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The morphology and taxonomy of species of the diatom genus *Asteromphalus* Ehr.

by

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with 33 plates and 3 tables

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INTRODUCTION.

1. General.

The diatom genus Asteromphalus is found frequently in the marine plankton around the world. Asteromphalus species are solely marine and mostly truly planktonic.

Some morphological studies have involved species of Asteromphalus, but few details have been shown and no study has been devoted to this genus. Furthermore, many species are commonly misidentified in routine plankton examinations, because identification is not always easy. One of the most characteristic features in Asteromphalus is the presence of hyaline rays radiating from a central hyaline area; this character is shared with other genera of the family Asterolampraceae, most of them now extinct. The systematics of Asteromphalus is mainly based on these rays and the central area, but both characters may vary in some species. Thus, a study of this genus is necessary.

This paper provides an investigation of the morphology and taxonomy of species of Asteromphalus, collected in several areas, especially from tropical and subtropical regions, in order to contribute to a partial revision and find common features and establish possible taxonomic relations within the genus.

2. Historic background and early treatments.

The genus Asteromphalus was erected by Ehrenberg (1844), with the description of seven species, A. darwinii Ehr. being the type species. Following Van Landingham (1967), only three of those species described are considered to be valid: A. darwinii, p. hookeri Ehr. and A. beaumontii Ehr., as four are considered to be synonyms. Since 1844, some other closely related genera have been created: Spatangidium Brébisson (Brébisson, 1857), Excentron Ralfs (Ralfs in Pritchard, 1861), Actinogramma Ehrenberg (Ehrenberg, 1872), Mesasterias Ehrenberg (Ehrenberg, 1872), and Liriogramma Kolbe, all of them now considered to be synonyms of Asteromphalus (Hustedt, 1930; Van Landingham, 1967; Thorrington-Smith, 1970).

After the early description of Asteromphalus species by Ehrenberg, many new species have been discovered and described. The following is an account of the history of the genus, but it is not exhaustive. Bailey (1856) included a new species, A. brookei Bail. in his paper on microscopic forms; Brébisson (1857) described four species (only three are now valid) under the genus Spatangidium; Greville (1859) described one new species, and in 1860 (Greville, 1860) attempted the first monograph of Asteromphalus (included in lsterolampra Ehr.), describing further new species. Wallich (1860) also described new species from the Indian Ocean; Ralfs (in Pritchard, 1861) proposed new combinations for many species originally described as Spatangidium and Asterolampra. Grunow (1870) described a very particular species: A. Pankoorensis Grunow; Castracane (1875, 1886) contributed new species, mainly from antarctic waters. Rattray (1889) made the second major revision within Asteromphalus, although he did not include some of the new species recently described by Castracane in 1886. In Schmidt's (1876-1899) Atlas of Diatoms, twelve species, including only one new are illustrated. Later, in 1905 Karsten (1905) found a number of Asteromphalus species, involving some new species. Further new species have been described by Mann (1907, 1937). Hustedt (1930) only dealt with four species in his large book on Centrales, and Mills (1933, cited by Van Landingham, 1967) listed 35 Asteromphalus species. Van Landingham's (1967) catalogue includes 41 valid species. Thorrington-Smith (1970) proposed two new combinations for species described as Liriogramma, and Simonsen (1974) gave the description of a new species, A. ingens, from the Indian Ocean.

Recent studies using electron microscopy were probably pioneered by Okuno (1951), who used mainly the transmission electron microscopy (TEM), but his observations on Asteromphalus show few details. Later, Helmcke & Krieger (1954) showed further observations on Asteromphalus species. However, from the supposed three species studied by electron microscopy listed by Desikachary (1956) and Hendey (1959), one had been misidentified (A. hooker] instead of A. heptactis (Bréb.) Ralfs, in Okuno, 1951), so by 1959, just two species, A. hookeri and A. humboldtii Ehr. had been so far studied. Geissler et al., 1961) provided further details of A. hookeri, and in 1964 Okuno (1964) included in his work on fossil diatoms some TEM observations on one Asteromphalus species, being one again misidentified as A. heptactis rather than A. darwinii.

In 1972 Hasle (1972) introduced some scanning electron microscopy (SEM) observations on one species of Asteromphalus which was not named, but it appears to be A. hookeri, when she was studying the rimoportulae in some diatoms. Fryxell & Hasle (1973) and Ross & Sims (1973) added new observations on Asteromphalus, showing general characteristics in relation to other genera in the Centrales. More recently, Gombos (1980) dealt with genera and species of the family Asterolampraceae, without including observations of Asteromphalus, but discussing relations within the family with comments on Asteromphalus. No more attempts have been made to study this genus.

3. Taxonomic relationships.

The genus Asteromphalus is currently included in the family Asterolampraceae, where Asterolamprd is a very closely related genus, being described earlier than Asteromphalus; both genera are extant. In the family Asterolampraceae are also included three other genera now extinct: Rvlandsia Grev., Bergonia Temp. and Discodiscus Gombos (Gombos, 1980). However, recent studies made by the author (to be published soon) appear to confirm the validity of the genus Spatanqidium, containing at the moment (pending further investigations) just one species: Spatangidium arachne Brébisson.

The fact that Asterolampra is the most closely realted genus to Asteromphalus is evident in some extant species like Asterolampra liarvlandica Ehr., and A. arevillei (Wall.) Grev. in relation to, for example, Asteromphalus variabilis (Grev.) Rattray. Perhaps this close relationship led Greville (1860) to consider Asteromphalus as a synonym of Asterolampra, in his monograph of the latter genus. The family Asterolampraceae is placed in the suborder Coscinodiscineae, order Centrales.

MATERIAL AND METHODS.

1. Source of material.

This study was carried out for the most part using preserved marine plankton samples. Some few samples were collected by the author, but the majority were supplied by colleagues and Institutions (listed in Table I). One fossil sample was obtained from Mr. B. Hartley. Permanent slides, including some type slides in several collections at Museums and Institutions were also observed.

The plankton samples came from different regions around the world, emphasis being placed on tropical and subtropical areas. In total 76 samples were analyzed (not all samples contained Asteromphalus species). Sixty-seven samples were collected from the tropical-subtropical Eastern Pacific Ocean: 30 from the Gulf of California, 31 from off the coast of Baja California, 5 from off the coasts of Mexico, and one from Peru. Four samples were obtained from the Indian Ocean, three from the Antarctic Ocean, one from Australian waters, and one sample from the Mediterranean Sea. The details of this material are given in Table I.

One sample of fossil material, already cleaned, from Yezzo Natanai, Japan was especially studied because it was known to contain *Asteromphalus* species.

In order to ensure the correct species identification and for further study, reference slides were observed. These slides from various collections were provided or loaned from the British Museum (Natural History) (BM) at London, the Naturhistoriska Riksmuseet (S) at Stockholm, the Muséum d'Histoire Naturelle (PC) at Paris, and the California Academy of Sciences (CAS) at San Francisco. The list of slides and details are given in Table II.

2. Methods.

All material used for light and electron microscopy was rinsed at least five times with destilled water. Permanent slides for light microscopy (LM) were made from rinsed and cleaned material. The method for cleaning diatoms followed that used by Simonsen (1974) and recomended by Hasle (1978), which is basically the oxidation of the organic material (using $KMnO_4$) followed by acid treatment (HC1). Identification, preliminary observations and measurements were made with an Olympus CH light microscope, phase contrast, and with an Olympus Bh with attached camera, phase contrast, bright field and differential interference contrast (Nomarski).

Rinsed and cleaned material was used for SEM. Drops of the prepared material were put onto coverslips, air-dried and then coated with gold-palladium in a coating unit. Some specimens previously identified were isolated with aid of a micropipette, and afterwards the above method was followed. The method of critical point drying (Medlin, 1978) was used for few samples, after rinsing and dehydration of these samples. The scanning electron microscope used was a Phillips 501, usually operated at 10-12 kv.

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3. Terminology.

In general, the terminology adopted in this study follows that proposed by Anonymous (1975) and Ross et al. (1979). Specific terminology for Asteromphalus follows Gombos (1980). However, some terms are proposed as new.

The following considerations are made: central portion, as denoted by Gombos (1980) is equivalent to the "central area" of many authors and the "hyaline area" of Greville (1860) (P1. 1, fig. 1).

There are two different kind *of rays:* those about the same width and length, denominated here 'Ordinary Rays', and the narrower and often longer or shorter ray, called here 'Singular Ray' (P1. 1, fig. 1, P1. 2, figs. la, lb). These two new terms were chosen to avoid confusion of position or function given by terms used by other authors. The singular ray had been named "obsolete ray" (Wallich, 1860; Castracane, 1886), "median ray" (Brébisson, 1857; Greville, 1860), "basal ray" (Ralfs in Pritchard, 1861), and "oblitered ray" (Castracane, 1886). None of these terms are now considered satisfactory for naming this structure, particularly since we know nothing of the function of these rays as yet. On the other hand, Ehrenberg (1844) had mentioned the term ordinis radii for all the other rays.

The term separating lines (Gombos, 1980) (P1. 1, fig. 1) refers to the terms "umbilical lines" (Greville, 1860; Castracane, 1886) and "partitions" used by many authors.

The term 'Indentation' is a new one for a structure described here for the first time and present in the valve margin, close to the singular ray (P1. 1, figs. 1, 4).

Other new proposal is the term 'Tympanum', which is the siliceous plate covering the ends of the rays ("ray holes") when the specimens are gently washed (P1. 1, figs. 2, 3).

Also used here is the term annulus (V. Styosch, 1977), the structure where silicification may start first in centric diatoms (Round & Crawford, 1981), located internally in Asteromphalus.

There are seven patterns of areolae found in the studied species of Asteromphalus; they are illustrated in P1. 2, figs. A-H, which also includes the areolae pattern of the closely related genus and species Spatanaidium arachne.

OBSERVATIONS.

Seventeen species have been studied by light and scanning electron microscopy. The taxonomic arrangement is newly proposed herein: separation into two subgenera, Asteromphalus and Liriogramma nov. stat., and further split into seven sections. The criteria taken into account for this separation were basically: shape of the cell, relative size of central portion, shape of separating lines, areolae pattern, and position of the indentation (regarding the singular ray).

Genus Asteromphalus Ehrenberg

Subgenus Asteromphalus

Section Pseudoasterolampra

Cells circular, slightly convex, with no mantle. Central portion round, extended about 1/2 of the valve diameter, separating lines straight. Singular ray about the same length as ordinary ones. Indentation inconspicuous, placed to the left or right side of singular ray. Areolae pattern very fine. Girdle with rows of poroids.

Asteromphalus vanheurckii Mann Pls. 3, 4.

Mann, 1907, p. 276, pl. 45, fig. 5.

Synonym ? : Asteromphalus hookeri Ehrenberg sensu Ricard, 1977, pl. 8, fig. 16.

Material: Coasts of Baja California (11), Mediterranean Sea (76).

In LM.- Cells circular and slightly convex. Central portion rounded, centric, extended one-half of the cell diameter, with its separating lines straight. Ten to twelve hyaline rays, some of them slightly curved and the singular ray thinner. Areolae pattern very fine, 14-15 / 10 um. Diameter: 60-77 um. P1. 3, fig. 1.

In SEM.- Cells discoid, convex (P1. 3, figs. 2, 3). Central portion flat, not easily distinguished, with separating lines poorly developed (P1. 3, fig. 3). The ordinary rays have ray holes and external openings of the rimoportulae, whilst the singular ray just bears a ray hole that differs slightly from the others (P1. 3, figs. 4, 6, 7); its rimoportula opens within the ray tube, although it can still be seen (P1. 4, fig. 3). Some specimens show a tympanum at the ends of the rays. Indentation is also present, but it is inconspicuous and simple, and may be placed to the left or right side of the singular ray (Pl. 3, fig. 3, Pl. 4, figs. 1, 2). Inside, the rimoportula at the singular ray is bigger than those of the ordinary rays (P1. 4, figs. 2, 6). The annulus is easily visible, stellate, at the very centre of the valve (P1. 4, figs. 4, 5).

The areolae are formed of rows of pores arranged in a quincunx pattern, which could be the simpliest type of pattern within <u>Asteromphalus</u> (type A, P1. 2) (P1. 3, fig. 5). The girdle in this species is the unique, of those studied, ornamented with striae, running in perpendicular rows (P1. 3, fig. 7, P1. 4, fig. 3).

Remarks: The whole cell in SEM may easily be confused with an <u>Asterolampra</u> species, because the central portion is not raised and not clearly defined. Also the singular ray is not the largest one, but it is about the same length as the ordinary ones. This species resembles <u>A. dallasianus</u> (Grey.) Ralfs in the shape of the cell and central portion, although the number of rays in A. <u>dallasianus</u> is between seven to nine. However, A.

vanheurckii is kept in a separate section mainly because of its particular areolae pattern and the characteristic of its indentation. This species is rather rare, with no secure report since its original description (Mann, 1907).

Section **Variabile**

Cells circular or subcircular, convex, no mantle or very low. Central portion angled, separating lines straight or bent. Singular ray differentiated just by being thinner than ordinary ones. Indentation inconspicuous, to the left of the singular ray. Areolae pattern fairly coarse.

Asteromphalus variabilis (Greville) Rattray Pls. 5, 6.
Rattray, 1889, p. 655.
Synonyms: Asterolampra variabilis Greville
Greville, 1860, p. 111, pl. 3, figs. 6-8.
Asteromphalus kinkeri Pantocsek
Pantocsek, 1892, pl. 24, fig. 357.
Asteromphalus grovei Pantocsek
Pantocsek, 1892, pl. 25, fig. 380.
Asteromphalus variabilis Greville
Ross & Sims, 1973, p. 107, figs. 28-31.

Material: Fossil (Yezzo Natanai, Japan).
Slides 2017 (B. Hartley), 347009 (CAS).

In LM.- Cells circular to subcircular, convex. Central portion angled, centric, occupying one-third of the cell diameter, with separating lines straight or slightly curved. Seven to ten hyaline rays, about the same length; ordinary rays slightly narrower close to their bases, the singular ray thinner than the others. Areolae pattern coarse, 8-9/ 10 um. Diameter: 73-94 um. P1. 5, fig. 1.
In SEM.- Cells discoid, convex, mantle absent or very low (P1. 5, fig. 2). Separating lines in the central

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portion are well developed (P1. 5, fig. 3). All rays, including the singular one, are sunk into the valve at their bases and for a short distance (P1. 5, figs. 2, 4). Ordinary rays are narrower at bases, becoming wider at ends; they have a ray hole and just below a small opening of the rimoportula (P1. pl. 5, figs. 4, 7). Their edges are limited by irregular rows of rather big pores, which do not penetrate the valve (P1. 5, figs. 6, 7). The singular ray has only a ray hole at its end, which is smaller than those at ordinary rays (P1. 5, figs. 4, 6). No tympanum was detected, as all specimens were cleaned. The indentation is almost absent, but just indicated by a very slightly discontinuity in the edge of the valve, next to the singular ray, to the left side (P1. 5, fig. 6). The rimoportulae inside appear the same as in the previous species, to say the one at the singular ray being bigger than the others, although most of the specimens were eroded and this character is hard to see (P1. 6, figs. 1, 3, 4). The annulus, easily seen, is stellate and centrally located (P1. 6, fig. 2).
The areolae have a basic quincunx pattern, but instead of a consecutive series of poroids, some of them become elongated and surround various other poroids (three to five) (type C, pl. 2). Sometimes this pattern becomes slightly irregular (P1. 5, fig. 2).
Remarks: This species was previously studied by Ross & Sims (1973). All their observations are consistent with those shown here, including the feature of the rays sunk into the valve.
Two species considered valid by Van Landingham (1967) are now placed as synonyms of A. variabilis: A. kinkeri and A. grovei (see above).

Section Genuina

Cells circular, subelliptic or elliptic, convex, mantle low. Central portion round or angled, separating lines straight, curved or bent. Singular ray thinner and often longer or shorter than ordinary ones. Indentation conspicuous, to the left side of the singular ray.

Areolae pattern fine.

Asteromphalus roundii Hernandez-Becerril sp. nov.
Pls. 7, 8.
Synonym: Asteromphalus elegans ? Greville sensu Hernandez-Becerril, 1987, p. 416, pl. 1, figs. 1, 2.
? Asteromphalus wvvilli Castracane sensu Subrahmanyan, 1946, p. 106, pl. 2, fig. 4, non fig. 87.

Material: Salina Cruz (64).

Valva Plana, fere circularis, diametro 67-72 um. Area centralis svmmetrica posita, 1/3 diametri valvae occupans. Partitiones rectae vel parum curvatae; radii 12-13, radius singularis rectus, angustior guam radii alii, gui parum curvati sunt. Areolae tenues. 11-12 in 10 um. Indentatio conspicua, in latere siniestro radii principalis. Rimoportulae solum ad fines radiorum, ills ad finem radii singularis major =am aliae. Appellatio in honorem Professoris F.E. Round. Habitat tvpus: Salina Cruz, Tehuantepec Sinus, Mexico.
Holotypus: Slide labeled 81750 Asteromphalus roundii, deposited in the British Museum (Natural History) (BM).
Isotypus: Slide labeled Asteromphalus roundii, deposited in the Diatom Collection of the Institute of Marine Sciences and Limnology, **UNAM** (MEXU-I).

In LM.- Cells usually circular and nearly flat. Central portion extended about one-third of the diameter of cell, rounded and centrally or slightly excentrally located, with separating lines straight. Twelve to thirteen hyaline rays run from the central portion, the singular ray being thinner and some of the ordinary rays being slightly curved. Areolae fine, 11-12/ 10 um. Diameter: 67-72 um. P1. 7, fig. 1.
In SEM.- Cells are discoid and flat (P1. 7, fig. 2). Ray hole and outer opening of the rimoportula at the end of

each ray, except the singular ray, where the rimoportula, as all Asteromphalus species studied, does open within the ray tube (P1. 7, figs. 4, 6, 7). This singular ray hole is bigger than all others (P1. 7, fig. 6). The indentation is located to the left of the singular ray and is very conspicuous (P1. 8, figs. 1, 2). Inside, the rimoportulae from ordinary rays are smaller than that in the singular ray (P1. 9, figs. 1, 4). The annulus can be observed placed slightly excentrically (P1. 8, fig. 3).

The areolae are arranged in the basic pattern of quincunx, but in here some poroids are elongated (as in A. variabilis), surrounding a single poroid (type B, P1. 2) (P1. 7, fig. 5).

Remarks: The morphology shown for this species seems to be common for a number of species included in the section Genuina (see also remarks for A. flabellatus (Bréb.) Greville). The commonest character is indeed the areolae pattern, and secondly the high number of rays (usually more than six, which may vary in most of the species).

Asteromphalus stellatus (Greville) Ralfs   Pls. 9, 10.
Ralfs in Pritchard, 1861,p. 838; Rattray, 1889, p. 660.
Synonym: Asterolampra stellata Greville
Greville, 1860, p. 124, pl. 4, fig. 20.

Material: Australian waters (75).
Slide 1938 (BM).

In LM.- Cell ovate to subelliptic, slightly convex. Central portion angled, sligthly excentric, about one-third to one-half of the cell diameter, with separating lines straight or curved. Nine to ten hyaline rays: the ordinary rays being wider at their bases becoming narrower near their ends, and those opposite to the singular ray are shorter than the others; the singular ray is thinner and longer. Areola pattern is rather

fine, 12-13/10 um. Diameter: 38-51 um (P1. 9, fig. 1).
In SEM.- Central portion presents its separating lines regular, without pores or processes (Pl. 9, figs. 2, 3). The same pattern described above regarding ordinary rays is found here (ray holes and an external opening of the rimoportula) (P1. 9, figs. 4, 7), although the ray hole of the singular ray is bigger and elongate (P1. 9, figs. 4, 6); this does not show an opening of the rimoportula to outside. The indentation is very conspicuous, to the left side of the singular ray (P1. 9, fig. 6). Inside, the rimoportula of the singular ray is the biggest (P1. 10, fig. 2). The annulus looks round, poorly apparent and excentric (P1. 10, fig. 3).
The areolae pattern is similar to that described for A. roundiy (type B, P1. 2) (P1. 9, fig. 5).
Remarks: A. stellatus is a very rare species, found just in the Indian Ocean, as the few reports indicate so far. Its rather small size and similarity with other species (namely A. flabellatus) makes positive identification difficult. When Greville (1860) described it, he was not very sure if it would be a good species.

Asteromphalus sp. P1. 11.

Material: Australian waters (75).

In LM.- Cells circular to subcircular, flat or slightly convex. Central portion round, nearly centric, extending to one-third of the cell diameter, with the separating lines straight or curved. Eleven to fifteen hyaline rays, all about the same length and some of the ordinary ones slightly curved; the singular ray is thinner. This singular ray is constricted in its separating line within the central portion. Areolae pattern fine, 11-12/10 um. Diameter: 72-83 um. P1. 11, fig. 1.
In SEM.- Cells drum-shaped, convex with mantle low (P1.

11, fig. 1). Central portion with no ornamentations, the separating lines being regular, with no pores (P1. 11, fig. 2). The pattern described earlier for ordinary rays is also found here. The singular ray has a bigger ray hole, which is different shaped as well, with no opening of its rimoportula to the outside (P1. 11, fig. 4). The identation is shown to be very conspicuous, placed to the left side of the singular ray (P1. 11, fig. 4). The rimoportulae from the inside present the same pattern as all precedent species (P1. 11, fig. 7). The annulus is well obvious, excentric. Some specimens showed their ray holes covered by the tympanum (P1. 11, fig. 6).

The areola arrangement follows the type B, previously described (A. roundii,) (P1. 11, fig. 5).

Remarks: This species is closely related to several other species in this section like A. roundii and A. stellatus. However, it could not be identified positively, because it presents some important differences: the pattern of rays, especially the character of the constriction in the singular ray. A. hiltonianus (Grey.) Ralfs (see ahead) could be possibly its closest allied, but the size and number of rays (A. hiltonianus has more than 15 rays) make hard the allocation in that species. A similar reason is given regarding to the relation with A. stellatus, which is very small. So, this species is left unidentified as its identification becomes unsatisfactory and, on the other side, a new species may result too precipitate.

Asteromphalus flabellatus (Brébisson) Greville Pls. 12, 13.

Greville, 1859, p. 160, pl. 7, figs. 4, 5; Schmidt, 1876, p1.38, figs. 10-12; Peragallo & Peragallo, 1897-1908, p. 406, figs. 4, 5; Hustedt, 1930, p. 498, fig. 279; Allen & Cupp, 1935, p. 123, fig. 22; Subrahmanyan, 1946, p. 105, fig. 85, non 81; Sournia, 1968, p. 25; Fryxell & Hasle, 1973, p. 75, figs. 11 a, b; Simonsen, p. 25.

Synonyms: Spatangidium flabellatum Brébisson

Brébisson, 1857, pl. 3, fig. 3.
Spatangidium peltatum Brébisson
Brébisson, 1857, p. 298, pl. 3, fig. 4.
Asterolampra flabellata (Bréb.) Greville
Greville, 1860, p. 116.
(non Asteromphalus flabellatus Bréb. sensu Skvortzow, 1931a, p. 121, pl. 2, fig. 14 = A. cleveanus Grunow)

Material: Coasts of Baja California (13, 15, 25, 29), Gulf of California (16, 18, 19-21, 23, 51, 54, 55, 57, 60), Australian waters (75).

Slides labeled "A. peltatum" (PC), "A. flabellatum" (PC).

In LM.- Cells subcircular or elliptic in valve view, slightly convex. Central portion rounded, about one-third to one-quarter of the diameter, separating lines straight. Eleven to thirteen hyaline rays, the singular ray usually longer and thinner; the ordinary rays are wider at their bases (near central portion), becoming narrower close to their ends. Areolae fine, 11-13/10 um. Diameter: 47-65 um. P1. 12, fig. 1.

In SEM.- Valves convex (P1. 12, fig. 2). Ordinary rays bear a ray hole at their ends and just below this an opening of the rimoportula (P1. 12, figs. 4, 6, 7). The singular ray has a bigger ray hole but no outer opening of the rimoportula (P1. 12, fig. 4). To the left of the singular ray, a typical identation is very conspicuous, extending well into the perimeter of the valve (P1. 12, fig. 6); at this point the areolae become discontinuous. Inside, again the rimoportula of the the singular ray is larger than the others (P1. 13, figs. 1, 3). The annulus is indistinct but stellate and excentric (P1. 13, fig. 2). The areolae pattern found here is of the type B (P1. 12, fig. 5).

Remarks: The closest related species of A. flabellatus should be A. cleveanus Grunow, which has been often placed as a synonym of the former (e.g. Sournia, 1968). The shape of the valve and the central portion make both species different; in addition it can be said that A. flabellatus has a higher number of rays (more than 10) than A. cleveanus (between seven and ten). Other closely related species is A. roundii, that observed by electron microscopy greatly resembles A. flabellatus. In LM the main difference is that A. flabellatus shows its ordinary rays wider at their base, becoming narrower close to the margin of the valve, while those in A, roundii are about the same width; in finer approach using SEM the difference in the annuli (round in A, roundii, small and stellate in A. flabellatus) can be seen.

Asteromphalus hiltonianus (Greville) Ralfs Pls. 14, 15.

Ralfs in Pritchard, 1861, p. 837; Rattray, 1889, p. 661.

Synonyms: Asterolampra biltoniana Greville
Greville, 1860, p. 117, pl. 4, fig. 5.
Asteromphalus wvvilli Castracane
sensu Karsten, 1907, p. 370, pl. 38, fig.4.

Material: Indian Ocean (68, 71).
Slides 1880, 1882, 42613 (BM).

In LM.- Cells circular and convex. Central portion rounded, occupying one-third of the cell diameter, separating lines straight or slightly curved, but not bent. Seventeen to eighteen hyaline rays, some of them slightly curved but all are of similar length; the singular ray is thinner. Areolae pattern fine, 11-12/10 um. Diameter: 98-109 um. P1. 14, fig. 1.

In SEM.- Cells convex with mantle low (P1. 14, fig. 2). The separating lines in the central portion are just marks in the valve (P1. 14, fig. 3). The ordinary rays have both rays holes and outer opening of the rimoportulae (P1. 14, fig. 4); singular ray bearing a larger ray hole with no opening of its rimoportula (P1. 14, fig. 6). The ray holes did not show the typical tympanum. Indentation is very conspicuous, to the left of the singular ray and as in A. flabellatus, extending well into the perimeter of the valve (P1. 14, fig. 6). Same pattern is found in here inside: the rimoportula at singular ray is larger than those at ordinary rays (P1. 15, figs. 1, 3). The annulus is also shown to be conspicuous and it is round and excentric (P1. 15, fig. 4). The areolae pattern is basically the same as type B (P1. 14, fig. 5). These areolae are continuous throughout, including the corners between sibling rays (P1. 15, fig. 2), unlike some specimens of A. eleaans Greville (see ahead).

Remarks: Species of large size, sharing many characteristics with those previously described within this section. Its closest link is believed to be A. eleaans (see description below).

Asteromphalus elegans Greville Pls. 16, 17.

