AFRICA

Amphora coffeaeformis (Agardh) Kützing: a revision of the species under light and electron microscopy

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Amphora coffeaeformis (Agardh) Kützing is frequently found in brackish waters. However, different concepts of this species found in the literature lead to confusion with respect to its true identity. In this study Agardh's type material from Carlsbad, as well as Kützing's samples from the same locality, have been examined using light and electron microscopy to establish the true concept of *A. coffeaeformis*. Based on these materials and on a number of specimens identical to the type specimens found both locally and from foreign sources, a revised and comprehensive description of *A. coffeaeformis* is given and is fully illustrated with photographs and electron micrographs. In the light of this new description numerous apparently well authenticated materials were re-examined. *Amphora salina* W. Smith is confirmed as a synonym of *A. coffeaeformis* while *A. aponina* Kützing is regarded as a variety, *A. coffeaeformis* var. *aponina comb. nov. Amphora lineata* Gregory and *A. taylori* Grunow are rejected as being synonymous although a close affinity to *A. coffeaeformis* is recognized. As a result of this study, the presence of *A. coffeaeformis* in southern Africa is confirmed although most of the present records under this name reflect another taxon, namely *A. veneta* var. *capitata* Haworth.

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Amphora coffeaeformis (Agardh) Kützing word dikwels in brakwater aangetref. Daar bestaan egter verwarring oor die ware identiteit van die spesie, as gevolg van die uiteenlopende beskouinge daaroor in die literatuur. In hierdie studie is Agardh se tipe-materiaal, asook Kützing se monsters, beide afkomstig van Karlsbad, lig- en elektronmikroskopies ondersoek om die ware identiteit van *A. coffeaeformis* te probeer vasstel. 'n Hersiene en omvattende beskrywing van *A. coffeaeformis* word gegee, gebaseer op hierdie monsters asook op verskeie voorbeelde wat identies is aan die tipes wat plaaslik en in die buiteland versamel is. Foto's en elektronmikrograwe word ter illustrasie geplaas. Verskeie oënskynlik eg-verklaarde monsters is, met die oog op die nuwe beskrywing, herondersoek. Dit het geblyk dat *Amphora salina* W. Smith 'n sinoniem van *A. coffeaeformis* is, maar dat *A. aponina* Kützing 'n variëteit, *A. coffeaeformis* var. *aponina comb. nov.*, daarvan is. *Amphora lineata* Gregory en *A. taylori* Grunow, hoewel aanverwant, is nie sinonieme van *A. coffeaeformis* nie. Die studie het bewys dat *A. coffeaeformis* wel in suidelike-Afrika gevind word, hoewel die meeste optekeninge onder bespreking van dié naam, 'n ander takson, naamlik *A. veneta* var. *capitata* Haworth is.

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1. Introduction

Amphora coffeaeformis (Agardh) Kützing is one of the most frequently recorded species from brackish water habitats, where it is often reported as being abundant (Kolbe 1927; Hustedt 1930; Patrick & Reimer 1975). It would therefore be logical to assume that the species is easily identifiable. However, when one consults the literature and is confronted with the wide variety of concepts for this species, this assumption is quickly dispelled. One is left with the impression that *A. coffeaeformis* is a fairly polymorphic species and, from an ecological point of view, can tolerate a very wide spectrum of environmental conditions.

Most descriptions in the literature are too brief to convey a good impression of the taxon and drawings illustrating it vary so greatly in respect of style, size and detail that it becomes impossible to formulate a proper concept of the species. Even photographic images and EM micrographs of material purported to be *A. coffeaeformis* indicate that often quite different taxa have been illustrated (Lewin & Lewin 1960; Anderson 1975; Ehrlich 1978).

A. coffeaeformis has been widely recorded from southern Africa, mostly from alkaline freshwater localities (Cholnoky 1968). This led to some doubt being cast on the accuracy of these identifications as the species is commonly believed to be mesohalobous (Lowe 1974), i.e. an organism inhabiting brackish waters of varying salt concentration. Re-examination of a large number of southern African samples containing *A. coffeaeformis* made it obvious that the taxon dealt with in these reports was not *A. coffeaeformis*. In the majority of cases it was later identified as *Amphora veneta* var. *capitata* Haworth (*cf.* Schoeman & Archibald 1978). While checking further records of the genus *Amphora* from southern Africa, it was evident that forms identifiable as *A. coffeaeformis* were placed either partially or wholly under other names. For example, in his paper on the diatoms from the Swakop River in South West Africa (Namibia), Cholnoky (1963) recorded *Amphora fluminensis* Grunow and also described a new species, *Amphora sydowii* Cholnoky, from the region. On checking these identifications, *A. fluminensis* was found to be *A. coffeaeformis*, while *A. sydowii* turned out to embrace three taxa, one of which was *A. coffeaeformis*. Misidentifications of this nature and a lack of critical discernment may be prevalent in many other southern African studies involving *A. coffeaeformis*, thus making the reliability of its identification doubtful.

Bearing this in mind and noting a similar situation in the literature, it seemed clear that a thorough revision of the species *A. coffeaeformis* was long overdue. Consequently, we have examined the type material as well as other authenticated material of *A. coffeaeformis* and several of the synonyms listed by VanLandingham (1967). This paper reports on our observations of these materials and attempts to provide a more comprehensive description of *A. coffeaeformis* through light and electron microscopy so that some of the confusion that exists in the interpretation of this species can be eliminated. Based on our concept of this species, we have furthermore attempted to reassess the validity of some of its synonyms.

2. Materials

Listed below are a number of materials in various diatom collections which have been used in this study. Symbols in parentheses either preceding or following each material number indicate the location of the relevant collection (Fryxell 1975). The abbreviation PIFW-NIWR reflects diatom slides in the National Institute for Water Research diatom collection in Pretoria, South Africa, while the abbreviations BM, BRM and LD indicate, respectively, slides from collections in the British Museum (Natural History), Bremerhaven and Lund.

2.1 Materials used in establishing the proper identity of *A. coffeaeformis* (Agardh) Kützing

The following material was examined: Agardh 4600 (LD); BM 18945 (Kützing 469); BM 78009 (Kützing collection); NIWR 383/7644 (PIFW) = SUN 37; BM 23126 (as *A. salina* W. Smith); NIWR sample SWA 227 (PIFW).

2.2 Materials used to investigate other concepts of *A. coffeaeformis* and the validity of various synonyms.

A large number of slides from various collections were examined to investigate what other diatomists have considered to be *A. coffeaeformis* or its synonyms. These slides are arranged in groups according to the taxon they are supposed to contain. In the lists below the slide numbers relevant to each group are given. Full details of these materials are supplied in those sections of the text where each material is discussed individually.

(a) *A. coffeaeformis* and its varieties: Cleve & Möller (1877–1882) Slide Nos 86, 91, 204, 262 (PIFW-NIWR); Hustedt Slide Nos U1,29, U1,30, U1,54 (BRM).

(b) *A. salina* W. Smith and its varieties: BM 23125, BM 23126 (BM); Eulenstein (1867) Slide No. 96 (PIFW-NIWR); Van Heurck (1884–1887) Types du Synopsis Nos 11, 12, 116 (PIFW-NIWR); Tempère & Peragallo (1889–1895) Slide Nos 415, 422, 520 (PIFW-NIWR); Cleve & Möller (1877–1882) Slide Nos 218, 255 (PIFW-NIWR).

(c) *A. aponina* Kützing: BM 18944, BM 25590 = H.L. Smith Diat. Spec. Type No. 29 (BM); Van Heurck (1884–1887) Types du Synopsis No. 257 (PIFW-NIWR).

(d) *A. taylori* Grunow: Van Heurck (1884–1887) Types du Synopsis No. 13 (PIFW-NIWR).

(e) *A. lineata* Gregory: BM 955, BM 956 (BM); Tempère & Peragallo (1889–1895) Slide Nos 161, 292 (PIFW-NIWR); Cleve & Möller (1877–1882) Slide Nos 155, 210 (PIFW-NIWR).

3. Methods

Methods for the preparation of slides from local material are described by Schoeman & Archibald (1976). For TEM and SEM studies the methods outlined by Schoeman & Archibald (1976), with improvements, (*cf.* Schoeman & Archibald 1977) were used.

Terminology used in this paper is that recommended by the Working Party on Diatom Terminology (Anon. 1975; Ross *et al.* 1979). In the text, place names describing the location at which samples were collected have been retained in the form and language in which they were originally published.

In addition to the materials mentioned above we also prepared permanent mounts of various TEM grids after they had been examined under the electron microscope. The grids were carefully removed from the TEM grid holder and transferred to a drop of Naphrax mounting medium on a glass slide. This was covered with a coverglass and the solvent of the mounting medium was then driven off by gentle heating. The mounted grid thus enables us to compare directly the appearance of the same specimen as it is seen under both the transmission electron microscope and the conventional light microscope. If the process is carried out carefully the specimens on the grid will not shift and they can easily be traced by comparison with the relevant TEM micrographs (*cf.* Table 1).

