) Potonié, 1956

1951 *Triletes marginatus* Dijkstra, p. 13, pl. 3, fig. 11
1956 *Minerisporites marginatus* (Dijkstra, 1951) Potonié, p. 68

Pl. 12, figs 1,2; pl.21, figs 3,4

Remarks:
The spores included here display the characters of the species as described by Dijkstra (1951).

Occurrence on Bornholm:
Rabekke and Robbedale Formations (Purbeck beds)

Minerisporites sp. cf. *M. marginatus* (Dijkstra, 1951) Potonié, 1956

Pl. 12, figs 3, 4

Remarks:
Some of the specimens Gry (1969) referred to *M. marginatus* are more weakly sculptured than those on which Dijkstra based the species. They are, therefore, only compared with it here.

Occurrence on Bornholm:
Rabekke and Robbedale Formations (Purbeck beds)

Minerisporites richardsonii (Murray, 1939) Potonié, 1956 emend. Harris, 1961

1939 *Triletes richardsoni* Murray, pp. 482,484, figs 9,10
1956 *Minerisporites richardsoni* (Murray, 1939) Potonié, p. 68
1961 *Triletes richardsoni* Murray, emend. Harris, p. 46, fig. 13A-H

Pl. 12, figs 5–8; Pl. 13, fig. 1; Pl. 21, fig. 5

Remarks:

The range of morphological variation that Harris (1961) considered to be acceptable for this species is quite wide as shown in his figures, and as is evident from our examination of his slides. In most respects the morphology of the specimens in Gry's collection accords with Harris' emended diagnosis. They do differ slightly, however; whereas the sculpture of the proximal face consists of meandering ridges forming an irregular reticulum, that on the distal face may be better defined and more regular in form than Harris allowed. On the other hand, the development of spines where the muri of the reticulum merge conforms with his description; these may be elevated to form processes up to 25 μm long, the longest structures usually being close to the triradiate flange.

Minerisporites institus Marcinkiewicz, 1960 is very similar and was placed in synonymy with *M. richardsonii* by Marcinkiewicz (1971). More recently she decided, however, that they are not the same because *M. institus* is larger and has (more) strongly developed auriculae (Marcinkiewicz, 1980).

Occurrence on Bornholm:
Bagå Formation

Minerisporites volucris Marcinkiewiz, 1960

1960 *Minerisporites volucris* Marcinkiewicz, p. 723, pl. 7, figs 1–3

Pl. 13, figs 2–5,7,8; Pl. 21, fig. 6

Remarks:
Marcinkiewicz's (1960) diagnosis of this species was based on observations of only one specimen 385 μm in diameter. The following characters were noted (freely translated and modified from the original description in Polish): spore body almost spherical; rays of triradiate suture extend to equator, bordered by transparent flanges about 50 μm in height; these merge with an equatorial flange (zona) to form delicately perforated auriculae extending to about 130 μm away from spore body; sculpture comprises numerous spines c. 55 μm long and c. 15 μm in basal width.

Gry's specimens clearly belong here. Marcinkiewicz remarked that the species most closely resembles *Minerisporites ales* (Harris, 1935) Potonié, 1956, differing from it primarily in possessing shorter and wider spines and in having a lower triradiate flange.

Occurrence on Bornholm:
Bagå Formation (Sorthat beds; Levka beds, coal-bearing succession; Levka beds, above coal-bearing succession)

Minerisporites sp.

Pl. 13, fig. 6; Pl. 14, fig. 1

Remarks:
This is a small species with an unevenly roughened/

scabrate surface and a fairly massive triradiate ridge. *Henrisporites delicatus* Marcinkiewicz, 1978 is normally spinose but Marcinkiewicz (1983) recovered specimens which lack any sculpture, and these appear to be similar to the spores illustrated here. The resemblance is, however, only superficial because the absence of spines on *H. delicatus* is interpreted to be a result of exinal degradation, and not a primary feature (Marcinkiewicz, 1983). This species is, in any case, much larger than the spores from Bornholm, whose diameters range from 230–300 μm.

Occurrence on Bornholm:
Bagå Formation

NATHORSTISPORITES Jung, 1958

Nathorstisporites hopliticus Jung, 1958

1958 *Nathorstisporites hopliticus* Jung, pp. 121–123, pl. 3, figs 1,5,6,9–11

Pl. 14, figs 2–8; Pl. 21, fig. 7

Remarks:
Specimens of this species consist of a spheroidal spore body with elevated, membraneous lips which obscure the laesurae. The basal part of the triradiate flange is of the same construction as the outer surface of the body, but the upper part appears solid and deeply incised. It is commonly difficult to distinguish the flange from adjacent appendages.

The contact faces are delineated by a low elevation that is subparallel to the equator, or by an alignment of coni or spines. The tips of these are often divided, and the surface of the wall between the large spines (up to 50 μm high and c. 30 μm in basal diameter) is also sculptured with small spines up to 10 μm high.

Bertelsen & Michelsen (1970) attempted to divide their collection of *Nathorstisporites* specimens into two groups according to the characters as set out by Jung (1958) for his two species, *N. hopliticus* and *N. peltasticus*, but found that they were left with a large, unassignable residual group. Another attempt at classification on the basis of distal sculpture being verrucate or capillate was also given up because the number of intermediate forms also made this impossible; hence, they recorded all their specimens as *N. hopliticus*.

On the basis of a TEM examination of a specimen from the Lower Jurassic of Bornholm, Kempf (1972) found the exoexine (perine in Kempf) to be c. 20 μm thick, excluding the sculpture, and its fine structure to differ from that of *Paxillitriletes*. The inner part of the wall was shown to comprise sporopollenin threads that are approximately 0.3 μm in diameter and arranged subparallel to the inner surface of the wall, whereas those of the outer zone are thicker and form an irregular network from which conical protruberances extend a further 20 μm and more, terminating in an almost solid sporopollenin mass. The elongate, often branched

processes that dominate the proximal surface close to the triradiate flange have hollow bases and, except where they merge with the reticulate outer surface of the exoexine, also consist largely of dense, homogeneous sporopollenin.

Occurrence on Bornholm:
Munkerup Member (Munkerup clay), Sose Bugt Member (Sosevig beds; Vellengsby clay; Ormebæk, white clay)

PAXILLITRILETES Hall & Nicolson, 1973

Paxillitriletes kristinae sp. nov.

Pl. 15, figs 1–8; Pl. 16, fig. 1; Pl. 21, fig. 8

Diagnosis:
Megaspore, trilete; mean maximum diameter of spore in polar view excluding auriculae and sculpture 310–390 μm (25 specimens). Laesurae extend to equator of body, bordered by lips c. 10 μm wide which extend into appendages up to 100 μm long and 10 μm in width, with pointed, bluntly rounded or expanded but flattened tips; amount of expansion up to 4 times width of process at mid-point of length. Adjacent to flange are one or two irregular rows of appendages of similar length to those on triradiate flange, but they are rounded rather than flattened in outline, and have rounded to pointed tips. Equator of spore is surrounded by a zona up to 25 μm wide interradially; this expands into auriculae in equatorial radial regions c. 70–120 μm wide and extending up to 100 μm away from spore body where they merge with ends of triradiate flange.

Sculpture comprises small, closely spaced, irregularly granular to murornate elements of varying length but of generally uniform height (up to 10 μm), giving surface a roughened, sugary appearance at low magnifications. On zona, sculptural elements are aligned normal to surface of spore body, giving it a finely ribbed appearance.

Cross-sections of broken specimens show exoexine to be c. 10–15 μm thick and composed of a three dimensional network of sporopollenin threads, the predominant orientation of which is subparallel to inner surface of wall. Alignment of sporopollenin threads is also evident on zona, triradiate flange and appendages, where they are mainly parallel to surface of these features. Exoexine is underlain by a thin (c. 1 μm) intexine, most of which also consists of a reticulate meshwork of sporopollenin threads similarly orientated mainly subparallel to surface of spore body; inner surface of this layer is, however, a thin, homogeneous membrane.

Derivation of name:
After EBK's daughter, Kristine Koppelhus

Holotype:

Pl. 21, fig. 8; slide HGHol/3, Borehole 246.207, 26.00m, Robbedale Formation, upper Berriasian

Remarks:
At least some of the specimens of this species were recorded by Gry (1969) as Thomsonia (now Paxillitriletes) cf. pseudotenella Dijkstra, 1951. This resembles P. kristinae in having a triradiate flange that bears long appendages which may splay out at their tips. It is, however, sculptured with cones and spines (Mädler, 1954; Batten, 1969) and has a proportionally smaller body. A reworked specimen of Paxillitriletes in a Tertiary deposit recorded by Collinson et al. (1985, fig. 4f) as P. sp. nov. is similar, but the undivided triradiate flange is higher and the appendages extending from it are proportionally shorter.

Paxillitriletes vittatus Kovach & Dilcher, 1985 has a similar wall structure (see for example, Kovach & Dilcher, 1985, pl. 1, figs 5–8; Kovach & Dilcher, 1988, pl. 4, figs 6,8).

Occurrence on Bornholm:
Rabekke and Robbedale Formations (Purbeck beds)

*Paxillitriletes phyllicus (Murray, 1939) Hall & Nicolson, 1973

1939 Triletes phyllicus Murray, p. 482, figs 7,8
1973 Paxillitriletes phyllicus (Murray, 1939) Hall & Nicolson, p. 320

Pl. 16, figs 2–4; Pl. 21, figs 9,13

Remarks:
P. phyllicus is a comparatively small megaspore with a prominent triradiate membraneous flange up to 100 μm high (according to Harris, 1961) that extends onto, and fuses with, an equatorial flange which is narrow interradially, but commonly expanded into small auriculae radially. The triradiate flange merges with these. It is regularly ribbed and may be somewhat sinuous but, unlike that in many species of Paxillitriletes, its outer margin is usually continuous. The equatorial flange is similarly constructed, but often with low muri of the surface reticulum extending onto it. The reticulum comprises ridges of varying height, mainly <5 μm on the proximal face away from the triradiate flange, but often somewhat more elevated on the distal face (10–20 μm). In addition, some muri may be prolonged into spines. Spinose elements dominate the sculpture towards the triradiate flange, and may be partly fused with it. They are usually not as long as the height of the flange; often they are only 1/2 to 2/3 of this.

Occurrence on Bornholm:
Bagå Formation (Korsodde and Onsbæk, coal-bearing beds; Boderne beds; Sorthat beds; Bagå beds; Levka beds, coal-bearing succession; Levka beds, above coal-bearing succession)

Paxillitriletes sp. cf. *P. pseudotenellus* (Dijkstra, 1951) Hall & Nicolson, 1973

1951 *Triletes pseudotenellus* Dijkstra, p. 12, pl. 3, figs 9,10

1973 *Paxillitriletes pseudotenellus* (Dijkstra) Hall & Nicolson, p. 320

Remarks:
The majority of the specimens from the "Purbeck beds" that Gry compared with *Paxillitriletes pseudotenellus* (recorded as *Thomsonia* cf. *pseudotenella*) are here considered to be *P. kristinae*. The remainder, including specimens noted to occur in the Levka beds, belong in other species. None looks sufficiently like *P. pseudotenellus* for it to be compared with that species.

Paxillitriletes rasmusii sp. nov.

Pl. 18, figs 1–8; Pl. 21, figs 12,18

Diagnosis:
Trilete megaspore, triangular in equatorial outline; maximum diameter 400–500 µm (25 specimens). Laesurae bordered by a flange from which extend flattened appendages of varying shape up to 150 µm high. At its extremities, flange merges with zona which is commonly expanded to form auriculae up to 200 µm wide and extending up to 200 µm from spore body. Proximal face finely reticulate, but with numerous spines up to 80 µm high extending from junctions of muri on spore body. Reticulum extends onto zona but muri become lower and towards angles, mainly orientated normal to equator. Distal face similarly sculptured but spinose extensions of reticulum are shorter (up to 50 µm) and more bluntly rounded.

Exoexine comprises a meshwork of sporopollenin threads, the predominant orientation of which is subparallel to outer surface of spore body. Appendages and both triradiate and equatorial flanges are composed of similar threads aligned mainly parallel to surface of these features.

Derivation of name:
After EBK's son, Rasmus Koppelhus

Holotype:
Pl. 21, fig. 18; slide HGHol/4, Borehole 246.307a, 5.60m, Skyttegård Member of the Rabekke Formation, lower Berriasian

Remarks:
Dijkstra (1951) described several species of *Triletes*, now referred to *Paxillitriletes* and one form of *Membranisporites* (*M. samarus*), which is morphologically similar, but none is closely comparable to *P. rasmusii*. This also applies to the other species of *Paxillitriletes* and to the only other *Membranisporites* (*M. trifoliaceus*) that have been described previously (see Batten & Kovach, 1990 for names and bibliographic data).

Occurrence on Bornholm:

Rabekke and Robbedale Formations

Paxillitriletes sp. cf. *P. reticulatus* (Mädler, 1954) Hall & Nicolson, 1973

1954 *Thomsonia reticulata* Mädler, p. 150, pl. 5, figs 14–19, 34

1973 *Paxillitriletes reticulatus* (Mädler, 1954) Hall & Nicolson, p. 319

Pl. 16, figs 5–7; Pl. 17, figs 1–3; Pl. 21, fig. 14

Description:
Megaspore, trilete; mean maximum diameter of spore in polar view excluding auriculae and sculpture 220–300 µm (25 specimens). Laesurae extend to equator of body, bordered by ribbed lips c. 20–30 µm wide and up to 80 µm high. Muri of reticulum of proximal face raised up into membraneous extensions that increase in elevation to approximately same height as triradiate flange. Equator of spore surrounded by a zona c. 10 µm wide interradially; in equatorial radial regions this expands into auriculae c. 20–30 µm wide and extending up to 50 µm away from spore body where they merge with ends of triradiate flange.

Sculpture on both proximal and distal faces is a clearly defined reticulum; muri 1–2 µm wide and up to 5 µm high, surrounding lumina of varying shape, up to 15 µm in diameter; on zona, muri are aligned normal to surface of spore body, giving it a ribbed appearance.

Cross-sections of broken specimens show exine to be made up of spongy exoexine up to 10 µm thick, composed of a three dimensional network of sporopollenin threads, the predominant orientation of which is subparallel to inner surface of wall. Alignment of sporopollenin threads is also evident on zona, triradiate flange and appendages, where they are mainly parallel to surface of these features. Exoexine is underlain by a thin (1 µm) intexine, most of which also consists of a reticulate meshwork of sporopollenin threads similarly orientated mainly parallel to the surface of the spore body; inner surface of this layer is, however, a thin, homogeneous membrane.

Remarks:
Gry appears to have recorded this species, perhaps along with others, as *Thomsonia* (now *Paxillitriletes*) *reticulata*. However, *P. reticulatus* (Mädler, 1954) Hall & Nicolson, 1973, the type species of the genus, was diagnosed as having "pilose sculpture along the tetrad rays or only in their immediate vicinity" (freely translated from Mädler, op. cit., p. 150); for scanning electron micrographs showing this character, see Pelzer & Reigel, 1982, pl. 1, fig. 7 (recorded as *P.* cf. *reticulatus*) and Schultz & Noll, 1987, pl. 7, fig. 6). The specimens shown here are not, however, sculptured in this way. *P. fairlightensis* Batten, 1969 is similar, and *P. lindstroemi* Huckreide, 1982 bears some resemblance to Gry's specimens, but again the triradiate flanges of both are

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bordered by discrete appendages rather than by membraneous muri.

Following his diagnosis of *Triletes gryensis*, Dijkstra (1961, p. 12) reported that "Dr Gry, during his visit to Heerlen, told us that he had found the same species in the Lower Wealden of Bornholm". It has not, however, been easy to determine which form Gry was meaning. One of those it most closely resembles is *P.* sp. cf. *P. reticulatus*, but for several reasons we do not think it is the same. The single specimen figured by Dijkstra (1961, pl. 1, fig. 14) looks different from topotype material we have examined; his description of the species does not entirely fit with the characters we have observed; and the specimens in Gry's collection that are closest morphologically to *T. gryensis* are better preserved.

Occurrence on Bornholm:
Rabekke and Robbedale Formations (Purbeck beds)

Paxillitriletes spp. 1-3

Pl. 17, figs 4–8; Pl. 21, figs 10, 11

Remarks:
Paxillitriletes sp. 1 bears some resemblance to *P. reticulatus* but the sculpture is more spinose, and the muri of the reticulum do not form elevated membraneous extensions adjacent to the triradiate flange (Pl. 17, fig. 4). *P.* sp. 2 is distinct in having a rugulate wall (Pl. 17, figs 5,7) and *P.* sp. 3 has a roughened/scabrate surface (Pl. 17, fig. 8), its uneven nature probably having been enhanced in most cases by the processes of degradation. It is typically triangular in shape with comparatively wide, flattened, finger-like processes extending upwards from the triradiate flange. In quite a few specimens a ridge runs parallel to the flange, and this may continue subequatorially adjacent to the inner part of the zona. In this respect it resembles *Sepisporites annulatus* Li & Batten 1987, but it differs from this species in other ways.