Greville, 1859, p. 161, pl. 7, fig. 6; Ralfs in Pritchard, 1861, p. 837, pl. 5, fig. 87; Schmidt, 1876, pl. 38, figs. 1, 2; Rattray, 1889, p. 660; Karsten, 1907, p. 370, pl. 38, fig. 3; Hendey, 1937, p. 269; Silva, 1953, p. 22, pl. 1, fig. 7; Sournia, 1968, p. 26, pl. 9, fig. 59; Hendey, 1971, p. 377, fig. 19.

Synonyms: Asterolammra eleaans (Greville) Greville
Greville, 1860, p. 118, pl. 4, fig. 16.
Asteromphalus wvvilli Castracane
Castracane, 1886, p. 134, pl. 5, fig. 6.
(non Asteromphalus eleaans Greville sensu Hernândez-Becerril, 1987, p. 414, pl. 1, figs. 1, 2 = A. roundii Hernandez-Becerril).

Material: Indian Ocean (68, 69, 71).
Slides 1778, 1880, 42613, 62698 (BM).

In LM.- Cells circular and convex. The central portion is round, extending one-third of the cell diameter, slightly excentric; separating lines are bent and in some specimens branched. There are seventeen to twenty hyaline rays, the singular ray being thinner but of

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similar length to the others. The areolae pattern is fine, 11-12/ 10 um. Diameter: 98-140 um. P1. 16, fig. 1. In SEM.- Cell discoid, convex with mantle low (P1. 16, fig. 2). The separating lines in the central portion are simple marks in the valve (P1. 16, fig. 3); some poroids are scattered in this portion, which do not appear to perforate the valve (P1. 17, fig. 2). Ray holes are about similar in size and shape, but that of the singular ray is longer; at this ray an external opening of the rimoportula is not present (P1. 16, fig. 4, P1. 17, fig. 3). In all other ray holes the rimoportulae open to outside in a small opening just below the ray hole (P1. 16, figs. 6, 7). Ray holes are covered by the tympanum as shown using untreated specimens (P1. 16, fig. 7, P1. 17, fig. 3). Again the indentation is very conspicuous, to the left of the singular ray (P1. 16, fig. 4). Inside, the rimoportula of the singular ray is larger than the others (Pl. 17, figs. 5, 6). The annulus is apparent in this species and excentrically placed (P1. 17, fig. 5).

The areolae pattern is type B as well (P1. 16, fig. 5); in some specimens, the areolae pattern is discontinuous between two sibling rays near the central portion, leaving a triangular hyaline area (P1. 17, fig. 4).

Remarks: The general appearence of <u>A. elegans</u> strongly resembles <u>A. hiltonianus,</u> both being of a similar size. <u>A. elegans</u> has a bent pattern of separating lines, whilst <u>A. hiltonianus</u> shows a straight pattern. The original description (Greville, 1859) and type material of <u>A. elegans</u> (BM, slide 1778) indicate a specimen having 13 rays, but still showing the bent pattern characteristic of this species; other slide in Greville's collection (BM, slido 1880) shows one specimen of 16 rays; Sournia (1968) has found specimens having between 12-29 rays. In the present material (Indian Ocean) specimens with less than seventeen rays or more than twenty were not found.

Asteromphalus imbricatus Wallich P1. 18.
Wallich, 1860, p. 46, pl. 2, fig. 9; Rattray, 1889, p. 661; Simonsen, 1974, p. 25, pl. 22, fig. 1.
Synonyms: Asterolampra imbricata (Wallich) Greville
Greville, 1860, p. 119, pl. 4, fig. 17.

Material: Indian Ocean (70), Australian waters (75).
Slides 1938, 42613 (BM).

In LM.- Cells subcircular to elliptical, plattened or slightly convex. Central portion rounded to stellate, extended to about one-half of the cell diameter, with separating lines bent in a zig-zag pattern. Ten to twenty-two rays of similar length with a somewhat thinner singular ray. Areolae pattern fine 9-10/ 10 um. Diameter: 43-78 um. P1. 18, fig. 1.
In SEM.- Central portion with separating lines formed of linear marks in the valve with no poroids (Pl. 18, figs. 2, 3). The same pattern described earlier for the ends of the rays is presented here: ordinary rays having ray holes and external opening of the rimoportula, the singular ray having a slightly smaller ray hole, rounded, with no opening of the rimoportula to outside, but visible when it opens within the ray tube (P1. 18, fig. 6). Indentation very conspicuous, to the left side of the singular ray (P1. 18, figs. 6, 7). Inside the rimoportula of the singular ray is the largest of all others (P1. 18, fig. 4). The annulus is not very apparent and is round and excentric. The areolae arrangement follows the type B (P1. 18, fig. 5).
Remarks: Species variable in the number of rays (from 10 to 22), A. imbricatus is easily recognizable by its rather extended central portion and the marked bent pattern of the separating lines. Despite its shape and size, A. imbricatus could be closely related to A. eleaans, in a possible sequence from radial to bilateral simetry. No specimen was available for studying by LM, thus slides from the BM were used for the light micrograph and the measurements.

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Asteromphalus ingens Simonsen Pls. 19, 20.
Simonsen, 1974, p. 25, pl. 21.

Material: Gulf of California (53, 58), Indian Ocean (68, 71).

In LM.- Cells subcircular with an undulate surface. Central portion round to elliptical, extending one-third to one-quarter of the diameter, centric or slightly excentric; separating lines are bent in a zig-zag pattern. Nine to thirteen hyaline rays with the singular ray being thinner and longer, and some of the ordinary rays are curved. Areolae very fine, 11-13/ 10 um. Diameter: 110-125 um. P1. 19, fig. 1.
In SEM.- Cell discoid with undulations coinciding with each ray, and mantle rather high (P1. 19, fig. 2, P1. 20, fig. 1). The central portion is slightly raised and somewhat undulated, with no apparent pores or processes (P1. 19, fig. 3). The ordinary rays have a ray hole and an external opening of rimoportulae, the singular ray has a larger ray hole and no opening of the rimoportula to the outside (P1. 19, figs. 4, 6, 7, P1. 20, fig. 2). Some ends of rays were found with a tympanum covering the ray hole. The indentation is found to the left of the singular ray (P1. 19, fig. 4). Inside, the same character of difference in relative size of rimoportulae is consistent in this species (P1. 19, figs. 3, 4, 6). The small round annulus is well-defined near the centre of the valve (P1. 20, fig. 5). The areolae are arranged like the type B (P1. 19, fig. 5).
Remarks: This species shows a fairly high mantle, in contrast with all species included in the section Genuina, but still the areolae pattern is kept. Its allocation, however, should be considered as preliminary.

Asteromphalus shadboltianus (Greville) Ralfs P1. 21.
Ralfs in Pritchard, 1861,p. 838; Schmidt, 1876, pl. 38, fig. 17, pl. 137, fig. 26; Rattray, 1889, p. 656.

Synonyms: Asterolampra shadboltiana Greville
Greville, 1860, p. 121, pl. 4, fig. 19.
Asteromphalus ovatus Castracane
Castracane, 1886, p. 132, pl. 5, fig. 7.

Material: Australian waters (75).

In LM.- Cells circular to subcircular, convex,. Central portion angled, about one-third to three-quarters of the cell diameter, slightly excentric; separating lines are straight, not bent. Seven hyaline rays are present, which do not reach to the edge of the valve, the singular ray is thinner and shorter than ordinary rays. Areolae pattern is fine, 9-11/ 10 um. Diameter (just one cell observed): 60 um. P1. 21, fig. 1.

In SEM.- Cell discoid and convex, mantle low (P1. 21, fig. 2). Central portion with no pores, the separating lines are simple linear marks in the valve (P1. 21, fig. 3). The ordinary rays are robust and have at their ends ray holes and openings of the rimoportulae (P1. 21, fig. 7). The singular ray just shows a ray hole, which appears to be smaller than those of the ordinary rays (P1. 21, fig. 6); this ray is even shorter than the others (P1. 21, fig. 4). Indentation is conspicuous, located to the left side of the singular ray (P1. 21, fig. 4). No observations were made of the inside, but it is assumed that the pattern of rimoportulae described for other species in the same section, is also present in this species. The areolae follow the arrangement of the type B (P1. 21, fig. 5).

Remarks: This is one of the few species in this section that apparently keep the number of rays unchanged. The other interesting character is the singular ray, which is shorter than the ordinary ones.

Asteromphalus roperianus (Greville) Ralfs Pls. 22, 23.
Ralfs in Pritchard, 1861, p. 838; Schmidt, 1876, pl. 38, fig. 15; Rattray, 1889, p. 657; Karsten, 1905, p. 90,

pl. 8, fig. 8; Hendet, 1937, p. 270; Sournia, 1968, p. 26, pl. 9, fig. 61; Simonsen, 1974, p. 26, pl. 22, fig. 2.

Synonyms: Asterolampra roperiana Greville
Greville, 1860, p. 120, pl. 4, fig. 14.
Asteromphalus roperianus var. atlantica Castracane
Castracane, 1886, p. 133, pl. 5, fig. 3.

Material: Indian Ocean (68, 69, 71), Australian waters (75).

Slide 1880 (BM).

In LM.- Cells nearly circular, convex. Central portion angled, excentric, about one-third to one-quarter of the cell diameter, with its separating lines straight. There are seven rays, the ordinary rays being about the same lenght and width, and the singular ray being thinner and often shorter than the others. Areolae pattern is fine, 11-13 10 um. Diameter: 70-175 um. P1. 22, fig. 1.

In SEM.- Cells drum-shaped and convex, mantle low (P1. 22, fig. 2). The separating lines in the central portion are marks in the valve (P1. 22, fig. 3). The pattern of rays holes and outer opening of rimoportulae in ordinary rays is repeated in this species, but the singular ray is shorter than the others and does not reach to the edge of the valve (P1. 22, fig. 4); the rimoportula opening in this ray does open within the ray tube, but it still can be seen (P1. 22, fig. 6). No tympanum was observed. The indentation is well defined, to the left side of the singular ray (P1. 22, fig. 6, P1. 23, fig. 6). Inside, the rimoportula of the singular ray is larger than those of ordinary rays (P1. 23, figs. 2, 4, 5, 7). The annulus is obvious, excentric and having stellate appearence (P1. 23, fig. 3). The areolae pattern is of the type B (P1. 22, fig. 5).

Remarks: A. roperianus is closely related to A. shadboltianus, mainly because both species have the same number of rays and this number does not change, and also due to the character of the singular ray, being shorter than the others.

Section Hookeri

Cells circular to subcircular, slightly convex, mantle low to moderately high. Central portion angled, separating lines straight or curved. Singular ray usually similar in length to the others. Indentation conspicuous, to the left of singular ray. Areolae pattern coarse.

Asteromphalus hookeri Ehrenberg Pls. 24, 25.
Ehrenberg, 1844, p. 200, pl. June, fig. 3; Ehrenbeg, 1854, pl. 35 A XXI, fig. 2; Ralfs in Pritchard, 1861, p. 826, pl. 11, fig. 34; Rattray, 1889, p. 656; Hendey, 1937, p. 270; Hustedt, 1958, p. 127, pl. 8, fig. 88 (non 89, nec 90).
Synonyms: Asteromphalus buchii Ehrenberg
Ehrenberg, 1844, p. 200, pl. June, fig. 4.
Asteromphalus cuviery Ehrenberg
Ehrenberg, 1844, p. 200, pl. June, fig. 7; Ehrenberg, 1854, pl. 35 A XXI, fig. 1.
Asterolampra hookeri (Ehrenberg) Greville
Greville, 1860, p. 114.
Asteromphalus antarcticus Castracane
Castracane, 1886, p. 135, pl. 16, fig. 11.
non Asteromphalus humboldtii Ehrenberg
Ehrenberg, 1844, p. 200, pl. June, fig. 6.
(non Asteromphalus Jiookerj Ehrenberg sensu Muller-Melchers, 1957, p. 114, pl. 5, fig. 9 = A. flabellatus (Bréb.) Grev.)

Material: Antarctic Ocean (72-74).
Slides 33558, 62720 (BM).

In LM.- Cells circular, nearly flat or slightly convex. Central portion angled, lying at the centre of the cell, ocupying one-third to nearly one-half of the diameter; the separating lines are straight or slightly curved, but not bent. Six to seven hyaline rays run from the central portion, usually straight, the singular ray is of similar length of the ordinary rays. Areolae pattern rather coarse, 7-8/ 10 um. Diameter: 43-78 um. P1. 24, fig. 1.

In SEM.- Cells discoid, slightly raised at rays, and mantle rather low (P1. 24, fig. 2, P1. 25, fig. 1). The same character, previously described, of ray holes and external opening of rimoportulae is also present for this species, regarding the ordinary rays (P1. 24, figs. 4, 7). The external opening of ordinary rays presents a labiate-like structure surrounding the aperture (P1. 24, fig. 6). The singular ray shows a ray hole differently shaped than the others (slightly eleongate) and no opening of its rimoportula to the outside is found (P1. 24, fig. 4). As in other species, the tympana cover the ray holes, at least in ordinary rays (P1. 24, fig. 6). The indentation occurs to the left of the singular ray and it is well-defined (P1. 24, fig. 4, P1. 25, fig. 1). The inner aperture of the rimoportula at the singular ray is larger than those of ordinary rays (P1. 25, fig. 3). The annulus is conspicuous, stellate and located near the centre (P1. 25, figs. 2, 4).

In this species the areolae pattern is similar to that of A.variabilis (type C), but in this case the pattern appears more regular, with elongate poroids surrounding various smaller poroids, in a quincunx arrangement (type D, P1. 2) (P1. 24, fig. 5).

Remarks: A. hookeri shows resemblances with those of the section Robusta (see ahead), but lacks a high mantle and the areolae pattern is different too. The species A. humboldtii Ehr. was found to be distinct from A.hookeri (see discussion), but remains the closest related species.

A number of described species (24) has been placed as synonyms of A. hookeri, including several valid species, by Van Der Spoel et al. (1973); the base for this is basically the number of rays. I strongly disagree with this as other important characters have not been estimated (e.g. areolae pattern, shape of separating lines).

Section Robusta

Cells circular, subcircular or elliptical, raised at rays, with mantle moderately high to high. Central portion round, separating lines bent in a zig-zag pattern. Singular ray slightly longer than others or of similar length. Indentation conspicuous, to the left of singular ray. Areolae pattern coarse.

Asteromphalus robustus Castracane Pls. 26, 27.

Castracane, 1875, p. 383, pl. 6, fig. 5; Hustedt, 1930, p. 496, fig. 278.

Synonym: Asteromphalus)rookei var. robustus (Castracane) Rattray

Rattray, 1889, p. 658.

(non A. robustus Castracane sense Manguin, 1954, pl. 15, fig. 7 = A. humboldtii Ehrenberg)

Material: Indian Ocean (69), Australian waters (75).
Slide 524 (1124) (S).

In LM.- Cells subcircular to elliptical, convex. Central portion round, extending to about one-third of the cell diameter, slightly excentric, with its separating lines bent. Eight to ten hyaline rays, all of similar length and width, but the singular ray is thinner. Areolae pattern rather coarse, being slightly coarser near the central portion,6-7/ 10 um. Diameter: 67-79 um. P1. 26, fig. 1.

In SEM.- Cells drum-shaped, raised at rays and with a high mantle (P1. 26, fig. 2, P1. 27, fig. 1). Ordinary rays robust, having at their ends a ray hole and an outer opening of the rimoportula (P1. 26, figs. 4, 6); in the singular ray, the ray hole differs in shape, about the same size as the others, but without an opening of its rimoportula to outside (P1. 26, fig. 6). Some specimens show the presence of the tympanum at the end of the rays (P1. 26, fig. 6). The indentation is very conspicuous, to the left of the singular ray (P1. 26, fig. 6). Inside, the pattern of bigger rimoportula belonging to the singular ray is again found in this species (P1. 27, figs. 3, 4). The annulus is small, round and excentric (P1. 27, fig. 2).

This species shows a characteristic areolae pattern, which is the basic arrangement in quincunx with bigger poroids surrounding small poroids (type E, P1. 2) (P1. 26, fig. 5). No elongate poroids are found in this pattern.

Remarks: Species evidently related to A. heptactis (Breb.) Ralfs (see next species), especially in the areolae pattern, the high mantle and the separating lines pattern (zig-zag). However, while A. heptactis keeps constant the number of rays (seven), in A. robustus the number may vary within a short range.

Asteromphalus heptactis (Brébisson) Ralfs Pls. 28, 29.
Ralfs in Pritchard, 1861, p. 838, pl. 8, fig. 21; Hustedt, 1930, p. 494, fig. 227; Lebour, 1930, p. 52, fig. 28 a; Gran & Angst, 1931, p. 454, fig. 32; Skvortzow, 1931b, p. 132, pl. 3, fig. 4; Cupp, 1943, p. 69, fig. 32; Wood, 1963, p. 193, pl. 2, fig. 30; Hendey, 1964, p. 96, pl. 24, fig. 5; Sournia, 1968, p. 25, pl. 9, fig. 58; Hendey, 1971, p. 377, fig. 21; Fryxell & Hasle, 1973, p. 72, figs. 6-10; Simonsen, 1974, p. 25; Ricard, 1977, pl. 8, fig. 13.

Synonyms: Spatangidium heptactis Brébisson Brébisson, 1857, p.296, pl. 3, fig. 2.

Spatangidium ralfsianum Norman
Norman in Greville, 1859, p. 161, pl. 7, figs. 7, 8.

Asterolampra heptactis (Brébisson) Greville
Greville, 1860, p. 122.

Asteromphalus ralfsianus (Norman) Grunow
Grunow in Schmidt, 1876, pl. 38, figs. 5-8.

Asteromphalus reticulatus Cleve
Cleve, 1873, p. 5, pl. 1, fig. 2.

Asteromphalus areolatus Mann
Mann, 1925, p. 30, pl. 6, fig. 5.

Material: Coasts of Baja California (09, 13, 25, 28-30), Gulf of California (16-19, 22, 23, 51-54, 57, 59), Pacific coasts of Mexico (62, 64, 65), Australian waters (75).

Slides labeled "A. heptactis", "A. brookei" (PC), 2258, 21673 (BM).

In LM.- Cells circular or subcircular with radial undulations. Central portion slightly angled or round, extending one-third to one-quarter of the cell diameter, and excentric. The separating lines are bent in a zig-zag pattern. There are seven rays, the singular one being thinner and longer. Areolae pattern very coarse, 5-6 10 um. Diameter: 68-165 um. P1. 28, fig. 1.

In SEM.- Cells discoid, with undulations corresponding to each ray, the mantle being high (P1. 28, fig. 2, P1. 29, fig. 1). Ray holes and outer opening of the rimoportulae are present in the rays, and the singular ray only shows a ray hole, bigger than that of the others, with no opening of the rimoportula to the outside (P1. 28, figs. 6, 7). Tympana are often found associated with ordinary rays, when the specimen is not treated with acid (P1. 28, fig. 6). The indentation in this species is obvious and placed on the left side of the singular ray (P1. 28, fig. 4, P1. 29, fig. 1). Inside, the rimoportula of the singular ray is also bigger than the others (P1. 29, figs. 3-5). The annulus is not well defined and is excentric (P1. 29, fig. 2). The areolae pattern is that of the type E (P1. 28, fig. 5), the same as A. robustus.

Remarks: As mentioned above, A. robustus is closely related to A. heptactis. The question that arises is if A. beaumontii Ehrenberg is conspecific with A. heptactis (in which case A. beaumontii has the priority), and what is the relation with A. ornithopus Karsten, because in appearence they are conspecific, just differing in the separating lines pattern (*p, ornithopus* has just one separating line bent, the remaining are straight). A large number of specimens were observed regarding the separating lines pattern and the evidence is that this pattern does not change. *A. heptactis* has a constant number of rays (seven).

Section Darwiniana

Cells circular and convex, with mantle low or moderately high. Central portion angled or round, separating lines bent in a zig-zag pattern. Number of rays constant. Singular ray often does not reach the edge of the valve. Indentation conspicuous, to the left of singular ray. Areolae pattern coarse.

Asteromphalus darwinii Ehrenberg Pls. 30, 31.
Ehrenberg, 1844, p. 200, pl. June, fig. 1; Ralfs in Pritchard, 1861, p. 837, pl. 5, fig. 86; Schmidt, 1876, pl. 38, fig. 16; Rattray, 1889, p. 663.
Synonyms: ? *Asteromphalus rosii* Ehrenberg
Ehrenberg, 1844, p. 200, pl. June, fig. 2.
Asterolampra darwinii (Ehrenberg) Greville
Greville, 1860, p. 116, pl. 4, figs. 12, 13.

Material: Fossil (Yezzo Natanai, Japan).
Slides 1942 (BM), 2017 (B. Hartley), 75001 (CAS).

In LM.- Cells circular and slightly convex. Central portion angled, occupying about one-third of the cell diameter, with the separating lines bent in a zig-zag pattern. Five hyaline rays, the singular ray being thinner and shorter than the others. Areolae pattern coarse, 7-8/ 10 um. Diameter: 63-72 um. P1. 30, fig. 1.
In SEM.- Cells discoid, slightly convex (P1. 30, fig. 2). In the central portion the separating lines are marked by rows of poroids and also small marks in the valve (P1. 30, fig. 3). The singular ray is shorter than the other four and does not extend to the edge of the valve, and is markedly irregular on its edges (P1. 30,

figs. 4, 6); its ray hole is smaller and differs in shape from those of the ordinary rays, and the rimoportula does not open to outside (P1. 30, fig. 6). The indentation is well visible, to the left side of the singular ray (P1. 31, fig. 6). The inner aperture of the rimoportula of the singular ray is larger than the others (P1. 31, figs. 2, 4, 7). The annulus is clearly visible, stellate shaped and occurs at the centre of the valve (P1. 31, figs. 3, 5).

The areolae pattern is of the type G (Pl. 2), consisting of bumps of hyaline areas with no poroids on them, but poroids are present in the flat areas; the arrangement still fits to a quincunx pattern (P1. 30, fig. 5).

Remarks: This species has been studied before by TEM, but misidentified as A. heptactis (Okuno, 1964, pl. 443), The observations shown there can allow little comparison, because they include only details of the areolae. A. darwinii has a constant number of rays (five), although as traditionally placed, A. rosii is possibly a synonym of A. darwinii, but having six rays instead of five. Further investigations are suggested, including the study of the type material. Other closely related species is A. brunii Pantocsek, which has a rather round and extended central portion, but same number of rays and separating lines pattern.

Subgenus Liriogramma (Kolbe) Hernandez-Becerril stat. nov.

Section Sarcophaga

Cells oblong with or without constrictions close to the apices, generally flat and with mantle low. Central portion reduced, separating lines straight to slightly curved, not bent. Number of rays constant; singular ray usually longer than ordinary ones, one of these is exactly opposite to the singular ray. Indentation not very conspicuous, to the left of the singular ray. Areolae pattern coarse.

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Asteromphalus sarcophagus Wallich   Pls. 32, 33.
Wallich, 1860, p. 47, pl. 2, fig. 12; Rattray, 1889, p. 666; Thorrington-Smith, 1970, p. 820, pl. 1, fig. 1; Simonsen, 1974, p. 26, pl. 22, figs. 3-6; Sournia et al., 1979, p. 184.
Synonym: Asterolampra sarcophaga (Wallich) Greville
Greville, 1860, p. 124.

Material: Australian waters (75).
Slide 61590 (BM).

In LM.- Cells oblong constricted close to their apices, with two main axis. Central portion excentric, occupying about one-third of the cell, with separating lines straight or slightly curved. Six hyaline rays, which vary in length and may be slightly curved, the singular ray being the longest and thinnest. Areolae pattern coarse, 8-9/ 10 um. Apical axis: 21-37 um, transapical axis: 20-24 um. P1. 32, fig. 1.
In SEM.- Valves flattened (P1. 32, fig. 2, P1. 33, fig. 1). The separating lines in the central portion are linear marks in the valve, with no apparent poroids (Pl. 32, fig. 3). The ordinary rays appear robust, raised, with ray holes and small external opening of the rimoportulae; their edges are irregular (P1. 32, fig. 6, Pl. 33, fig. 2). The singular ray is less robust but longer and thinner, with edges more regular (P1. 32, fig. 4). Indentation is not well defined, located to the left side of the singular ray (P1. 32, fig. 4). Inside, the rimoportula at the singular ray is larger than those of ordinary rays (P1. 32, fig. 4, P1. 33, figs. 4, 5). The annulus is small, nearly centric.
The areolae follows the type F (P1. 2), which also has raised bump-like areas having small poroids on them surrounded by other bigger poroids in the periphery of these bumps (P1. 32, fig. 5).
Remarks: This is a very characteristic species that however fits with the Asteromphalus circumscription (see discussion). Despite claims by some authors (e.g.

Simonsen, 1974; Sournia et al., 1979) that this species could be a malformation or even monstruos form of other species, I do think that it is a good and valid species; this is supported by the evidence shown here: A. sarcophagus has its own structure, quite different from other species. In addition, the proposed forms by Thorrington-Smith (1970) show a similarity in shapes and sizes with no intermediate forms of other species. A. sarcophagus is evidently related to species of the former genus Liriogramma, presently known as Asteromphalus: A. hustedtii (Kolbe) Thorrington-Smith and A. pettersonii (Kolbe) Thorrington-Smith; all the three species have six rays. Wether the two latter species are poorly developed forms of A. sarcophagus is not clear, but al least they show a slightly different areolae pattern (coarser). It is hard to relate, as suggested by Simonsen (1974), A. heptactis with A. sarcophagus, although the areolae pattern possibly is on the same line of evolution.

DISCUSSION.

1. Morphology.

The general morphology of the species studied is similar to other *genera* within the suborder Coscinodiscineae, mainly the genus Coscinodiscus Ehr. Earlier studies have shown this similarity (Fryxell & Hasle, 1973; Ross & Sims, 1973). Fryxell & Hasle (1973) have mentioned the main characters: the cribrum that is external, with the foramina internal, and the morphology and position of the rimoportulae. However, the posession of a hyaline central portion and a number of hyaline rays clearly separate Asteromphalus and Asterolampra from, for example Coscinodiscus. Some previous descriptions, mainly using TEM have been briefly given by Desikachary (1956), and indicate that "the areolae are compound and partially open to the inside".

The distinctive character of the valve morphology of

Asteromphalus raises a number of questions of which the most obvious is the possible function of the rays. Whereas thin siliceous plates (tympanum) are often found over their outer opening, particularly in gently washed or cleaned preparations, little evidence exists to suggest that the inner slit are similarly covered. They may be 'closed' only by the plasmolemma and apart from a suggestion that they may contain bacteria (Crawford, pers. comm.) there is not clear proposal as to their function.

Despite previous studies illustrating the differences between ray holes located at the singular ray and those at ordinary rays (Fryxell & Hasle, 1973, fig. 11 b), no comment has been made. The ray hole had been called a pseudonodulus by Fryxell & Hasle (1973), but this term is incorrect for this structure (Simonsen, 1975; Gombos, 1980).