On analysing the data concerning dimensions and striae counts found in the literature, we found that our striae counts do not always tally with those given by other authors. This may be attributed to two factors. Firstly, it may be ascribed to the site where counts were made. In most papers the actual site is not given, and one is left to assume that counts were made across the central parts of the valve. To obviate this problem we would like to state clearly that our striae counts are always made along the raphe (Schoeman & Archibald 1976). Striae counts designated as near the centre signify that the site of the counts was on either side of the central nodule or central area and not across the central nodule. Other discrepancies may result from misidentification. These may not be easy to detect, particularly if there is no illustration to confirm the identity of the species under review.

For a description of the frustule construction in *Amphora*, reference should be made to Schoeman & Archibald (1979).

4. Observations and Discussion

Our first task in this study was to establish the true concept of *A. coffeaeformis*. To accomplish this we began by examining Agardh's (1827) type material from Carlsbad (Agardh No. 4600) on a slide prepared by Reimer. We also obtained a small portion of this exsiccata material for examination under the electron microscope (EM), from which we were able to mount a few specimens as permanent preparations (see Tables 1 & 2). Furthermore, we examined two sets of material in the Kützing collection in the British Museum (Natural History) originating from Agardh's type locality, Carlsbad (Kützing 1844: 108). These were Kützing material No. 469 prepared on slide BM 18945, and an unnumbered sample (labelled in Kützing's own handwriting as originating from Carlsbad) mounted on slide BM 78009. In addition to this we were provided with exsiccata material of the Agardh

Table 1 Permanent slides of marked specimens mounted on TEM grids and illustrated in the plates

Figure Nos	Material	Taxon	Slide No.	England Finder No.
104–106	Agardh No. 4600	*A. coffeaeformis*	NIWR 422/8438	L37/3
107, 108	Agardh No. 4600	*A. coffeaeformis*	NIWR 422/8438	L37
153	W. Smith: Iford	*A. salina*	NIWR 422/8434	K37
154	W. Smith: Iford	*A. salina*	NIWR 422/8435	L39
155	W. Smith: Iford	*A. salina*	NIWR 422/8435	L39/1
163–165	Kützing No. 393	*A. aponina*	NIWR 422/8429	J38
167	Kützing No. 393	*A. aponina*	NIWR 422/8430	N39

Note: *A. salina* = *A. coffeaeformis*; *A. aponina* = *A. coffeaeformis* var. *aponina comb. nov.*

Table 2 NIWR reference slides prepared from authenticated exsiccatae materials

Material	Taxon	Slide No.	Comments
Agardh No. 4600 (Carlsbad)	*Frust. coffeaeformis* = *A. coffeaeformis*	NIWR 422/8433	Several specimens
Kützing 469 (Carlsbad)	*A. coffeaeformis*	NIWR 422/8428	Several specimens
W. Smith: Iford	*A. salina*	NIWR 422/8427	Several specimens
Kützing No. 393 (Abano)	*A. aponina*	NIWR 422/8426	Specimen at K44/4–K45/3 (England Finder Coordinates)

Note: *A. salina* = *A. coffeaeformis*; *A. aponina* = *A. coffeaeformis* var. *aponina comb. nov.*

type gathering as well as Kützing No. 469, which we examined under TEM and SEM. Having observed these samples we were able to formulate a good concept of *A. coffeaeformis*. Using this concept as a basis we were then in a position to examine a large number of materials containing *A. coffeaeformis* or taxa presently regarded as synonymous with this species. These materials came not only from the well known type slide collections of Eulenstein (1867), Van Heurck (1884–1887), Cleve & Möller (1877–1882) and Tempère & Peragallo (1889–1895), but also from more recent gatherings by Hustedt (BRM) and our local material (PIFW-NIWR). Some of these did indeed contain forms identical with true *A. coffeaeformis*, while others were either definitely not *A. coffeaeformis* or had points of similarity with this species but displayed other features which made it difficult for us to accept them as truly synonymous.

In the paragraphs below each material is discussed separately with our comments on what we feel taxa represented in these materials should be.

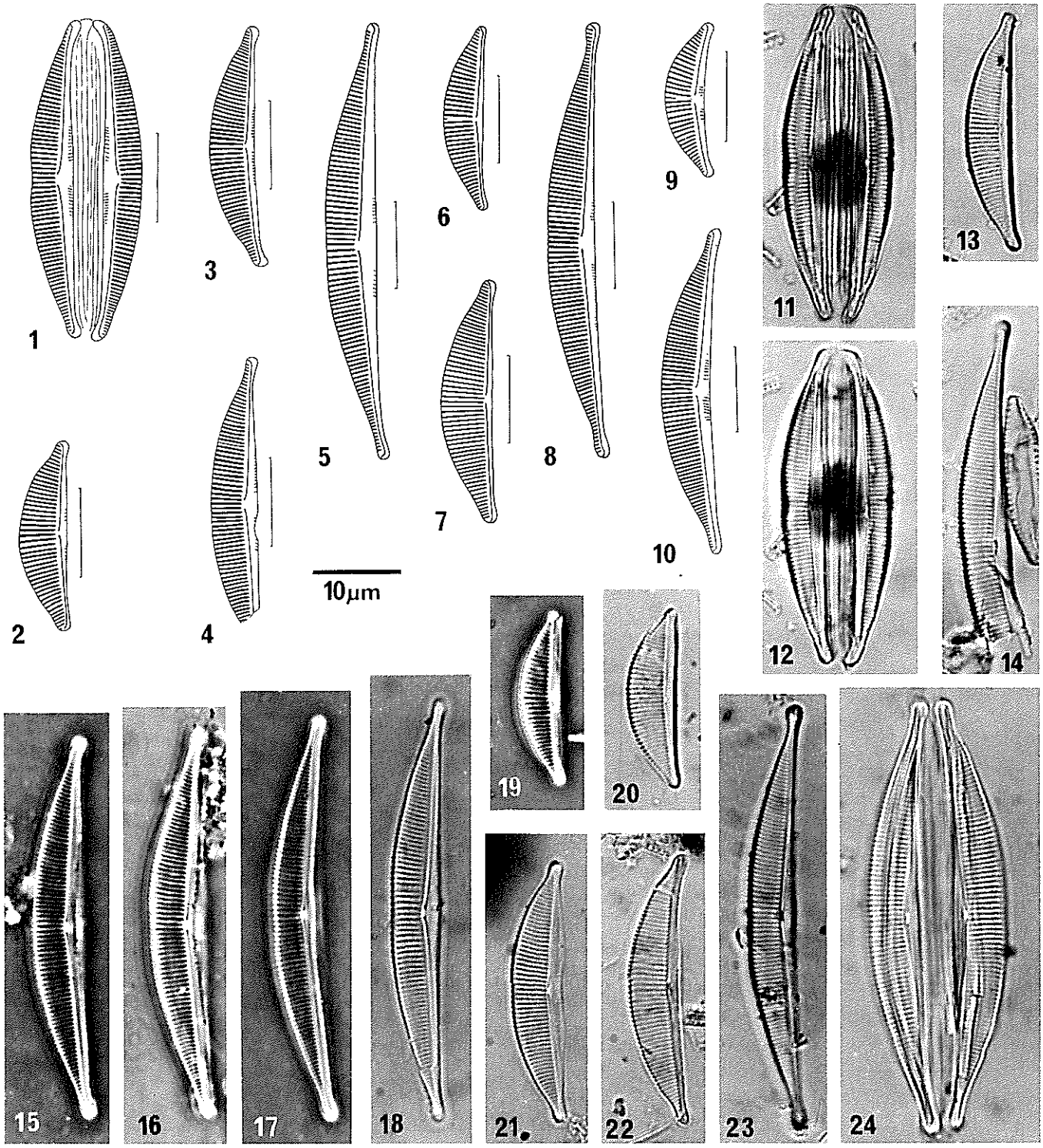
4.1 *A. coffeaeformis* (Agardh) Kützing: Type and other identical material

On comparing specimens (Figures 1–8, 11–24, 100–116) from the three Carlsbad materials mentioned above we could find no significant differences between them. We can therefore regard these forms as truly representing Agardh's taxon, *A. coffeaeformis*. At the same time this questions the validity of the variety, *A. coffeaeformis* var. *fischeri* Kützing (1844: 108). Apart from containing *A. coffeaeformis*, the slide BM 18945 is also designated as the type slide for the var. *fischeri*. Kützing's (1844) description of the variety suggests that it differs from *A. coffeaeformis* merely on the degree of convexity of the valve or frustule margins, var. *fischeri* being 'mediae magis turgida'. However, all the specimens observed on the slide BM 18945 are rather long and narrow and show no greater degree of convexity of the valves than specimens of equivalent length in Agardh's type material. On the other hand many of the smaller examples in Agardh's material (Agardh No. 4600) and on slide BM 78009 are relatively broader and therefore more convex than the specimens on slide BM 18945. These shorter and broader examples, furthermore, form a graded series with the long narrow forms in the same samples. We therefore reject the var. *fischeri* as a variety of *A. coffeaeformis* and include it in the natural range of variation of the species.