Occurrence on Bornholm:
Bagå Formation; Rabekke and Robbedale Formations

STRIATRILETES van der Hammen, 1955 ex Potonié, 1956

Striatriletes sulcatus (Dijkstra, 1951) Potonié, 1956

1951 *Triletes sulcatus* Dijkstra, p. 11, pl. 2, fig. 3
1956 *Striatriletes sulcatus* (Dijkstra) Potonié, p. 42

Pl. 17, fig. 9; Pl. 21, fig. 16

Remarks:
Of the morphological characters of the specimens referred to this species, the most significant is that the muri on the contact areas are radially orientated and extend onto the distal face, thus conforming with the characters of the type material.

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Occurrence on Bornholm:
Rabekke and Robbedale Formations (Purbeck beds)

TRILEITES Erdtman, 1945 ex Potonié, 1956

Trileites candoris Marcinkiewicz, 1960

1960 *Trileites candoris* Marcinkiewicz, p. 717, pl. 1, fig. 6

Pl. 19, figs 1–3; Pl. 21, fig. 15

Description:
The very few specimens of this species in Gry's collection are mostly broken or occur only as fragments. All are large, ranging from c. 750–1150 μm in diameter, and have clearly delineated to prominent triradiate ridges 10–40 μm high and 10–20 μm in basal width. These extend to about 1/2 the radius of the spore and are connected at their extremities by equally prominent, slightly sinuous curvaturae of similar dimensions.

The exine of fragmentary remains is seen to consist of a very thick (c. 40 μm; Harris, 1961: 20 to more than 50 μm; Kempf, 1972) exoexinal layer beneath which is a much thinner (<1 to 2 μm) membraneous intexine. Kempf (1972) has demonstrated that the exoexine consists of three layers.

Remarks:
T. candoris was erected by Marcinkiewicz (1960) on the basis of a single, laterally compressed specimen somewhat elongated about the polar axis and 800 μm in diameter. The other characters noted were that the surface of the spore is smooth and glossy, and both the triradiate ridges and curvaturae are well developed, the latter being about 20 μm in width and wavy in form.

On the basis of about 30 specimens from the Middle Jurassic of Yorkshire, Harris (1961) described more comprehensively very similar forms which he named *Triletes turbanaeformis*. This was later considered to be a junior synonym of *T. candoris* on the basis of priority of publication (Marcinkicwicz, 1981, p. 82).

Margaritatisporites regalis Marcinkiewicz 1962 is very similar, if not identical to *T. candoris*. The original diagnosis (description) was also based on only one specimen of closely comparable size and appearance. According to Marcinkiewicz (1962, pp. 473, 491) the arcuate ridges are only faintly indicated, but the single photograph shows them to be well developed.

Occurrence on Bornholm:
Sose Bugt Member (Sosevig beds), ?Galgeløkke Member, Bagå Formation (Korsodde and Onsbæk, coal-bearing beds; Boderne beds; Sorthat beds; Bagå beds; Levka beds, coal-bearing succession; Levka beds, above coal-bearing succession)

Trileites murrayi (Harris, 1961) Marcinkiewicz, 1971

1961 *Triletes murrayi* Harris, pp. 64,66, figs 20A-F, 21A-B

1971 *Trileites murrayi* (Harris) Marcinkiewicz, p. 31, pl.1, figs 6–8

Pl. 19, fig. 4; Pl. 21, fig. 19

Remarks:
Gry's reference of the spores with the characters of this species to *T. murrayi* was invalid at the time of publication because he failed to formally transfer the species from *Triletes* to *Trileites* by giving details of the basionym as required by the ICBN. This was not done until two years later (Marcinkiewicz, 1971).

This smooth-walled species can vary enormously in size. Harris (1961) gives a range of 250–1400 μm, but regarded those smaller than 500 μm in diameter as abortive. The triradiate ridge is typically short (1/3 spore radius), *c.* 60 μm broad, 40 μm high, and sharply delineated by marginal grooves 10–20 μm broad. Contact areas are usually undifferentiated but may be suggested by low, poorly defined ridges. The exoexine is very thick (30–50 μm), beneath which is a thin (*c.* 2 μm) intexine.

Occurrence on Bornholm:
Bagå Formation (Korsodde and Onsbæk, coal-bearing beds; Boderne beds; Bagå beds; Levka beds, above coal-bearing succession)

VERRUTRILETES van der Hammen, 1955 ex Potonié, 1956 emend. Binda & Srivastava, 1968

Verrutriletes franconicus Jung, 1960

1960 *Verrutriletes franconicus* Jung, pp. 137,138, pl. 36, figs 12–20

Pl. 19, figs 5–8; Pl. 21, fig. 17

Remarks:
The spores identified as *V. franconicus* are mostly subcircular in equatorial outline and comparatively small (*c.* 400 μm in diameter), thin walled (*c.* 5–7 μm), and weakly sculptured with grana, coni, small verrucae and/or rugulae up to 15 μm in basal diameter and 10 μm high. The larger sculptural elements are confined in most specimens to the contact areas. In reflected light the remainder of the surface of the spore usually has a roughened to granular appearance. The triradiate ridges are often fairly prominent (*c.* 15–25 μm in basal width and up to 40 μm high) and usually connect with more weakly delineated subequatorial curvaturae.

The combination of a thin exine, a comparatively subdued sculpture of coni and/or small verrucae usually restricted to proximal interradial regions, and relatively prominent triradiate ridges which merge with curvaturae serve to distinguish this species from most of the other spore-types that are attributable to *Verrutriletes*. Jung (1960) compared the species to *Hughesisporites ionthus* (Harris, 1935) Potonié, 1956, but concluded that, despite a superficial resemblance, there are significant differences in morphology.

The specimen of *V. franconicus* figured by Bertelsen & Michelsen (1970) has a slightly sinuous triradiate ridge and more clearly delineated low verrucae on the contact areas. It also lacks curvaturae, and is larger than the Gry's specimens, most of which are only just over 200 μm in maximum diameter.

Occurrence on Bornholm:
Munkerup Member (Munkerup clay), Sose Bugt Member (Sosevig beds, Vellengsby clay)

Affinities

A recent increase in the number of systematic studies on the megaspores of extant plant species in which use has been made of scanning and transmission electron microscopy has helped to put morphological analyses of their fossil predecessors into botanical perspective. Particularly important for classifying both modern and fossil forms is the structure of their walls. Although we have not yet attempted any transmission electron microscopy of Gry's material we have, where possible, examined cross-sections under the SEM using broken specimens and fragments.

It is clear, both from our study and by comparison with observations made previously by ourselves and others in the literature, that most, if not all of the megaspores in Gry's collection are probably referable to the heterosporous lycopod orders Selaginellales and Isoetales. Although positive evidence of affinity for some is lacking, none appears to be the product of water ferns.

It is possible to divide the collection into four groups as follows:

1. Affinity unknown because there are no data (published or unpublished) on the structure of the their walls: *Aneuletes patera; Verrutriletes franconicus.* (As noted in the systematic section, *A. discus* is unlikely to be a megaspore.)
2. Affinity uncertain because although information about wall structure is available (e.g. in Hueber, 1982; Waksmundzka, 1986; Batten & Ferguson, 1987, and herein), both this and the gross morphol-

ogy of the spores are not closely comparable with the characters of any modern forms, and they have not been found *in situ* in remains of fossil plants: *Cabochonicus carbunculus; Echitriletes; Hughesisporites.*
3. Affinity probably lies with the Isoetales because the structure of the exine closely resembles that of the acid-resistant part of the wall of modern representatives of this order (cf. sections in, for example, Pettitt, 1966; Batten, 1988, Kovach & Dilcher, 1988; Archangelsky & Villar de Seoane, 1990; this paper): all of the species of *Henrisporites, Minerisporites* and *Paxillitriletes.*
4. Affinity probably lies with the Selaginellales because the structure of the wall is more compact, and in most species the exoexine is thicker than is usually the case for isoetalean products (cf. sections in, for example, Kempf, 1970, 1972; Bergad, 1978; Minaki, 1985; Batten, 1988; Taylor & Taylor, 1988; Koppelhus & Batten, 1989; Morbelli, 1990; this paper): all of the species of *Bacutriletes, Erlansonisporites, Horstisporites, Maexisporites, Nathorstisporites, Striatriletes* and *Trileites.*

Only one taxon in Gry's collection is reliably attributable to a particular fossil plant species. This is *Nathorstisporites hopliticus*, which has been closely linked to the heterosporous lycopod *Lycostrobus scottii* by a number of authors (e.g. Harris, 1926, 1935, 1946; Reissinger, 1952; Lundblad, 1956; Jung, 1958, 1960).

Stratigraphic value

Gry (1969) showed that megaspores are of value for the stratigraphic subdivision and correlation of the Jurassic (and earliest Cretaceous) rocks on Bornholm, as is evident from the taxonomic associations listed in the section on material and methods above. Our reassessment of his assemblages in the light of an examination of selected specimens under the SEM and a larger body of literature than was available in 1969 has shown that his general conclusions on the ages of the associations he recognised are still valid except for those of the "Purbeck beds".

Among the age data plotted on Figure 5 are the maximum ranges for the previously published taxa recorded from the succession. Comparison of these with Gry's records of occurrences noted above show that the associations recorded for the different formations are consistent with them. Some of the taxa, such as *Erlansonisporites sparassis*, *Horstisporites harrisii*, *Maexisporites soldanellus* and *Trileites murrayi*, are relatively long-ranging, even allowing for possible misidentifications on which these plots are based (taken from Kovach & Batten 1989, slightly modified). Others, such as *Aneuletes patera*, *Bacutriletes corynactis*, *Echitriletes lanatus*, *Minerisporites volucris* and *Verrutriletes francon-*

icus have more restricted stratigraphic distributions and hence may serve as local "markers" for certain parts of the column. However, even those that have less restricted ranges can be important in the context of first and last appearances and associations with other taxa, such as *Horstisporites areolatus* and *Nathorstisporites hopliticus*.

Some of Gry's identifications have been questioned, required emendation and/or been nomenclaturally updated, as indicated in both the introductory discussion and from our handling of the taxa described in the systematic section of this paper. Those forms placed in comparison with other published species cannot be identified more positively until larger assemblages of newly acquired samples are analysed. Some previously undescribed species are present in his slides for which textual and photographic documentation is provided here. A few other species still require comprehensive analysis. This cannot be done until more and/or better preserved specimens have been obtained.

It is anticipated that this will be accomplished in a subsequent paper using new material which we hope will also enable us to give greater precision to some of the ranges of the species within the Bornholm succes-
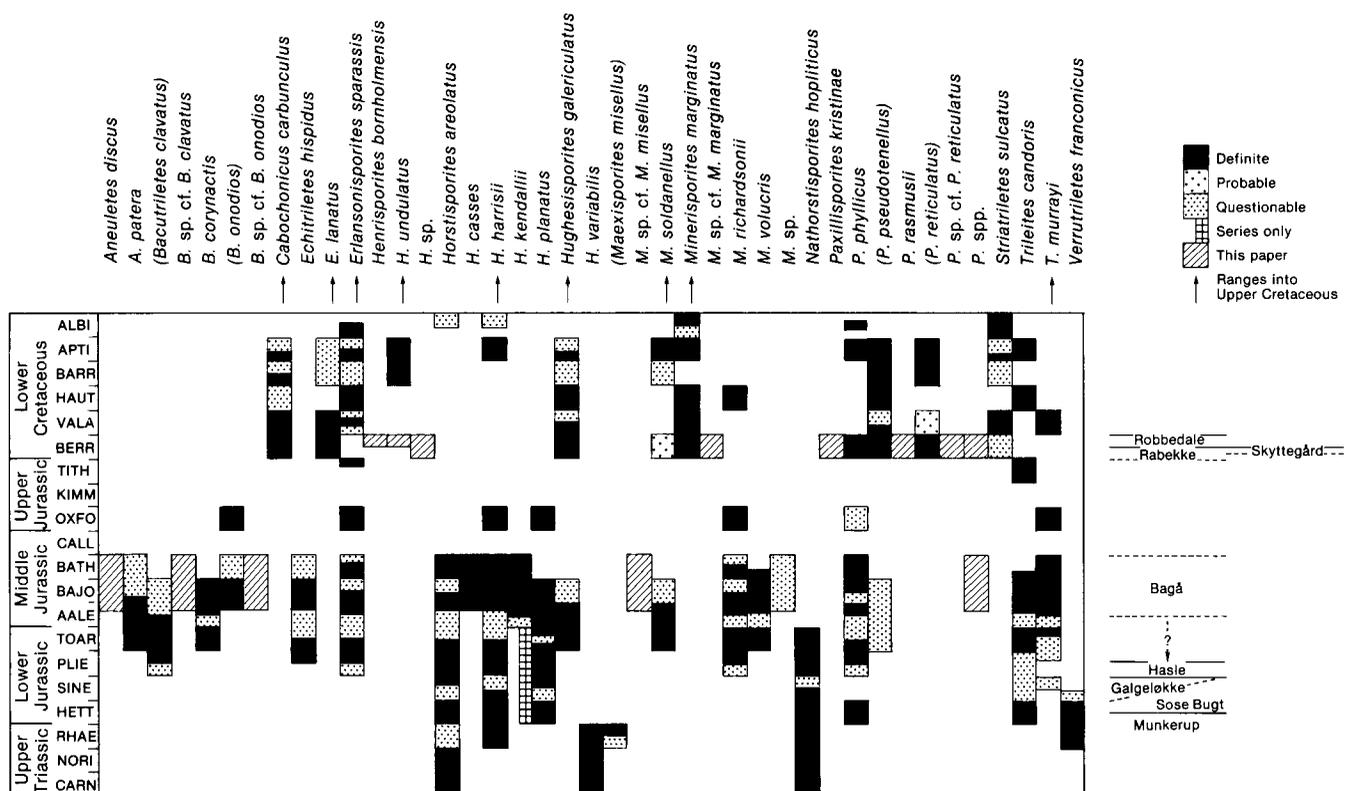
Fig. 5. Known ranges within Upper Triassic and younger mesozoic deposits of previously described species encountered in Gry's collection (adapted and slightly modified from Kovach & Batten, 1989) plotted alongside stratigraphic occurrences of the taxa placed in comparison and the new species.

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sion. Unfortunately, the levels from which many of the assemblages in Gry's collection have come are not precisely located stratigraphically; indeed only very basic information is available for the majority. Our analysis has shown the need to resample the outcrops and any borehole sections that are currently accessible in order to clarify the ranges of the taxa in the light of current interpretations of age and the stratigraphic development of the succession. Hence the ranges of the new species and those taxa that are placed in comparison with previously published species are generalised to the maximum age-ranges of the formations concerned, pending further biostratigraphic analysis.