The rimoportulae occur at the end of each ray, although outside openings are present only in ordinary rays, as the rimoportula of the singular ray opens within the ray tube; the internal aperture of this rimoportula is larger than those in ordinary rays. All the rimoportulae in Asteromphalus species are curved processes; there are rimoportulae in genera of the family Coscinodiscaceae (e.g. Coscinodiscus) which are relatively smaller and not exactly curved (Fryxell & Hasle, 1973), while in most of the species of the genus Azpeitia Peragallo, the rimoportulae are very short, with a "little neck" and oval slits running parallel to the marginal tangent (Fryxell et al., 1986), and in some Actinocyclus Ehrenberg species the rimoportulae have an inflated lip (e.g. Andersen et al., 1986).

Hasle (1972) and Fryxell & Hasle (1973) have shown details of the rimoportulae in two species of Asteromphalus (A. hookeri and A. heptactis), but no mention of difference among rimoportulae was made. The question of why the rimoportula of the singular ray is bigger can not be answered yet. Brooks (1975a, 1975b) showed the presence of two different sizes in the rimoportulae of Coscinodiscus species: rimoportulae and macrorimoportulae. The homology with Asteromphalus species is, however, difficult to establish. Although the different rimoportulae within the suborder Coscinodiscineae have been thought to serve a same function (Fryxell & Hasle, 1973), there are opinions that their function may be distinct (Andersen et al., 1986).

Another interesting question concerns the nature and possible function of the valve indentation and the discontinuity in the areolae pattern at the edge of the valve. The corresponding projection of the valvocopula is to be expected, but its function remains unexplained despite the regular appearence of this feature in all species of Asteromphalus and, in all cases but two, in the same position suggests that it must serve a function. The only other feature similar is the opening between valve ridges of sibling valves of Lithodesmium, but the indentation here are at opposite ends of the mantle and can not have similar functions. Fryxell & Hasle (1973) illustrated the indentation in A flabellatus, but omitted any reference to it. The structure has not been reported from any Asterolampra species and my own observations show it to be absent.

In agreement with some authors (Fryxell & Hasle, 1973; Ross & Sims, 1973), the present observations show the loculate areola in the Asteromphalus species studied, with the foramen inside and the velum (cribrum) outside. The areolar pattern presents the same general arrangement of small poroids in quincunx in all species studied and this could be valid for all Asteromphalus species. As variations of the general pattern, rather elongate poroids may replace the common round poroids (type B), or several round poroids may aggregate (types C, D); other patterns include the hexagonal arrangement of large poroids (type E), the raised type, which has a round raised area with small poroids (type F), or the raised type without poroids which are in a flat area (type G). Finaly, it is worth to mention the Roperialike type, present in Spatangidium arachne (traditionaly considered an Asteromphalus species), where poroids are arranged in circles, but keeping the same basic allignement in quincunx (type H).

Inside views of the valves reveal the presence of the annulus, which may be in various shapes and positions, depending on each species. The annulus may be stellate, circular, subcircular, and it can be placed in the very centre or slightly excentrc. It is likely from this that it is the inside layer of the valve that is formed first, as the annulus is the structure where silicification may start first, in centric diatoms (Round & Crawford, 1981).

The main characters that can be used to distinguish the different species of Asteromphalus, from light and electron microscopy, are given in Table III. Summarising, they are: size, number of rays, shape of central portion and separating lines, areolae pattern, the position and relative size of the indentation, and shape and position of the annulus. The characters that may vary in a single species are the size and the number of rays (Van Der Spoel et al., 1973, found even intervalvar variation in one Asteromphalus species: one valve having one ray less than the other one in the same frustule).

More studies, however, are recomended on the morphology of the genus, especially the variation in a same species and possible intergrades among species.

2. Taxonomy and contribution to a partial revision.

On the basis of all the characters mentioned above, the grouping of species has been attempted. I have proposed two subgenera and seven sections to include most of the valid species of Asteromphalus. The observations made here also led me to propose an emended diagnosis of the genus:

Cells solitary, discoid; valves circular, subcircular, elliptic, ovate or oblong in shape, flat or convex. Central portion hyaline and circular, angled or stellate, reduced or extended (occupying between 1/6 to 1/2 of the valve diameter). Hyaline rays numerous, varying from four to twenty-nine, those apart from the singular ray (usually thinner and longer or shorter) are termed ordinary rays, being usually wider than the singular ray, and may be curved and vary slightly in width throughout. All rays end in a ray hole when the tympanum (that covers it) is lost due to cleaning or dissolution. The ordinary rays have an external opening of the rimoportula; each ray bears one rimoportula at its end close to the valve margin, the rimoportula of the singular ray being larger than those of the ordinary rays. Separating lines radiate from the very centre or from other parallel separating lines, which form the base of the singular ray; the separating lines may be branched, and are straight, curved or bent. Segments between rays have areolae which may be coarse or fine in pattern (6 to 14 areolae/ 10 um). An indentation next to the singular ray may be located to one side of it, on the valve edge, and corresponding to the indentation is a projection of the girdle (valvocopula).

Since the work of Rattray (1889), no revision of Asteromphalus has been attempted. Mills (1933, cited by Van Landingham, 1967) and Van Landingham (1967) have listed the species they considered to be valid, but this was made without a critical appraisal of the characters. Furthermore, only two authors have attempted to make an infrageneric classification: Ralfs (in Pritchard, 1861) proposed two groups (subgenera ?), and Rattray (1889) proposed three groups (sections ?). These two classifications are not useful at present because they did not take into account important characters like the areolae pattern, the pattern of separating lines, and others just shown in this study (indentation, annulus, etc.); thus, the earlier classifications are to be changed in the light of new observations made by light and electron microscopy.

Accordingly, I propose to make the following

taxonomic changes:
New combination:
Asterolampra centraster (Johnston) Hernandez-Becerril comb. nov.
Basionym: Asteromphalus centraster Johnston, 1860, Quat. J. Microsc. Sci., p. 12, pl. 1, fig. 10.
The lack of a singular ray means that this species must be considered a true Asterolampra species.

Asteromphalus wiville-thompsonianus O'Meara
O'Meara, 1877, p. 57, pl. 1, fig. 5.
This species can not be considered as a Asteromphalus species, because it lacks a singular ray. It should be regarded as an imperfect form of Asterolampra marylandica Ehrenberg. No further report of this species has been made since its original description.

New synonymies:
Asteromphalus humboldtii Ehrenberg
Ehrenberg, 1844, p. 200 pl. June, fig. 6.
Synonyms: Asteromphalus challengerensis Castracane
Castracane, 1886, p. 134, pl. 5, fig. 2, non pl. 9, fig. 2.
Asteromphalus Xegularis Karsten
Karsten, 1905, p. 90, pl. 8, fig. 12.
Asteromphalus robustus Castracane fo.
sensu Manguin, 1954, p. 15, pl. 2, fig. 7.
non Asteromphalus hookeri Ehrenberg
Ehrenberg, 1844, p. 200, pl. June, fig. 3.
This species has been placed as a synonym of A, hookeri (most probably since Greville, 1860). However, material from the Antarctic Ocean (permanent preparations) have revealed the presence of A. humboldtii, indeed closely related to A. hookeri, but being more robust and larger (diameter = 91-106 um), with the base of the singular ray differently shaped from that of A. hookeri, and also a high number of rays (more than 8) which are quite robust, and the areolae pattern is slightly coarser, 6-7/ 10 um. Type material has unfortunately not been

studied. Material studied here corresponds to slides 33558 (BM) and 149056 (CAS).

Asteromphalus dallasianus (Greville) Ralfs
Ralfs in Pritchard, 1861, p. 836.
Synonym: AsterolamprA dallasiana Greville
Greville, 1860, p. 115, pl. 4, fig. 10.
This species must be considered as a valid Asteropmphalus species, because observations made of the type material (BM, slide 2196) showed the presence of the singular ray.

Asteromphalus senectus Tempére et Brun
Tempére & Brun in Schmidt, 1896, pl. 202, fig. 17.
non Asteromphalus humboldtii var. senectus Tempére gt Brun
Tempére & Brun in Schmidt, 1896, pl. 202, fig. 17.
Species that should be considered a valid one, as it is completely different from A. humboldtii which has been related to. Probably its closest link is A. darwinii.

Asteromphalus brunii Pantocsek
Pantocsek, 1892, pl. 21, fig. 309.
Synonym: ? Asteromphalus urbanii Julilj
Jurilj, 1957, p. 32, pl. 5, fig. 2.
A. urbanii is apparently conspecific with A. brunii. Now the question arises wether or not both are conspecific with A.darwinii. It was considered wise to keep them separated, mainly because A. brunii (and A. urbanii) has a central portion circular rather than angled, and relatively larger than A. darwinij.

A number of species considered valid by Van Landingham (1967) have been previously reallocated in what, I consider to be their appropiate taxonomic position: A. antarcticus, A. qrovei, A. kinkeri and A. ovatus. With all these propositions, the number of valid Asteromphalus species is 40, including the A. leboimei Manguin (Manguin, 1957) (considered a new form of A. hookeri by Van Der Spoel et aj., 1973), the new

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combinations made by Thorrington-Smith (1970), the species described by Simonsen (1974), the new species described herein, and _Asteromphalus_ sp., also described here. However, as some species are little known and fairly rare, further studies on them should be carried out soon. Three species traditionally considered to be _Asteromphalus_ are not included here (as they are thought to belong to another genus: _Spatangidium):_ A. _nankoorensis_ Grunow, A. _nanus_ Mann and _Spatangidium arachne_ Brébisson.

The classification, including the valid species considered in this study, except _A.trigonus_ Schmidt, is the following:

Genus _Asteromphalus_ Ehrenberg

Subgenus Asteromphalus

I. Section Pseudoasterolampra

1. _A. vanheurckii_ Mann *

II. Section Variabile

2. _A. variabilis_ (Grev.) Rattray *
3. _A. moronensis_ (Grev.) Schmidt
4. _A. dallasianus_ (Grev.) Ralfs

III. Section Genuina

5. _A. roundii_ Hernandez-Becerril *
6. _A. stellatus_ (Grev.) Ralfs *
7. _Asteromphalus_ sp. *
8. _A. flabellatus_ (Bréb.) Greville *
9. _A. cleveanus_ Grunow
10. _A. hiltonianus_ (Grev.) Ralfs *
11. _A. elegans_ Greville *
12. _A. imbricatus_ Wallich *
13. _A. ingens_ Simonsen *
14. _A. wallachianus_ (Grev.) Ralfs
15. _A. shadboltianus_ (Grev.) Ralfs *
16. _A. roperianus_ (Grev.) Ralfs *
17. _A.rarus_ Rattray

IV. Section Hookeri

18. A. hookeri Ehrenberg *
19. A. humboldtii Ehrenberg

V. Section Robusta

20. A. hungaricus Pantocsek
21. A. brookei Bailey
22. A. diminitus Mann
23. A. robustus Castracane *
24. A. heptactis (Bréb.) Ralfs *
25. A. beaumontii Ehrenberg
26. A. ornithopus Karsten

VI. Section Darwiniana

27. A. depyi Pantocsek
28. A. senectus Tempére et Brun
29. A. emergens *Mann*
30. A. eminens Mann
31. A. hyalinus Karsten
32. A. cholnokyi Julilj
33. A. brunii Pantocsek
34. A. darwinii Ehrenberg *
35. A. parvulus Karsten
36. A. leboimei Manguin

Subgenus Liriogramma (Kolbe) Hernandez-Becerril

VII. Section Sarcophaga.

37. A. sarcophagus Wallach *
38. A. hustedtii (Kolbe) Thorrington-Smith
39. A. petersonii (Kolbe) Thorrington-Smith

* Species studied here.

3. Phylogenetic and taxonomic relationships.

Many of its morphological characters make the genus Asteromphalus very distinctive, but its belonging to the family Asterolampraceae has no doubt. As mentioned earlier, this family includes five genera: Asterolampra, Asteromphalus, Bergonia, Rvlandsia and Discodiscus

(Gombos, 1980). Another genus that may be related is Brightwellid Greville, but this was placed outside the family by Ross & Sims (1973), who believed its chambers can not be to the rays in Asterolampra or Asteromphalus. In addition, Gombos (1980) discussed palaeontological evidence to suggest thet the genus Brightwellia is "an independent branch of the Coscinodiscaceae and is not on the main development line to the Asterolampraceae". Simonsen (1979) included Brightwellia in the family Asterolampraceae. I concur with Ross & Sims (1973) and Gombos (1980) that Brightwellia should not be considered as a member of the family Asterolampraceae and its relation with the family is possibly due to evolution in parallel.

According to Gombos (1980) the Asterolampraceae are linked to Coscinodiscus, as the latter represents the ancestor of the family, through species like Bergonia primitiva Gombos. Asteromphalus and Asterolampra are the only extant genera in the family, and it is likely that Asteromphalus evolved from Asterolampra, because fossil evidence indicates that Asterolampra is an older genus than Asteromphalus (Gombos, 1980). However, although Gombos (1980) suggests that Asterolampra uraster Grove et Sturt constitutes a link between the two genera, it is possible that other exist, for instance, Asteromphalus vanheurckii and A. variabilis. In fact, these two species may easily be misidentified as Asterolampra species due to the valve shape and the poor differenciation of the singular ray, and also because the areolae patterns are similar and the indentation is ill-defined.

Despite that some authors mention a low number of Asteromphalus species (e.g. five extant species, according to Ricard, 1987; Van Der Spoel et al., 1973, mentioned that many species, if not all Asteromphalus species, are morphs or ecotypes of A. hookeri, placing it as the type species of the genus), it is evident that a range of species can be found within the genus. Some of them share a number of characters and therefore may be related. The species grouped here within the section Genuina share the character of areolae pattern and that of the indentation position, however, A. eleaans, A, imbricatus and A. ingens show a bent pattern in the separating lines, unlike the other members of the section. The inclusion of A. ingens should be considered as preliminar.

4. Aspects of biogeography.

On the basis of available information and my own observations, an attempt has been made to give some general patterns of distribution of as many species as possible. Some species show a rather limited distribution and may be considered as typical species.

A. North or south cold-water (occasionally found in temperate regions).

A. beaumontii Ehr. ?
A. brookei Bailey
A. darwinii Ehr.
A. hookeri Ehr.
A. humbodltii Ehr.
A. hvalinus Karsten
A. leboimet Manguin
A. parvulus Karsten

B. Cosmopolitan.

A. heptactis (Bréb.) Ralfs

C. World-wide warm-water (occasionally found in temperate regions).

A. dallasianus (Grey.) Ralfs
A. flabellatus (Bréb.) Ralfs
A. moronensis (Grey.) Schmidt
A. robustus Castracane
A. roperianus (Grey.) Ralfs 1
A. vanheurckii Mann
A. variabilis (Grey.) Rattray
A. wallachanus (Grey.) Ralfs

D. Tropical and subtropical.

A. cleveanus Grunow
A. roundii Hernândez-Becerril

A. hiltonianus (Grey.) Ralfs A. shadboltianus (Grey.) Ralfs
A. hustedtii (Kolbe) Thor.-Sm. Asteromphalus sp.

E. Indo-Pacific (endemic ?).

A. elegans Grev. 2 A. petersonii (Kolbe) Thor.-Sm.
A. ingens Simonsen A. sarcophagus Wallich 3

F. Indian Ocean (endemic ?).

A. imbricatus Wallich A. stellatus (Grev.) Ralfs

1: According to Sournia (1968) and Simonsen (1974) there are few reports of this species from the Antarctic Ocean.
2: According to Sournia (1968) A. elegans has been also found in the Mediterranean Sea.
3: Reported from the Antarctic Ocean (Sournia et al., 1979).

5. Final remarks.

The present work is far to complete the revision of Asteromphalus, but it is a contribution to. the morphology and taxonomy of the genus, in a modern context. Further studies are to be necessary, including the investigation of the morphology of species not included here, as well as the study of the variation in a same species, which should involve experimental work (cultures, life cycles, etc.). The function of some particular structures, such as the rays, tympanum, marginal valve indentation has been only suggested here, thus investigation should be made on this subject.

Species identification should consider as many characters as possible, in order to ensure it positive. In the literature, a high number of species allocations are misidentifications. The use of electron microscope is practical, but even using light microscope species identification can be reached.

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REFERENCES.

Allen, W.E. & E.E. Cupp. 1935. Plankton diatoms of the Java **Sea**. Ann. Jardin Bot. Buitenzorg 44: 101-224.

Andersen, R.A., L.K. Medlin & R.M. Crawford. 1986. An investigation of the cell wall components of Actinocyclus subtilis (Bacillariophyceae). J. Phycol. 22: **466-479.**

Anonymous. 1975. Proposals for the standardization of diatom terminology and diagnoses. Nova Hedwigia, Beih. 53: 323-354.

Bailey, J.W. 1856. Notice of microscopic forms found in the surrounding of the Sea of Kamschatka. Am. J. Sci. Arts, 2nd ser. 22: 1-7, pl. 1.

Brébisson, A. de. 1857. Description de quelques nouvelles diatomées observées clans le guano du Pérou, et formant genre Spatangidium. Bull. Soc. Linn. Normandie 2: 292-298, pl. 3.

Brooks, M. 1975a. Studies on the genus Coscinodiscus. I. Light, transmission and scanning electron microscopy of C. concinnus Wm. Smith. Bot. Mar. 18: 1-13.

Brooks, M. 1975b. Idem. II. Light, transmission and scanning electron microscopy of C. asteromphalus Ehr. Bot. Mar. 18: 15-27.

Castracane, F. 1875. Contribuzione alla florula delle diatomee del Mediterraneo ossia esame del contenuto nello stomaco di una salpa pinnata pescata a Messina. Atti Acad. Pontif. Nuovi Lincei 28: 377-396, pl. 6.

Castracane, F. 1886. Report of the diatomaceae collected by H.M.S. Challenger during the years 1873-1876. Rep. Sci. Res. Voyage H.M.S. Challenger during the years 1873-1876, Bot. 2: 1-178, 30 pls.

Cleve, P.T. 1873. On diatoms of the Arctic Sea. Bih. K. Svenska Vetensk. Hand. 1 (13): 1-28, 3 pls.

Cupp, E.E. 1943. Marine plankton diatoms of the west coast of Wort America. bull Scripps Inst. Oceanogr. 5 (1): 1-238.

Desikachary, T.V. 1956. Electron microscope studies on diatoms. J. Roy. Microsc. Soc., ser III 76: 9-36.

Ehrenberg, C.G. 1844. Einige vorlaufige Resultate der Untersuchungen der von der Sudpolreise des Captain Ross, so wie von den Herren Schayer and Darwin zugekommenen Materialen uber das Verhalten des kleinsten Lebens in den Oceanen and den grossten bisher zuganglichen Tiefen des Weltmeers. Ber. Akad. Wiss. Berlin, 1884: 182-207.

Ehrenberg, C.G. 1854. Mikrogeologie. Das Erden and Felsen schaffende Wirken des unsichtbaren kleinen selbstandigen Lebens auf der Erde. Vol. II. Atlas. Leopold Voss, Leipzig. 31 pp., 40 pls.

Ehrenberg, C.G. 1872. Mikrogeologische studien uber das kleinste Leben der Meeres-Tiefgrunde aller Zonen and dessen geologischen Einfluss. Phys. Abb. Akad. Wiss. Berlin, 1972: 131-398, 12 pls.

Fryxell, G.A. & G.R. Hasle. 1973. Coscinodiscineae: some consistent pattern in diatom morphology. Nova Hedwigia, Beih. 45: 69-96.

Fryxell, G.A., P.A. Sims & T.P. Watkins. 1986. Azpeitia (Bacillariophyceae): related genera and promorphology. Syst. Bot. Monogr. 13. 74 pp.

Geissler, U., J. Gerloff, J.-G. Helmcke, W. Krieger & B, Reimann. 1961. Diatomeenschalen im elektronenmikroskopischen Bild. In: Helmcke, J.-G. & kW. Krieger (Eds.) Idem. Teil 3. J. Cramer, Weinheim. 44 pp., pls. 201-300.

Gombos, A.M. 1980. The early history of the diatom family Asterolampraceae. Bacillaria 3: 227-272.

Gran, H.H. & E.C. Angst. 1931. Plankton diatoms of the Puget Sound. Publ. Puget Sound Biol. Stat. Univ. Washington 7:417-516.

Greville, R.K. 1859. Description of diatomaceae observed in California guano. Quat. J. Microsc. Sci. 7: 155-166.

Greville R.K. 1860. A. monograph of the genus <u>Asterolampra,</u> including <u>Asteromphalus</u> and <u>Spatangidum.</u> Trans. Microsc. Soc. London, n.s. 8: 102-124.

Grunow, A. 1870. Algae. Reise der Osterreichischen Fregatte Novara. Bot Theil. Wien. 1-104, 11 pls.

Hasle, G.R. 1972. Two types of valve processes in centric diatoms. Nova Hedwigia, Beih. 39: 55-78.

Hasle, G.R. 1978. Diatoms. In: Sournia, A. (Ed.). Phytoplankton manual. UNESCO. Paris. pp. 136-142.

Helmcke, J.-G. & W. Krieger. 1954. Diatomeenschalen im elektronenmikroskopischen Bild. Teil 2. 24 pp., pls. 103-200.

Hendey, N.I. 1937. The plankton diatoms of the Southern Seas. Discovery Rep. 16: 151-364.

Hendey, N.I. 1959. The structure of the diatom cell wall as revealed by electron microscope. J. Quekett Microsc. Club, ser. 4, 5: 147-175.

Hendey, N.I. 1964. An introductory account of the smaller algae of British costal waters. Parts IV and V. Bacillariophyceae. Fish. Inv. ser. IV. HMSO. London. 317 pp., 45 pls.

Hendey, N.I. 1971. Some marine diatoms from the Galapagos Islands. Nova Hedwigia 22: 371-422.

Hernandez-Becerril, D.U. 1987. Especies de fitoplancton tropical del Pacifico Mexicano. I. Diatomeas y silicoflagelados. Rev. Lat-amer. Microbiol. 29: 413-428.

Hustedt, F. 1930. Die Kieselalgen Deutschlands, Osterreichs and der Schweiz. In: Rabenhorst, L. Kryptogamenflora. Akad. Verlag. Leipzig. 7 (1): 1-920.

Hustedt, F. 1958. Diatomeen aus der Antarktis and dem Sudatlantik. Deutsch. Antark. Exped., 1938-1939 Wiss. Ergebn. 2 (3): 103-191, pls. 3-13.

Johnson, C. 1860. Description of diatomaceae, chiefly of those found in "Elide" lower California guano. Quat. J. Microsc. Sci. 8: 11-21.

Jurilj, A. 1957. Dijatomeje sarmatskog mora okoline Zagreba. Priridslovna Istrazivanja 28. Acta Biologica I. Jugoslay. Akad. Znanosti umjet. Zagreb. 5-143 pp., 40 pls.

Karsten, G. 1905. Das Phytoplankton des Antarktischen Meeres nach der deutschen Tiefsee-Expedition 1989-1899. Wiss. Ergebn. deutsche Tiefsee-Exped. "Valdivia", II, 2 (1): 1-136, pls. 1-19.

Karsten, G. 1907. Das Indische Phytoplankton. Wiss. Ergebn. deutsche Tiefsee-Exped. "Valdivia", II, 2 (3): 221-548, pls. 35-54.

Lebour, M.V. 1930. The plankton diatoms of northern seas. Ray. Soc. Pub. 116: 1-244, 4 pls.

Manguin, E. 1954. Diatomées marines de file Heard (Australian Antarctic Research Expedition). Rev. Algol., n. ser. 1 (1): 14-24.

Manguin, E. 1957. Premier inventarie des diatomées de la Terre Adelie Antarctique. Espéces nouvelles. Rev. Algol. 3: 111-134.

Mann, A. 1907. Report of the diatoms of the Albatross voyages in the Pacific Ocean, 1888-1904. Cont. U.S. Nat. Herb. 10: 221-442, inc. pls. 44-54.

Mann, A. 1925. Marine diatoms of the Philippine Islands. Bull. Smithsonian Inst., U. S., Natl. Mus. 100: 1-182, 39 pls.

Mann, A. 1937. Diatoms. Australasian Antarctic Expedition 1911-1914. Sci. Rep. Ser. C-Zoology & Botany 1(): 1-82, 6 pls.

Medlin, L.K. 1978. The use of critical point drying for cleaned diatom valves. Bacillaria 1: 169-177.

Muller-Melchers, F.C. 1957. Plankton diatoms of the "Toku-Maru" voyage (Brazil coast). Bol. Inst. Oceanogr. 8 (1-2): 111-137.

Okuno, H. 1951. Electron microscopical study on antarctic diatoms (1). J. Jap. Bot. 26 (10): 305-310.

Okuno, H. 1964. Fossil diatoms In: Helmcke, J.-G. & W. Krieger (Eds.). Diatomeenschalen im elektronmikroskopischen Bild. Tell 5 J. Cramer, Weinheim. 48 pp., pls. 414-513.

O'Meara, M.A. 1877. On the diatomaceous gatherings made at Kerguelen's land by H.N. Moseley. M.A. H.M.S. "Challenger". J. Linn. Soc., Botany 15: 55-59.

Pantocsek, J. 1892. Beitrage zur Kenntniss der fossilen Bacillarien Ungarns. III Teil. W. Junk, Berlin. 42 pls.

Peragallo, H. & M. 1897-1908. Diatomées marines de France et des districts maritimes voisins. M.J. Tempére. Grez-sur-Loing. 491 pp., 137 pls.

Pritchard, A. gt Al. 1861. A history of the Infusoria, including Desmidiaceae and the Diatomaceae British and foreign. Whitaker & Co., London. 938 pp., 40 pls.

Rattray, J. 1889. Revision of the genus Coscinodiscus and some allied genera. Proc. Roy. Soc. Edimburgh 16: 449-692.

Ricard, M. 1977. Les peuplements de diatomées des lagons de 1'archipel de la Societé (Polynésie Frangaise): Floristique, écologie, structure des peuplements et contribution a la production primaire. Rev. Algol. 12 (3-4): 143-336.

Ricard, M. 1987. Atlas du phytoplancton marin. Vol. II. Diatomophycées. C.N.R.S., Paris. 297 pp.

Ross, R. & P.A. Sims. 1973. Observations on family and generic limits in the centrales. Nova Hedwigia, Beih. 45: 97-130.

Ross, R. et al. 1979. An amended terminology for the siliceous components of the diatom cell. Nova Hedwigia, Beih. 64: 513-533.

Round, F.E. & R.M. Crawford. 1981. The lines of evolution of the Bacillariophyta. I. Origin. Proc. Roy. Soc. London B 211: 237-260.

a..

Schmidt, A. 1876-1899. Atlas der Diatomaceenkunde, pls. 38, 137, 202. Leipzig.

Silva, E.S. 1953. Diatomaceas do plancton marinho de Angola. An. Junta Inv. Ultramar 8 (2): 7-72, 11 pls.

Simonsen, R. 1974. The diatom plankton of the Indian Ocean expedition of R.V. "Meteor" 1964-1965. Meteor. Forsch., Reih. D. 19: 1-66, 41 pls.

Simonsen, R. 1975. On the Pseudonodule of the centric diatoms, or Hemidiscaceae reconsidered. Nova Hedwigia, Beih. 53: 83-97.

Simonsen, R. 1979. The diatom system: ideas on phylogeny. Bacillaria 2: 9-71.

Sournia, A. 1968. Diatomées planctoniques du Canal de Mozambique et de file Maurice. Mem. ORSTOM 31: 1-120, 13 pls.