After comparing the Carlsbad materials discussed above with local examples we confirm that *A. coffeaeformis* does occur in southern Africa. Sample SUN 37 (=NIWR slide No. 383/7644) from the Sundays River in the eastern Cape Province of South Africa provided many examples (Figures 9, 10, 25–29, 117–152) identical to the Carlsbad forms. Figures 160–162 illustrate an example of true *A. coffeaeformis* from the Etosha National Game Park in South West Africa/Namibia (*cf.* NIWR sample SWA 227). Data from these examples have therefore been included in our new description of this species.

In addition to the data mentioned above our description incorporates information obtained from a few slides on which, we are positive, the proper *A. coffeaeformis* is present. These slides containing specimens under the name *A. salina* (BM 23126 — Figures 30–34; Eulenstein No. 96 — Figures 45, 46; Tempère & Peragallo No. 422 — Figures 61–64, and No. 520 — Figures 65, 66; Van Heurck Type du Synopsis No. 12 — Figures 49, 50) are discussed in paragraphs 5 and 6.

In our new description of *A. coffeaeformis* which follows we have not included data from the literature as the considerable variation in the concept of this species makes it

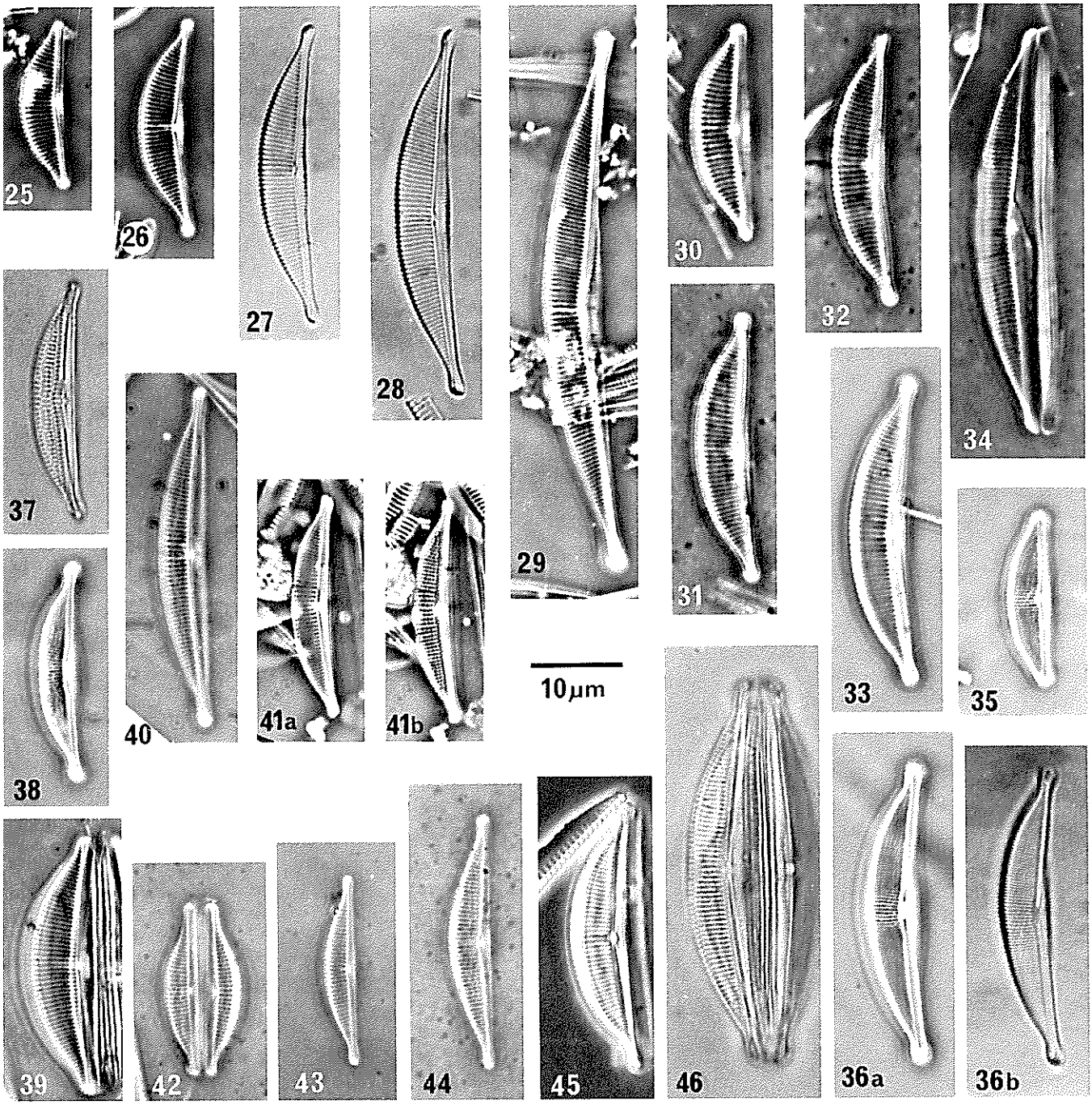


Figures 1–24 *Amphora coffeaeformis* (Agardh) Kützing. Figures 1–4, 11–14: Agardh No. 4600, Carlsbad (Syntype), as *Frustulia coffeaeformis* Agardh (Figures 11, 12 — same specimen in different focus). Figures 5, 15–18: BM 18945 — Kützing mat. No. 469, Carlsbad. Figures 6–8, 19–24: BM 78009 — Kützing material, Carlsbad. Figures 9, 10: NIWR 383/7644 — Sundays River, South Africa (sample SUN 37). × 1 500. Figures 11, 13, 18, 21, 24 – bright field illumination. Figures 12, 14, 20, 22, 23 – oblique-bright field illumination. Figures 15–17, 19 – phase contrast illumination.

unreliable. Nevertheless, we have incorporated data supplied by Patrick & Reimer (1975) since Reimer examined the Agardh type material.

(a) Species description based on light microscopy (LM). Figures 1–34, 45, 46, 49, 50, 61–66

Frustules elliptical to lanceolate with ends protracted into relatively broad (and sometimes truncate) subrostrate to rostrate poles. Girdle bands numerous, finely striate. Valves semilanceolate, somewhat elongate in large specimens; dorsal margin convex, sometimes slightly flattened or indented at the centre in the larger specimens; ventral margin generally straight with a slight central inflation, or weakly concave; poles somewhat ventrally deflected, protracted into subrostrate, rostrate or capitate apices of varying lengths; valve length 14,0–55,0 μm, valve breadth 3,5–7,3 μm. Raphe filiform, fairly close to the ventral margin, with more or less straight raphe branches sloping gently upwards