Acknowledgments

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Appendix

Boreholes referred to in the text and their geographical location:

244.83, Hasle Klinkerfabrik clay pit
244.105, Hasle Klinkerfabrik clay pit
244.232, Bakkegård
246.207, Robbedale

246.279, Nylars
246.307(a), Skyttegård
247.130, Eskegård
247.130(f), Eskegård
247.131(c), Eskegård
247.134, Hundshale/Saxebro

PLATE 1

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Figs 1–3, *Aneuletes patera* (from Anholt-4 borehole); all same specimen. 1, whole spore in proximal view, ×300. 2, close-up of part of presumed proximal face showing surface "swellings" (verrucate to rugulate elements), ×900. 3, proximal subequatorial surface showing granulate-rugulate wall, surface perforations, and granular to vermiform appearance of sporopollenin, ×9000. Figs 4–7, *Aneuletes discus* (from borehole 244.105, Hasle Klinkerfabrik clay pit). 4, general view, ×150. 5, close-up of rough, presumably at least partly degraded surface of same specimen; no distinctive sculpture, ×1000. 6, portion of brittle wall in cross-section of specimen illustrated in fig. 7, showing homogeneous appearance and conchoidal fractures, ×2500. 7, section of whole specimen, ×400.
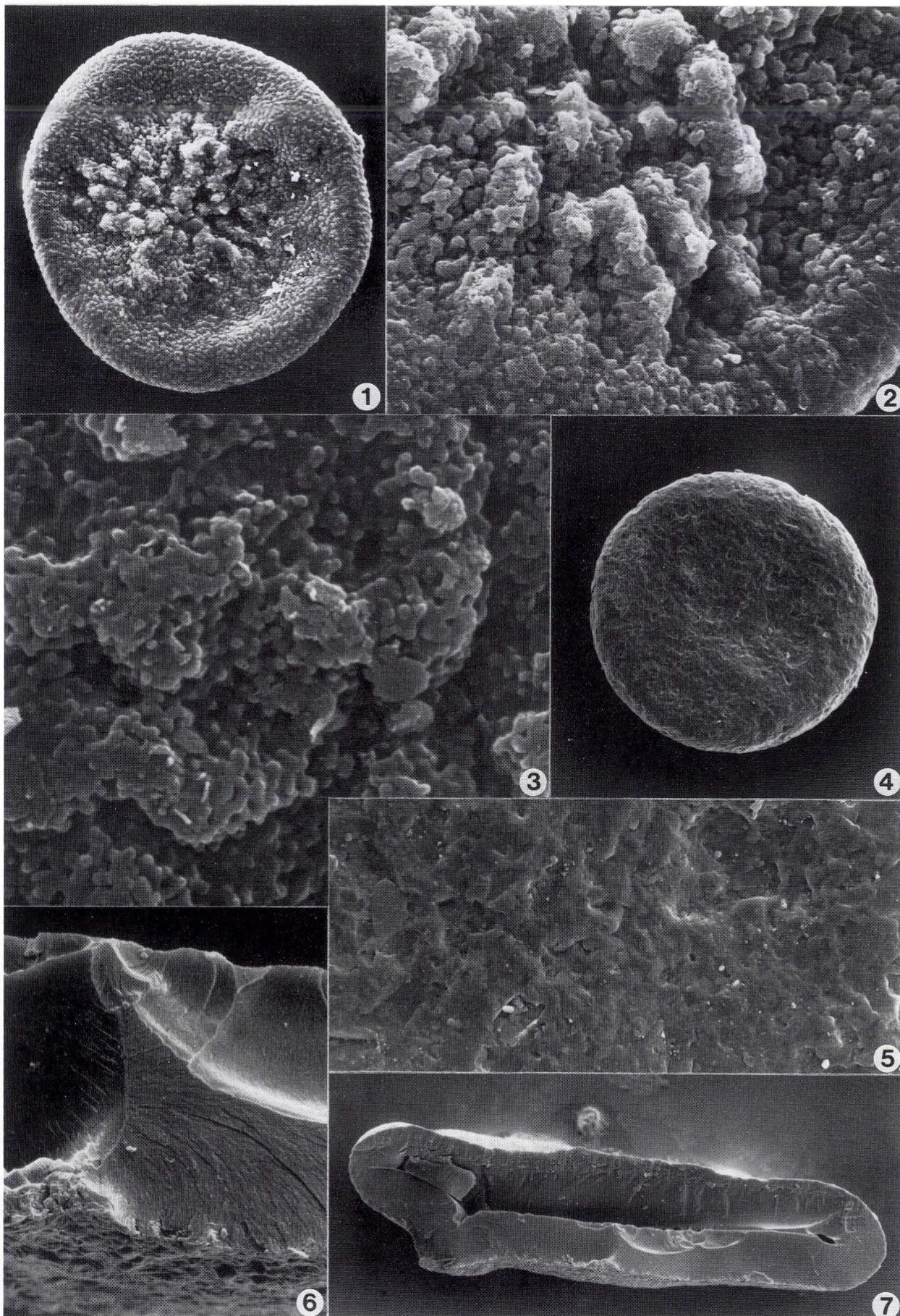
Plate 1

PLATE 2

Fig. 1, *Aneuletes discus,* section of wall, same specimen as shown on Pl. 1, fig. 7, ×5000.

Fig. 2, *Aneuletes*-like body (from Sose Bugt outcrop), ×150.

Figs 3–5, *Bacutriletes* sp. cf. *B. clavatus* (from slide 13, Gry's collection, Hasle Klinkerfabrik clay pit); all same specimen. 3, oblique view of whole spore, ×120. 4, close-up of part of proximal surface close to equator, ×5000. 5, close-up of triradiate ridge and adjacent proximal surface, ×500.

Fig. 6, *Bacutriletes* sp. cf. *B. onodios* (from borehole 244.83, Hasle Klinkerfabrik clay pit), proximal view, ×200.
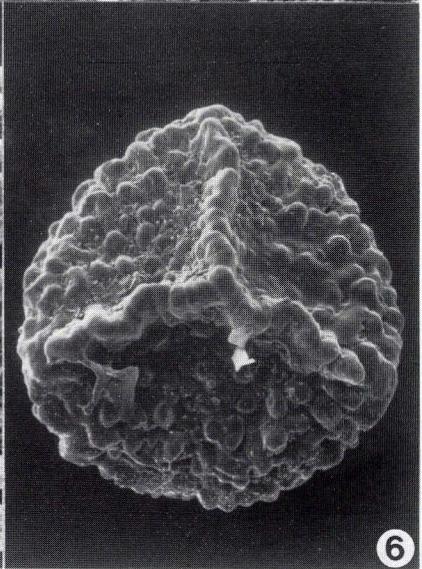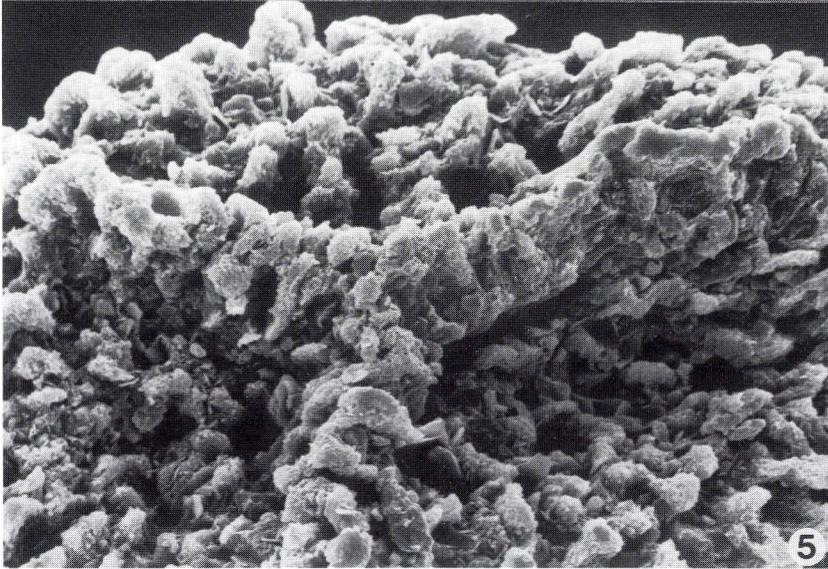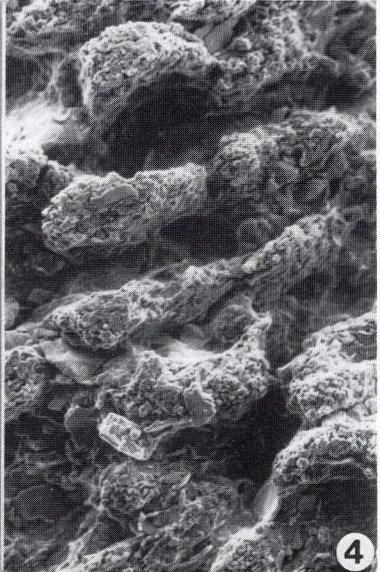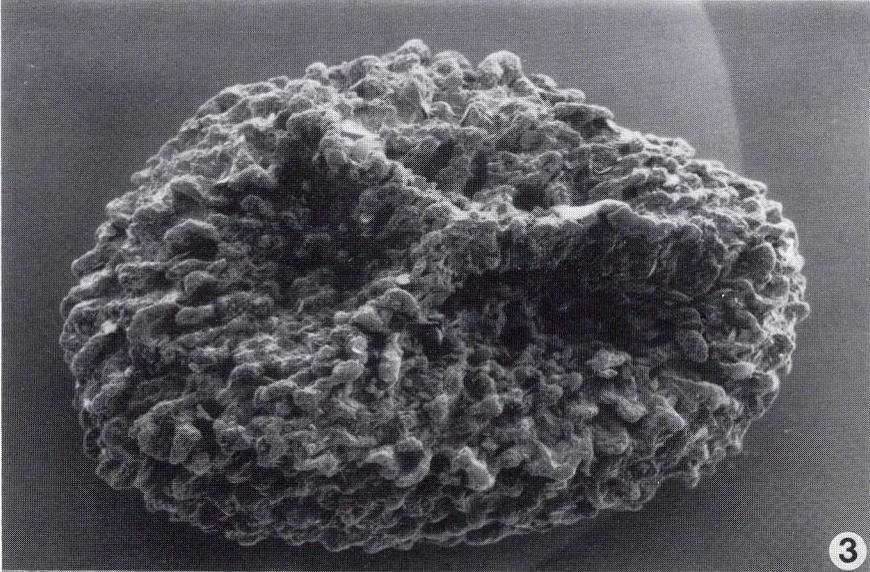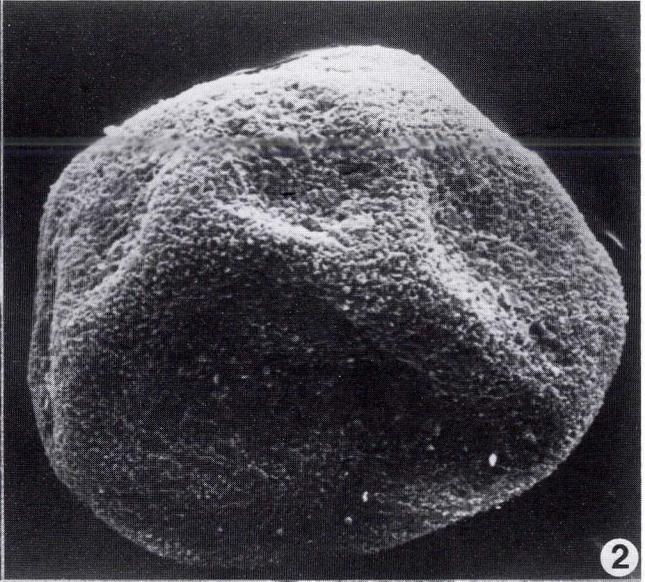
Plate 2

PLATE 3

Figs 1–5, *Bacutriletes corynactis* (from slide 15, Gry's collection, Hasle Klinkerfabrik clay pit). 1, whole specimen in lateral view, ×200. 2, broken specimen; portion of transverse section of exoexine and basal part of an appendage showing reticulate construction, ×5000. 3, section though broken appendage of specimen illustrated in fig. 1, ×10000. 4, part of fractured wall of another specimen showing membraneous intexine beneath much thicker exoexine, ×1700. 5, close-up of some baculate-clavate appendages, same specimen as in figs 1 and 3, ×2500.

Figs 6–8, *Caboconicus carbunculus* (from Skyttegård outcrop); all same specimen. 6, general view, ×125. 7, detail of outer surface of exoexine, ×4000. 8, close-up of some of the pitted gemmae, ×1000.
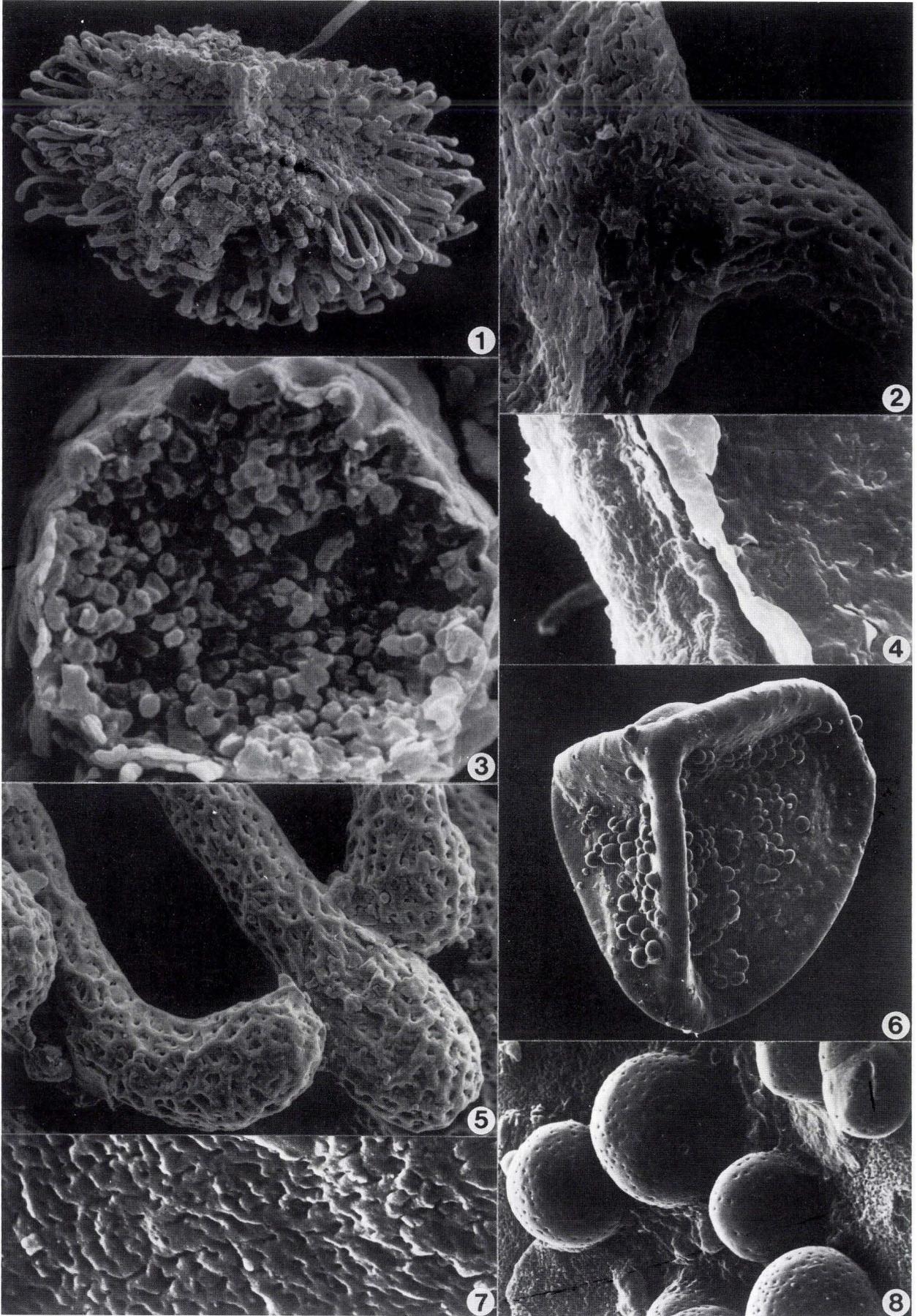
Plate 3

PLATE 4

Figs 1–5, *Bacutriletes* sp. cf. *B. onodios*. 1, oblique view of spore from borehole 246.279, Nylars, ×200. 2, same specimen, detail of contact area and trilete ridge, ×400. 3–5, broken specimen from borehole 246.279, Nylars. 3, general view showing comparatively thin, membraneous intexine beneath much thicker exoexine, ×200. 4, close-up of proximal polar area, ×500. 5, section of part of proximal, rather dirty, spongy exoexine, ×2000.