Skvortzow, B.W. 1931a. Marine diatom from the Kanazawa oyster experimental station of Japan. Philippine J. Sci. 41 (1): 119-127, 2 pls.

Skvortzow, B.W. 1931b. Marine littoral diatoms from environs of Vladivostok. Philippine J. Sci. 41 (1): 129-150, 6 pls.

Sournia, A., J.-R. Grail & G. Jacques. 1979. Diatomées et dinoflagellés planctoniques d'une coupe meridienne dans le sud de 1'ocean Indien (campagne "Antiprod I" du Marion-Dufresne, mars 1977). Bot. Mar. 22: 183-198.

Stosch, H.A. von 1977. Observations on Bellerochea and Streptothecq, including descriptions of three new planktonic diatom species. Nova Hedwigia, Beih. 54: 113-166.

Subrahmanyan, R. 1946. A systematic account of the marine plankton diatoms of the Madras coast. Proc. Indian Acad. Sci., sect. B 24 (4): 85-197.

Thorrington-Smith, M. 1970. Some new and little-know planktonic diatoms from the West Indian Ocean. Nova Hedwigia, Beih. 31: 815-835.

Van Der Spoel, S., G.M. Hallegraeff & R.W.M. Van Soest. 1973. Notes on variation of diatoms and silicoflagellates in the South Atlantic Ocean. Netherlands J. Sea Res. 6 (4): 518-541.

Van Landingham, S.L. 1967. Catalogue of fossil and recent genera and species and their synonyms. Part I. Acanthoceras through Bacillaria. J. Cramer, Lehre. pp. 1-493.

Walllich, G. C. 1860. On the siliceous organisms found in digestive cavities of the salpes, and their relation to the Flint Nodules of the chalk formation. Trans. Microsc. Soc. London, n.s. 8: 36-55, pl. 2

Wood, E.J.F. 1963. Studies on Australian and New Zealand diatoms. VI. Tropical and subtropical species. Trans. Roy. Soc. New Zealand, Botany 2 (15): 189-218.

Table I. Plankton samples used for this study (Light and electron microscopy).

No.	Samples	Location	Cruise	Source
		Coasts of **Baja** California	CICIMAR-CIB **8508**	CIB
01		26' 41' N 112° 39' W		
02		25° 53' N 112° 58' W		
03		25° 43' N 113° 17' W		
04		26° 10' N 113° 09' W		
05		26° 00' N 113° 18' W		
06		25° 50' N 113° 46' W		
07		26° 27' N 113° 19' W		
08		26° 18' N 113° 38' W		
09		26° 07' N 113° 57' W		
10		26° 25' N 113° 50' W		
11				
12		26° 14' N 114° 29' W		
13		26° 52' N 114° 01' W		
14		26° 24' N 114° 20' W		
15		26° 32' N 114° 40' W		
		Gulf of California	GOLCA **8606**	CIB
16		27° 28' N 111° 25' W		
17		27° 45' N 110° 53' W		
18		27° 31' N 111° 20' W		
19		27° 49' N 111° 55' W		
20		27° 59' N 111° 36' W		
21		28° 13' N 111° 14' W		
22		28° 24' N 111° 52' W		
23		28° 38' N 112° 28' W		
		Coasts of Baja California	CIB-CICIMAR 8605	CIB
24		26° 25' N 114° 17' W		
25		26° 35' N 113° 58' W		
26		26° 15' N 114° 36' W		
27		26° 29' N 113° 34' W		
28		26° 19' N 113° 48' W		
29		26° 03' N 113° 39' W		
30		26° 13' N 113° 19' W		
31		26° 23' N 113° 00' W		
32		25° 47' N 112° 38' W		
33		25° 37' N 112° 57' W		
34		25° 09' N 113° 05' W		
35		24° 45' N 112° 25' W		
36		24° 01' N 112° 23' W		
37		24° 19' N 112° 34' W		
38		23° 55' N 111° 05' W		
39		23° 27' N 111° 12' W		

	Gulf of California	GOLCA 8411	CICIMAR
40-49			
	Gulf of California	CORTES II (1985)	ICML
50	25° 02' N 108° 32' W		
51	25° 33' N 110° 59' W		
52	26° 51' N 110° 06' W		
53	28° 10' N 112° 48' W		
54	29° 12' N 112° 31' W		
55	29° 48' N 114° 20' W		
56	31° 17' N 114° 22' W		
57	28° 09' N 111° 41' W		
58	26° 59' N 111° 50' W		
59	23° 08' N 109° 27' W		
60	21° 38' N 106° 31' W		
	Pacific Ocean coasts of Mexico	CORTES II (1985)	ICML
61	21° 28' N 105° 20' W		
62	22° 45' N 108° 53' W		
63	20° 49' N 105° 41' W		
64	Salina Cruz	Author	Author
65	Maruata	Author	Author
66	Chamela		IB
67	Pacific coasts of Peru		IB
	Indian Ocean	Discovery **1964**	IOS
68	01° 51' S 67° 46' E		
69	07° 01' S 67° 20' E		
70	13° 14' S 57° 41' E		
71	07° 28' S 54° 48' E		
	Antarctic Ocean	Discovery 1937	IOS
72	57° 45' S 65° 42' W		
73	53° 17' S 37° 14' W		
74	63° 33' S 60° 33' W		
75	Australian waters		UB1
76	Mediterranean Sea		UB2

CIB= Centro de Investigaciones Biologicas de Baja California Sur, A.C., La Paz, B.C.S., Mexico.

CICIMAR= Centro Interdisciplinario de Ciencias del Mar (IPN), La Paz, B.C.S., Mexico.

ICML= R. Cortés-Altamirano, Instituto de Ciencias del Mar y Limnologia (UNAM), Estacibn Mazatlén, Sin., Mexico.

IB= S. Gomez-Aguirre, Instituto de Biologia (UNAM), México, D.F., Mexico.

IOS= C. Chingley, Institute of Oceanographic Sciences, Wormley, Surrey, England.

UB1= F.E. Round, University of Bristol, Dept. of Botany, Bristol, England.

UB2= L.K. Medlin, University of Bristol, Dept. of Botany, Bristol, England.

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Table II. References and type slides used for this study (Light microscopy).

British Museum (Natural History), London (BM).
Greville Collection.
1330 "Asterolampra wallachiana"
1634
1778
1880 "Asterolampra hiltoniana"
1882
1938
1941
1942
2196 "Asterolampra dallasiana"
2257
2258
Roper Collection.
21672
21673
Barker Collection.
62720 Asteromphalus ovatus Castr.
62698 "Asteromphalus wvvilli" Castr.
Deby Collection.
14336
Wallich Collection.
61590
Comber Collection.
33558 "Challenger"
Adams Collection
450
Payne Collection.
42613
R.I. Firth Collection.
35657

Naturhistoriska Riksmuseet, Stockholm (S).
522 (1118)

Museum d'Histoire Naturelle, Paris (PC).
slides are labeled as follows:
Asteromphalus heptactis Bréb. (Guano de Perou)
}Asteromphalus flabellatus Bréb. (Guano de Perou)
Asteromphalus brookei Bailey (Guano de Bolivie)
Asteromphalus peltatum Bréb. (Guano de Perou)
Asteromphalus beaumontii Ehr. (Guano de Perou)

California Academy of Sciences, San Francisco (CAS).
75001 A. darwinii Grev. A.L. Brigger
75003 A. hyalinus A.L. Brigger
149056 Asteromphalus hookeri Ehr. A.L. Brigger
347009 Asteromphalus brookeii Bail. R.I. Firth

B. Hartley Particular Collection.
2017

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Table III. Major characteristics in the *Asteromphalus* species studied.

Asteromphalus species	Size (um)	Number of rays	Shape & sep. lines in central portion	Areolae pattern	Indentation features	Annulus shape & position	Variation main source
A. vanheurckii	60-77	10-12	Rounded, straight	Very fine 14-15/10	(-) consp., right or left	Stellate, centric	
A. variabilis	73-94	7-10	Angled, straight-curved	Coarse, 8-9/10	(-) consp., left side	Stellate, centric	No. rays
A. roundii	67-72	12-13	Rounded, straight	Fine, 11-12/10	(+) consp., left side	Round, excentric	
A. stellatus	38-51	9-10	Rounded, straight-curved	Fine, 12-13/10	(*) consp., left side	Round, excentric	Size
Asteromphalus sp.	72-83	11-15	Rounded, straight-curved	Fine, 11-12/10	(') consp., left side	Round, excentric	No. rays
A. flabellatus	47-65	11-13	Rounded, straight-curved	Fine, 11-13/10	(+) consp., left side	Stellate, excentric	Size
hiltonianus	98-109	17-18	Rounded, straight-curved	Fine, 11-12/10	(r) consp., left side	Round, excentric	
A. ele9ans	90-140	17-20 *(13)	Rounded, bent	Fine, 11-12/10	(') consp., left side	Round, excentric	No. rays Size
A. imbricatus	43-78	10-22	Rounded, bent (zig-zag)	Fine, 9-10/10	(*) consp., left side	Round, excentric	No. rays Size

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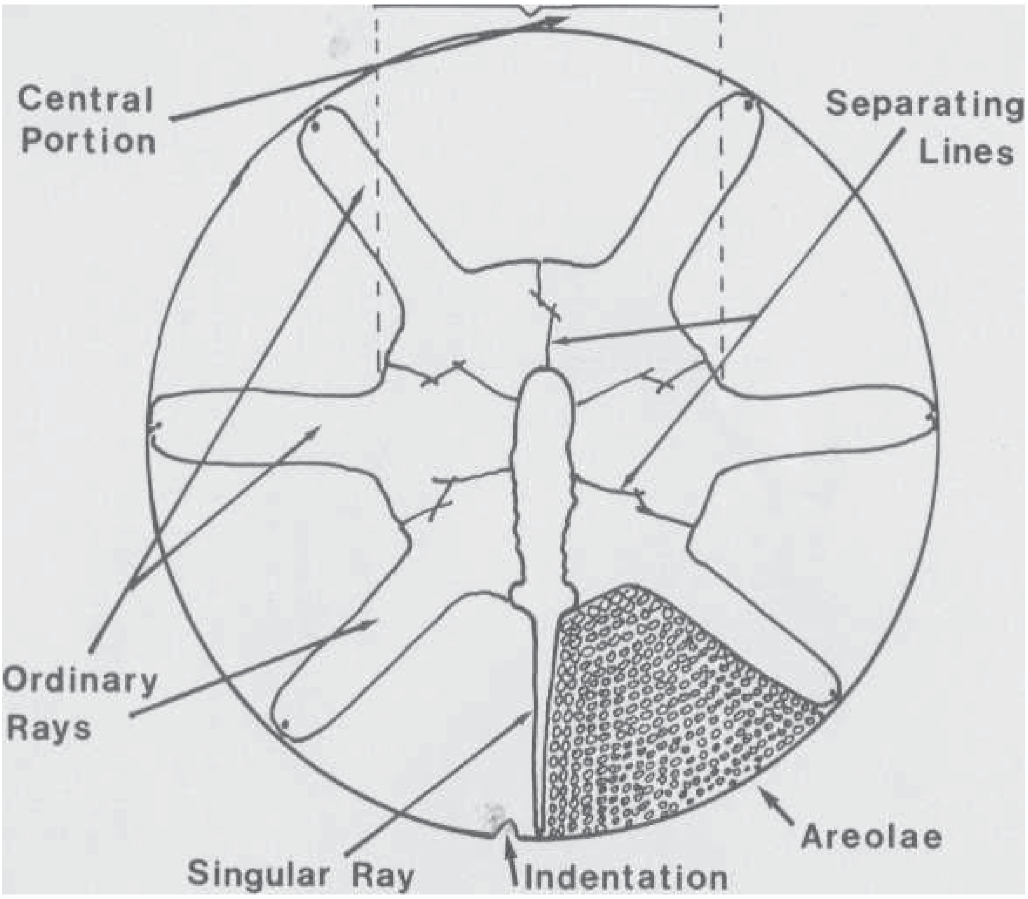
A, ingens	110-125	9-13	Rounded-elliptic bent (zi9-zag)	Fine, 11-13/10	(+) consp., left side	Round, centric	No. rays
A. shadboltianus	60	7	Angled, straight	Fine, 9-11/10	(+) consp., left side		
A. roperienus	70-175	7	Angled, straight-curved	Fine, 11-13/10	(+) consp., left side	Stellate, excentric	Size
A. hookerii	43-78	6-7	Angled, straight-curved	Coarse, 7-8/10	(+) consp., left side	Stellate, centric	
A. robustus	67-79	8-10	Rounded, bent	Coarse, 6-7/10	(*) consp., left side	Round, excentric	
A. heptactis	68-165	7	Rounded, bent (zi9-zag)	Very coarse 5-6/10	(+) consp., left side	Round, excentric	Shape, size
A. darwinii	63-72	5	Angled, bent	Coarse, 7-8/10	(+) consp., left side	Stellate, centric	
A, sarcophagus	21-37	6	Angled, straight-curved	Coarse, 8-9/10	(+) consp., left side	Round, centric	

* Number of rays as originally described (Greville, 1859).



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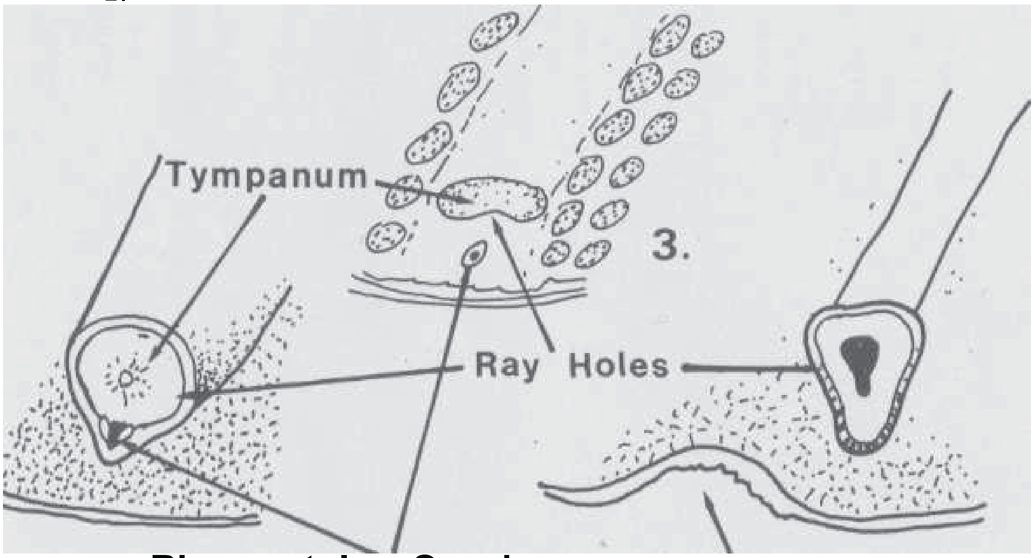
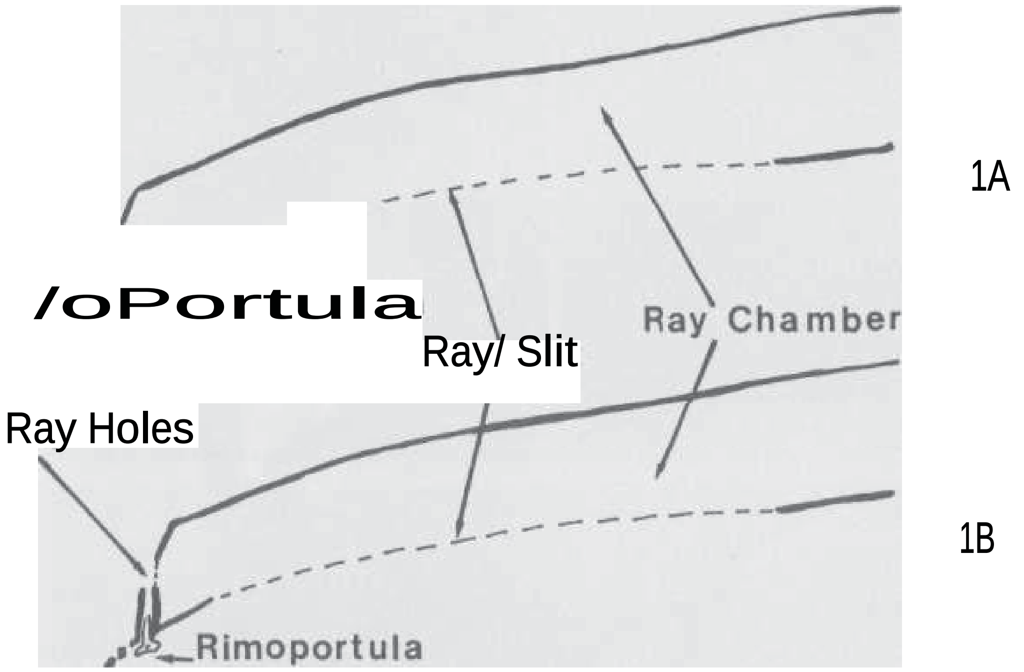
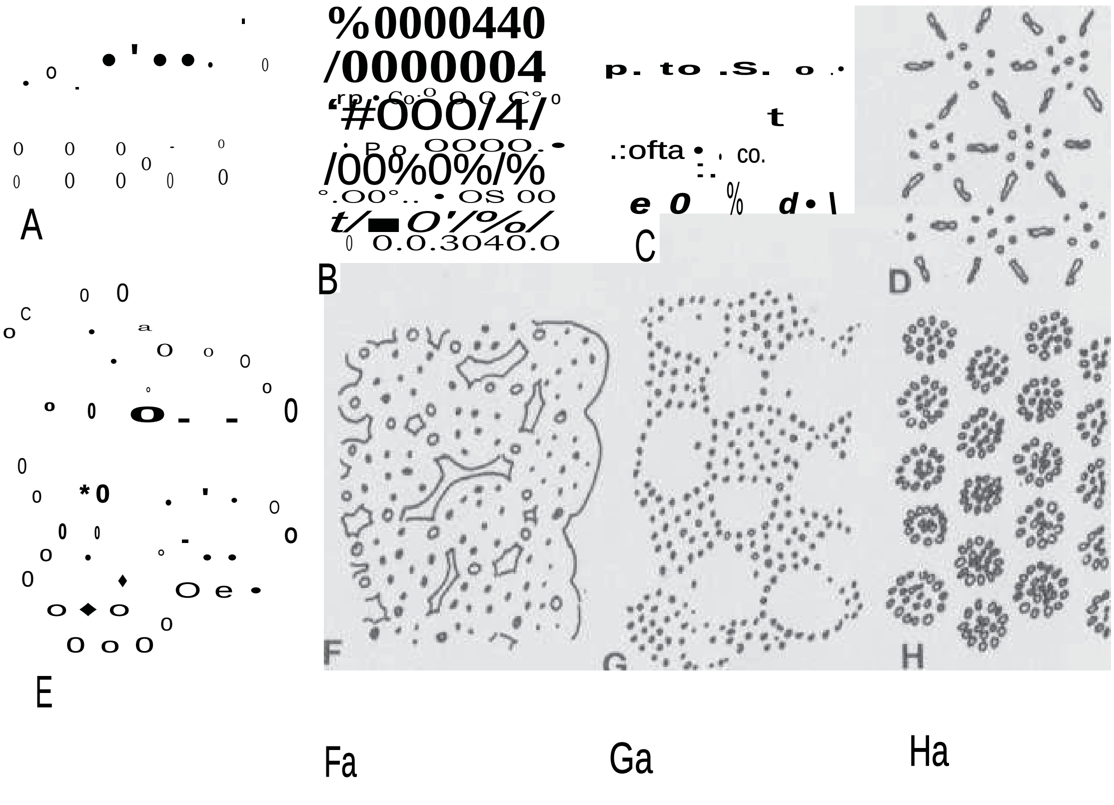


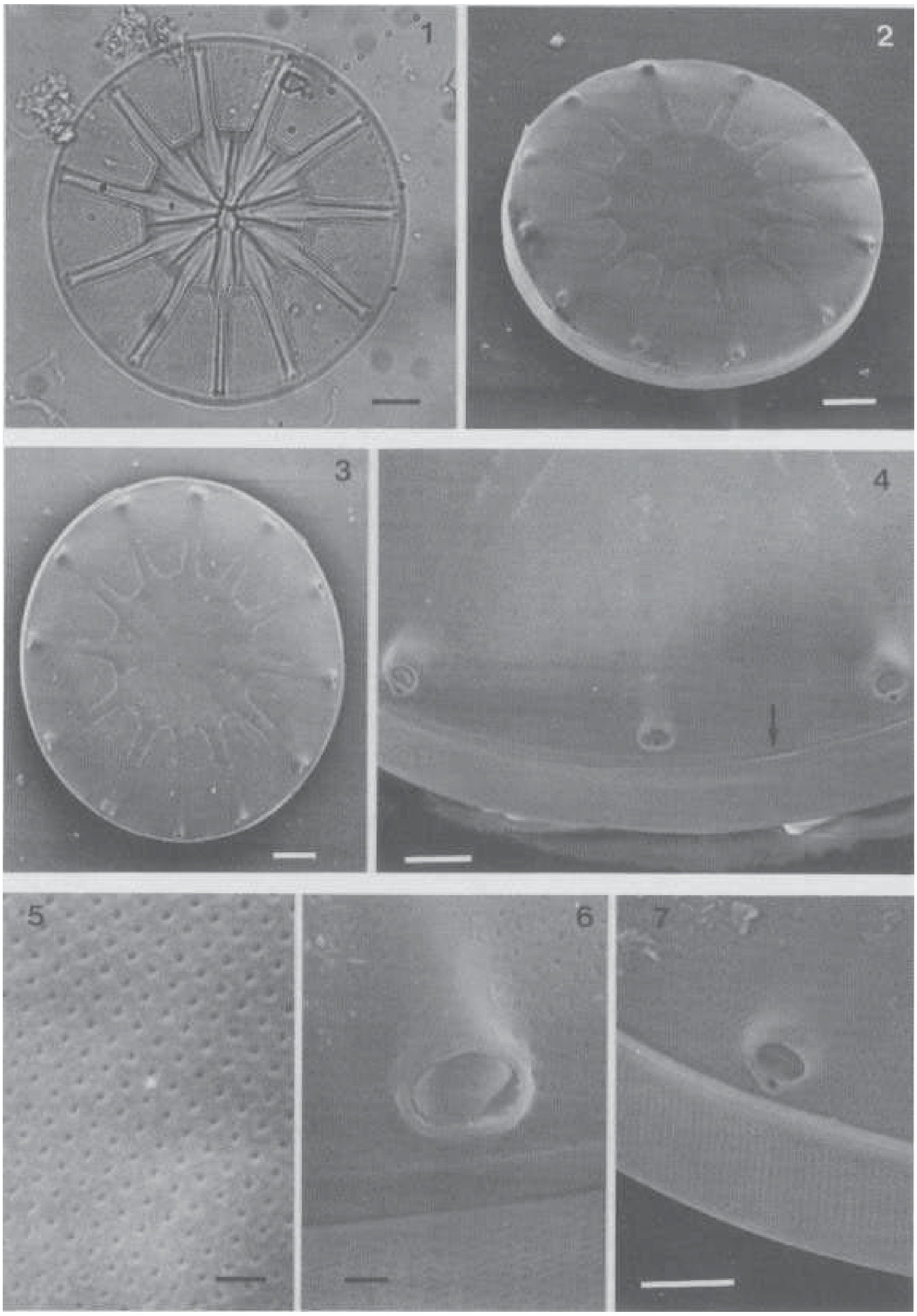
2. 4.

P1. 1. Fig. 1. Diagram to illustrate terminology in a valve of a typical species of Asteromphalus. Fig. 2. End of an ordinary ray showing structures (A. hookeri). Fig. 3. End of an ordinary ray in the closely related genus Spatangidium (S. arachne). Fig. 4. End of a singular ray showing the indentation (A. flabellatus).