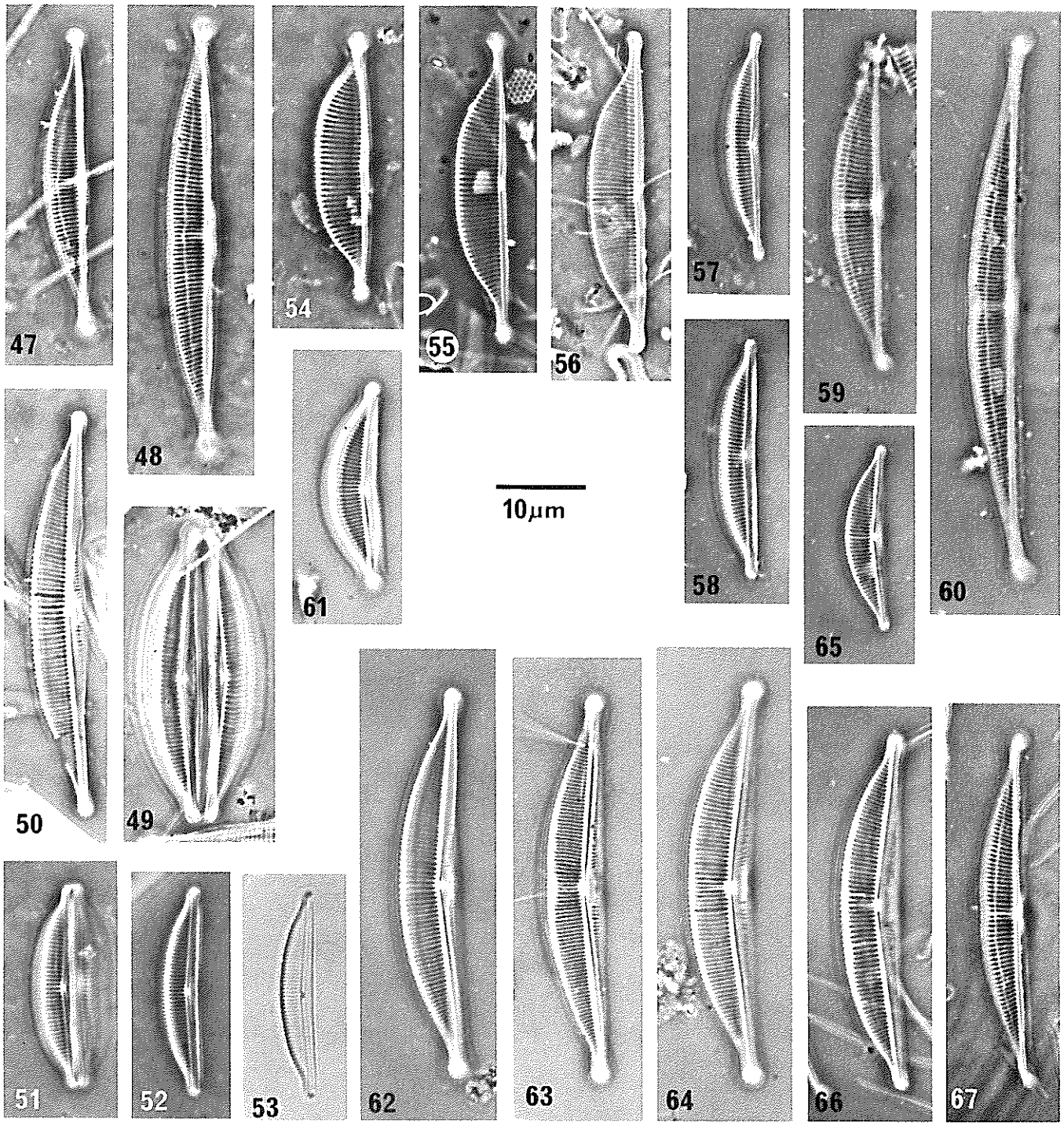
Figures 25–46 Figures 25–29: *A. coffeaeformis* — NIWR 383/7644, Sundays River, South Africa (sample SUN 37). Figures 30–34: *A. salina* W. Smith — BM 23126 Iford (Syntype) = *A. coffeaeformis*. Figure 35: '*A. coffeaeformis*' *sensu* Cleve & Möller slide No. 86 = *A. veneta* Kützing. Figure 36a,b: '*A. coffeaeformis*' *sensu* Cleve & Möller slide No. 86 = *A. veneta* var. *capitata* Haworth (same specimen). Figure 37: '*A. coffeaeformis*' var. *salinarum* Grunow *sensu* Cleve & Möller slide No. 204 = ? *A. acutiuscula* Kützing. Figure 38: '*A. coffeaeformis*' *sensu* Cleve & Möller slide No. 262 = *A. veneta* var. *capitata* Haworth. Figure 39: *A. coffeaeformis* — Hustedt slide No. U1,29, Carlsbad. Figure 40: '*A. coffeaeformis*' *sensu* Hustedt slide No. U1,30, Bad Nauheim. Figure 41a,b: '*A. coffeaeformis*' *sensu* Hustedt slide No. U1,54, Kuripan, Java (same specimen). Figures 42–44: '*A. salina*' *sensu* W. Smith slide BM 23125, Belfast. Figures 45, 46: *A. salina* — Eulenstein slide No. 96, Isigny = *A. coffeaeformis*. × 1 500. Figures 25, 26, 29–36a, 38–45 — phase contrast illumination. Figures 27, 28, 36b — oblique-bright field illumination. Figures 37, 46 — bright field illumination.

from the poles to the central nodule; central pores small but distinct and somewhat dorsally deflected; terminal fissures not always distinct, but when visible fairly abruptly directed to the dorsal side; conopeum sometimes faintly visible as a slightly brighter band crossing the proximal ends of the dorsal striae. Axial area narrow, linear, following the line of the raphe on the dorsal side. Central area on the dorsal side absent, on the ventral side an expanded area generally reaching the margin, but sometimes bounded by shortened ventral striae. Dorsal transapical striae slightly radial throughout, usually more strongly so at the poles, somewhat undulate near the centre of the valve and often slightly arcuate towards the poles; structure indistinct; (16)17–24(26) in 10 µm near the centre along the raphe, slightly denser towards the poles, (20)22–30 in 10 µm; ventral striae short marginal dashes increasing in length towards the centre, 21–36 in 10

μm near the centre and somewhat denser at the poles.

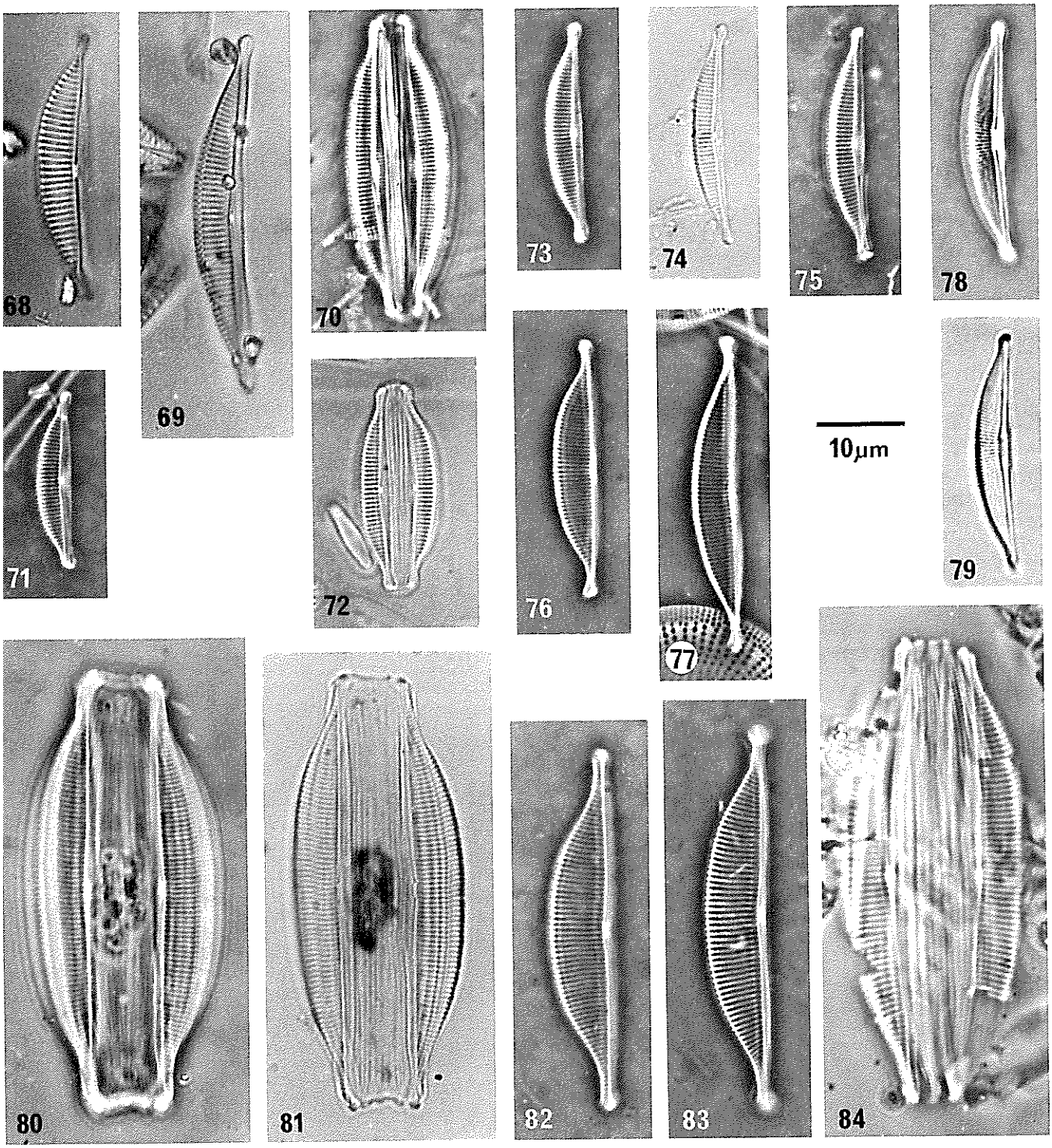
(b) Species description based on electron microscopy (EM)

Under EM the general characteristics of the frustule and valve as seen under LM are confirmed, but certain features are more clearly observed. SEM studies of an entire frustule (Figures 135, 136) show that the pervalvar axis is strongly curved so that the valvar planes of both valves subtend each other in an extremely obtuse angle (Figures 110, 111). In dorsal aspect the girdle is broad and convex (Figures 115, 135, 136), while in ventral view it is more or less concave and considerably narrower (Figures 110, 111). The structure of the individual elements of the girdle is not particularly clear to us at present, but it appears to be similar to that described by Gotoh (1980) for an unnamed species of *Amphora*. Each girdle element is a band, open at one end, and having a more



Figures 47–67 Figures 47, 48: *'A. salina' sensu* Van Heurck slide No. 11 = *A. hybrida* Grunow. Figures 49, 50: *'A. salina' sensu* Van Heurck slide No. 12 = *A. coffeaeformis*. Figures 51–53: *'A. salina'* var. *sensu* Van Heurck slide No. 12 (Figures 52, 53 — same specimen). Figures 54–56: *'A. salina' sensu* Van Heurck slide No. 116 = *A. taylori* Grunow. Figures 57, 58: Tempère & Peragallo slide No. 415, Knocke, Belgique = ? *A. coffeaeformis* var. Figures 59, 60: Tempère & Peragallo slide No. 415, Knocke, Belgique = *A. hybrida* Grunow. Figures 61–64: *A. salina* — Tempère & Peragallo slide No. 422 = *A. coffeaeformis*. Figures 65, 66: *A. salina* — Tempère & Peragallo slide No. 520 = *A. coffeaeformis*. Figure 67: *'A. salina' sensu* Tempère & Peragallo slide No. 520 = *A. hybrida* Grunow. × 1 500. Figures 47–52, 54–67 — phase contrast illumination. Figure 53 — bright field illumination.