Figs 6–8, *Echitriletes lanatus* (from borehole 247.307a, Skyttegård). 6, 7, same specimen. 6, proximal view, ×170. 7, close-up of part of proximal face close to equator, ×500. 8, fragment of wall of another specimen (from borehole 247.134 between Hundshale and Saxebro) in cross-section showing inner portion of spongiose exoexine and intexine which has partly pulled away from it, ×3000.
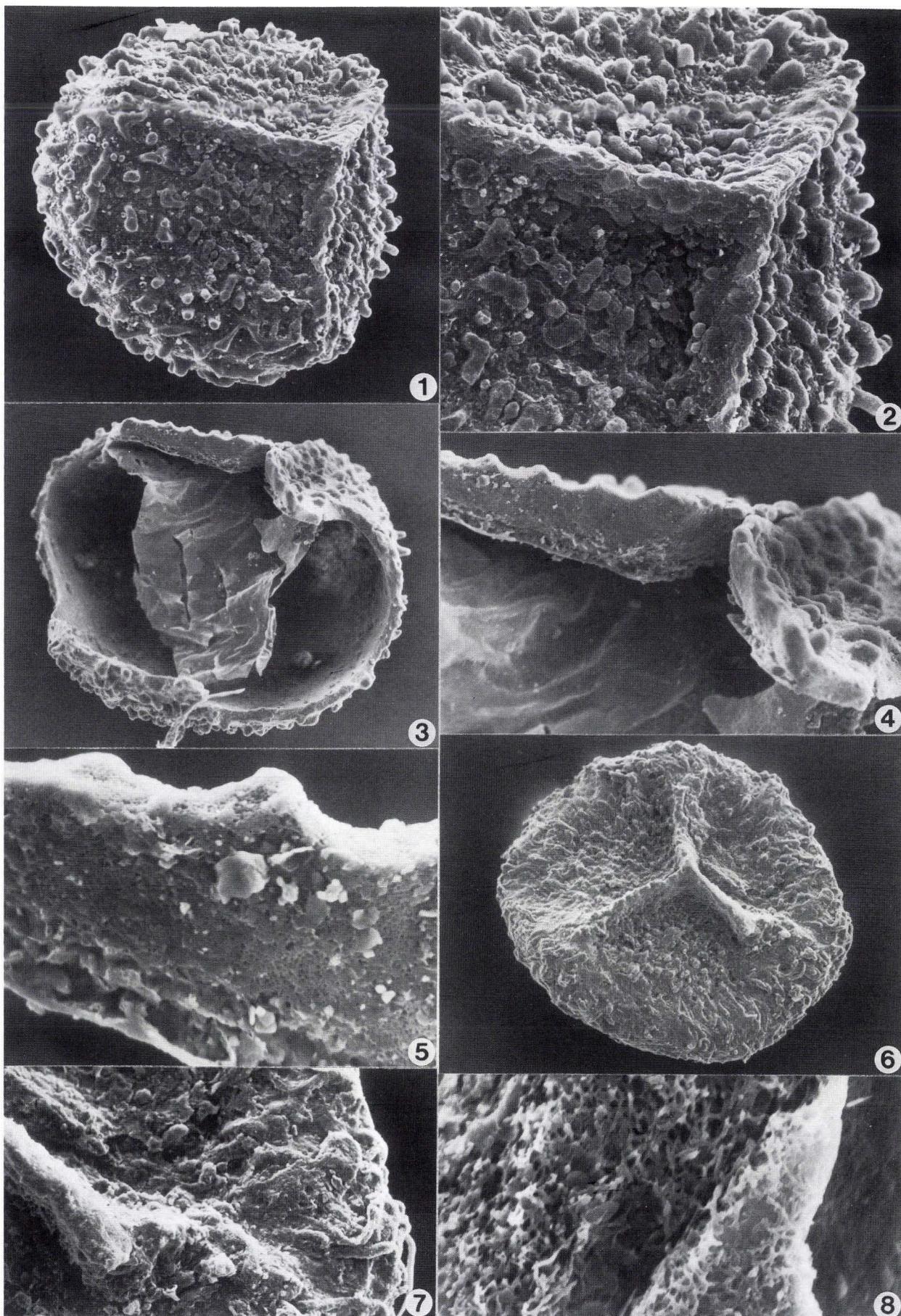
Plate 4

PLATE 5

Figs 1, 2, *Erlansonisporites sparassis*. 1, close-up of reticulate sculpture of specimen from Homandshald outcrop shown in fig. 2, with adhering inorganic particulate detritus, ×700. 2, proximal view, ×150.

Figs 3, 4, *Henrisporites undulatus*. 3, oblique-lateral view of spore from borehole 246.207, Robbedale, ×150. 4, close-up of part of contact area of same specimen, ×500.

Figs 5, 7, *Henrisporites* sp. from borehole 247.130f, Eskegård. 5, proximal view, ×160. 7, same specimen, close-up of part proximal face and zona, ×450.

Figs 6, 8, *Henrisporites undulatus*. 6, laterally compressed example from borehole 246.207, Robbedale, ×150. 8, same specimen, detail of surface of exoexine showing reticulate construction, ×6000.
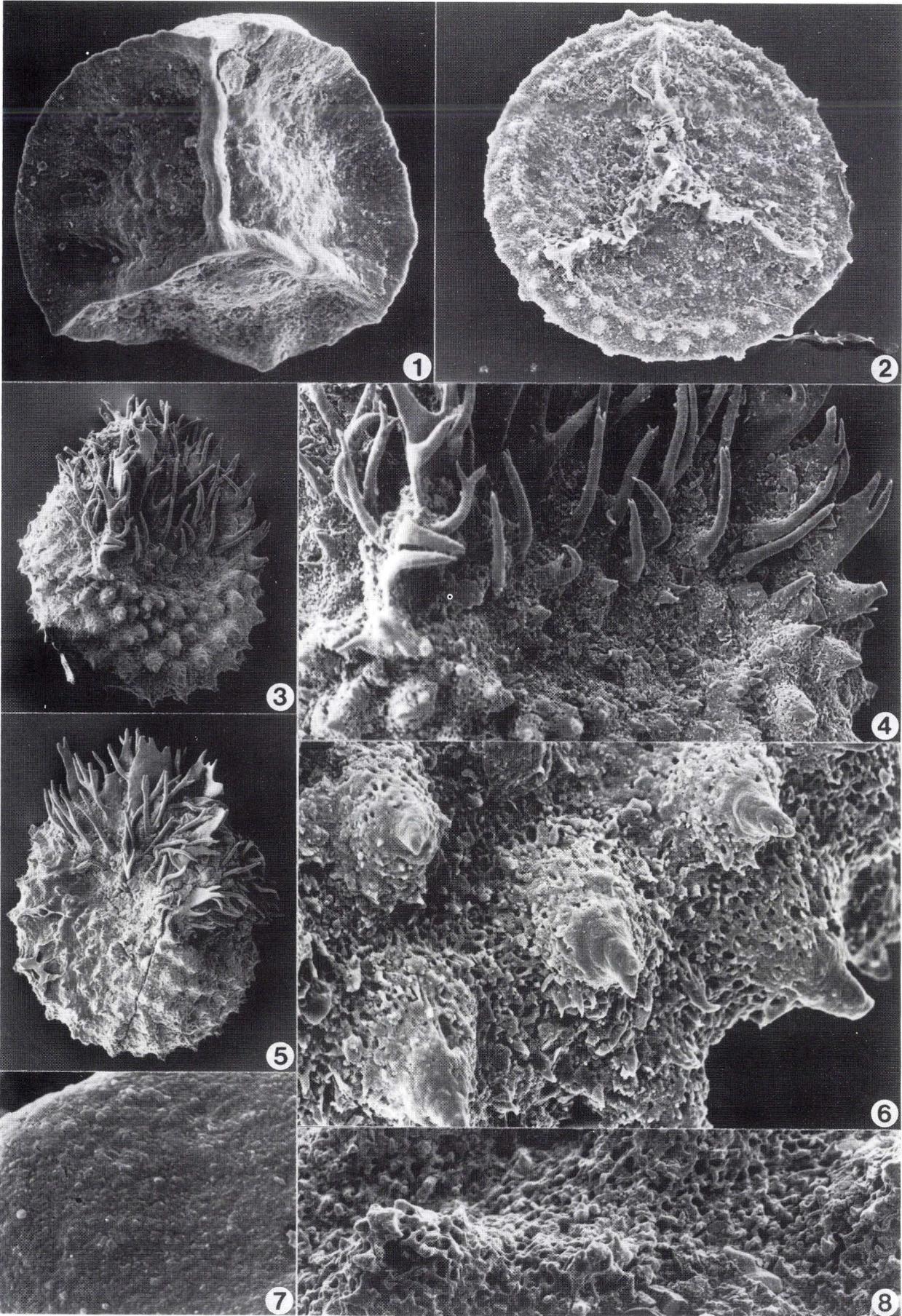
Plate 5

PLATE 6

Figs 1–8, *Henrisporites bornholmensis*; 1, proximal view of specimens from borehole 246.207, Robbedale, ×150. 2, distal view of another specimen from same borehole, ×150. 3, same specimen as in Fig. 1; part of contact area, ×500. 4, proximal view of a third specimen from borehole 246.207, ×160. 5–8, all same broken specimen from borehole 247.131c, Eskegård. 5, proximal view, ×150. 6, section of wall showing spongiose exoexine extending into triradiate flange, and membraneous intexine, ×2000. 7, close-up of contact area, ×500. 8, surface of zona, ×6000.

Plate 6

PLATE 7

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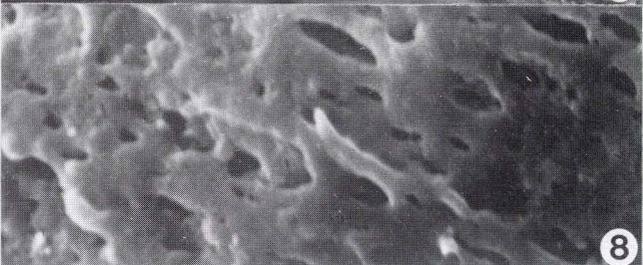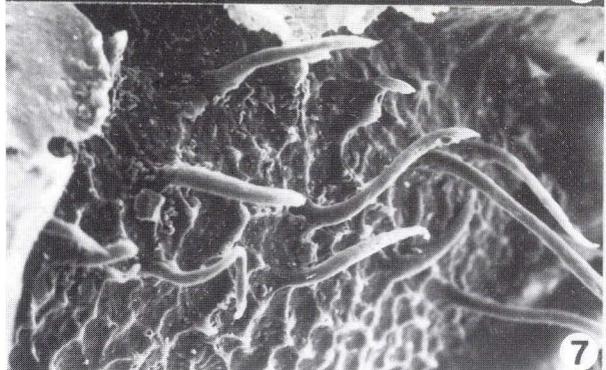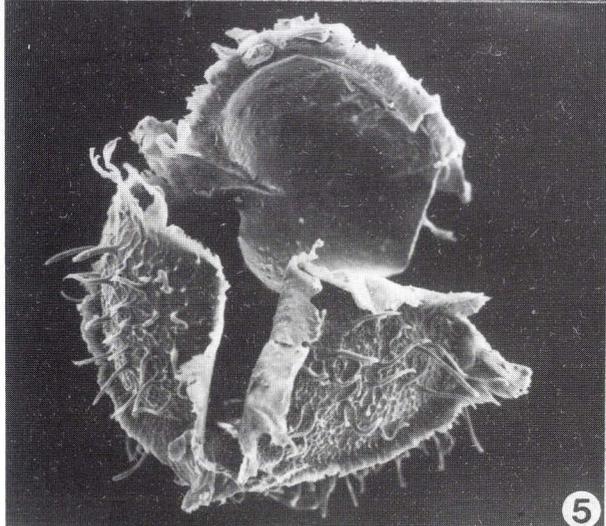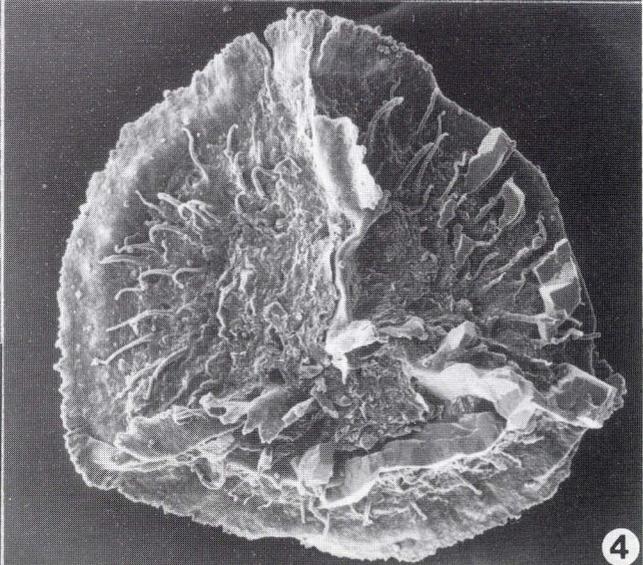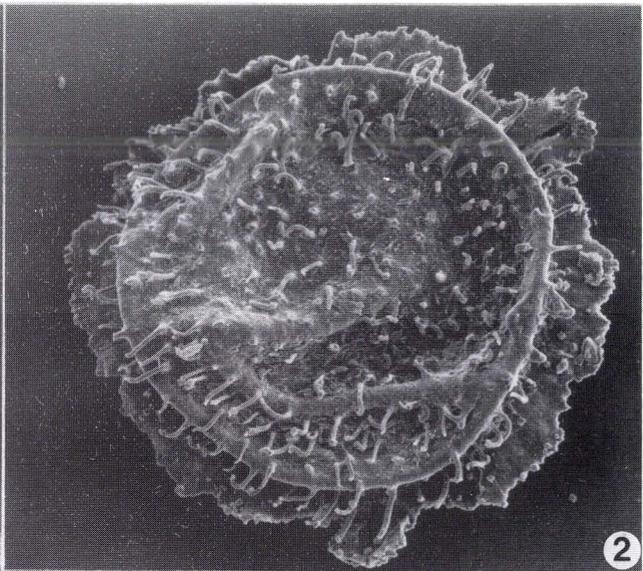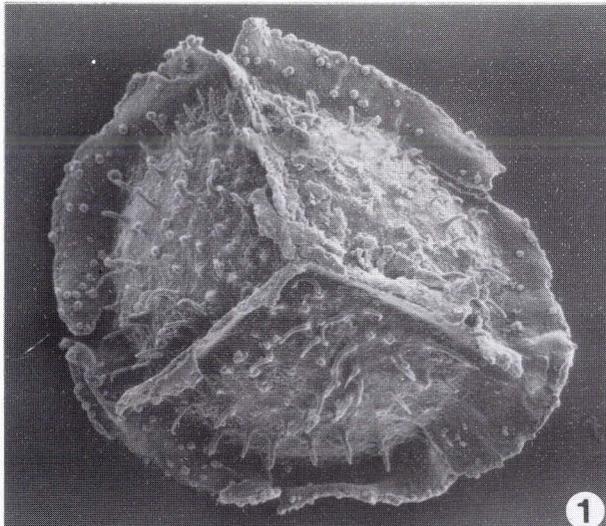
Figs 1–8, *Horstisporites areolatus*. 1, proximal view of spore from Hasle Klinkerfabrik clay pit, ×100. 2, close-up of part of proximal surface of same specimen, ×500. 3, proximal view of another example from Rønne Formation outcrop, ×120. 4, close-up of part of proximal face of same specimen, ×300. 5–8, all same broken specimen from Rønne Formation outcrop, 5, showing thin intexine peeling away from inner surface of exoexine, ×500. 6, close-up of reticulum, ×1000. 7, detail of wall layers, ×1300. 8, inner surface of intexine, ×7500.
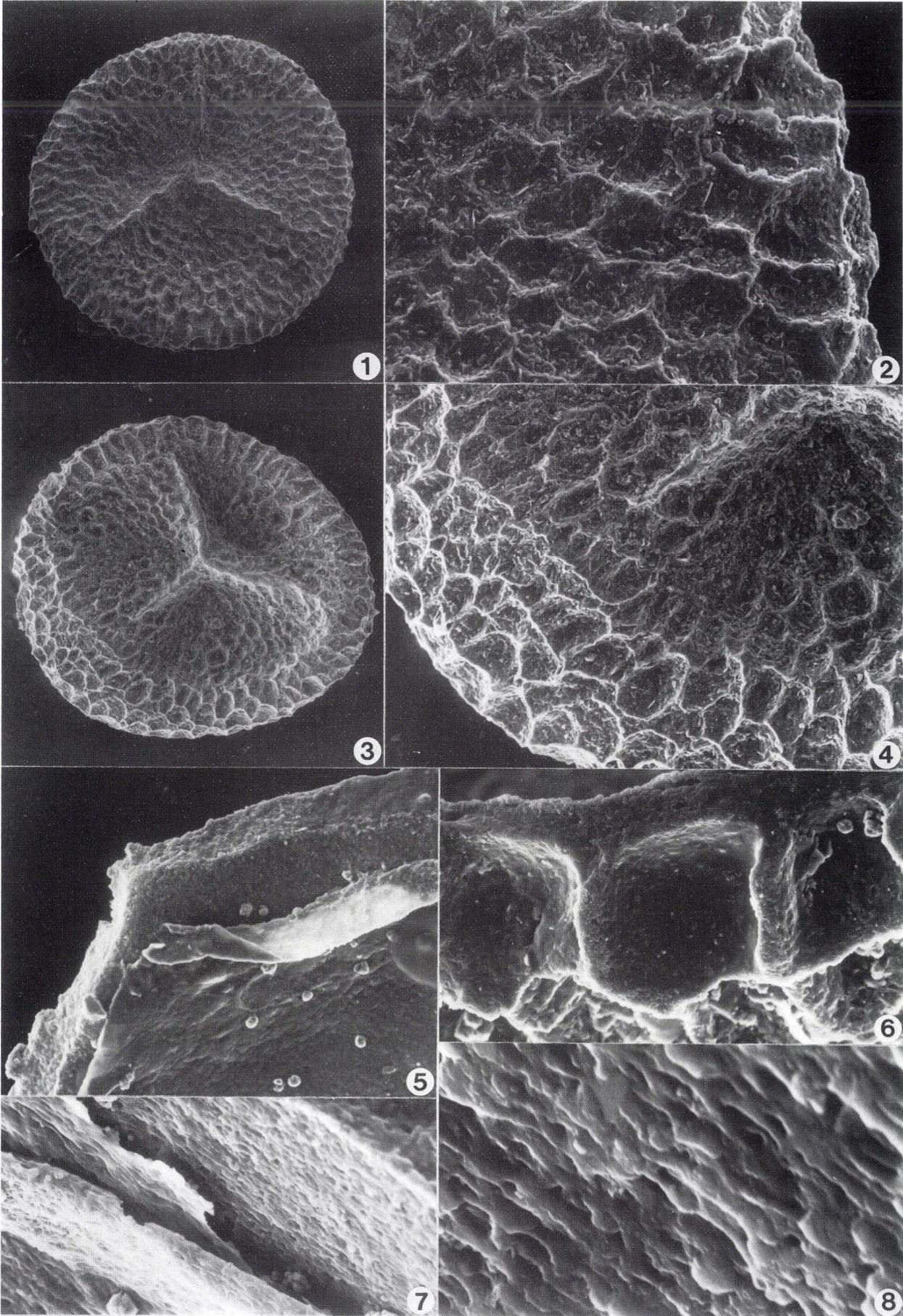
Plate 7