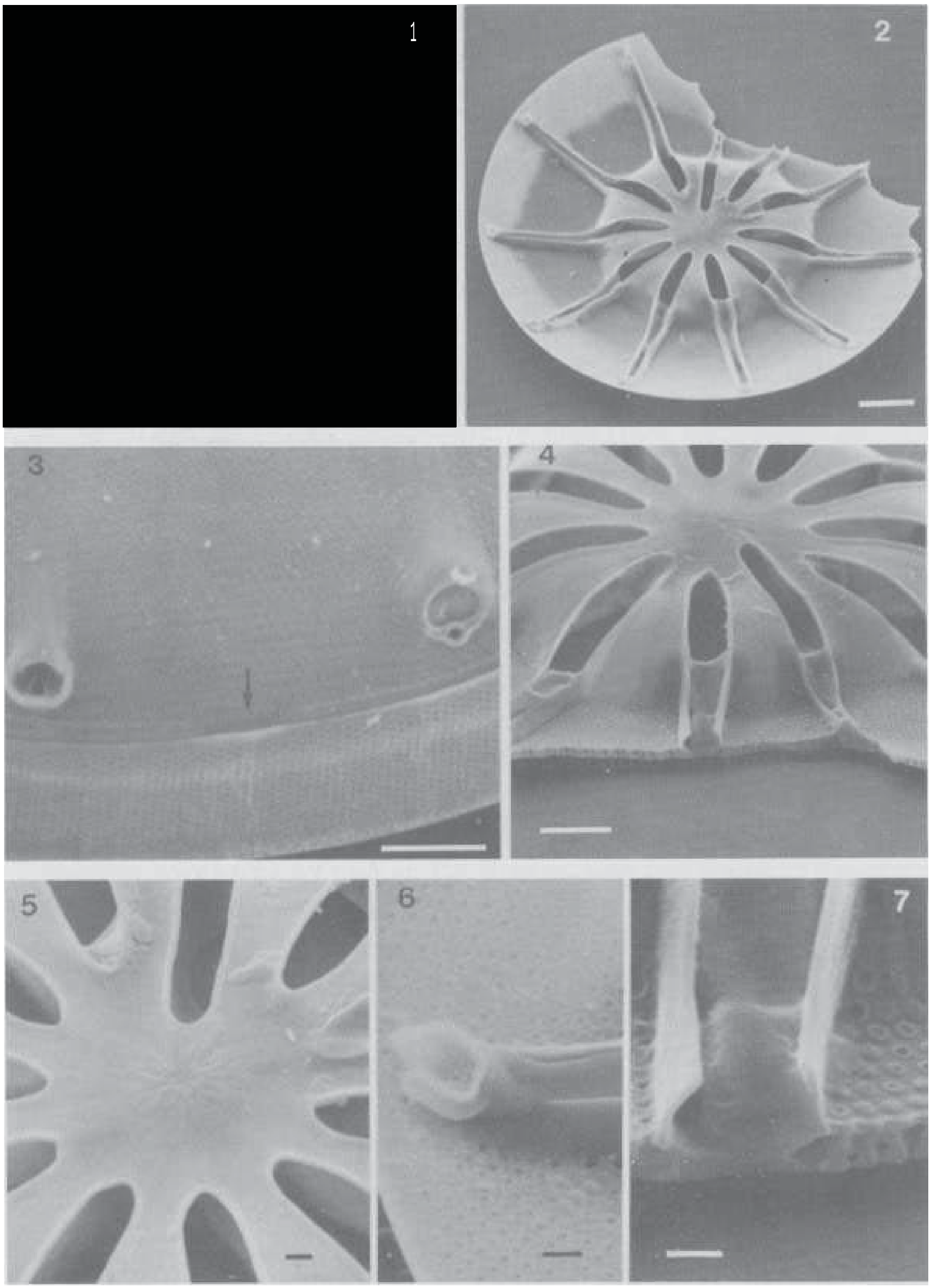




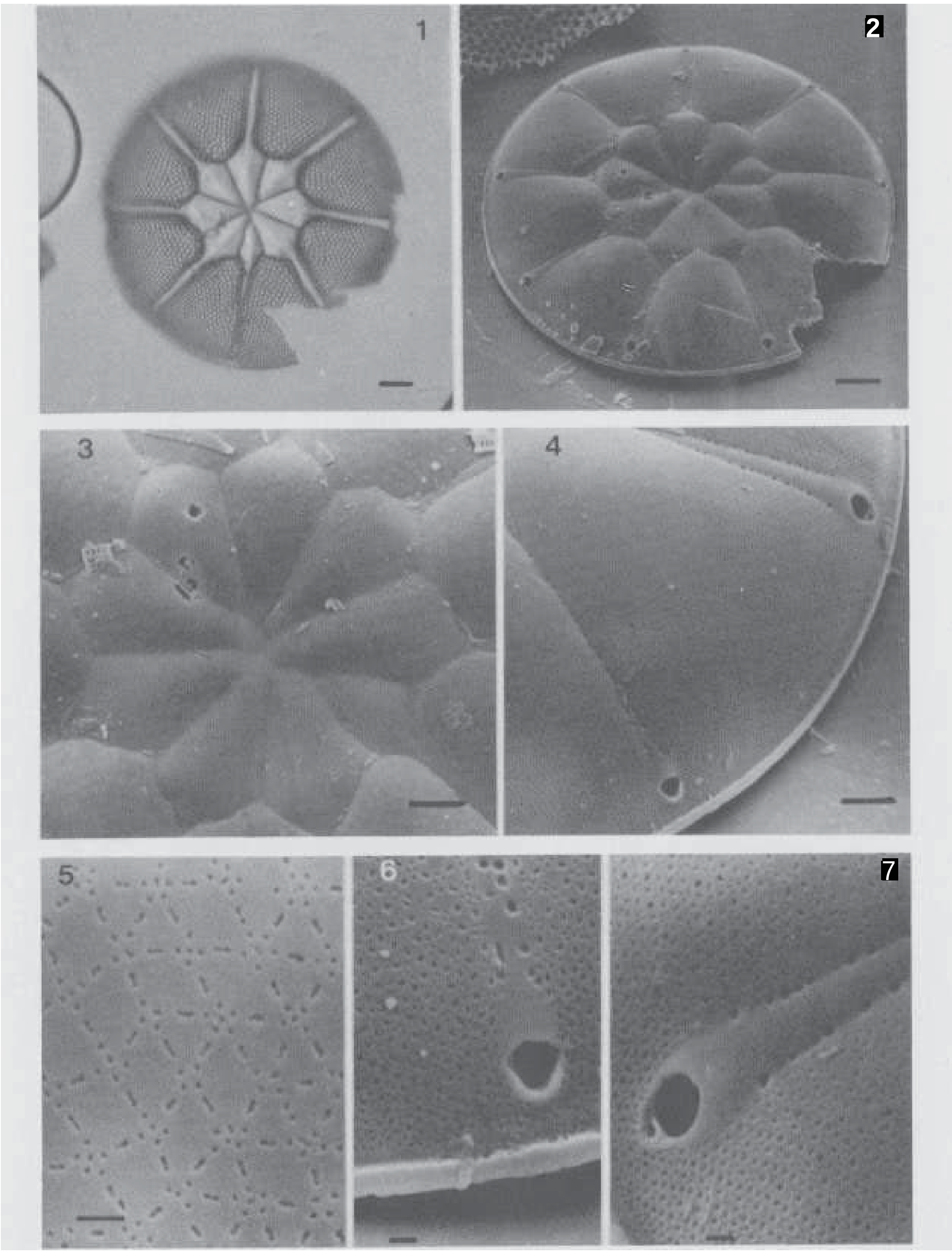
Pl. 2. Figs. la, lb. Cross section of a singular ray (la) and of an ordinary ray (lb). Figs. A-H. Types of areolae pattern in Asteromphalus (A-G) and Spatangidium (H) species. Fa, Ga, Ha are profiles of the areolae.



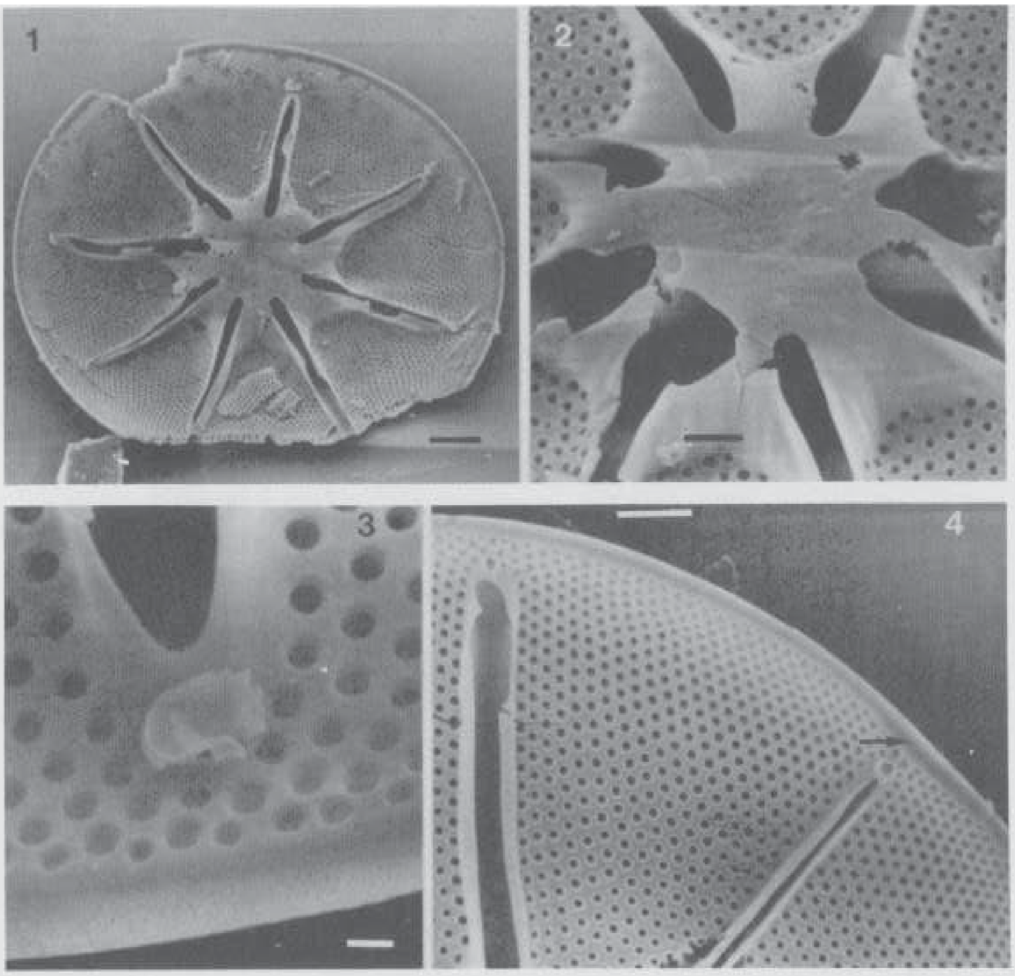
P1. 3. Asteromphalus vanheurckii. Fig. 1. A complete valve, LM. Fig. 2. A whole frustule, SEM. Fig. 3. Valve view of a complete frustule, SEM. Fig. 4. Part of frustule showing singular and ordinary rays. The arrow points the indentation. Note the striae on the girdle, SEM. Fig. 5. Areolae pattern, SEM. Fig. 6. Singular ray showing tympanum, SEM. Fig. 7. Ordinary ray, SEM. Scale bars = 10 um, Figs. 1-3, = 5 um, Figs. 4, 7, = 1 um, Figs. 5, 6.



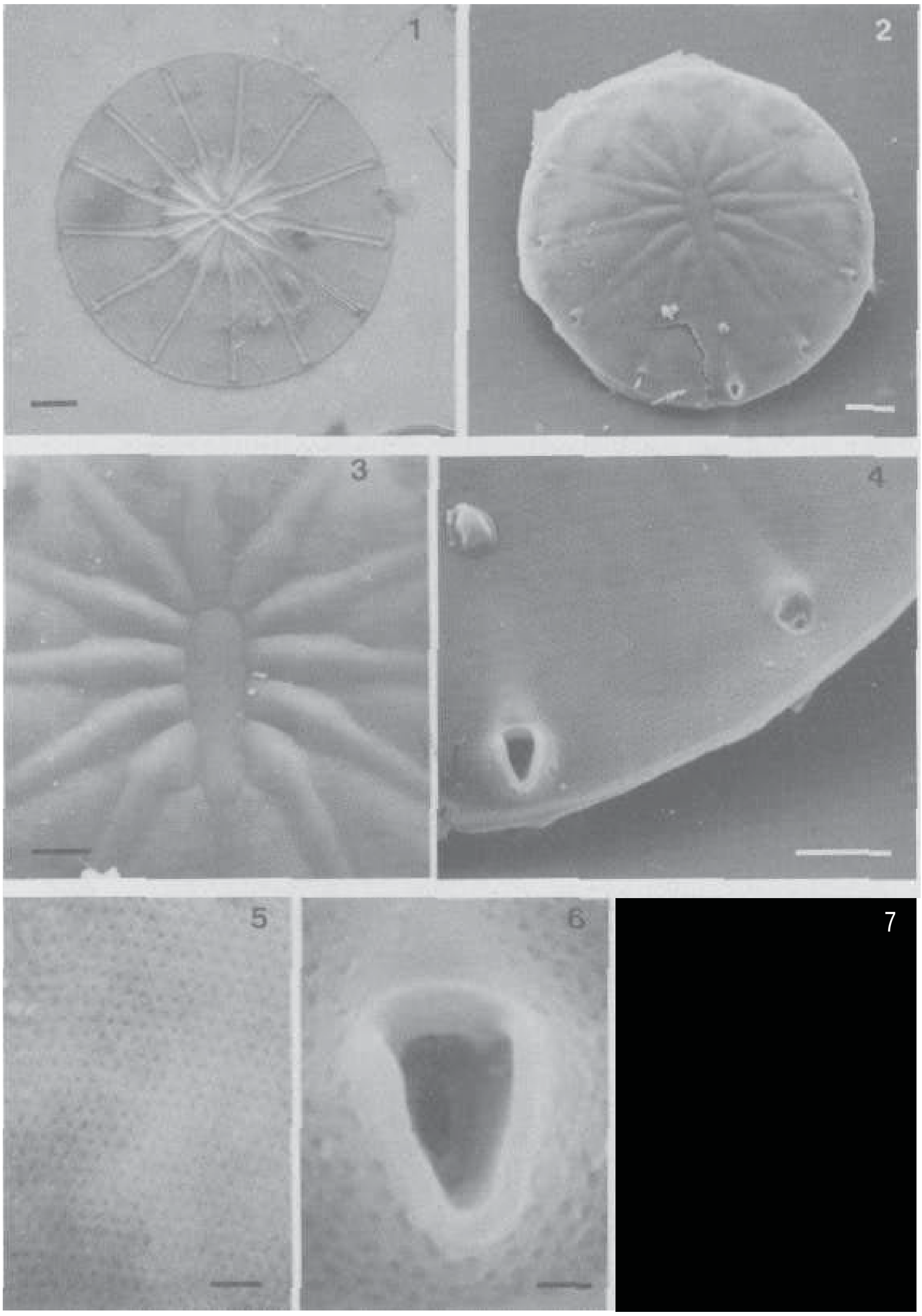
Pl. 4. <u>Asteromphalus</u> <u>vanheurckii.</u> Fig. 1. Ordinary ray (left) and singular ray (right). Arrow points the indentation (left side to the singular ray), SEM. Fig. 2. Inside view of a broken valve, SEM. Fig. 3. Singular ray (left) and ordinary ray (right). Arrow points the indentation (right side of the singular ray), SEM. Fig. 4. Inside view showing the annulus and a section of the cribrum, SEM. Fig. 5. Inside view of the annulus, SEM. Fig. 6. Rimoportula of an ordinary ray, SEM. Fig. 7. Section of the cribrum and the ray tube, SEM. Scale bars = 10 um, Fig. 2, = 5 um, Figs. 1, 3, 4, = 1 um, Figs. 5-7.



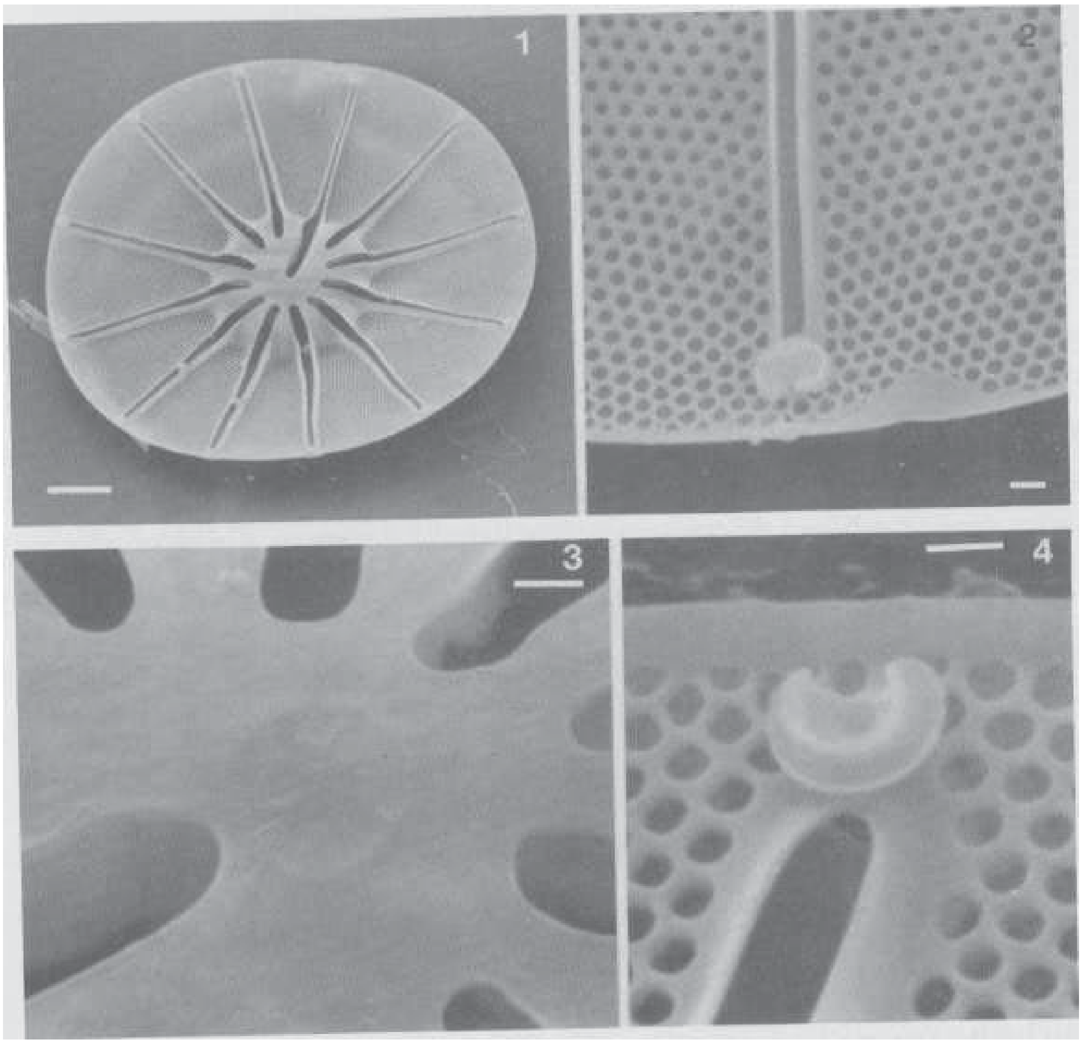
Pl. 5. Asteromphalus variabilis. Fig. 1. Partially broken valve, LM. Fig.2. Another broken valve, SEM. Fig. 3. Detail of the central portion, SEM. Fig. 4. Singular ray (left) and ordinary ray (right), SEM. Fig. 5. Areolae pattern, SEM. Fig. 6. Singular ray. Arrow points the indentation, SEM. Fig. 7. Ordinary ray, SEM. Scale bars = 10 um, Figs. 1, 2, = 5 um, Figs. 3, 4, = 1 um, Figs. 5-7.



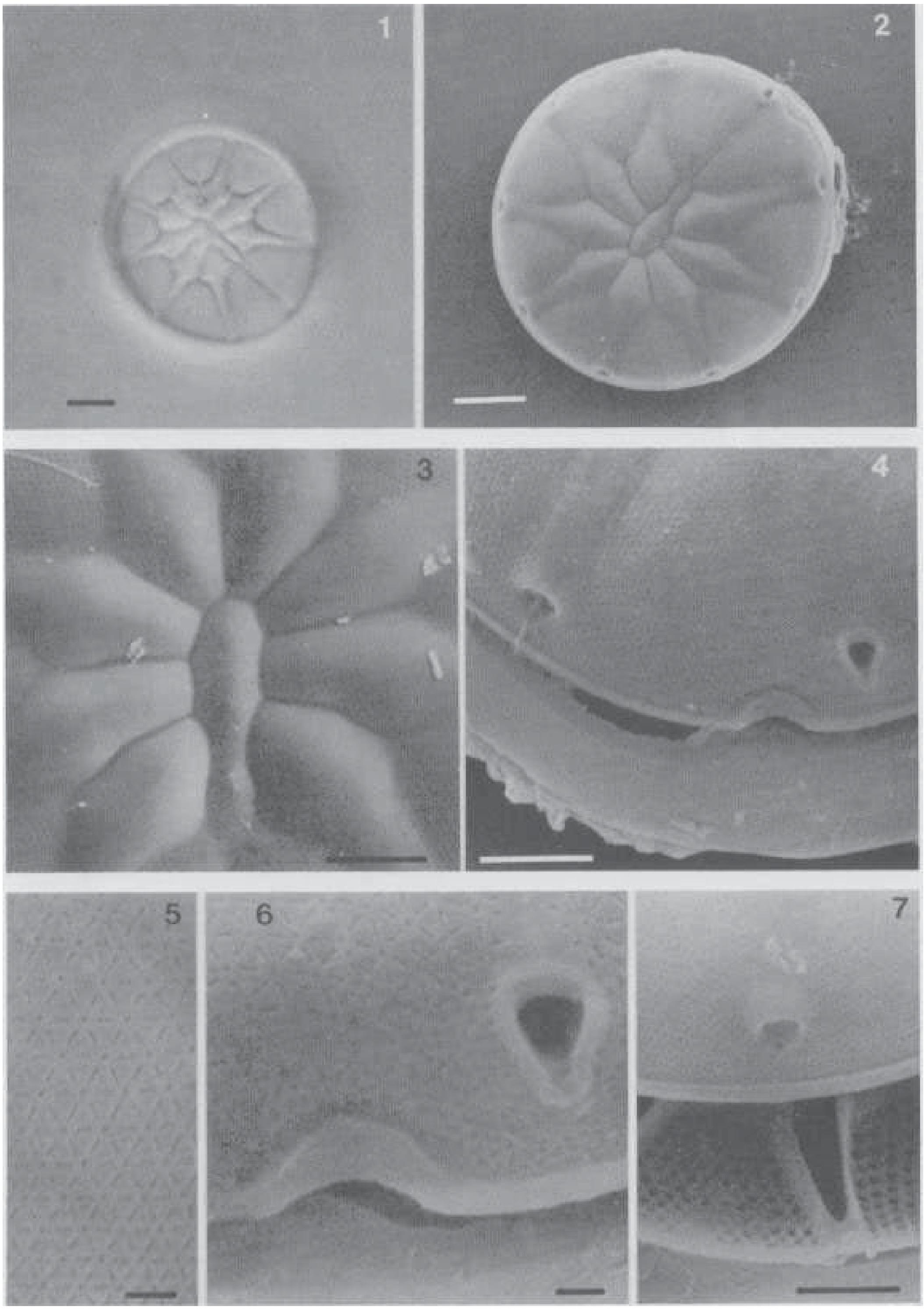
Pl. 6. Asteromphalus variabilis. Fig. 1. Inside view o a valve, SEM. Fig. 2. Inside view showing the annulus SEM. Fig. 3. Rimoportula of an ordinary ray, SEM. Fig 4. Rimoportula of an ordinary ray (lefy) and of singular ray (right). Arrow points the indentation, SEM Scale bars = 10 um, Fig. 1, = 5 um, Figs. 2, 4, = 1 um Fig. 3.



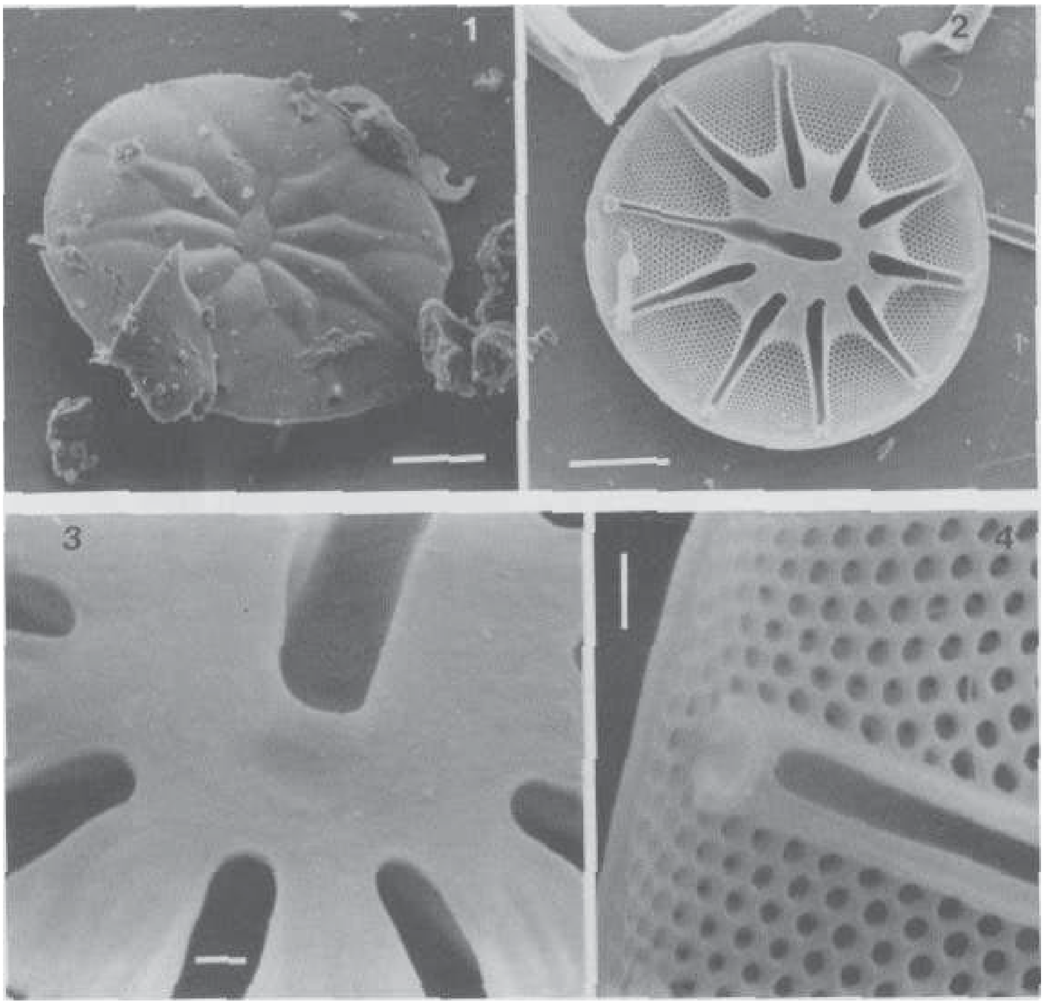
P1. 7. Asteromphalus roundii. Fig. 1. A complete valve, LM. Fig. 2. A complete valve, SEM. Fig. 3. Detail of the central portion, SEM. Fig. 4. Singular ray (left) and ordinary ray (rigth). Arrow points the indentation (partially seen), SEM. Fig. 5. Areolae pattern, SEM. Fig. 6. Ray hole (no tympanum) of the singular ray, SEM. Fig. 7. Ray hole (no tympanum) of an ordinary ray, SEM. Scale bars = 10 um, Figs. 1, 2, = 5 um, Figs. 3, 4, = 1 um, Figs. 5-7.



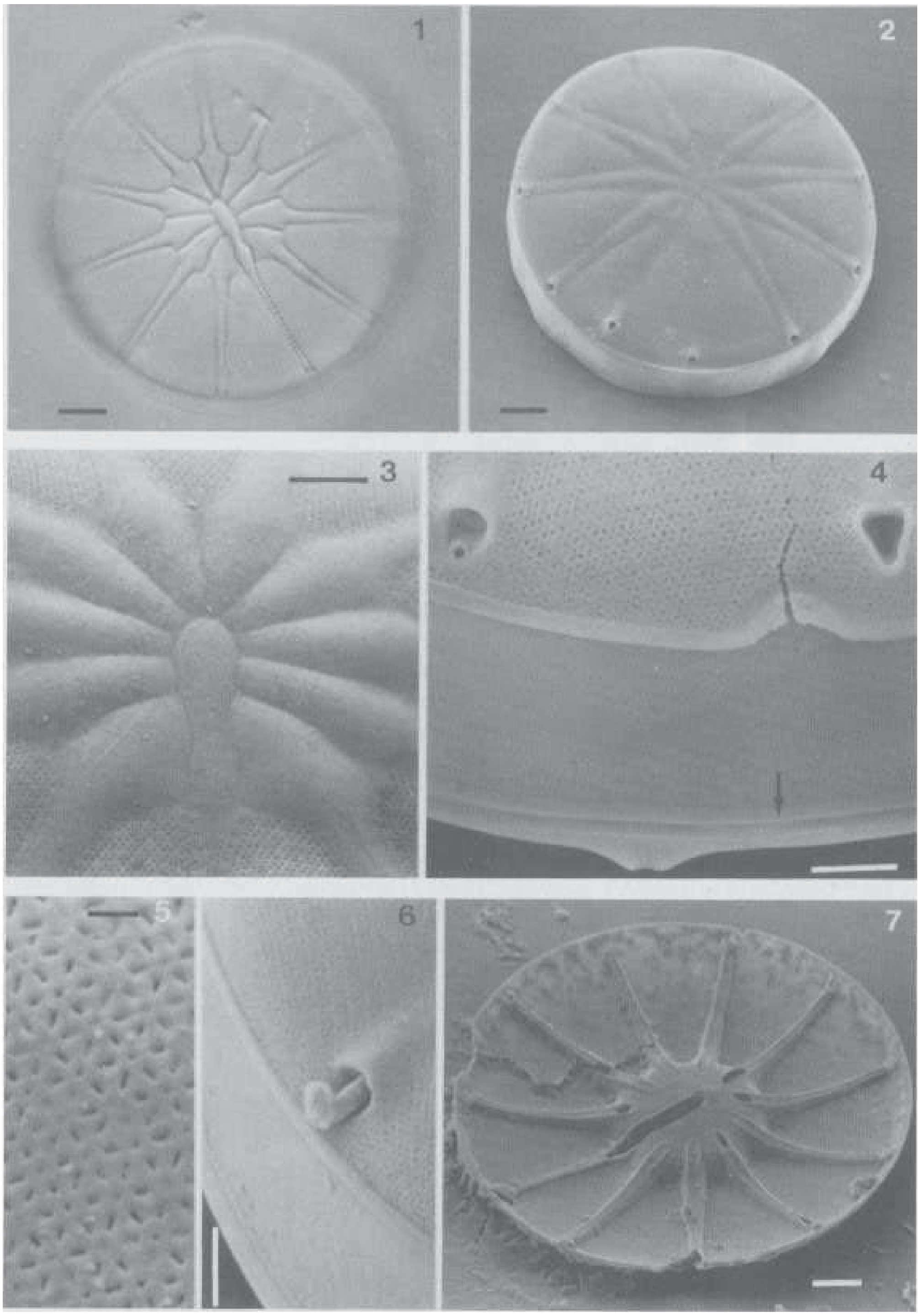
P1. 8. psteromphalus roundii. Fig. 1. Inside view of a valve, SEM. Fig. 2. Rimoportula of singular ray. Indentation can be seen to the right, SEM. Fig. 3. Detail of the annulus from inside, SEM. Fig. 4. Rimoportula of an ordinary ray, SEM. Scale bars = 10 um, Fig. 1, = 1 um, Figs. 2-4.