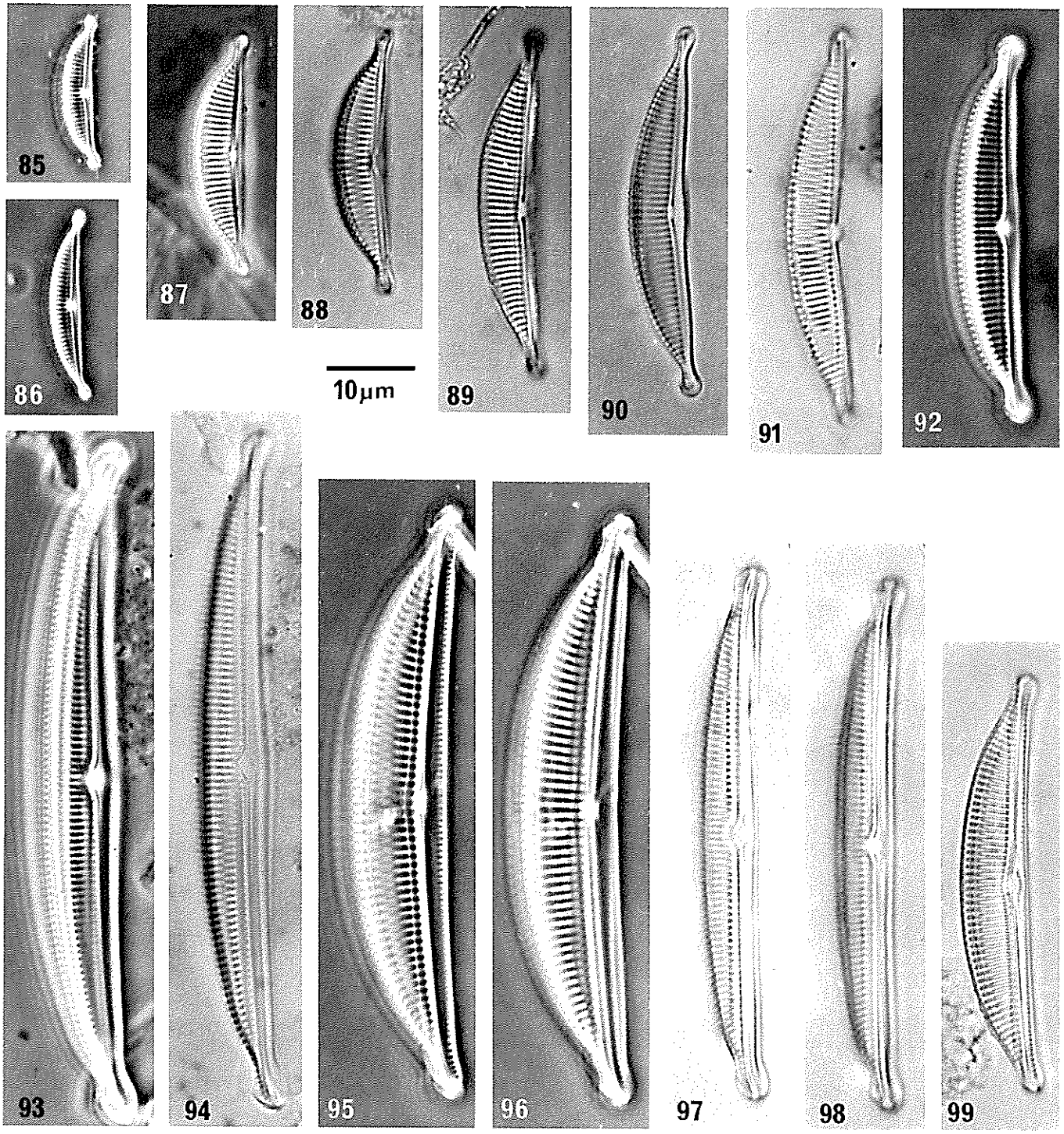
: less thickened axial rib. On either side of this rib there is a ngle row of linear, oval or roundish pores (37–45 in 10 m). Each band is bordered on the outside by a narrow atureless region (Figures 109, 137, 138). In our local ecimens the axial rib of the girdle bands is progressively ore strongly developed in each successive band in an lvalvar direction (Figures 136–138), although in the type aterial (Agardh No. 4600) the axial ribs appear to show no such differentiation with development (Figure 115). Under SEM the valve face is flat and curves smoothly over into a relatively high dorsal mantle lying more or less at right angles to the valve face (Figures 111, 147, 156, 157, 159). Along the transition line between these two regions there is usually a weak longitudinal costa which barely interrupts the striae in their passage from valve face to mantle (Figures 142, 145). In some cases (Figure 143) this costa may not be



Figures 68–84 Figures 68, 69: '*A. salina*' var. *sensu* Cleve & Möller slide No. 255. Figures 70–75: *A. aponina* Kützing — BM 18944 (Syntype), Kützing mat. No. 393, Abano = *A. coffeaeformis* var. *aponina comb. nov.* Figures 76, 77: '*A. aponina*' *sensu* H.L. Smith slide No. 29 (BM 25590) = *A. taylori* Grunow. Figures 78, 79: '*A. aponina*' *sensu* Van Heurck slide No. 257 = *A. veneta* var. *capitata* Haworth (same specimen). Figures 80–83: *A. taylori* Grunow — Van Heurck slide No. 13 (Syntype). Figures 80, 81: frustule (same specimen). Figure 84: *A. lineata* Gregory — BM 956 (Type ?), Glenshira. × 1 500. Figures 68, 69, 72, 74, 81 — bright field illumination. Figures 70, 71, 73, 75–78, 80, 82–84 — phase contrast illumination. Figure 79 — oblique-bright field illumination.

distinguishable. In contrast, other specimens appear to develop a low external ridge along this costa towards the centre of the valve (Figures 111, 156, 157). In TEM the longitudinal costa (Figures 102, 130, 132) may not always be clearly visible owing to the position in which the valve is lying.