PLATE 8

Fig. 1, *Horstisporites areolatus* from Rønne Formation outcrop, equatorial view, ×140.
Figs 2–8, *Horstisporites harrisii*. 2, oblique-proximal view of spore from borehole 244.83, Hasle Klinkerfabrik clay pit, ×150. 3–5, another example from Munkerup Member outcrop. 3, oblique-proximal view, ×120. 4, close-up of equatorial surface, ×500. 5, sculpture of contact area, ×1000. 6, specimen from Hasle Klinkerfabrik clay pit, ×100. 7, section of wall of broken specimen from Rønne Formation outcrop showing exoexine and intexine, but fragment is dirty; hence structural details are obscured, ×500. 8, close-up of part of contact face and equatorial area of specimen in Fig. 6, ×100.
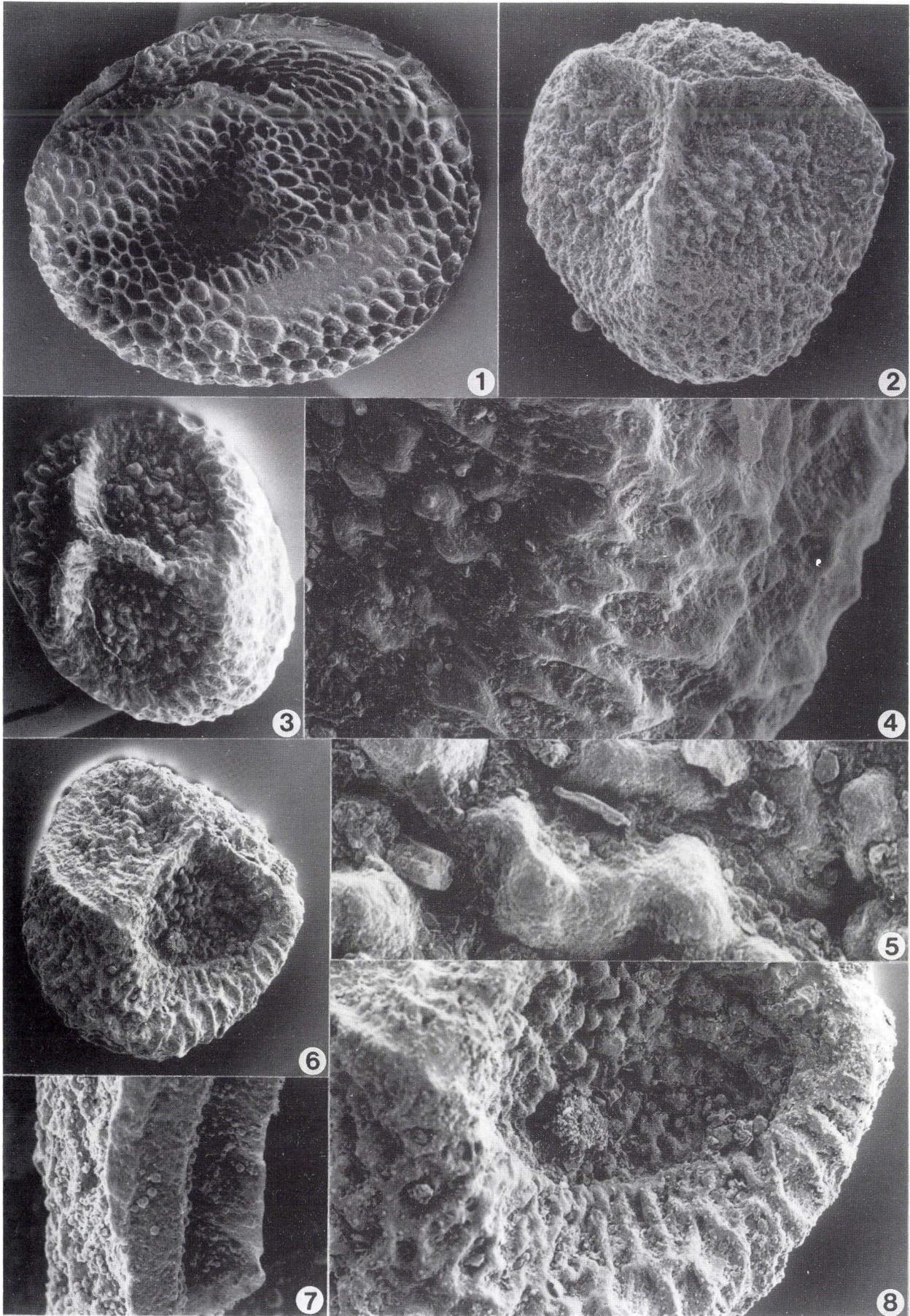
Plate 8

PLATE 9

Figs 1–5, *Horstisporites planatus*. 1–4, all same specimen from Sose Bugt Member outcrop. 1, proximal view, ×200. 2, close-up of contact area, ×400. 3, same as 2 but at higher magnification, ×1600. 4, detail of surface of sculptured exoexine on proximal face, ×5000. 5, apparently granular distal surface of another specimen from same outcrop; at higher magnification it is seen to be reticulate, ×150.

Figs 6–9, *Hughesisporites galericulatus*, all same specimen from borehole 246.307a, Skyttegård. 6, proximal view, ×200. 7, close-up of part of triradiate ridge and adjacent appendages, ×550. 8, close-up of proximal surface away from triradiate area, ×2000. 9, as for 8, detail, ×5000.
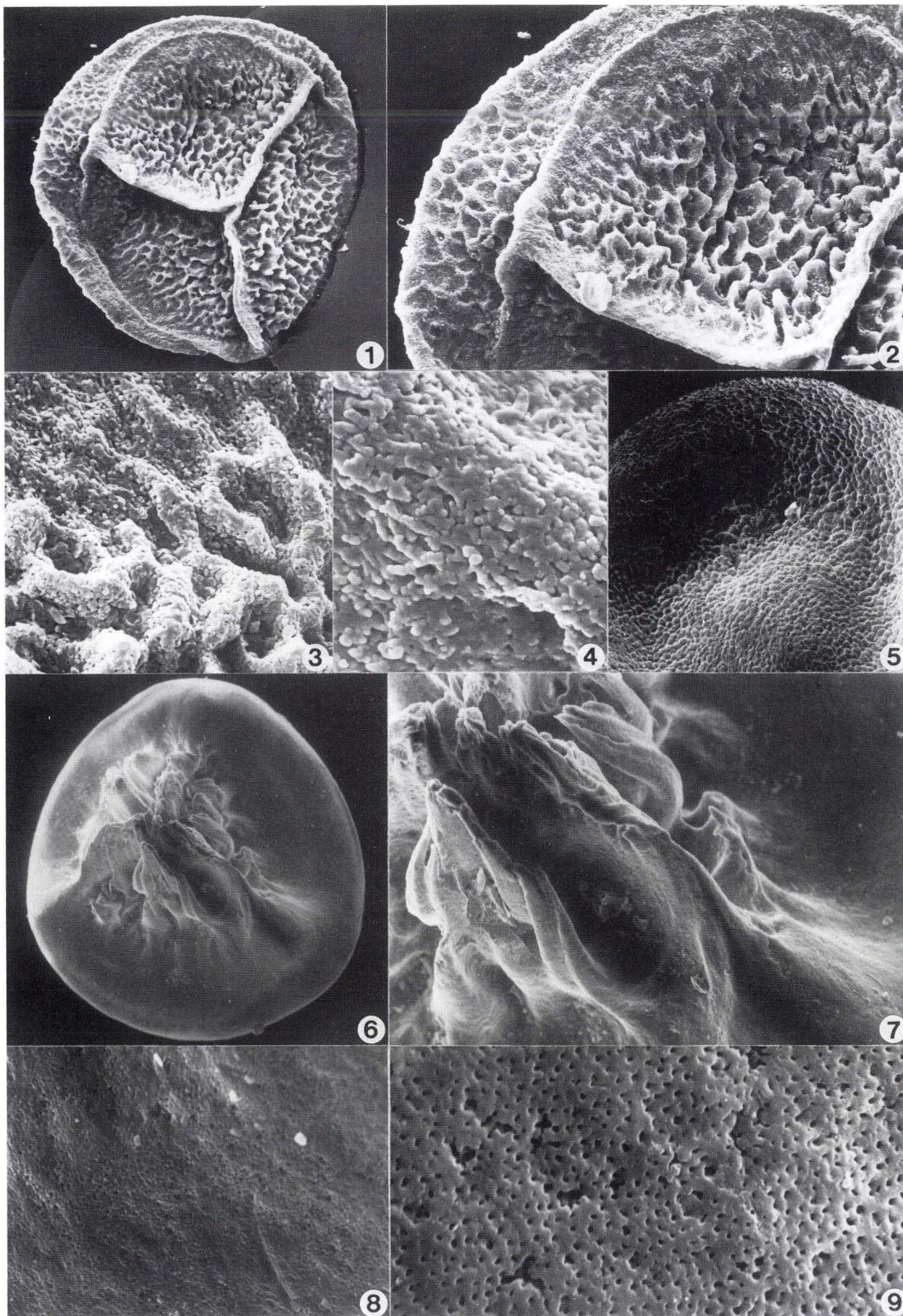
Plate 9

PLATE 10

Figs 1, 3, *Hughesisporites galericulatus* from Skyttegård outcrop. 1, specimen broken in half, ×250. 3, cross-section of distal exoexine, ×2000.

Figs 2, 4–8, *Hughesisporites variabilis* from borehole 244.105, Hasle Klinkerfabrik clay pit. 2, 4, 6, same specimen. 2, proximal view, ×100; for reflected light photograph of same specimen, see Pl. 20, fig. 17. 4, close-up of triradiate ridge and rugulate sculpture of adjacent proximal face, ×500. 6, surface of exoexine of proximal face close to equator, ×5000. 5, 7, 8, another specimen from same borehole. 5, proximal view, ×100. 7, detail of equatorial surface area; reticulation of surface partly plugged with extraneous matter, ×5000. 8, detail of surface of triradiate ridge, similarly affected by particulate detritus, ×5000.
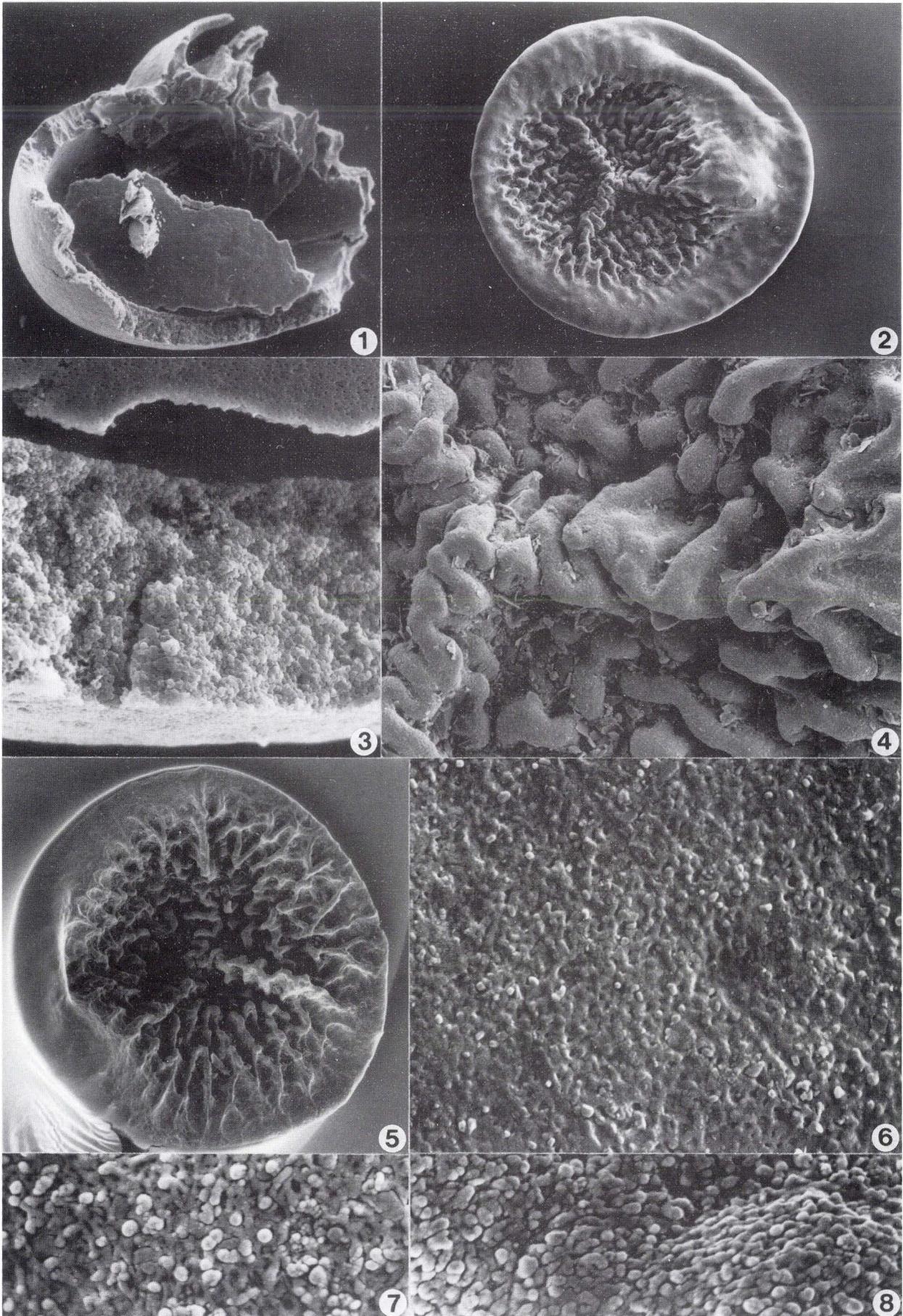
Plate 10