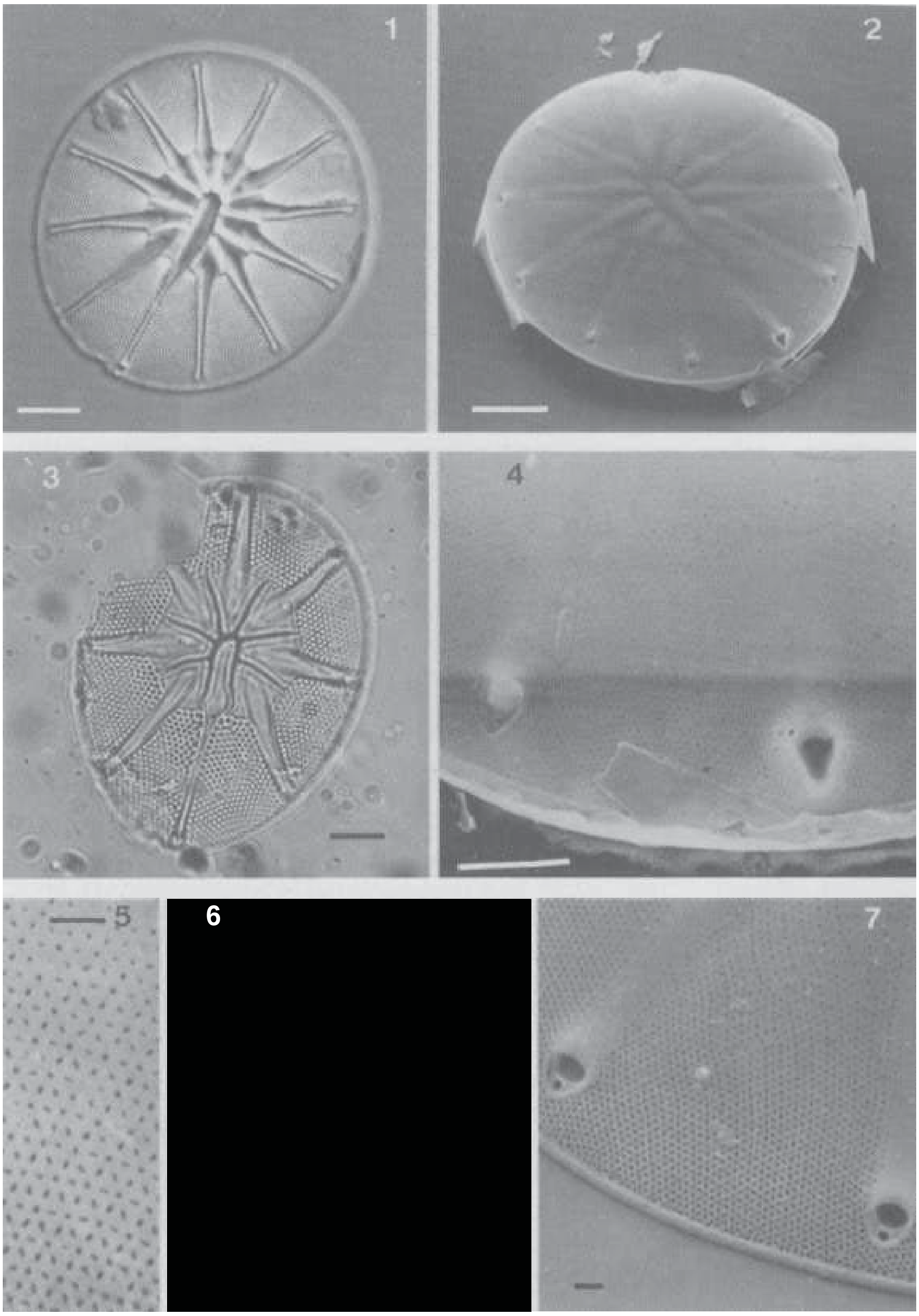
P1. 9. psteromphalus stellatus. Fig. 1. Complete valve, LM. Fig. 2. **A** whole frustule, SEM. Fig. 3. Detail of the central portion, SEM. Fig. 4. Ordinary ray (left) and singular ray (right). Note indentation to the left of the singular ray, SEM. Fig. 5. Detail of the areolae pattern, SEM. Fig. 6. Singular ray with the indentation to the left side, SEM. Fig. 7. Detail of an ordinary ray, SEM. Scale bars = 10 um, Figs. 1, 2, = 5 um, Figs. 3, 4, 7, = 1 um, Figs. 5, 6.



P1. 10. Asteromphalus stellatus. Fig. 1. **A** complete valve, SEM. Fig. 2. Inside *view* of a valve, SEM. Fig. 3. Inside view showing the annulus, SEM. Fig. 4. Rimoportula of an ordinary ray, SEM. Scale bars = 10 um, Figs. 1, 2, = 1 um, Figs. 3, 4.



Pl. 11. Asteromphalus sp. Fig. 1. A complete valve, LM. Fig. 2. A whole frustule, SEM. Fig. 3. Detail of the central portion, SEM. Fig. 4. Ordinary ray (left), singular ray (right) and indentation next to the singular ray. Arrow points the indentation in the other valve, SEM. Fig. 5. Areolae pattern, SEM. Fig. 6. Tympanum ? of an ordinary ray, SEM. Fig. 7. Inside view of the valve, SEM. Scale bars = 10 um, Figs. 1, 2, 7, = 5 um, Figs. 3, 4, 6, = 1 um, Fig. 5.



P1. 12. Asteromphalus flabellatus and A. cleveanus. Fig. 1. Complete valve, LM. Fig. 2. Complete valve, SEM. Fig. 3. Valve of A. cleveanus, LM. Fig. 4. An ordinary ray (left) and singular ray (right), SEM. Fig. 5. Detail of the areolae pattern, SEM. Fig. 6. Singular ray with the indentation to the left side, SEM. Fig. 7. Two ordinary rays, SEM. Scale bars = 10 um, Figs. 1-3, = 5 um, Fig. 4, = 1 um, Figs. 5-7.

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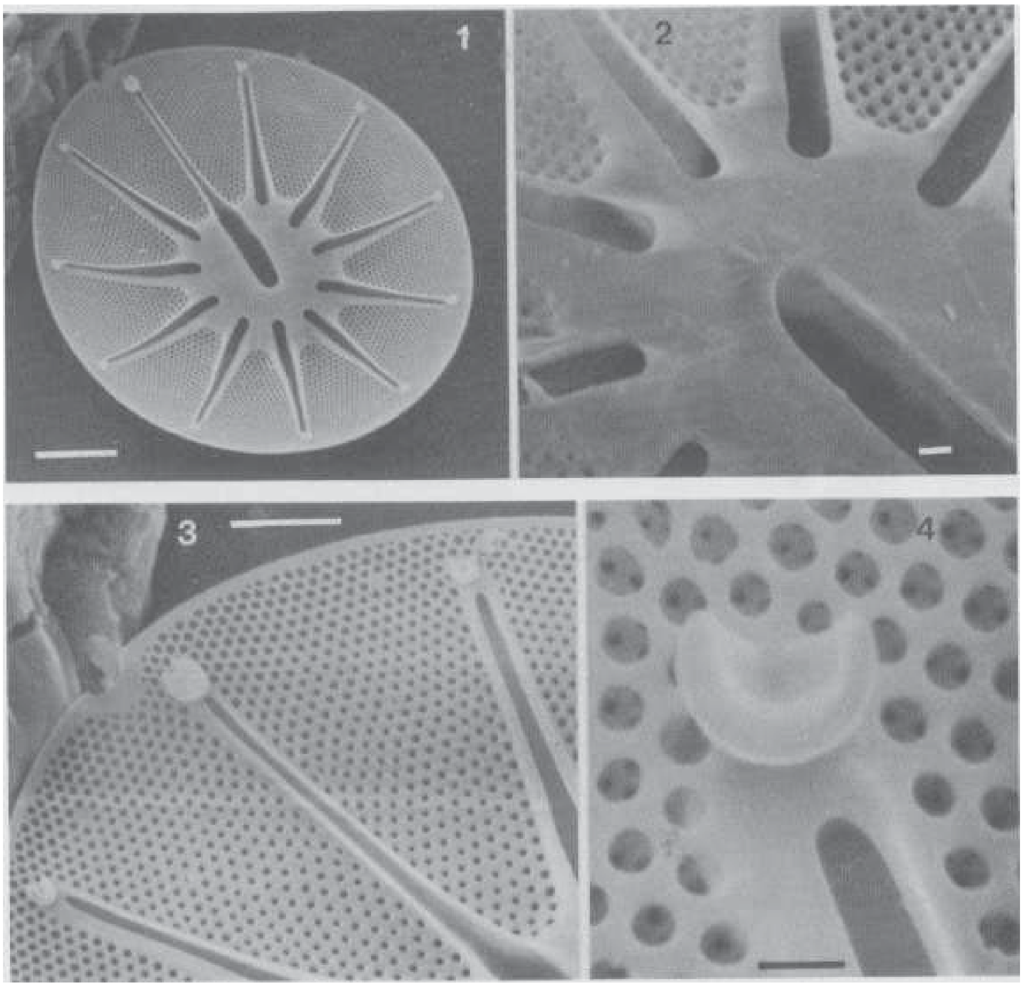
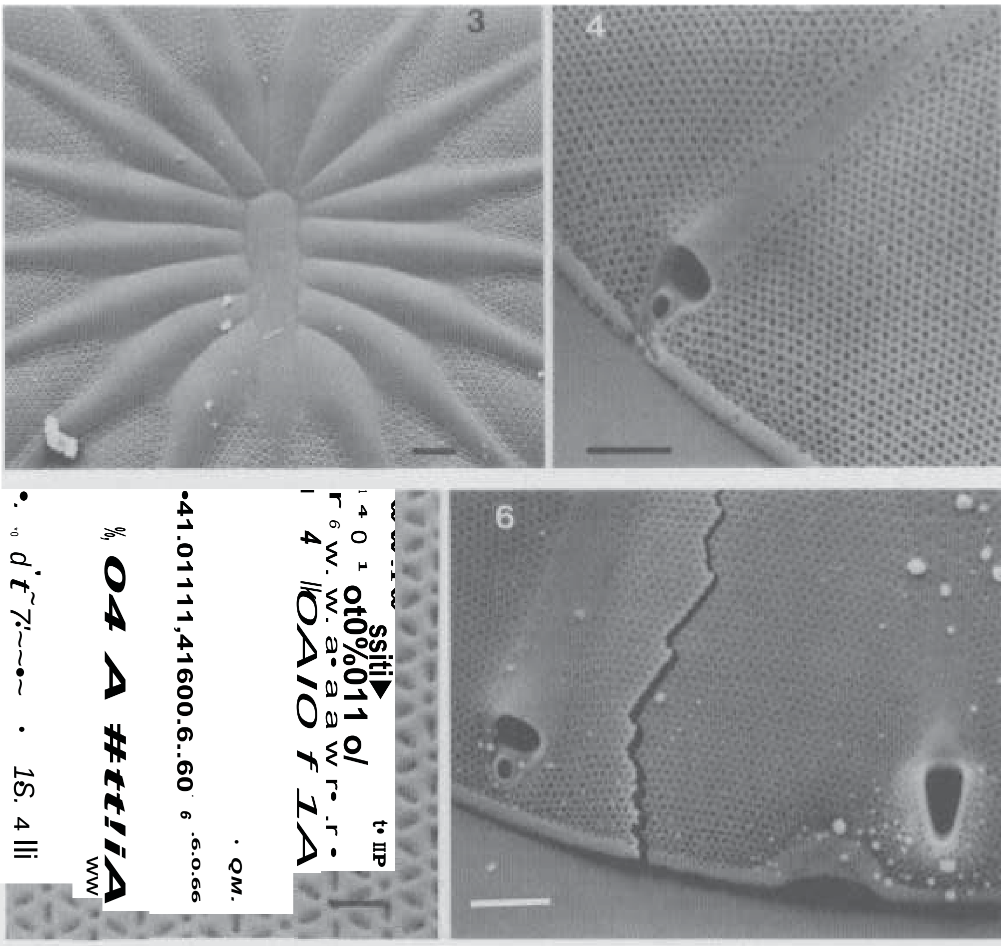


Pl. 13. Asteromphalus flabellatus. Fig. 1. Inside view of a valve, SEM. Fig. 2. Inside view showing the annulus, SEM. Fig. 3. Rimoportulae at the ends of the rays. The larger is that of the singular ray. The indentation is also apparent, SEM. Fig. 4. Rimoportula of an ordinary ray, SEM. Scale bars = 10 um, Fig. 1, = 5 um, Fig. 3, = 1 um, Figs. 2, 4.



Pl. 14. Asteromphа
valve, LM. Fig. 2.
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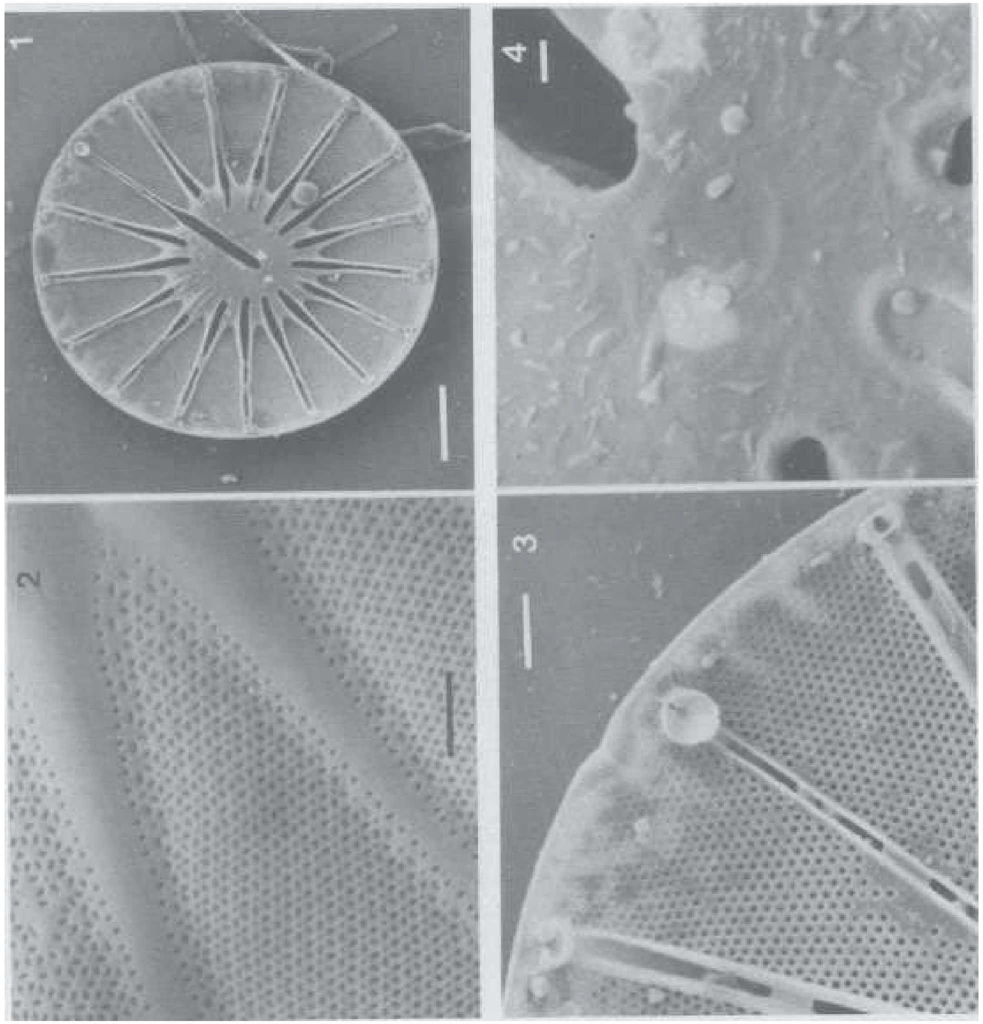
Fig. 5.



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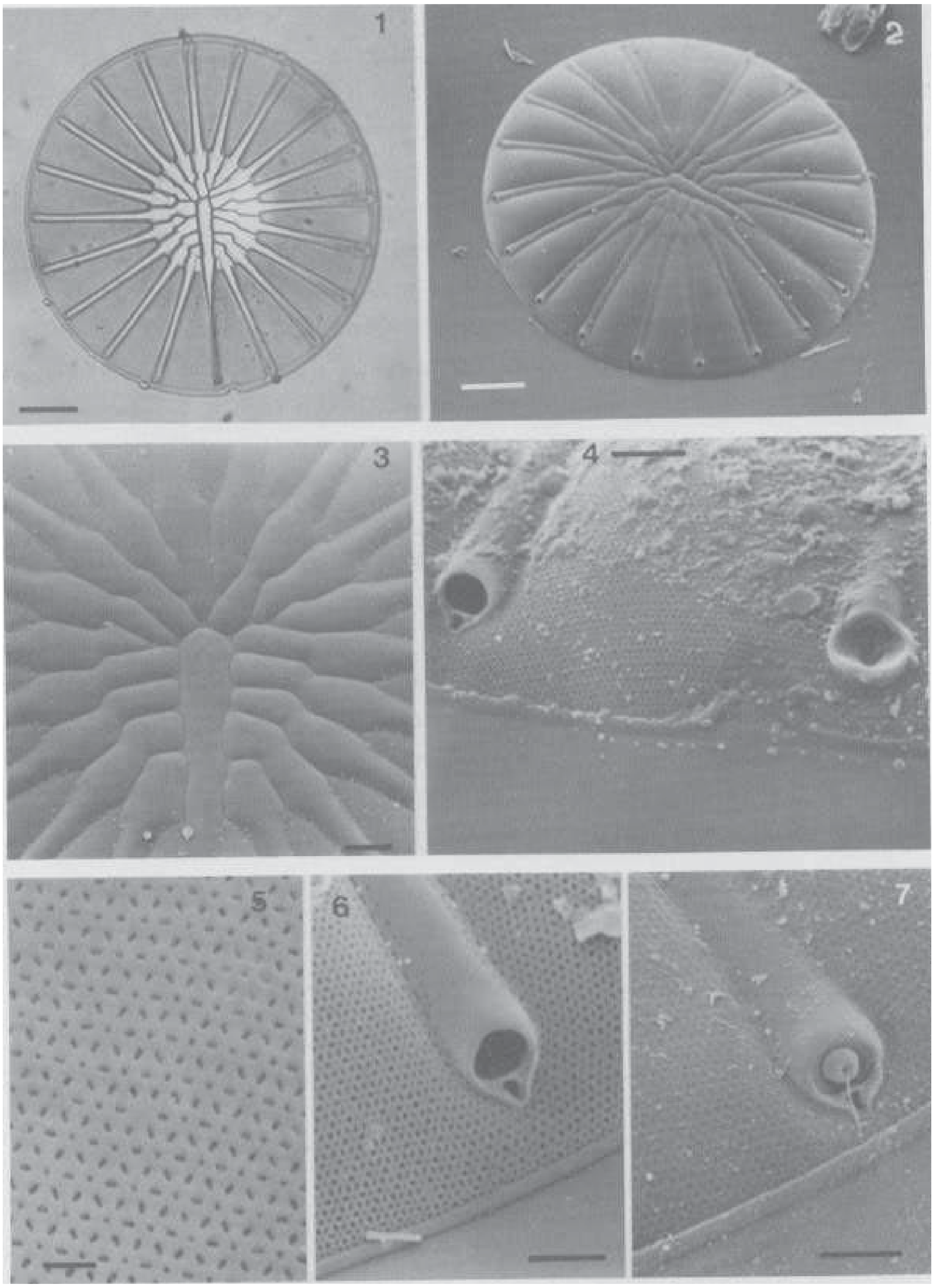
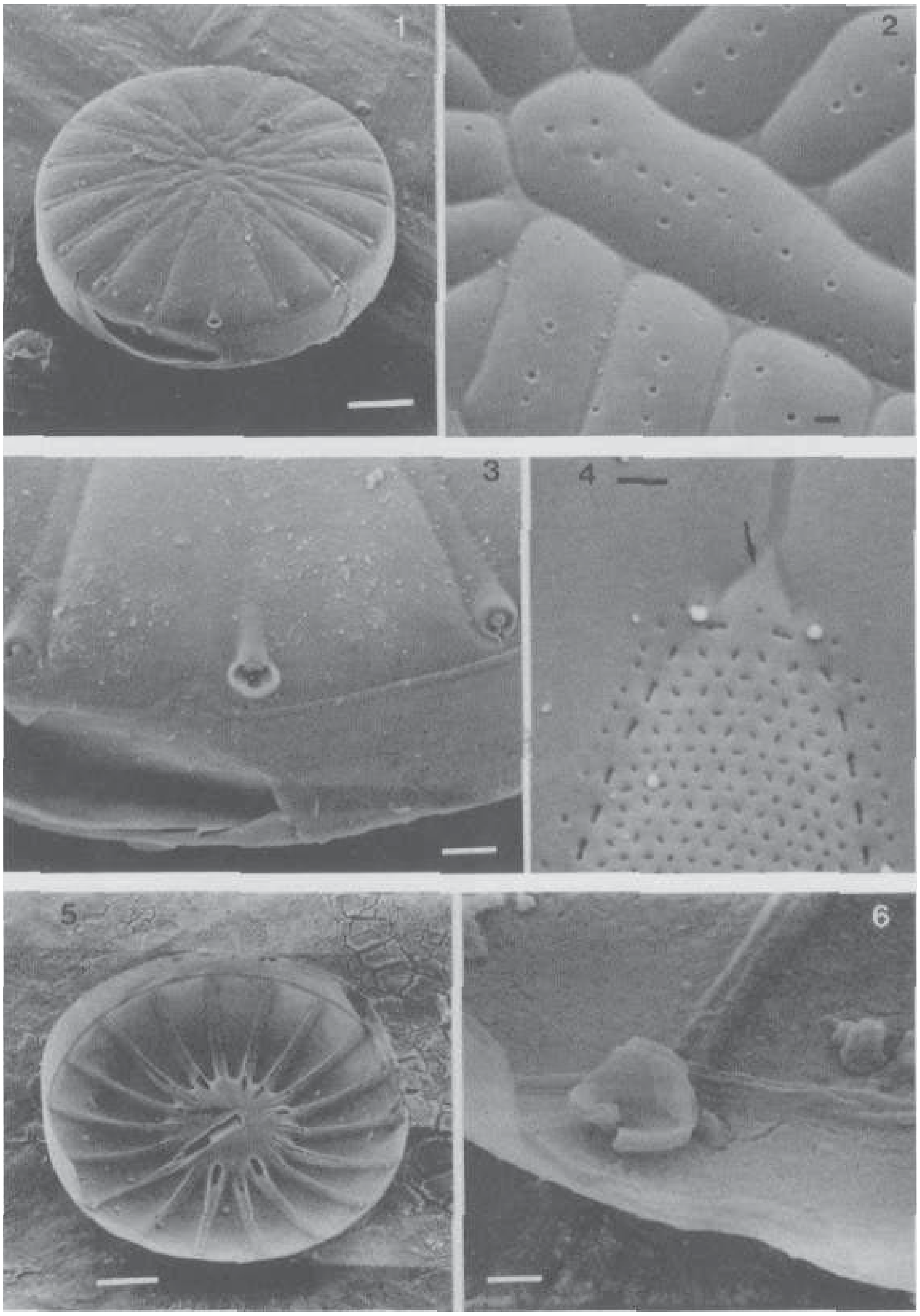
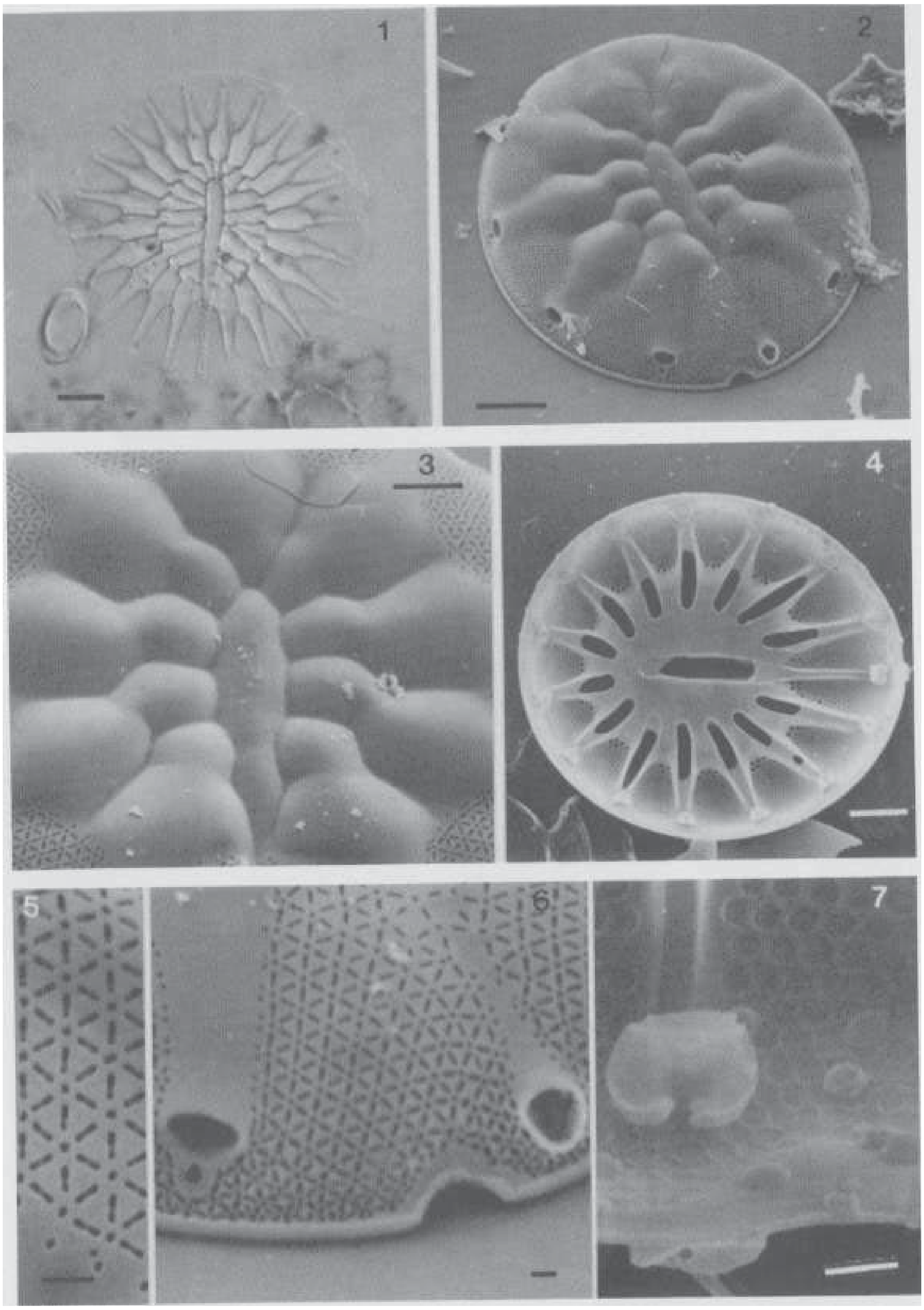


Pl. 16. Asteromphalus elegans. Fig. 1. Complete valve, LM. Fig. 2. Complete valve, SEM. Fig. 3. Central portion, SEM. Fig. 4. An ordinary ray (left) and singular ray (right) with the indentation to the left of the singular ray, SEM. Fig. 5. Detail of the areolae pattern, SEM. Fig. 6. An ordinary ray showing the ray hole and external opening of the rimoportula, SEM. Fig. 7. An ordinary ray showing the tympanum covering the ray hole, SEM. Scale bars = 20 um, Figs. 1, 2, = 5 um, Figs. 3, 4, 6, 7, = 1 um, Fig. 5.