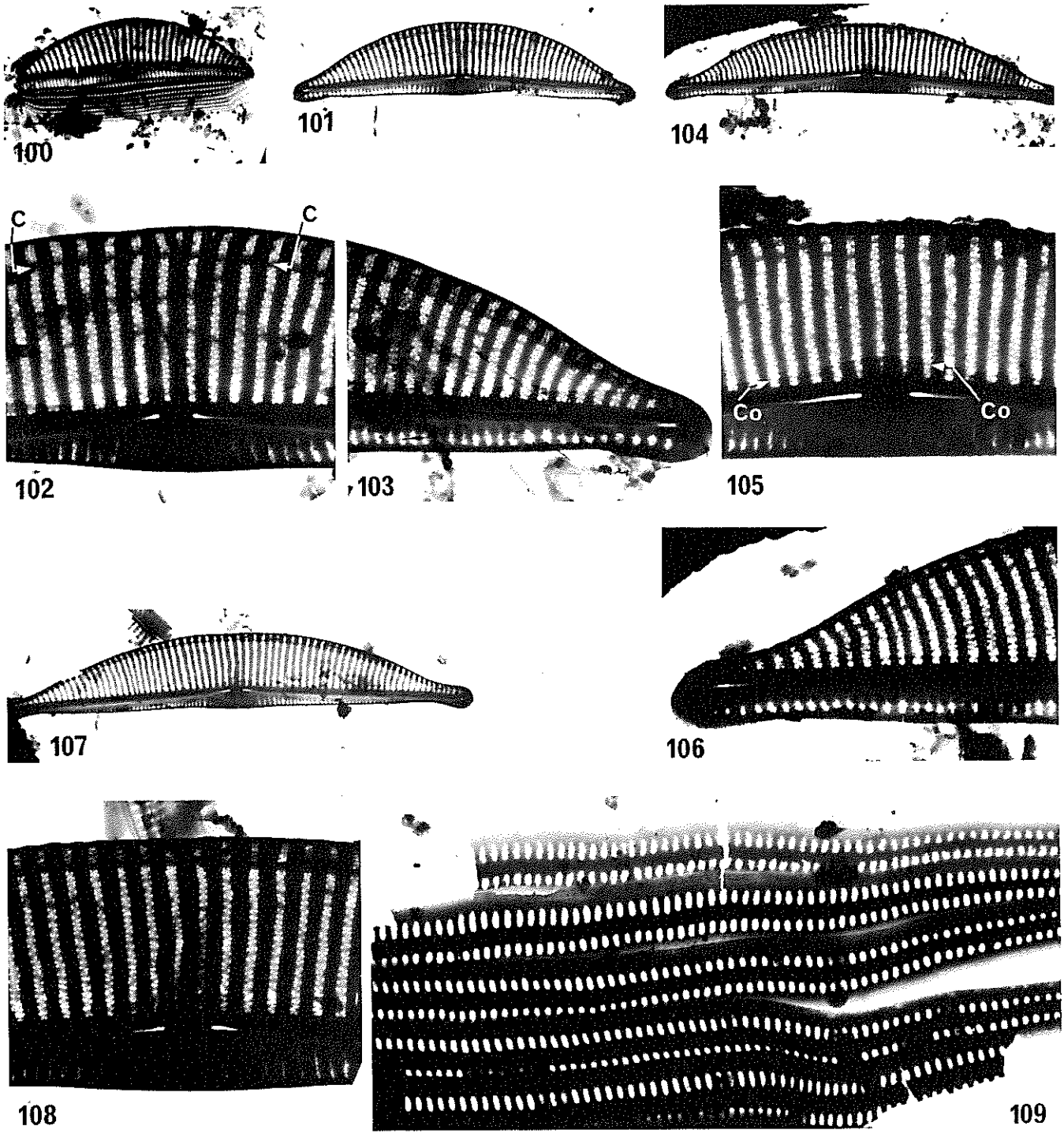
There is a prominent axial rib (Figures 111, 144) running the length of the valve near the ventral margin. This rib has a narrow extension along its dorsal margin, the conopeum (Figures 141, 143, 145, 146, 156–158), behind which lies a canal. The conopeum does not appear to be firmly attached at the central nodule but is fused to the terminal nodule where it is slightly expanded (Figures 146, 158). It is a thin structure and can sometimes be seen in TEM as a narrow shadow band crossing the proximal ends of the dorsal striae (Figures 105, 124, 126, 134). The external raphe fissure opens along the axial rib as a narrow slit. At the central nodule the central pores are small expansions of the raphe



Figures 85–99 Figures 85, 86: *'A. lineata'*? — Tempère & Peragallo slide No. 161. Figures 87–91: *'A. lineata'*? or *'A. salina'*? — Tempère & Peragallo slide No. 292 = ? *A. acutiuscula* Kützing (*cf.* BM 18173 = Kützing mat No. 252 — Genoa). Figures 92–94: ? *'A. lineata'* — Cleve & Möller slide No. 155 (Figures 93, 94 — same specimen). Figures 95, 96: ? *'A. lineata'* Gregory — Cleve & Möller slide No. 155 (same specimen). Figures 97, 98: ? *'A. lineata'* — Cleve & Möller slide No. 210 (same specimen). Figure 99: ? *'A. lineata'* — Cleve & Möller slide No. 210. × 1 500. Figures 85–87, 92, 93, 95, 96 — phase contrast illumination. Figures 88–91, 94, 97–99 — bright field illumination.

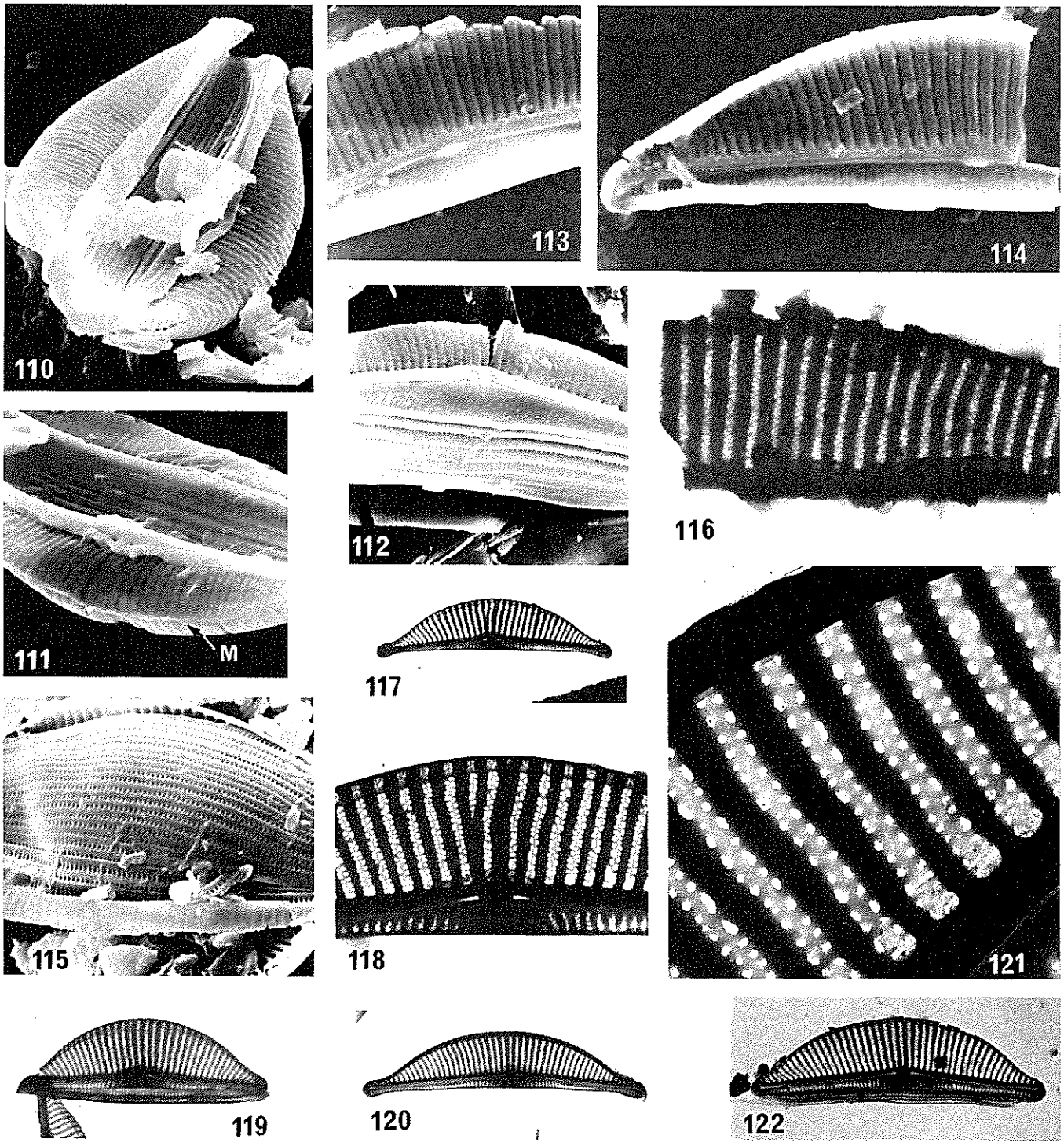
ssure (Figures 111, 139, 141, 143, 157), while at the erminal nodule the raphe ends in a short dorsally deflected erminal fissure (Figures 146, 158). Internally the axial rib ppears to be slightly raised (Figure 147) with a narrow ongue-like expansion at the central nodule (Figures 113, 47–150, 159). The internal raphe fissure is a narrow slit unning mainly along the ventral edge of the axial rib Figures 147, 150). At the central nodule it terminates on ither side of the tongue-like expansion (Figures 113, 150), while at the poles it ends in the terminal nodule (Figures 151, 152). In some TEM micrographs the relative positions of the external and internal raphe fissures may be seen (Figure 154).