PLATE 11

Figs 1, 2, *Maexisporites* sp. cf. *M. misellus*, specimen from Hasle Klinkerfabrik clay pit. 1, proximal view, ×200. 2, detail of sculptured surface, ×7500.
Figs 3–8, *Maexisporites soldanellus*. 3, 4, 7, same specimen from Hasle Klinkerfabrik clay pit. 3, proximal view, ×100. 4, close-up of triradiate ridge and part of adjacent proximal face, ×400. 7, part of ridge at slightly higher magnification, ×500. 5, 6, fragment from Hasle Klinkerfabrik clay pit. 5, cross-section of exoexine showing closely spaced rods of sporopollenin which give wall a granular appearance, ×10000. 6, reticulate outer surface of exoexine, ×10000. 8, lateral view of another specimen from borehole 244.83, Hasle Klinkerfabrik clay pit, ×200.
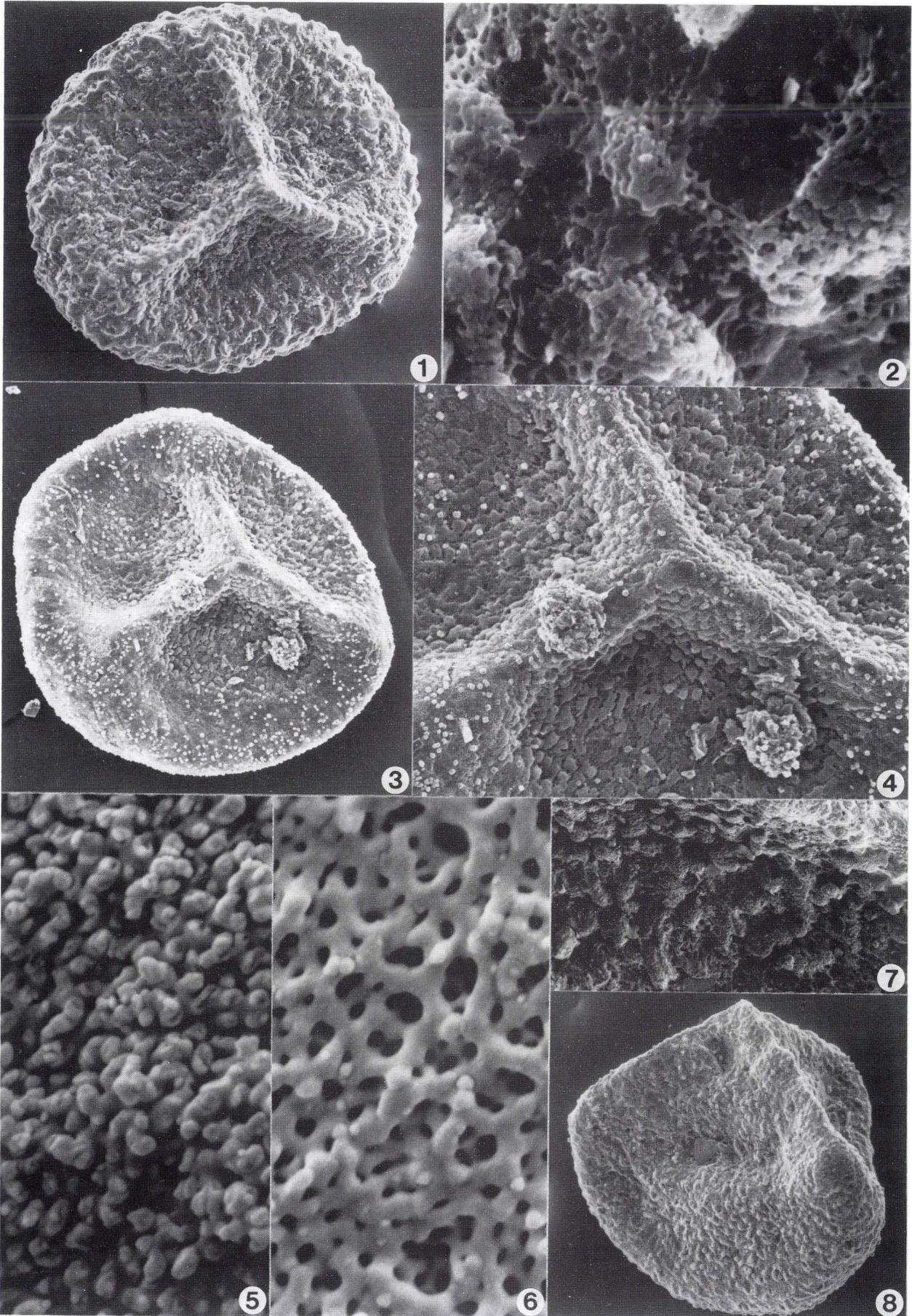
Plate 11

PLATE 12

Figs 1, 2, *Minerisporites marginatus*. 1, oblique-lateral view of damaged spore from Eskegård outcrop, ×200. 2, close-up of proximal surface of same specimen, ×2500.

Figs 3, 4, *Minerisporites* sp. cf. *M. marginatus*, same specimen from borehole 247.130f, Eskegård. 3, proximal view, ×200. 4, close-up of part of triradiate ridge, zona and proximal surface, ×700.

Figs 5–8, *Minerisporites richardsonii*. 5, oblique-proximal view of spore from borehole 244.105, Hasle Klinkerfabrik clay pit, ×150. 6, close-up of surface of same specimen, ×2000. 7, lateral view of another specimen, Hasle Klinkerfabrik clay pit, ×200. 8, lateral view of a third specimen, Hasle Klinkerfabrik, ×150.
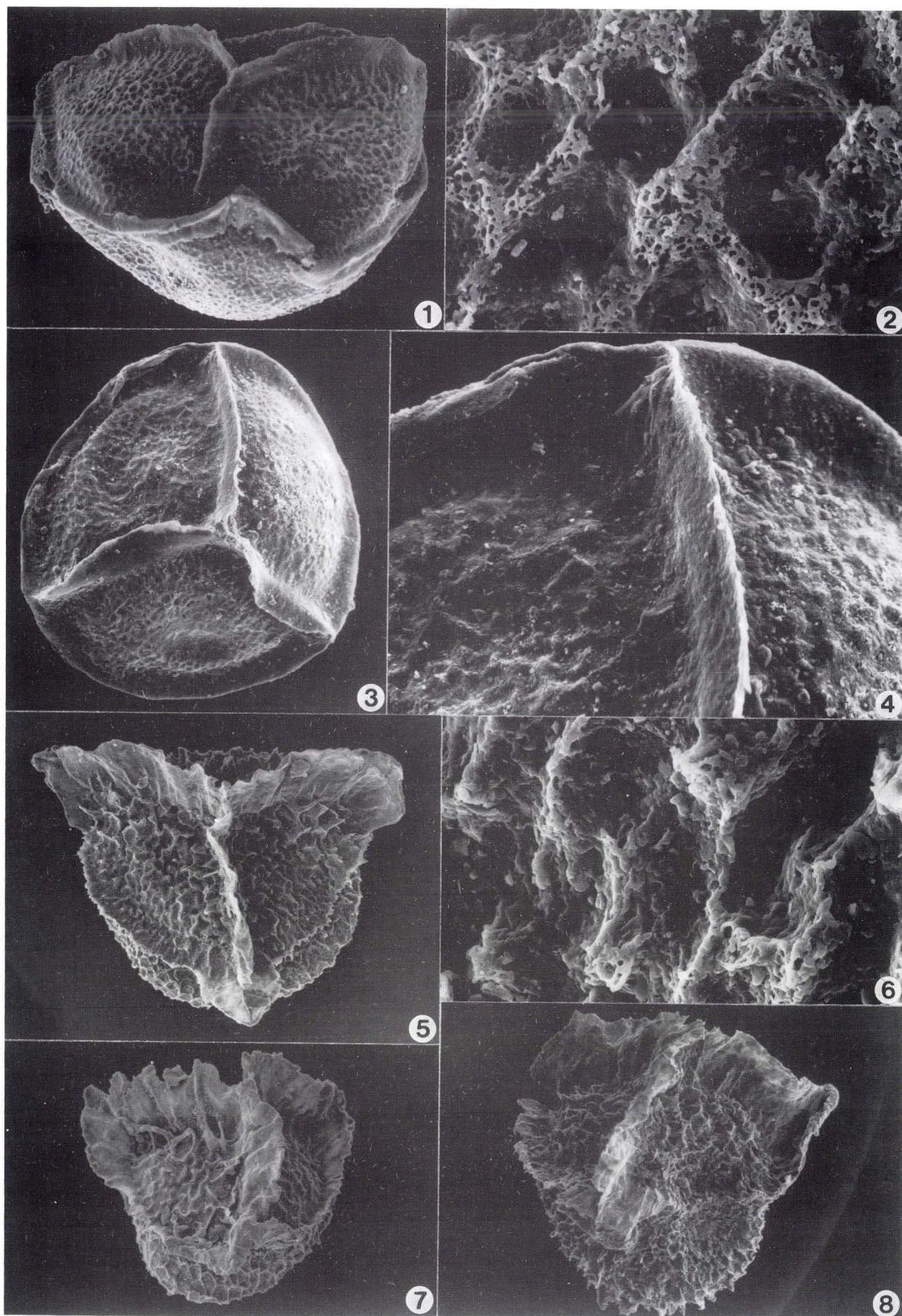
Plate 12

PLATE 13

Fig. 1, *Minerisporites richardsonii* from Hasle Klinkerfabrik clay pit, proximal view, ×150.

Figs 2–5, 7, 8, *Minerisporites volucris*. 2–4, 8, all same specimen from borehole 244.105, Hasle Klinkerfabrik clay pit. 2, part of triradiate flange and proximal face showing spinose sculpture, ×400. 3, equatorial view of laterally compressed specimen, ×140. 4, part of distal surface showing closely spaced spines, ×400. 8, close-up of auriculate development of zona, ×500. 5,7, another specimen from same borehole. 5, lateral view, ×150. 7, close-up of flattened spinose elements of distal sculpture, ×1000.

Fig. 6, *Minerisporites* sp. from borehole 247.130f, Eskegård, proximal view, ×200.
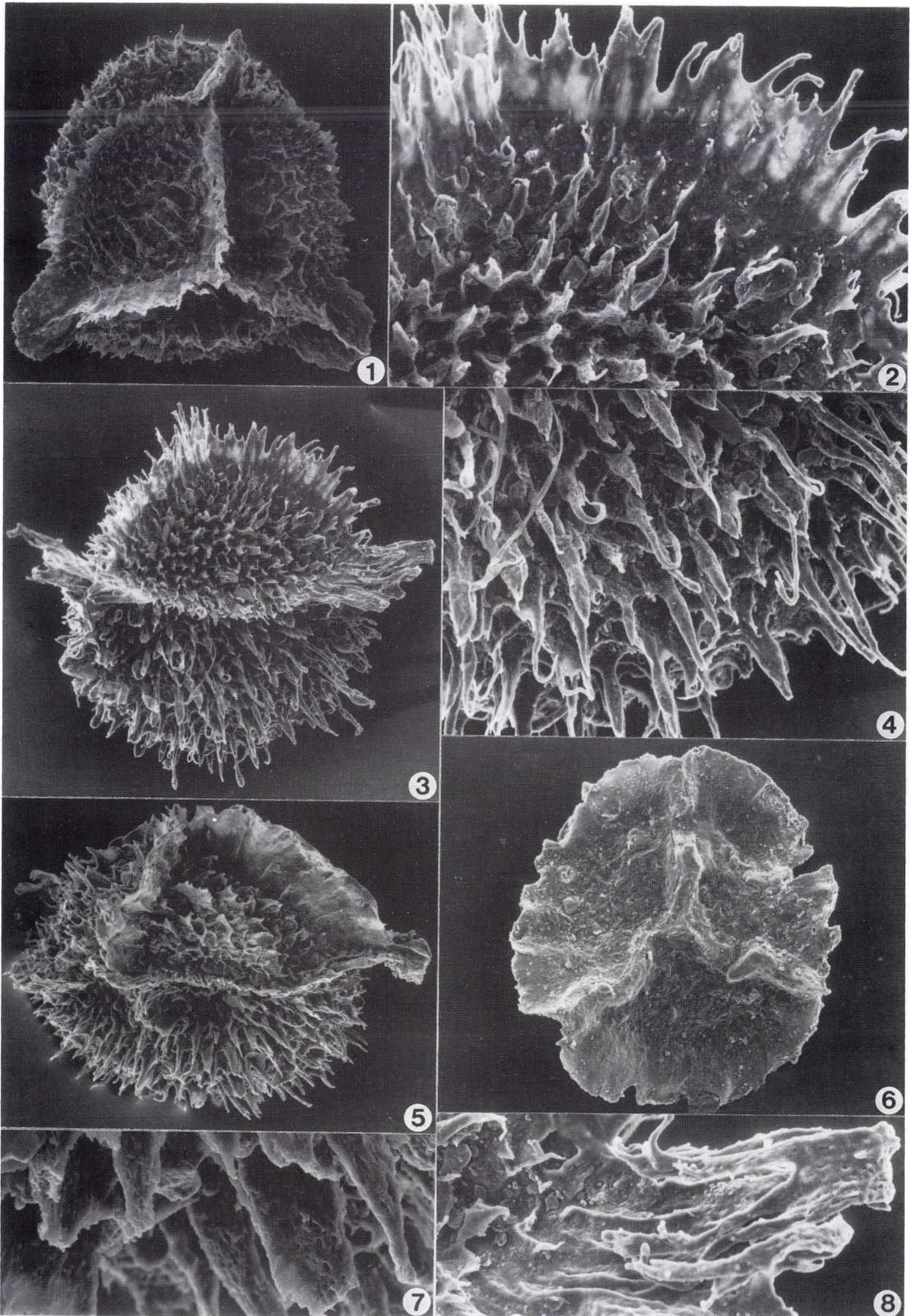
Plate 13

PLATE 14

Fig. 1, *Minerisporites* sp. from borehole 247.130f, Eskegård, proximal view, ×300.

Figs 2–8, *Nathorstisporites hopliticus*, all from Munkerup Member outcrop. 2, proximal view of very degraded specimen, ×150. 3, 4, 6–8, all same specimen from Munkerup Member outcrop. 3, equatorial view, ×100. 4, close-up of part of equatorial region and proximal surface, ×300. 6, close-up of part of distal surface, ×750. 7, close-up of part of scabrate, homogeneous surface of proximal appendage, ×2500. 8, close-up of subequatorial part of proximal surface, ×1000. 5, lateral view of another specimen from same locality, ×100.
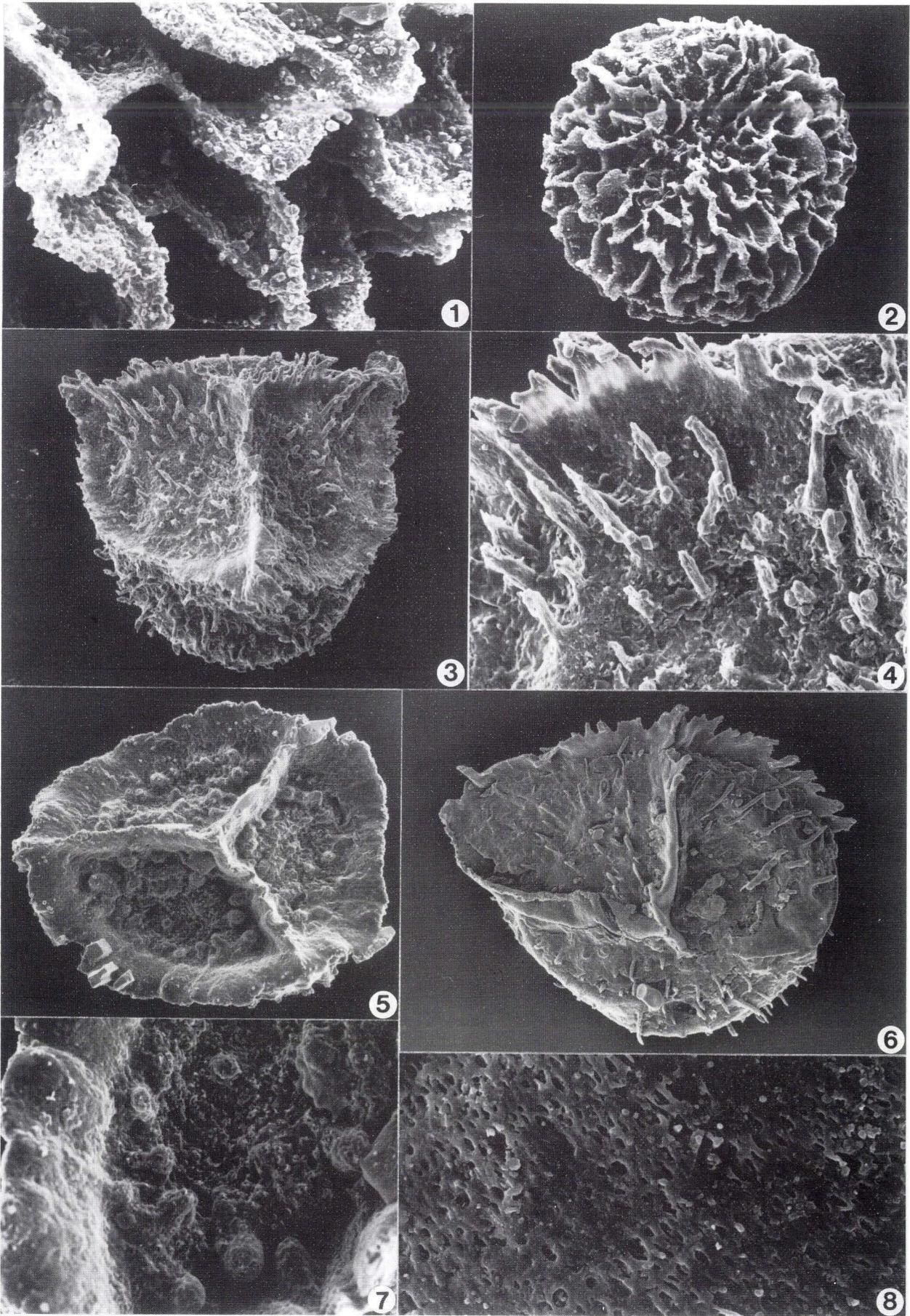
Plate 14