P1. 17. Asteromphalus elegans. Fig. 1. A whole frustule, SEM. Fig. 2. Detail of the central portion showing some poroids, SEM. Fig. 3. Different types of rays, the middle one is the singular ray, SEM. Fig. 4. Discontinuity of the areolae at corners formed between two sibling rays (arrow), SEM. Fig. 5. Inside view of the valve, SEM. Fig. 6. Rimoportula of the singular ray, SEM. Scale bars = 20 um, Figs. 1, 5, = 5 um, Fig. 3, = 1 um, Figs. 2, 4, 6.



Pl. 18. Asteromphalus imbricatus. Fig. 1. Complete valve, LM. Fig. 2. Complete valve, SEM. Fig. 3. Detail of the central portion, SEM. Fig. 4. Inside view of the valve, SEM. Fig. 5. Areolae pattern, SEM. Fig. 6. An ordinary ray (left) and singular ray (right) showing the indentation located to the left of the singular ray, SEM. Fig. 7. Detail of the rimoportula of the singular ray, and part of the indentation, SEM. Scale bars = 10 um, Figs. 1, 2, 4, = 5 um, Fig. 3, = 1 um, Figs. 5-7.

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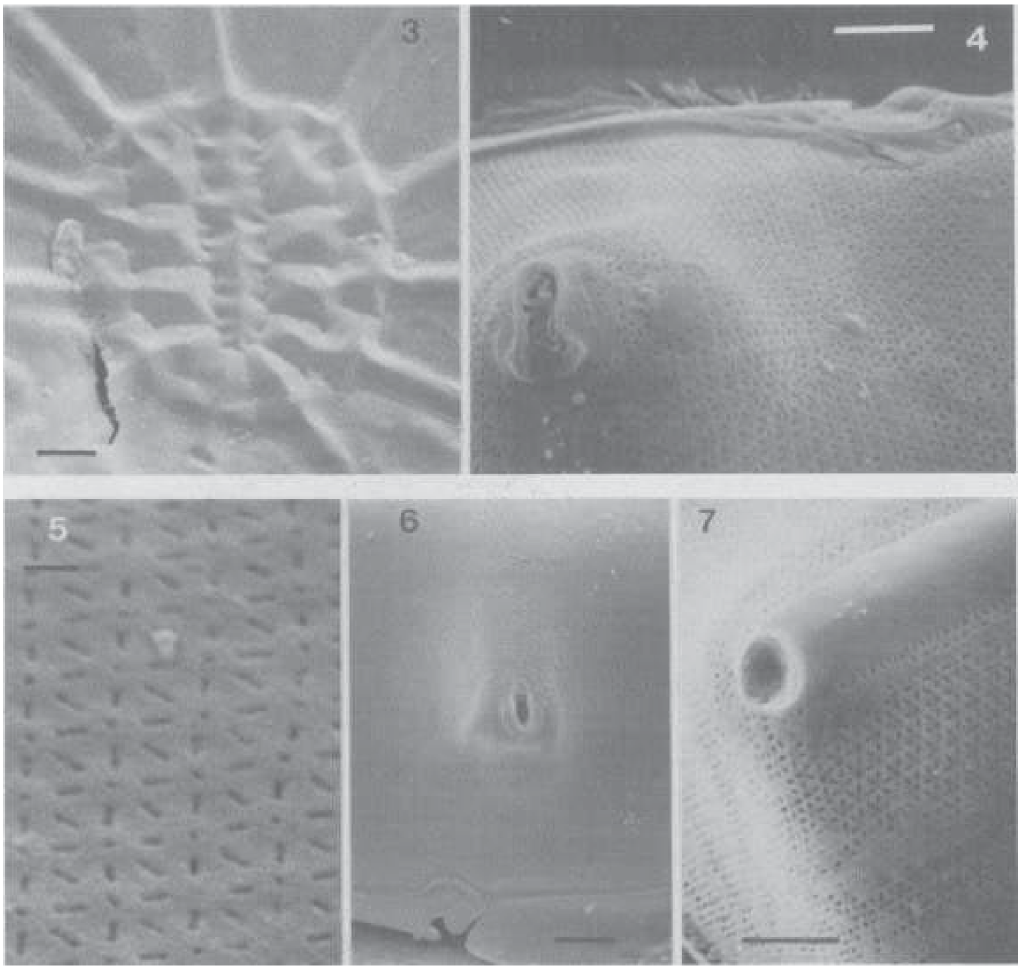
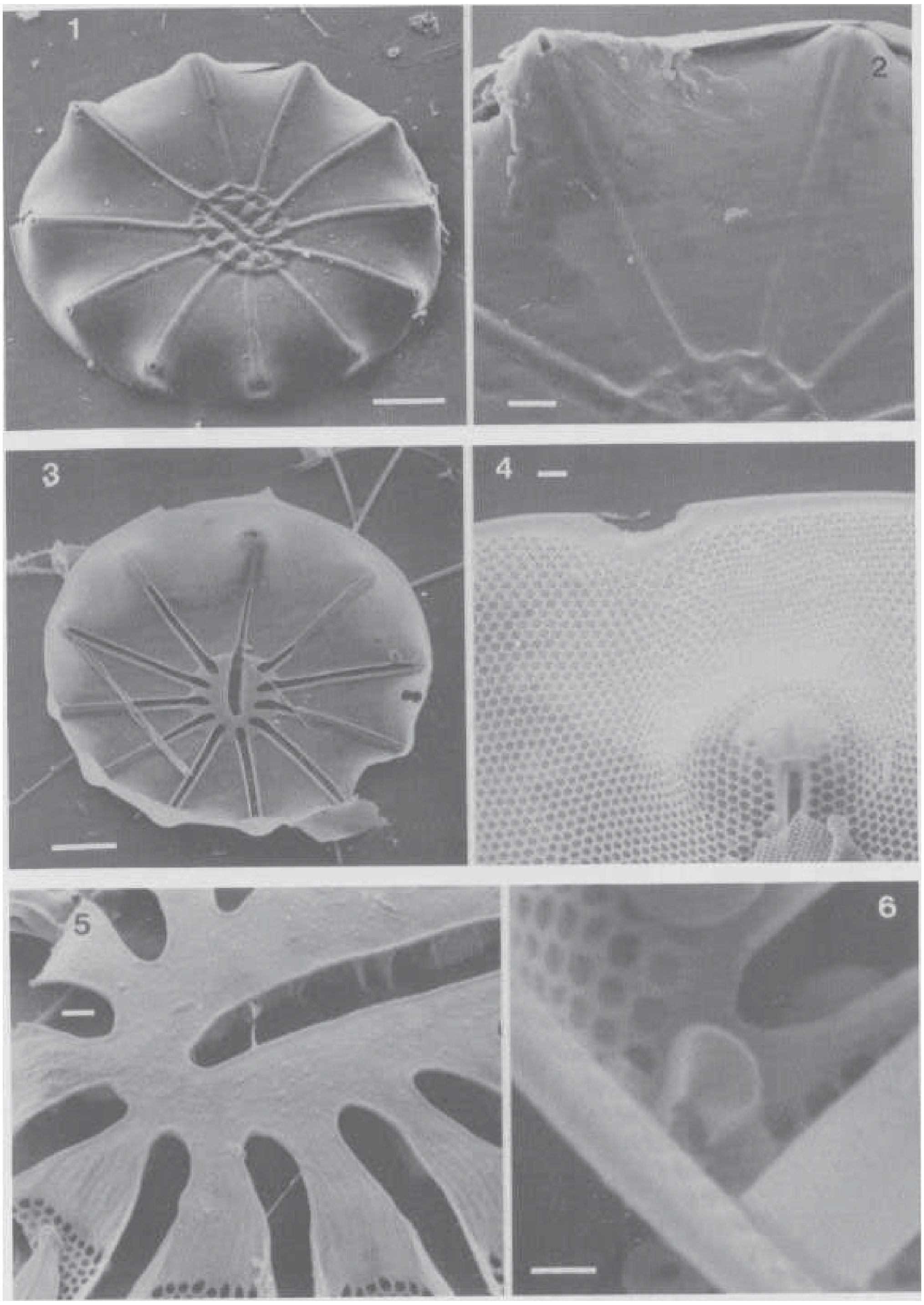


P1. 19. <u>Asteromphalus</u> <u>ingens.</u> Complete valve, LM. Fig. 2. Complete valve, SEM. Fig. 3. Detail of the central portion, SEM. Fig. 4. Ray hole of the singular ray and indentation, SEM. Fig. 5. Areolae pattern, SEM. Fig. 6. Singular ray and indentation, SEM. Fig. 7. An ordinary ray showing the tympanum, SEM. Scale bars = 20 um, Figs. 1, 2, = 5 um, Figs. 3, 4, 6, 7, = 1 um, Fig. 5.



P1. 20. Asteromphalus ingens. Fig. 1. Another complete valve, SEM. Fig. 2. Singular ray (left) and an ordinary ray (right), SEM. Fig. 3. Inside view of the valve, SEM. Fig. 4. Detail of the rimoportula of the singular ray and the indentation, SEM. Fig. 5. Detail of the annulus, SEM. Fig. 6. Rimoportula of an ordinary ray, SEM. Scale bars = 20 um, Figs. 1, 3, = 5 um, Fig. 2, = 1 um, Figs. 4-6.

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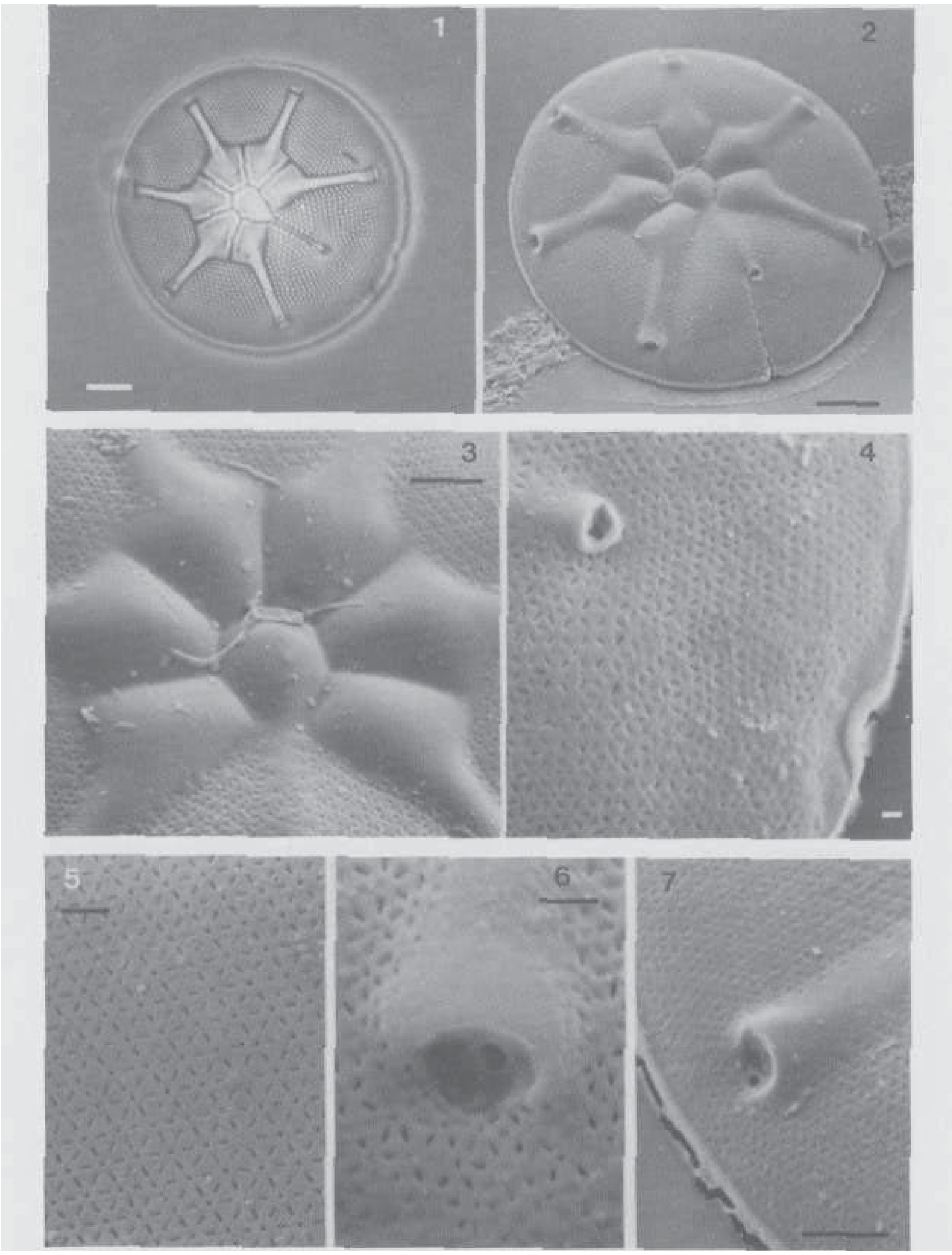
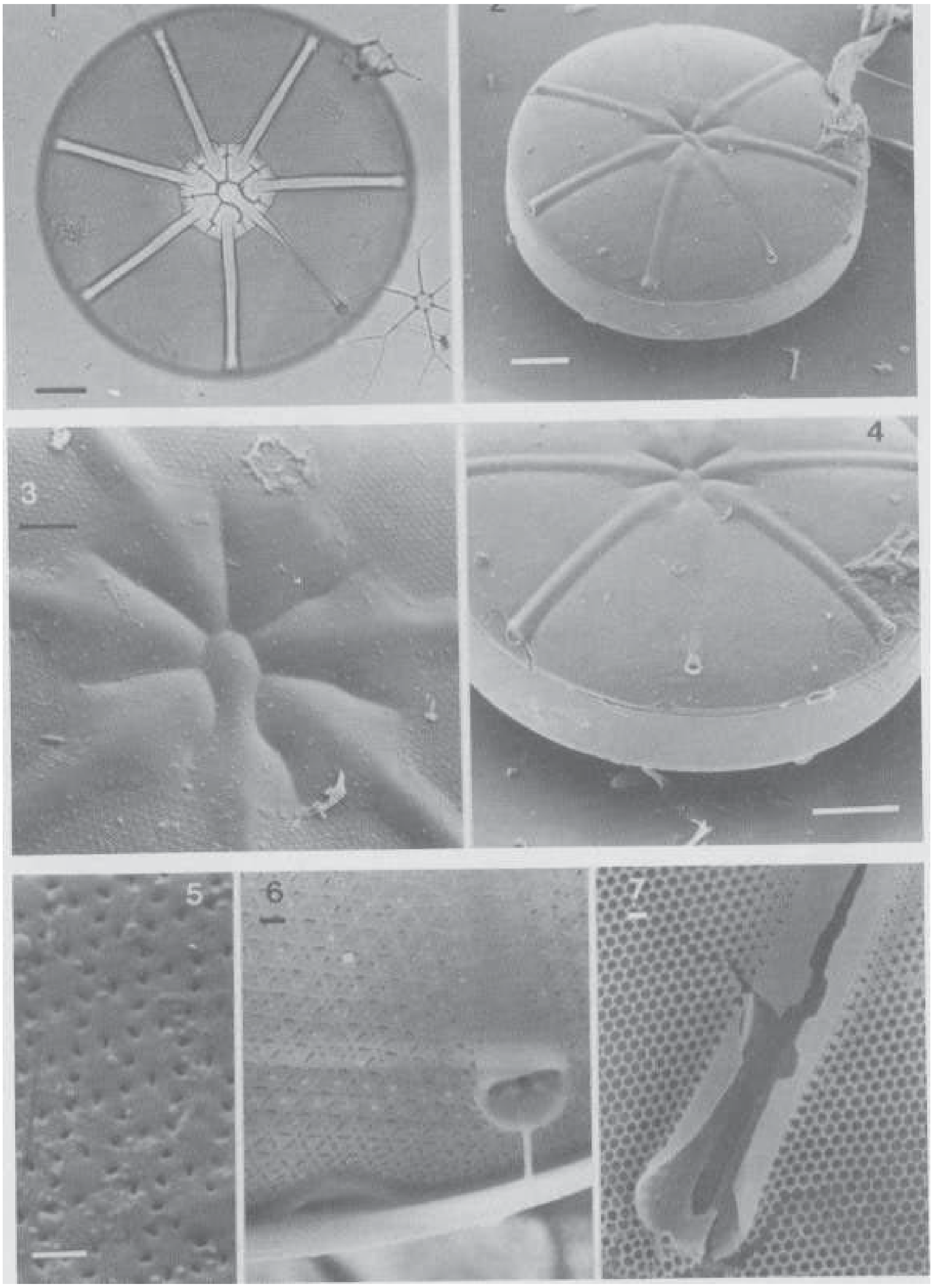
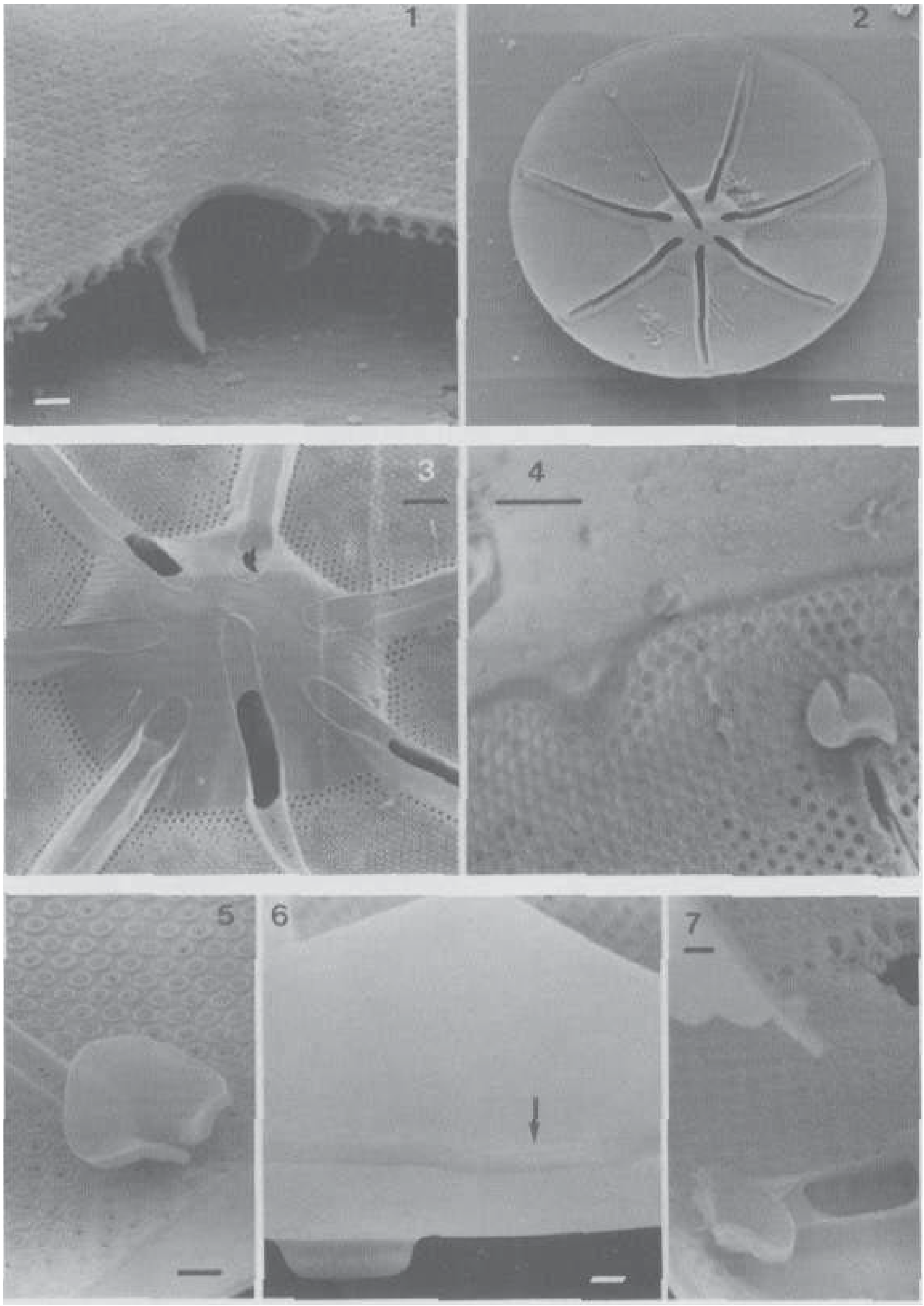


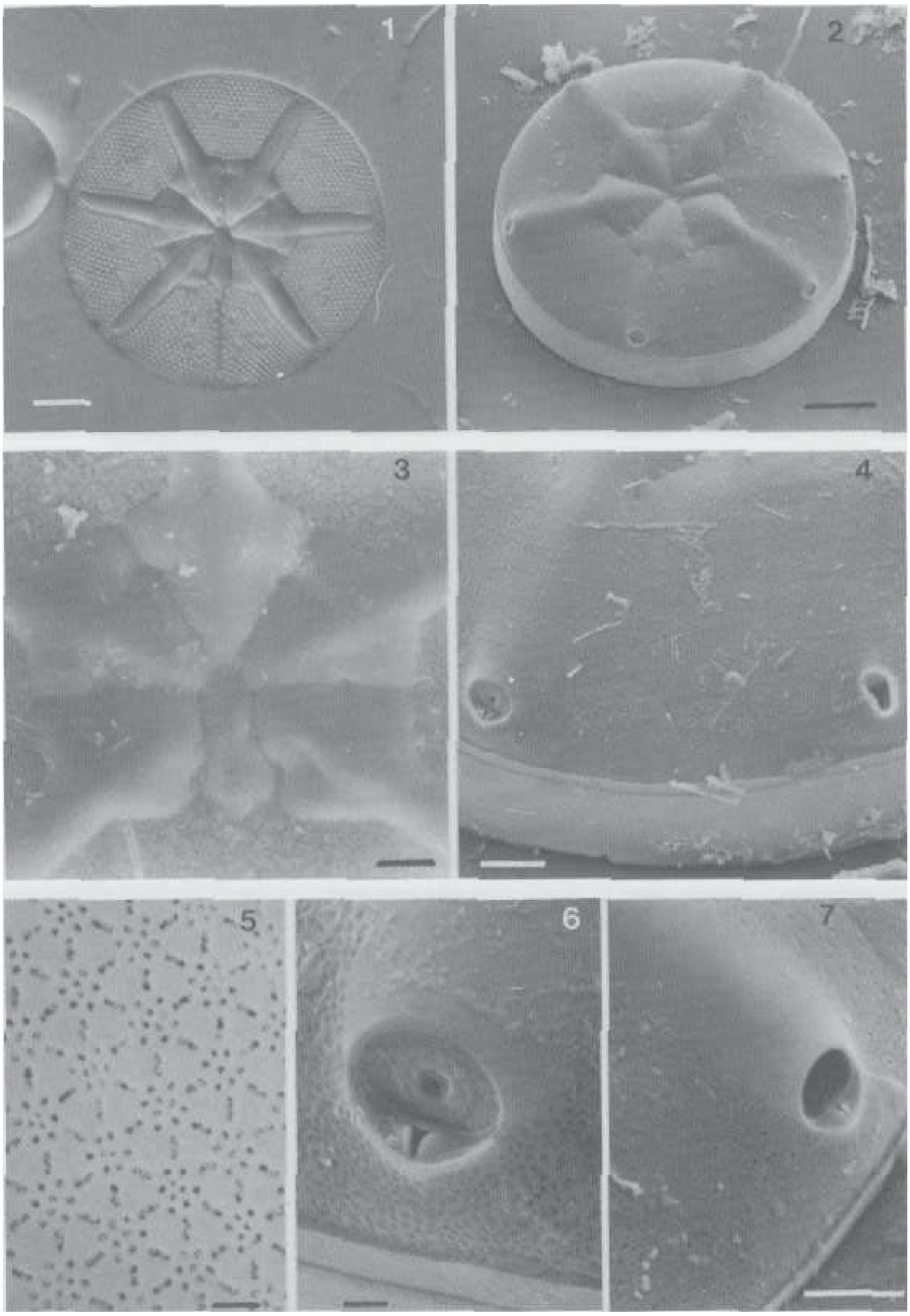
Pl. 21. <u>AsteromDhalus</u> <u>shadboltianus.</u> Fig. 1. A complete valve, LM. Fig. 2. The same valve, SEM. Fig. 3. Central portion, SEM. Fig. 4. Ray hole of the singular ray and indentation, SEM. Fig. 5. Areolae pattern, SEM. Fig. 6. Detail of the ray hole of the singular ray showing the tympanum partially broken, SEM. Fig. 7. An ordinary ray, SEN. Scale bars = 10 um, Figs. 1, 2, = 5 um, Figs. 3, 4, 7, = 1 um, Figs. 5, 6.