The dorsal striae are formed by regularly spaced, narrow, transapically elongate depressions of the inner surface of the basal siliceous layer (Figures 113, 114, 147–150, 159). The outer wall of these depressions is perforated by a double row of fine pores varying in size and shape, and irregularly



Figures 100–109 Figures 100–109: *A. coffeaeformis* — Agardh No. 4600 (Syntype) as *Frustulia coffeaeformis*. TEM. Figure 100: Valve with attached girdle bands. Figures 101–103: Valve with centre (Figure 102) and pole (Figure 103) enlarged; note longitudinal costa (C) in Figure 102. Figures 104–106: another valve with centre (Figure 105) and pole (Figure 106) enlarged; note conopeum (Co) indicated in Figure 105. Figures 107, 108: larger valve with centre enlarged. Figure 109: Portion of five girdle bands enlarged. Figures 100, 101, 104, 107: × 2 200. Figures 102, 103, 105, 106, 108, 109: × 7 525.

arranged although tending towards alternate (Figures 102, 103, 105, 106, 108, 116, 118, 128, 131, 150, 154, 155, 161, 162). Each pore row contains between 51 and 93 puncta in 10 μm. In some of the TEM micrographs cited here a third row of smaller pores may be observed between the double row of pores forming the striae (Figures 131, 155). Continuations of the striae on the dorsal mantle have the same structure (Figures 132, 138). The ventral striae (Figures 102, 103, 118, 120, 134, 152–155) are narrower and much shorter than the dorsal striae, although towards the centre of the valve they become progressively longer. Below the central nodule the ventral striae are usually interrupted (Figures



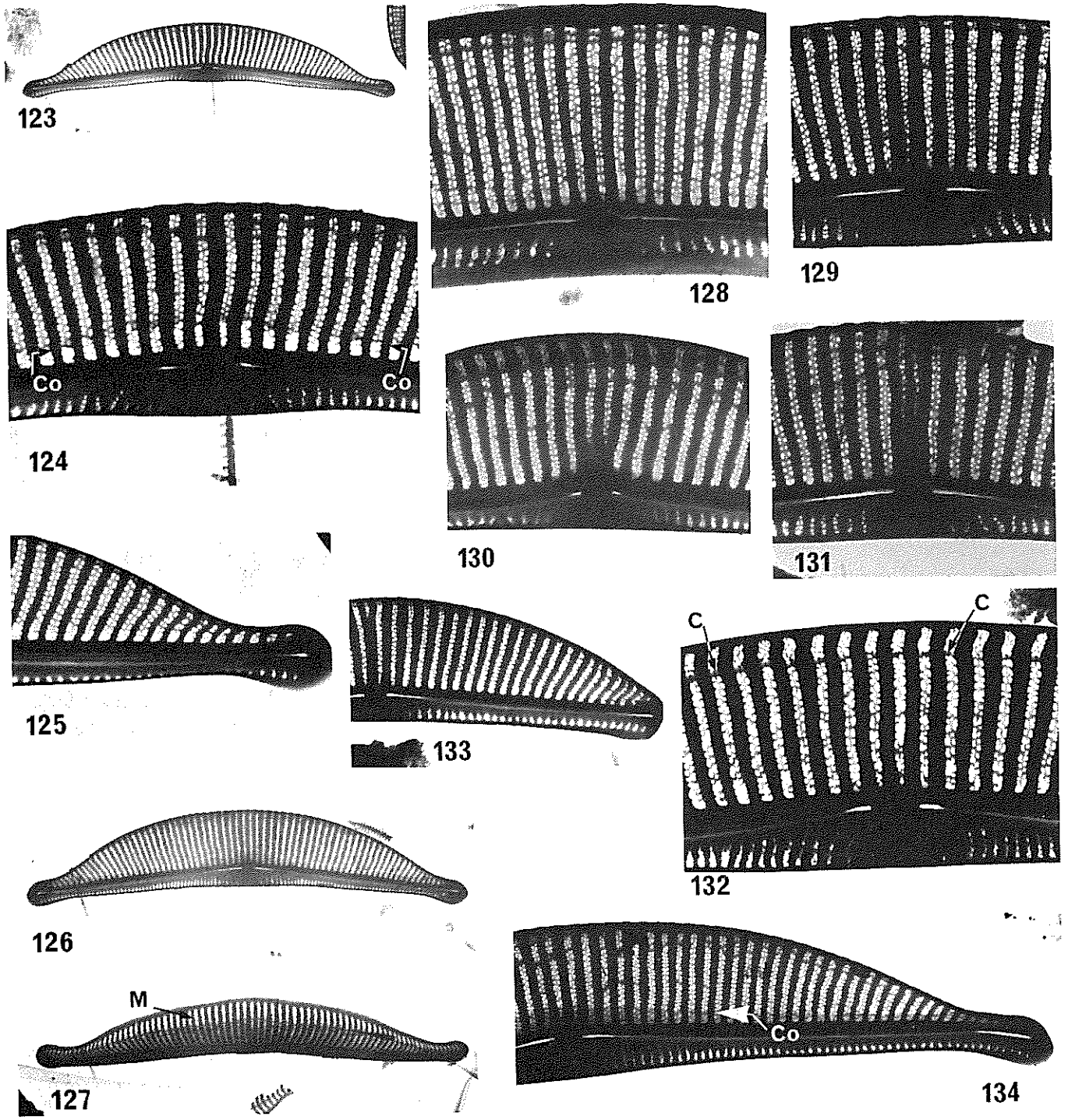
Figures 110–122 Figures 110–115: *A. coffeaeformis* — Agardh No. 4600 (Syntype) as *Frustulia coffeaeformis*. SEM. Figure 110: frustule viewed from ventral side; note girdle bands. Figure 111: part of another frustule from the ventral side; note dorsal mantle (M) separated from the valve face by a weak longitudinal costa. Figure 112: part of a valve with attached girdle bands. Figures 113, 114: internal views of the centre (Figure 113) and a pole (Figure 114) of different valves. Figure 115: dorsal view of part of a frustule showing convex girdle. Figure 116: *A. coffeaeformis* — Kützing mat. No. 469 (Carlsbad). TEM. Fragment of valve to show striae structure. Figures 117–122: *A. coffeaeformis* — Sundays River, South Africa (sample SUN 37). TEM. Figures 117, 118: a valve with centre enlarged. Figure 119: another valve with some girdle bands attached. Figures 120, 121: a valve with a section enlarged to show striae structure. Figure 122: valve with a few girdle bands attached. Figures 110–112, 115: × 4 300. Figures 113, 114: × 6 000. Figures 116, 118: × 7 525. Figures 117, 119, 120, 122: × 2 200. Figure 121: × 25 000.

102, 105, 118), but sometimes a few very short marginal striae may be found (Figure 129). The structure of the ventral striae is very similar to that of the dorsal striae and consists of a double (the longer striae near the centre) or single row of somewhat finer puncta. Towards the central nodule the ventral striae are radial but become convergent towards the poles where they number between 29 and 42 in 10 μm.

4.2 Other materials under the name *A. coffeaeformis*

(a) Cleve & Möller slide No. 86 (Gottland, Boge) = NIWR 64/1262

On this slide we examined specimens (Figures 35, 36) identified by Cleve & Möller as *A. coffeaeformis* var. It is clear, however, that they cannot be related to *A. coffeaeformis* or *A. salina*. They are in fact two varieties of *A. veneta* Kützing, viz. the var. *veneta* (Figure 35) and the var. *capitata* Haworth (Figure 36). For descriptions of these see Schoeman & Archibald (1978; 1979). Also consult paragraphs 4.2(d) and 4.6(b).



Figures 123–134 Figures 123–134: *A. coffeaeformis* — Sundays River, South Africa (sample SUN 37). TEM. Figures 123–125: a valve with centre (Figure 124) and a pole (Figure 125) enlarged; note conopeum (Co) in Figure 124. Figures 126, 127: a valve in valve face view (Figure 126) and tilted to expose the dorsal mantle (M-Figure 127). Figures 128–132: centres of some valves showing variations in striae development above the central nodule; note longitudinal costa (C) in Figure 132. Figures 133, 134: half valves showing variation in polar shape; note conopeum (Co) in Figure 134. Figures 123, 126, 127: × 2 200. Figures 124, 125, 128–132: × 7 525. Figure 133: × 4 560. Figure 134: × 4 800.

(b) Cleve & Möller slide No. 91 (Isigny, Normandy) = NIWR 64/1267

Cleve & Möller identified certain specimens on this slide as *A. coffeaeformis* var. (=*A. salina* W. Smith). Unfortunately the quality of this slide did not permit clear focussing on the structural details of the valves. Nevertheless we accept these forms as being representatives of *A. coffeaeformis* proper.

(c) Cleve & Möller slide No. 204 (Oakland, California) = NIWR 69/1380

Specimens on this slide (Figure 37) were identified by Cleve & Möller as *A. coffeaeformis* var. *salinarum* Grunow. It is, however, evident from the relatively distinct puncta of the striae and the presence of a more or less clearly visible conopeum that they do not belong to *A. coffeaeformis*. VanLandingham (1967) treats the var. *salinarum* as a synonym of *A. acutiuscula*. At present we follow this interpretation although we do not have a clear concept of the latter.

(d) Cleve & Möller slide No. 262 (Geysir, lower fire-hole basin, Iceland) = NIWR 72/1438

Cleve & Möller listed *A. coffeaeformis* as present on this slide. We observed no true representatives of this species but only forms (Figure 38) fitting the description of *A. veneta* var. *capitata* Haworth (*cf.* paragraph 4.2(a)).

(e) Hustedt slide No. U1,29 (Carlsbad) — BRM

The specimens (Figure 39) on this slide are confirmed as *A. coffeaeformis*. The slide is marked as being from Carlsbad, Agardh's type locality, but we do not know whether this is Hustedt's own gathering or whether it was made from Agardh's or Kützing's materials.