PLATE 15

Figs 1–8. *Paxillitriletes kristinae*. 1, proximal view of spore from borehole 244.232, Bakkegård, ×140. 2, close-up of processes adjacent to, and comprising part of, triradiate flange of same specimen, ×400. 3, close-up of zona of second spore, Skyttegård outcrop, ×1500. 4, part of proximal face of same specimen with broken appendages adjacent to triradiate flange, ×330. 5, part of broken specimen from borehole 246.307a in cross-section showing membraneous intexine beneath much thicker, spongiose exoexine, ×1000. 6, cross-section of exoexine of another fragment underlain by a closely adhering membraneous intexine, Skyttegård outcrop, ×2000. 7, proximal view of specimen from borehole 246.207, Robbedale, ×150. 8, sculpture of proximal surface of same specimen as fig. 4, ×1500.
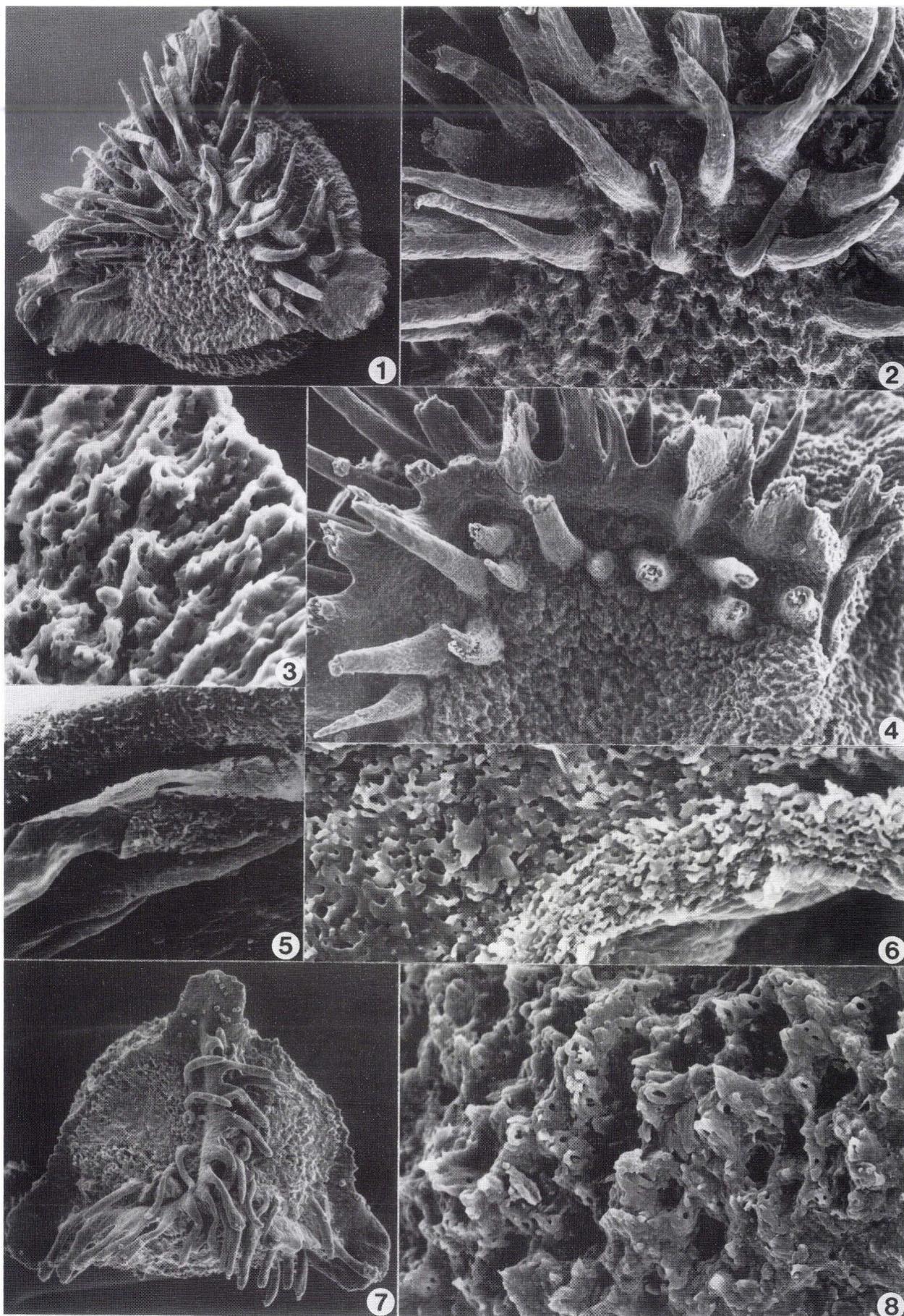
Plate 15

PLATE 16

Fig. 1, *Paxillitriletes kristinae*, oblique-lateral view of specimen from borehole 244.232, Bakkegård, ×140.

Figs 2–4, *Paxillitriletes phyllicus*, all same specimen from Skyttegård outcrop. 2, lateral view, ×220. 3, proximal sculpture, ×1000. 4, part of proximal face showing triradiate flange, adjacent membraneous processes and reticulum, ×400.

Figs 5–7, *Paxillitriletes* sp. cf. *P. reticulatus* from borehole 246.307a, Skyttegård. 5, lateral view, ×250. 6, close-up of part of proximal sculpture and membraneous elevations adjacent to triradiate flange, ×500. 7, detail of proximal reticulum showing spongiose exoexine, ×2000.
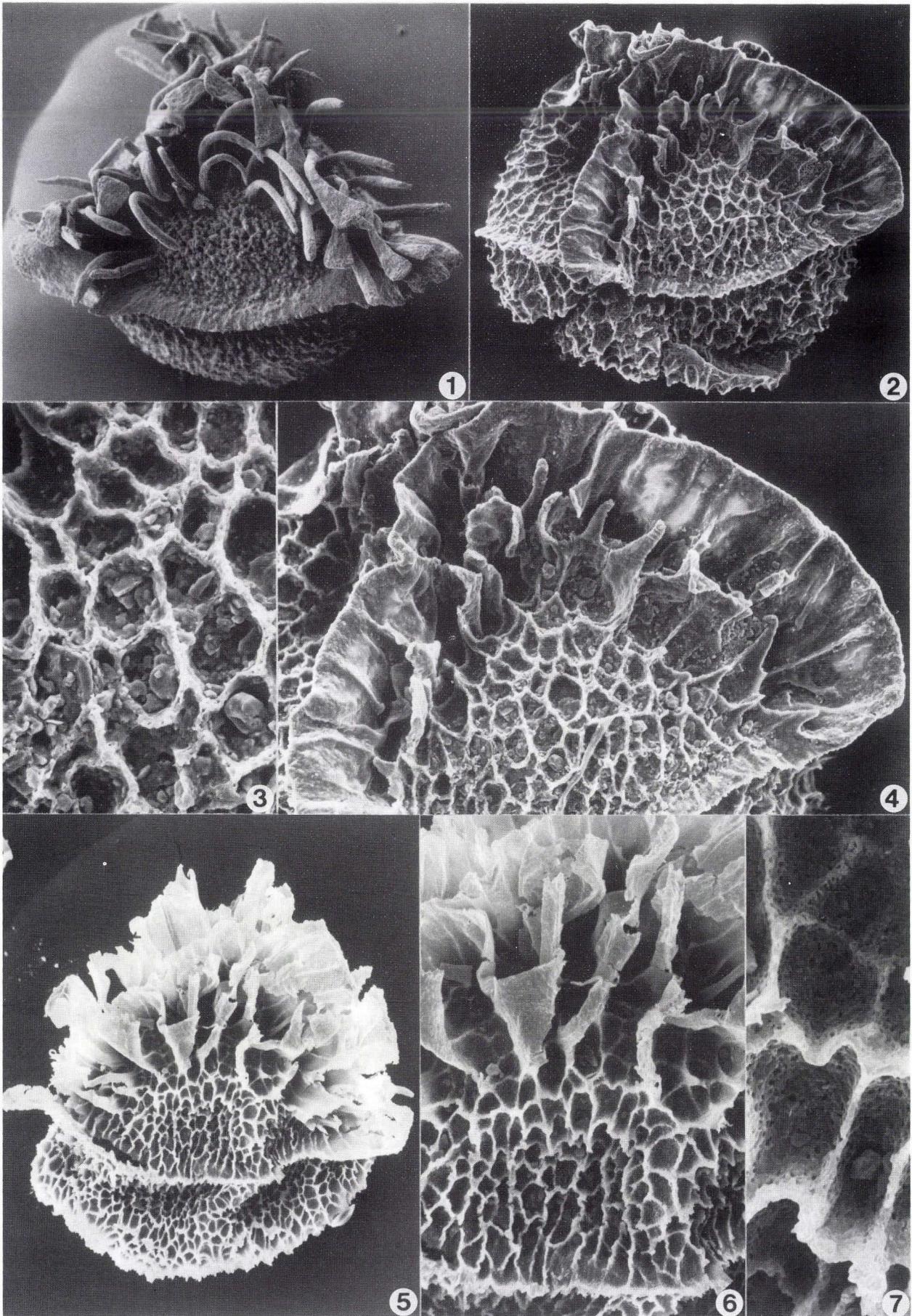
Plate 16

PLATE 17

Figs 1–3, *Paxillitriletes* sp. cf. *P. reticulatus*, all same specimen, from borehole 246.307a, Skyttegård. 1, lateral view, ×170. 2, part of ribbed triradiate flange, ×1000. 3, reticulate sculpture on distal surface, detail, ×3000.

Fig. 4, *Paxillitriletes* sp.1 from Skyttegård outcrop, oblique-lateral view, ×200.

Figs 5–7, *Paxillitriletes* sp. 2, all same specimen from Hasle Klinkerfabrik clay pit. 5, oblique-proximal view, ×250. 6, part of zona and appendages adjacent to triradiate flange, ×2000. 7, close-up of rugulate sculpture on proximal face, ×1000.

Fig. 8, *Paxillitriletes* sp. 3 from Vellengsby outcrop, proximal view, ×150.

Fig. 9, *Striatriletes sulcatus* from borehole 244.83, Hasle Klinkerfabrik clay pit, oblique-proximal view, ×200.
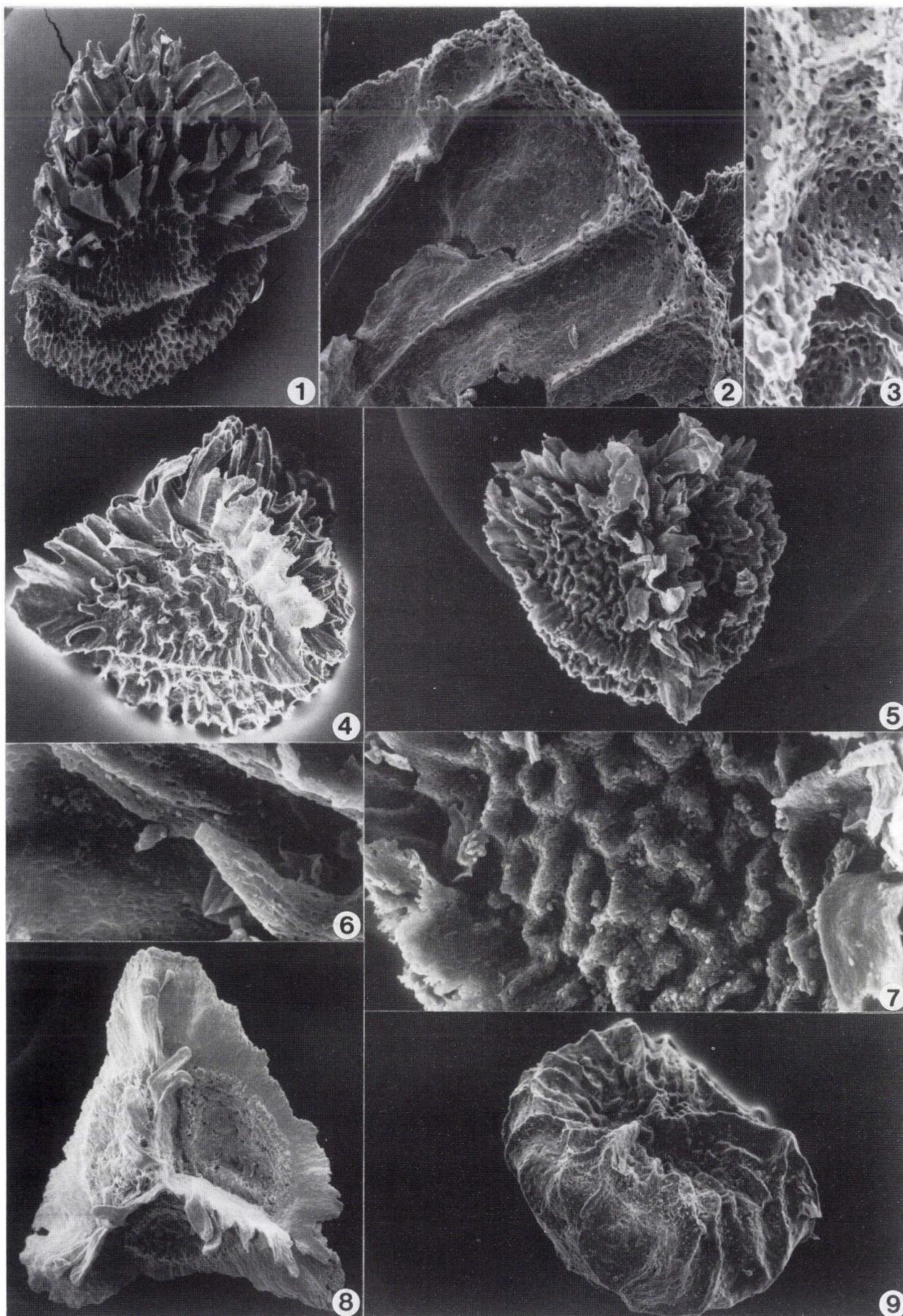
Plate 17

PLATE 18

Figs 1–8, *Paxillitriletes rasmusii*. 1–4, all same specimen from Skyttegård outcrop. 1, proximal view, ×100. 2, close-up of part of proximal face showing triradiate flange, sculpture of contact area and zona, ×250. 3, proximal sculpture at higher magnification, ×1000. 4, detail of outer surface of exoexine, ×5000. 5–8, second specimen, Skyttegård outcrop. 5, equatorial view, ×120. 6, surface of auricula, ×400. 7, distal surface beneath zona, ×400. 8, close-up of spinose sculpture of proximal face, ×400.
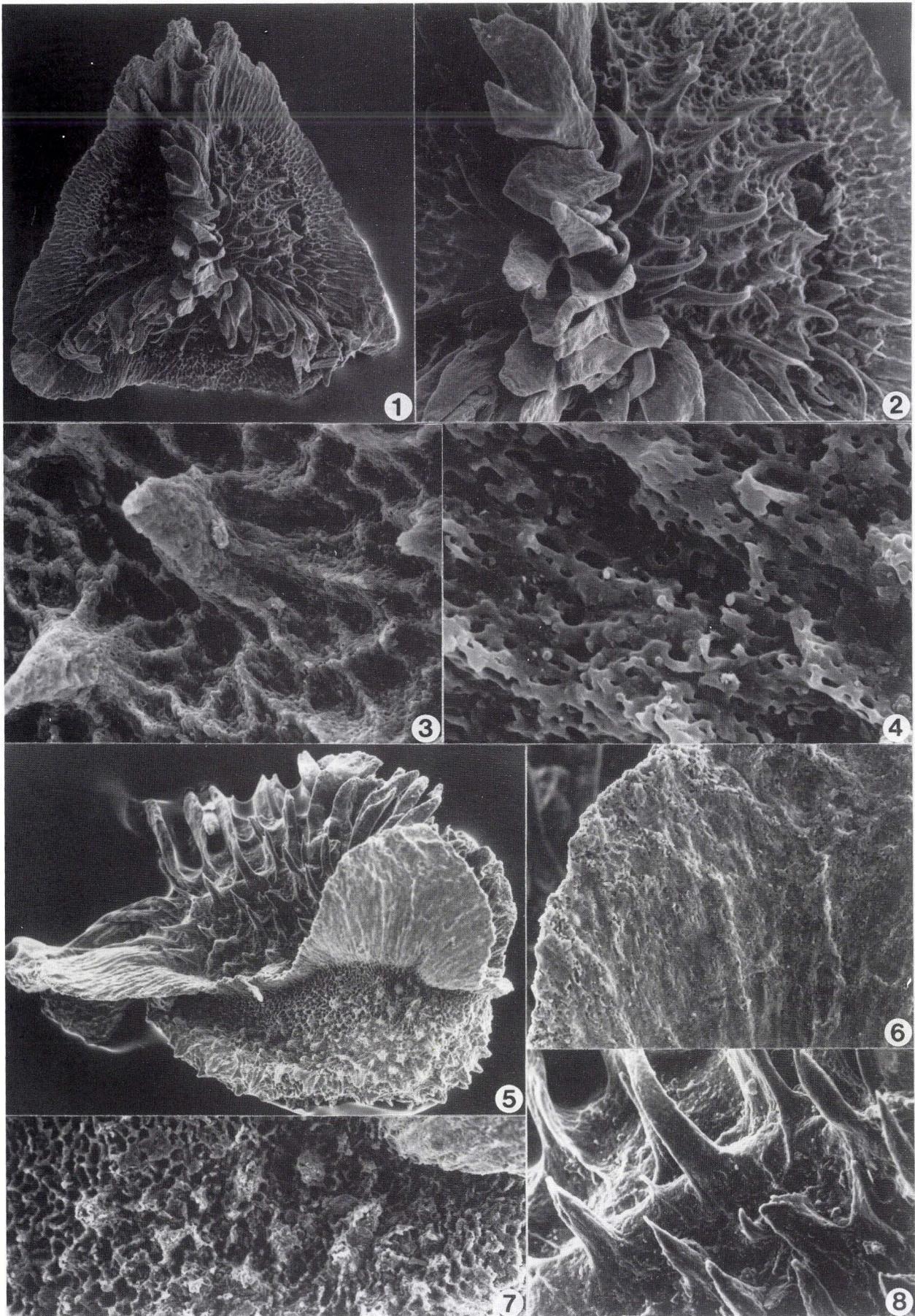
Plate 18