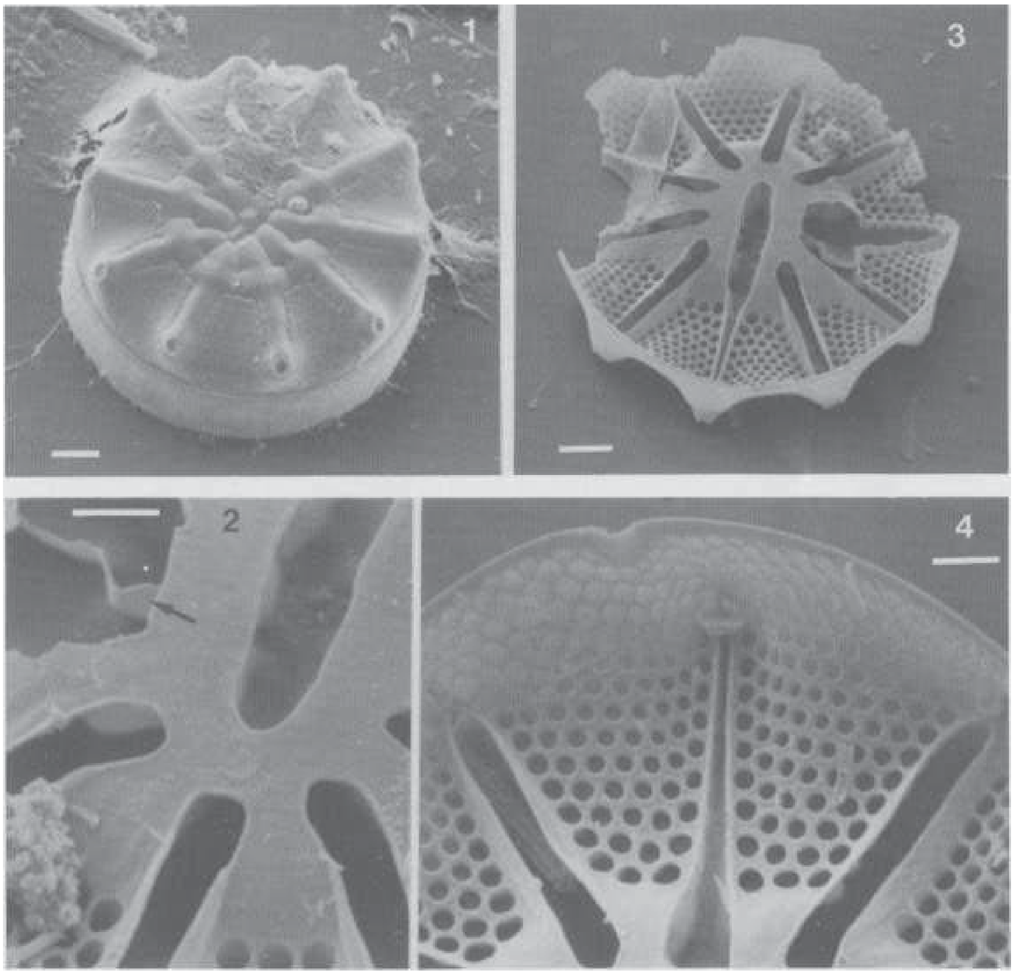
Pl. 22. Asteromphalus roperianus. Fig. 1. Complete valve, LM. Fig. 2. A whole frustule, SEM. Fig. 3. Central portion of valve, SEM. Fig. 4. Part of the frustule showing the singular and ordinary rays, SEM. Fig. 5. Areolae pattern, SEM. Fig. 6. Singular ray showing the indentation to the left of the singular ray, SEM. Fig. 7. An ordinary ray broken showing the ray slit and the external opening of the rimoportula, SEM. Scale bars = 20 um, Figs. 1, 2, 4, = 5 um, Fig. 3, = 1 um, Figs. 5-7.



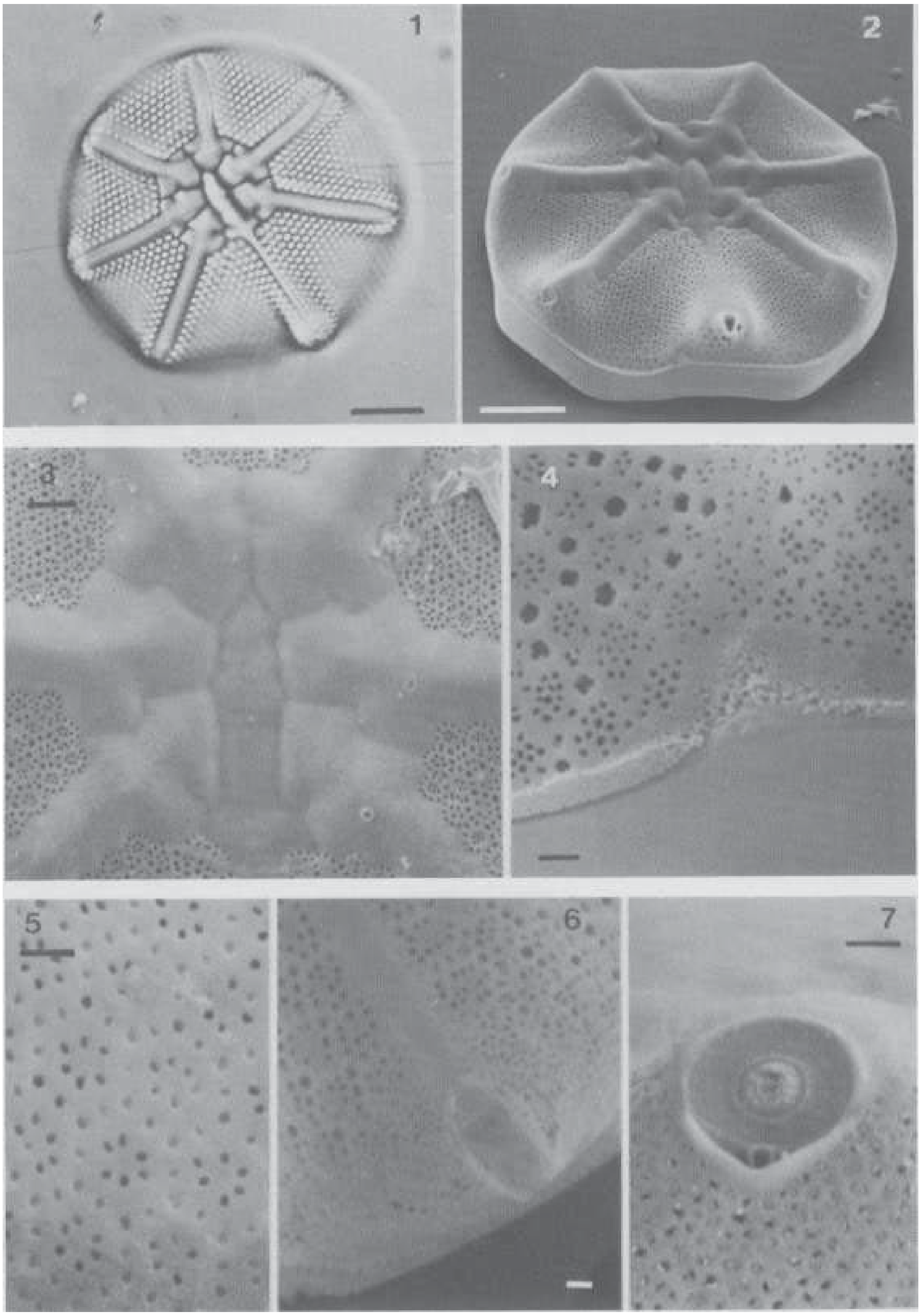
Pl. 23. Asteromphalus roperianus. Fig. 1. Section of an ordinary ray showing the ray slit, SEM. Fig. 2. Inside view of a valve, SEM. Fig. 3. Detail of the central portion from inside showing the annulus, SEM. Fig. 4. Rimoportula of the singular ray and the indentation located to the left side, SEM. Fig. 5. Rimoportula of the singular ray, SEM. Fig. 6. Detail of the indentation (arrow), SEM. Fig. 7. Rimoportula of an ordinary ray, SEM. Scale bars = 20 um, Fig. 2, = 5 Um, Figs. 3, 4, = 1 um, Figs. 1, 5-7.



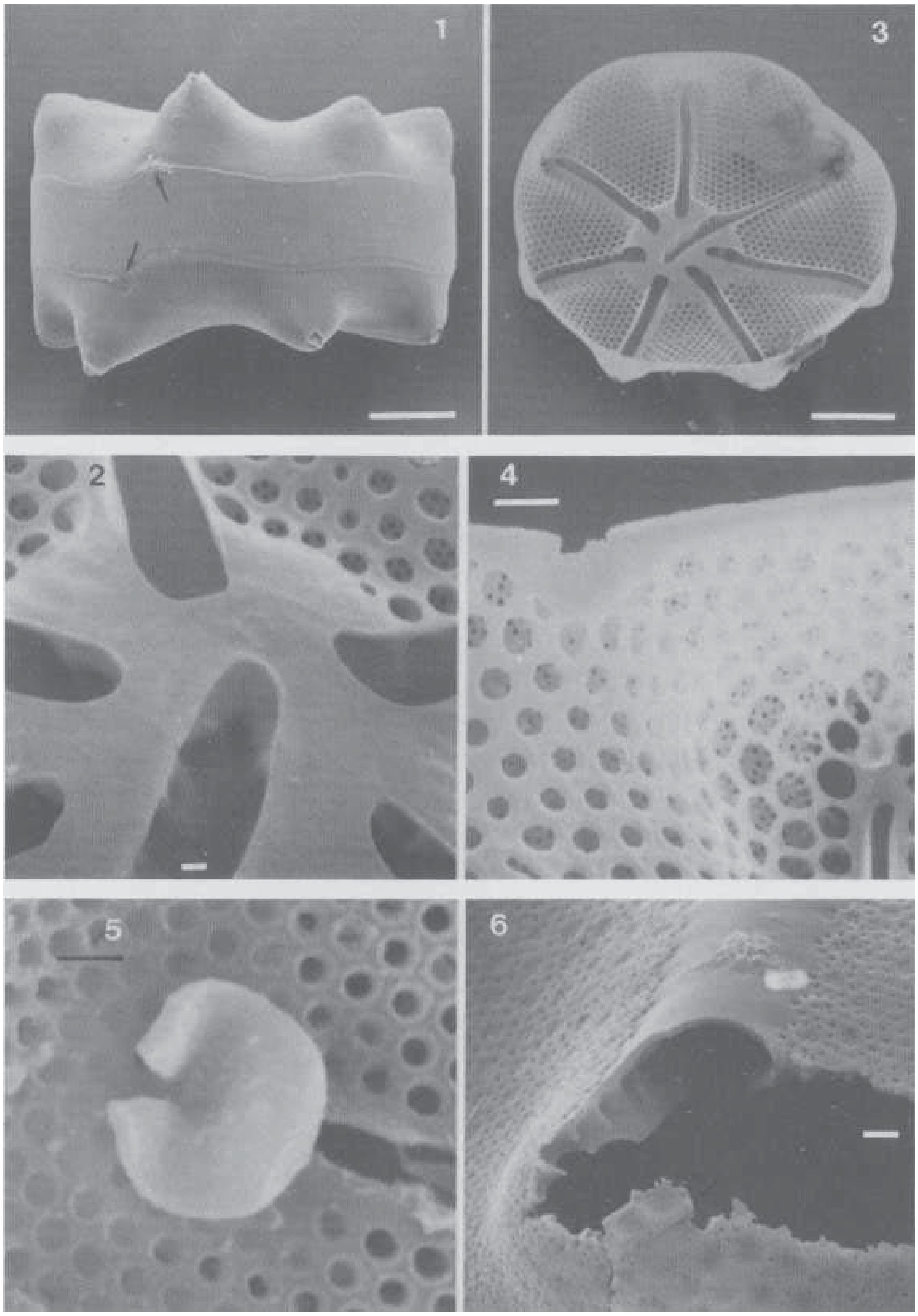
Pl. 24. <u>Asteromphalus</u> <u>hookeri.</u> Fig. 1. Complete valve, LM. F'.g. 2. A whole frustule, SEM. Fig. 3. Detail of the central portion, SEM. Fig. 4. Ordinary ray (left) and singular ray (right), SEN. Fig. 5. Areolae pattern, SEM. Fig. 6. Detail of an ordinary ray with the ray hole covered by the tympanum. Note the labiate outer opening of the rimoportula, SEM. Fig. 7. Ordinary ray showing the ray hole, SEM. Scale bars = 10 um, FigS. 1, 2, = 5 um, Figs. 3, 4, 7, = 1 um, Figs. 5, 6.



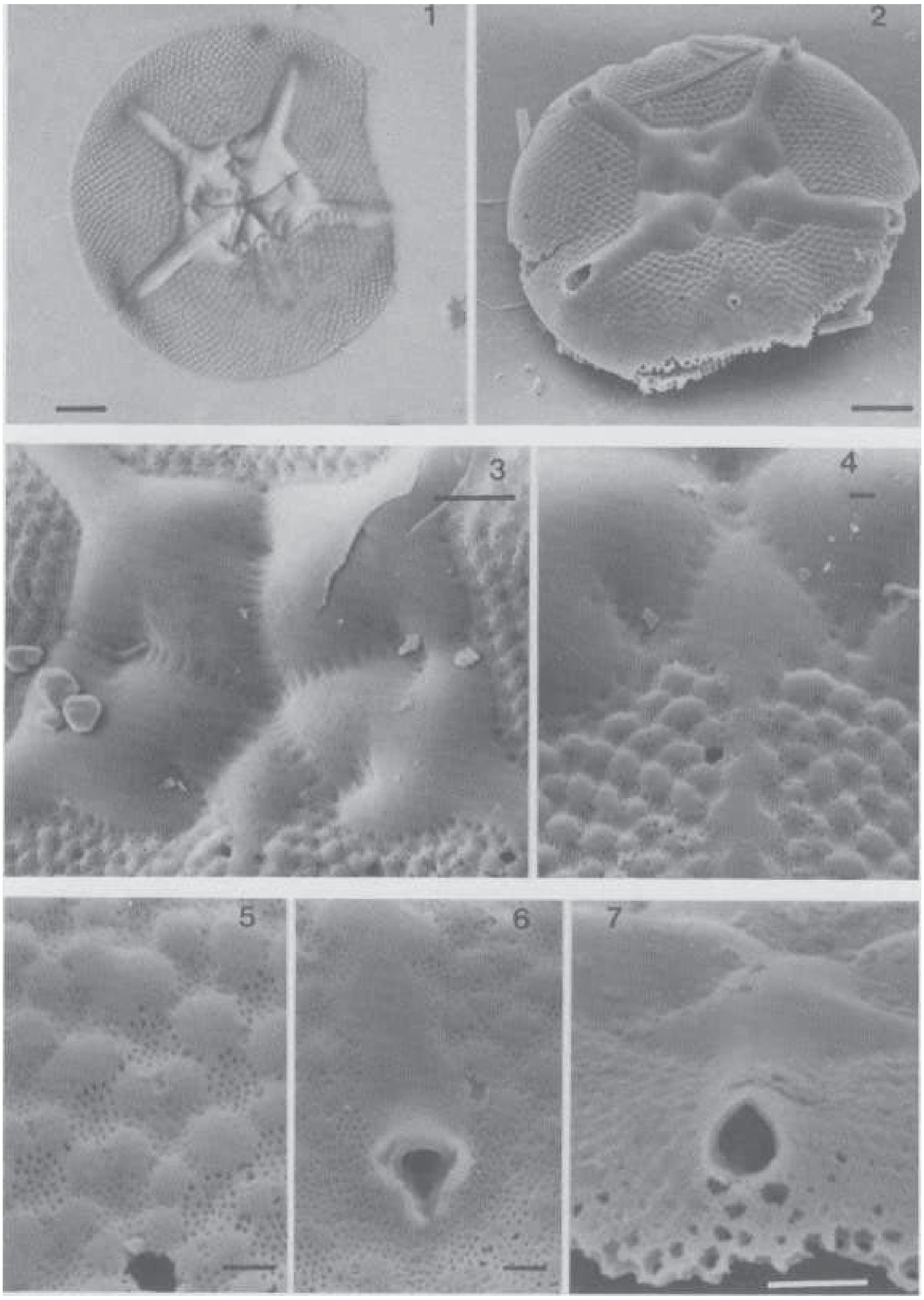
Pl. 27. <u>Asteromphalus</u> <u>robustus.</u> Fig. 1. A whole frustule, SEM. Fig. 2. Inside view of the valve, SEM. Fig. 3. Detail of the annulus, and a visible separating line (arrow), SEM. Fig. 4. Rimoportulae of three rays, the middle one (the largest) corresponds to the singular ray, SEM. Scale bars = 10 um, Figs. 1, 3, = 5 um, Figs. 2, 4.



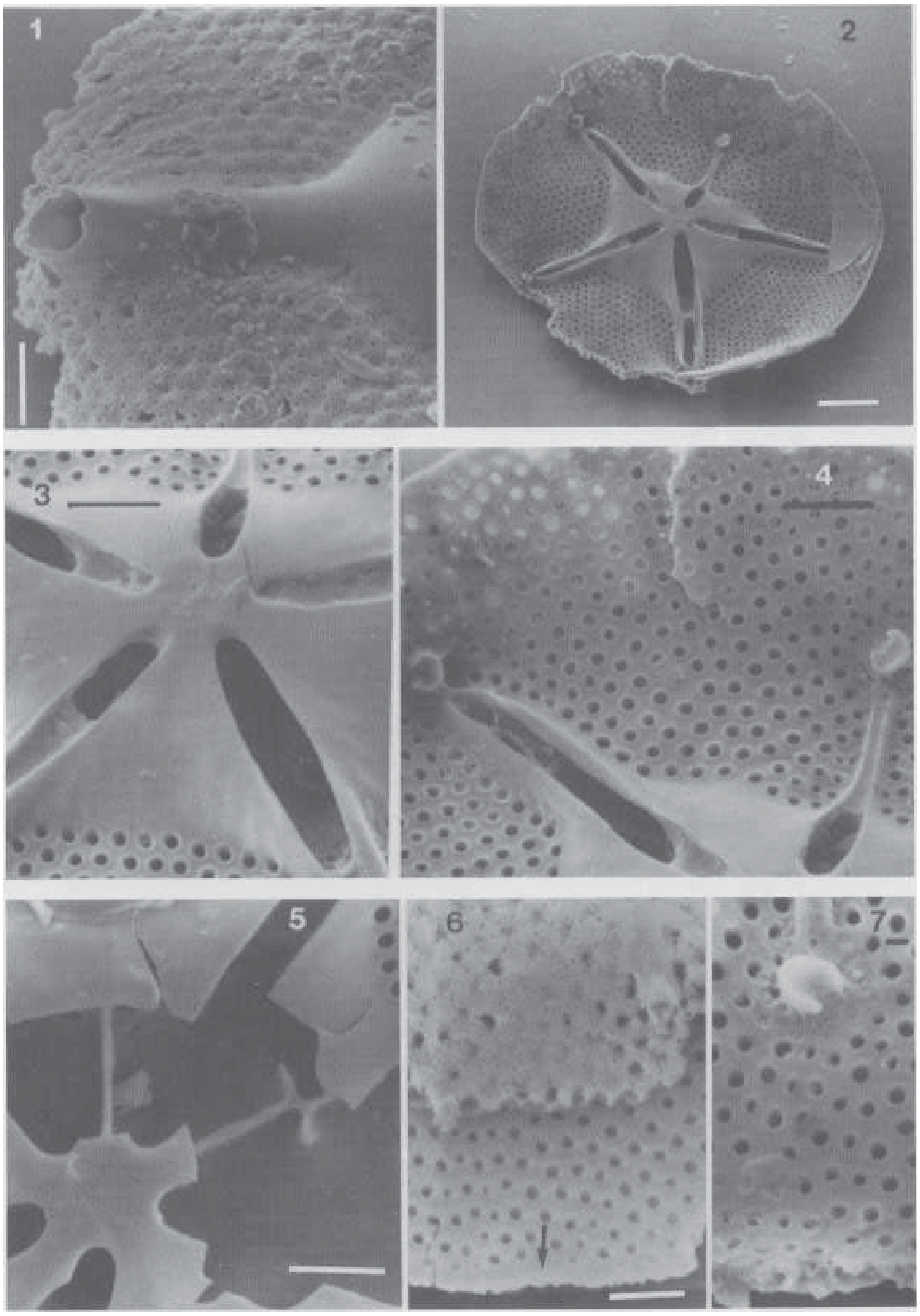
P1. 28. p,steromphalus heptactis. Fig. 1. Complete valve, LM. Fig. 2. Whole frustule, SEM. Fig. 3. Detail of the central portion, SEM. Fig. 4. Detail of the indentation, SEM. Fig. 5. Areolae pattern, SEM. Fig. 6. Rah hole of the singular ray, SEM. Fig. 7. An ordinary ray covered by the tympanum, SEM. Scale bars = 20 um, Figs. 1, 2, = 5 um, Fig. 3, = 1 um, Figs. 4-7.



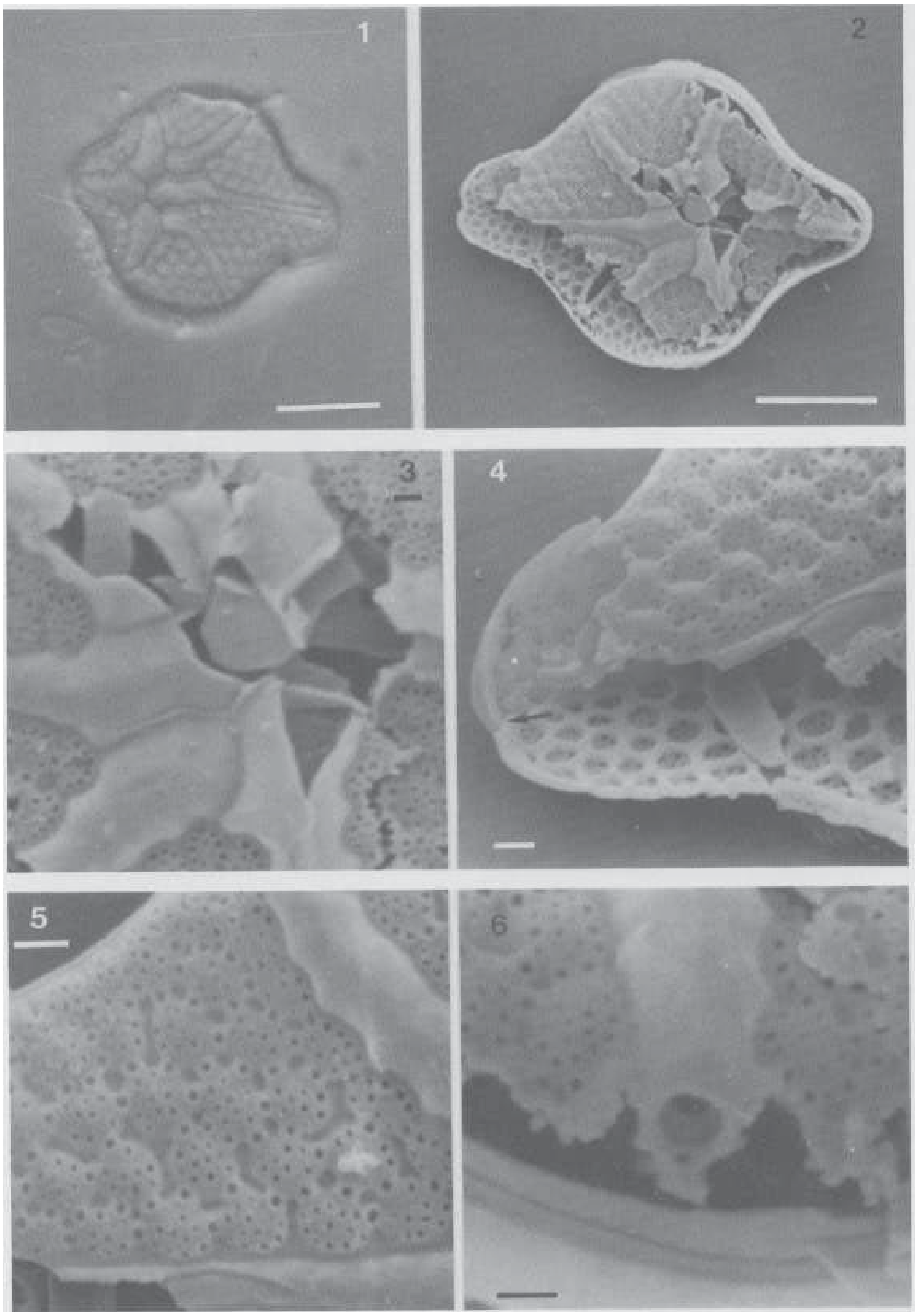
Pl. 29. Asteromphalus heptactis. Fig. 1. Complete frustule in girdle view. The arrow points the indentation in both valves (to the left of the singular ray), SEM. Fig. 2. Inside view of a valve, SEM. Fig. 3. Inside view showing the annulus, SEM. Fig. 4. Rimoportula of the singular ray and the indentation, SEM. Fig. 5. Rimoportula of the singular ray, SEM. Fig. 6. Section of an ordinary ray, SEM. Scale bars = 20 um, Figs. 1, 2, = 5 um, Fig. 4, = 1 um, Figs. 3, 5, 6.



Pl. 30. Asteromphalus darwinii. Fig. 1. Complete valve, LM. Fig. 2. Valve slightly broken, SEM. Fig. 3. Detail of the central portion, SEM. Fig. 4. Part of the singular ray and the areolae, SEM. Fig. 5. Areolae pattern, SEM. Fig. 6. Ray hole of the singular ray, SEM. Fig. 7. Ray hole and external opening of the rimoportula in an ordinary ray, SEM. Scale bars = 10 um, Figs. 1, 2, = 5 um, Figs. 3, 7, = 1 um, Figs. 4-6.



Pl. 31. Asteromphalus darwinii. Fig. 1. An ordinary ray showing the ray hole, SEM. Fig. 2. Inside view of the valve, SEM. Fig. 3. Inside view of the central portion with the annulus at the centre, SEM. Fig. 4. Two rimoportulae, at an ordinary ray (left) and at singular ray (right), SEM. Fig. 5. Detail of the annulus and separating lines, SEM. Fig. 6. Indentation (arrow) and singular ray, SEM. Fig. 7. Rimoportula of the singular ray, SEM. Scale bars = 10 um, Fig. 2, = 5 um, Figs. 1, 3-6, = 1 um, Fig. 7.



Pl. 32. *.steromphalus sarcophagus.* Fig. 1. Complete valve, LM. Fig. 2. A partially broken frustule, SEM. Fig. 3. Detail of the central portion, SEM. Fig. 4. Edge of the valve showing the presence of the rimoportula (arrow) and the rimoportula of the singular ray, SEM. Fig. 5. Areolae pattern, SEM. Fig. 6. Ray hole of an ordinary ray, SEM. Scale bars = 10 um, Figs. 1, 2, = 1 um, Figs. 3-6.