PLATE 19

Figs 1–3, *Trileites candoris,* broken specimen from Hasle Klinkerfabrik clay pit. 1, proximal view, ×100. 2, perforated outer surface of exoexine of contact area, ×3000. 3, transverse section of exoexine, ×3000.
Fig. 4, *Trileites murrayi* from borehole 247.131, Eskegård, proximal view, ×270.
Figs 5–8, *Verrutriletes franconicus.* 5, oblique-lateral view of spore from Sose Bugt outcrop, ×300. 6, oblique view of another specimen from same locality, ×300. 7, close-up of wall adjacent to triradiate ridge, ×1000. 8, surface detail, ×5000.

Plate 19
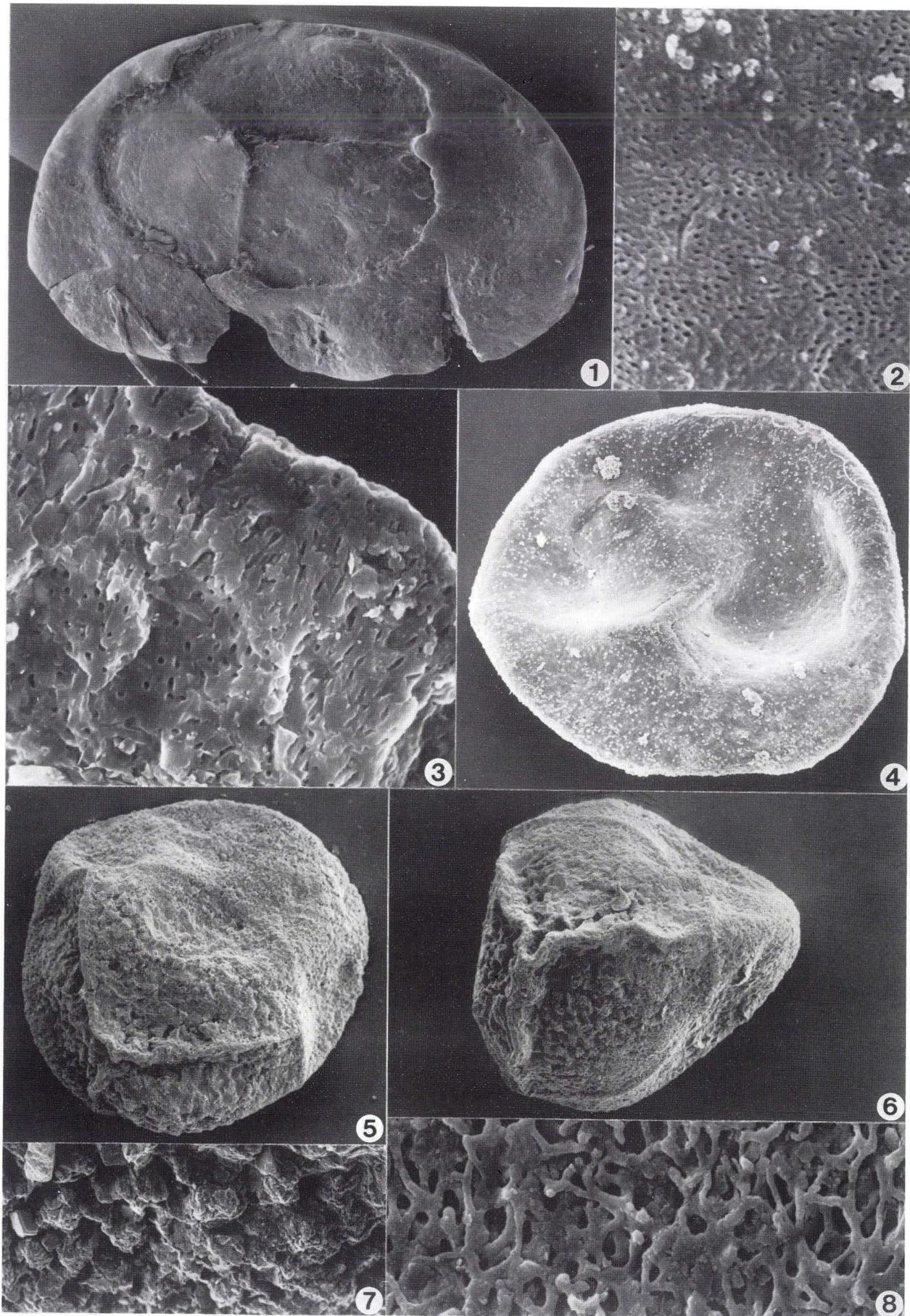
PLATE 20

Except where otherwise indicated, all magnifications *c.* ×75. All specimens are stored in slides labelled according to name of taxon, plate and figure references below.

Fig. 1, *Aneuletes patera*

Fig. 2, *Aneuletes discus*, holotype, HGHol/1: for details, see systematics section

Fig. 3, *Bacutriletes* sp. cf. *B. clavatus*

Fig. 4, *Bacutriletes corynactis*

Figs 5, 6, *Cabochonicus carbunculus*

Fig. 7, *Echitriletes hispidus*

Fig. 8, *Echitriletes lanatus*

Figs 9, 10, *Erlansonisporites sparassis*

Figs 11, 12, *Horstisporites areolatus*, same specimen; 11, proximal face, 12 distal face; both ×50

Fig. 13, *Horstisporites harrisii*

Figs 14–16, *Horstisporites planatus*; 14 & 15, ×100; 16, ×250

Fig. 17, *Hughesisporites variabilis*

Fig. 18, *Hughesisporites galericulatus*

Figs 19, 20, *Henrisporites bornholmensis*; 19 is holotype, HGHol/2: for details, see systematics section
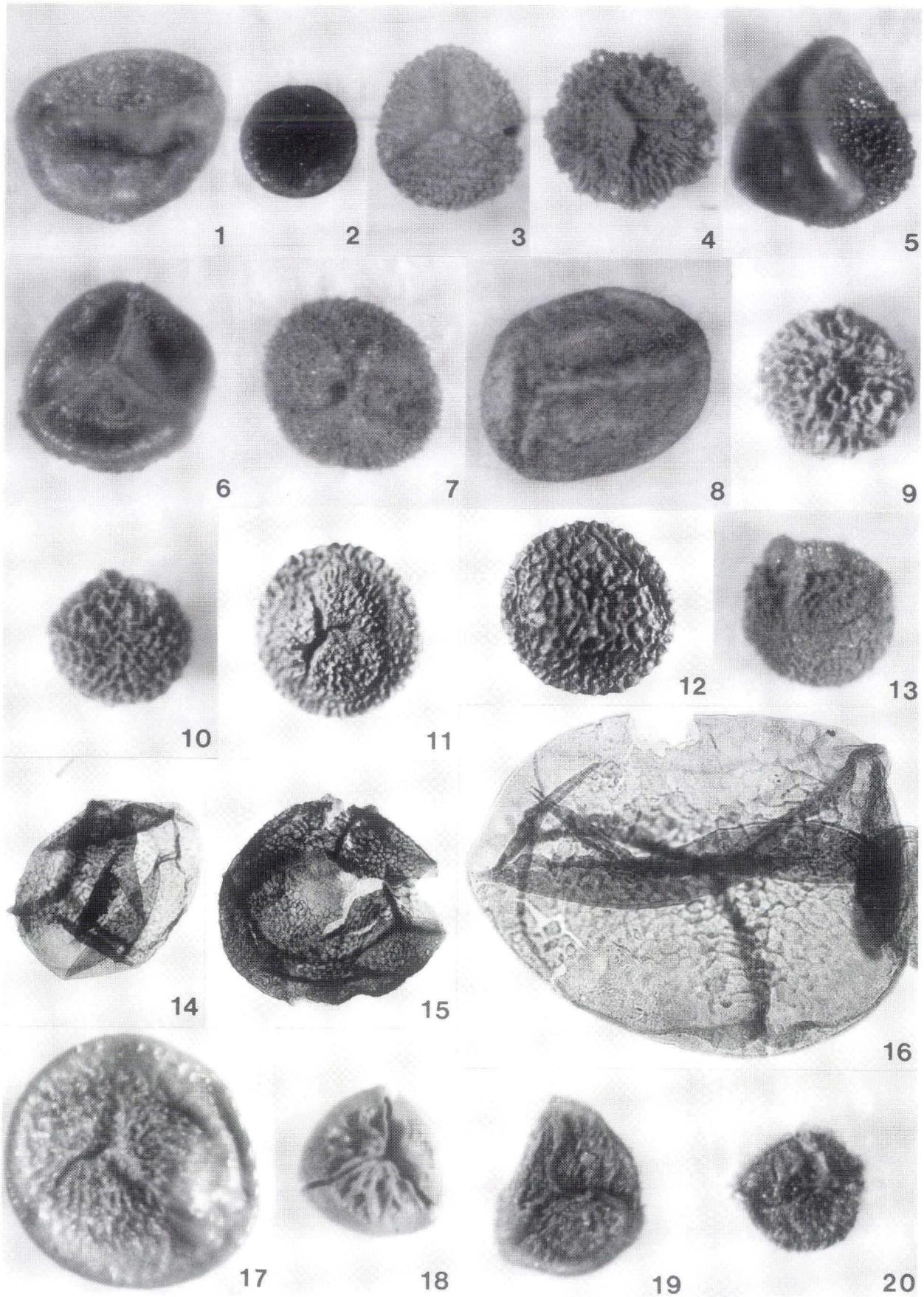
Plate 20

PLATE 21

Except where indicated, all magnifications *c.* ×75. All specimens are stored separately in slides labelled according to name of taxon, plate and figure references below.

Figs 1, 2, *Maexisporites soldanellus*

Figs 3, 4, *Minerisporites marginatus*

Fig. 5, *Minerisporites richardsonii*

Fig. 6, *Minerisporites volucris*

Fig. 7, *Nathorstisporites hopliticus*

Fig. 8, *Paxillitriletes kristinae*, holotype, HGHol/3: for details, see systematics section

Figs 9, 13, *Paxillitriletes phyllicus*

Figs 10, 11, *Paxillitriletes* sp. 3

Figs 12, 18, *Paxillitriletes rasmusii*; 12, *c.* ×37.5; 18 is holotype, HGHol/4: for details see systematics section

Fig. 14, *Paxillitriletes* sp. cf. *P. reticulatus*

Fig. 15, Three specimens of *Trileites candoris, c.* ×37.5

Fig. 16, *Striatriletes sulcatus*

Fig. 17, *Verrutriletes franconicus*

Fig. 19, Five specimens of *Trileites murrayi,* ×37.5

Plate 21
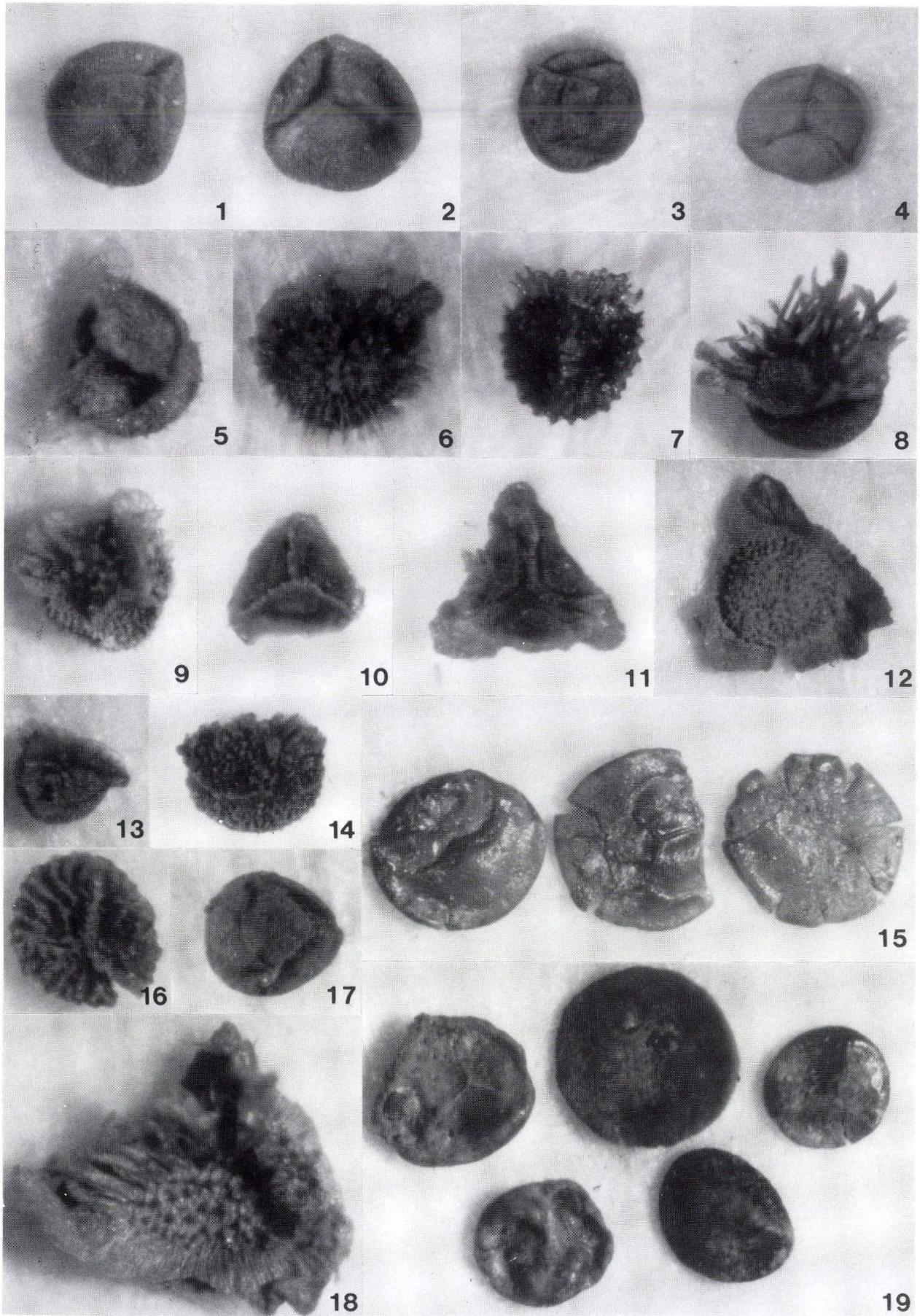
This paper presents a detailed systematic treatment of megaspores in Helge Gry's plant microfossil collection from the Jurassic and lowermost Cretaceous of Bornholm, Denmark. Thirty-seven taxa, four of which are new, are described and illustrated. Their botanical affinities and biostratigraphic potential are discussed.