(f) Hustedt slide No. U1,30 (Bad Nauheim) — BRM

We are reluctant to accept Hustedt's identification of specimens on this slide (Figure 40) as *A. coffeaeformis*. In many respects they resemble fairly closely our concept of *A. coffeaeformis* and it is difficult to define clearly the points of difference. These lie mainly in the structural appearance of the dorsal and ventral striae. Hustedt's (1930: 344, Figure 634) illustration of *A. coffeaeformis* reflects very closely the specimens on this slide.

(g) Hustedt slide No. U1,54 (Kuripan, Java) — BRM

The specimens on this slide provide a third variation of Hustedt's concept of *A. coffeaeformis*. The Javanese forms (Figures 41a, 41b) differ markedly in their distinctly punctate striae and therefore cannot be closely related to *A. coffeaeformis*. The true identity of these specimens has not yet been established.

4.3 *Amphora salina* W. Smith: Type material

The type slide for *A. salina* is BM 23126, prepared in 1887 from material gathered by W. Smith (1853) at Iford, Sussex, in September 1852. We examined this slide and observed a fair number of specimens. These (Figures 30–34) agree in all details with *A. coffeaeformis* as observed on the syntype slide (No. 4600 Lund prepared by C.W. Reimer *ex* Herb. Agardh, Lund — No. 4600). Our light microscope observations were verified by examination of the syntype material of both *A. coffeaeformis* and *A. salina* under the electron microscopes (Figures 100–115, 153–159 respectively). On this basis we confirm that *A. salina* and *A. coffeaeformis* are conspecific and that *A. salina* is correctly regarded as a later synonym of *A. coffeaeformis*.

4.4 Other materials under the name *A. salina*

(a) BM 23125 (Belfast, July 1853) — BM

This is a slide prepared from W. Smith's diatom gathering made in July 1853 at Belfast and is labelled *A. salina*. On the grounds of their striae structure (Figures 42–44), which is more or less distinctly punctate, we cannot relate these specimens to *A. salina* (= *A. coffeaeformis*) nor can we identify them with any other *Amphora* taxon known to us.

(b) Eulenstein slide No. 96 (Isigny, Gallia) = NIWR 80/1596

This slide, labelled *Amphora salina* Sm., was prepared from material gathered from Isigny (*cf.* Cleve & Möller slide No. 91 in paragraph 4.2(b) above). The slide contains mainly frustules but its condition is generally not good. Nevertheless we consider these specimens (Figures 45, 46) to be true representatives of *A. coffeaeformis*.

(c) Van Heurck slide No. 11 (Anvers, Belgique) = NIWR 1/11

The slide is specifically marked '*Amphora salina* W. Smith' but according to the relevant booklet accompanying each set of Van Heurck's slides (Grunow in Van Heurck 1884–1887: Séries 1, p. 3) the slide also contains *A. lineolata* Ehrenberg fo. *minor*. Apart from this taxon we noted one other abundant *Amphora* form (Figures 47, 48) which we assume was designated *A. salina* by Grunow. These specimens differed significantly in structure from the typical *A. salina* (= *A. coffeaeformis*) and can be identified with *A. hybrida* Grunow (in Van Heurck 1884–1887: 4, slide No. 12; see following material).

(d) Van Heurck slide No. 12 (Blankenberghe, Belgique) = NIWR 1/12

This is the syntype slide for *A. hybrida* Grunow and these specimens were clearly distinguishable. In addition, Grunow listed *A. salina* v.v.v. which we presume indicates a number of varieties of this species. In this regard we did observe a few examples (Figures 49, 50) of *A. coffeaeformis* (syn. *A. salina*) but there were also a number of specimens of a form (Figures 51–53) resembling *A. coffeaeformis* in some respects. At present we cannot identify this form with *A. coffeaeformis* proper but accept that it may be a variety. A similar form (Figures 57, 58) was found on a Tempère & Peragallo slide (No. 415, 1st. Ed.) of material from Knocke in Belgium (*cf.* paragraph 4.4(f)).

(e) Van Heurck slide No. 116 (Creswell, Angleterre) = NIWR 6/116

In his inventory of species occurring on this slide, Grunow (in Van Heurck 1884–1887: 37) mentions only one *Amphora* species, *A. salina*. The specimens (Figures 54–56) observed on this slide do not fit our concept of *A. coffeaeformis* but agree well with '*Amphora taylori* Grunow' (for further comments on this taxon see paragraph 4.7).

(f) Tempère & Peragallo (1st Ed.) slide No. 415 (Knocke, Belgique) = NIWR 49/966

Of the five species of *Amphora* listed for this slide (*cf.* Tempère & Peragallo 1889–1895: 205) three present no problem in their recognition. However, some difficulty was experienced in identifying *A. acutiuscula* and '*A. salina*' (= *A. coffeaeformis*). On examining the slide we observed two forms which may represent these two species. It is impossible to know which Tempère & Peragallo intended as which, as, from our examination of the previous slides (see above) both these forms have been assigned to '*A. salina*'. However, having examined a large array of samples in this study, we can now identify one of the forms (Figures 59, 60) as *A. hybrida* Grunow while the other (Figures 57, 58) may be a variety of *A. coffeaeformis* (*cf.* paragraph 4.4 (d)).

(g) Tempère & Peragallo (1st Ed.) slide No. 422 (Shark River, New Jersey, U.S.A.) = NIWR 49/973

The specimens (Figures 61–64) were identified correctly as *A. salina* which is synonymous with *A. coffeaeformis*.

(h) Tempère & Peragallo (1st Ed.) slide No. 520 (Calvados, France) = NIWR 54/1071

Tempère & Peragallo (1889–1895: 252) list only one *Amphora* species for this slide under the name *A. salina*. Our examination of the slide showed that there are actually two species present but they were probably regarded as one taxon. One of the species (Figures 65, 66) is indeed correctly identified as *A. salina* (= *A. coffeaeformis*) while the other is *A. hybrida* (Figure 67).

(i) Cleve & Möller slide No. 218 (Malmö, Sweden) = NIWR 70/1394

Specimens on this slide are in poor condition and much of their structure is obscure. Consequently we cannot make any positive identification of these forms.

(j) Cleve & Möller slide No. 255 (Hourdel, Embouchure de la Somme) = NIWR 72/1431

Here also the condition of the slide made it difficult to determine with certainty what the specimens are. Cleve & Möller (1877–1882: Part 5, p. 4) list *A. salina* var. as being common. However, the specimens (Figures 68, 69) observed on this slide are clearly not the proper *A. coffeaeformis* (syn. *A. salina*) but we have not been able to assign them to another taxon. Owing to a fairly conspicuous conopeum and coarser striation they may be related to *A. acutiuscula*.

4.5 *Amphora aponina* Kützing: Type material

BM 18944, a slide prepared by the British Museum (Natural History) from material (Kützing No. 393 — Abano) in the Kützing collection, is marked as the type slide for *A. aponina*. Cleve (1895) cited *A. aponina* as a synonym of *A. coffeaeformis*, presumably following De Toni's (1891–1894) taxonomic notes on *A. aponina*. This interpretation is still adhered to in VanLandingham (1967: 193 and 202). We examined the type slide and found numerous specimens (Figures 70–75) resembling *A. coffeaeformis* very closely, but with certain subtle differences. In contrast, the valves of *A. aponina* appeared to be more linear-lanceolate with a length:breadth ratio for specimens of an equivalent length greater than in *A. coffeaeformis*. The range in breadth of *A. aponina* covers only the lower breadth range of *A. coffeaeformis*. The valves observed were 17–35 μm long, and 3,6–4,5 μm broad. Although the striae density (dorsal striae: 20–23 in 10 μm near the centre, 23–30 in 10 μm at the poles; and ventral striae: 30–36 in 10 μm near the centre and up to 42 in 10 μm at the poles) falls within the range for *A. coffeaeformis*, TEM studies (Figures 163–168) revealed certain differences in their structure. It appeared that the striae in *A. aponina* were slightly broader and were perforated by two rows of larger puncta (43–66 in 10 μm), giving the striae a coarser appearance (*cf.* Figures 121, 166). Figure 168 illustrates a specimen with unusual striae structure in which a large degree of fusion of the puncta appears to have taken place. Our observations of *A. aponina* under SEM (Figures 169–171) were unable to demonstrate any further clear distinctions between this species and *A. coffeaeformis*.

On the grounds of the differences we observed, *A. aponina* cannot be equated exactly with *A. coffeaeformis*. On the other hand the high degree of similarity between these two taxa does not allow *A. aponina* to stand on its own as a species. We therefore consider *A. aponina* to be a variety of *A. coffeaeformis*, and its correct name should therefore be *A. coffeaeformis* var. *aponina* (Kützing) *comb. nov.*

4.6 Other materials under the name *Amphora aponina*

(a) H.L. Smith Diat. Spec. Typ. No. 29 = BM 25590 (BM)

H.L. Smith's slide contained numerous specimens of a form (Figures 76, 77) which he identified as *A. aponina*. These could not, however, be related to the *A. aponina* on the type slide as discussed above, but we believe them to be akin to, if not the same as, '*A. taylori* Grunow' (see paragraph 4.7 below).

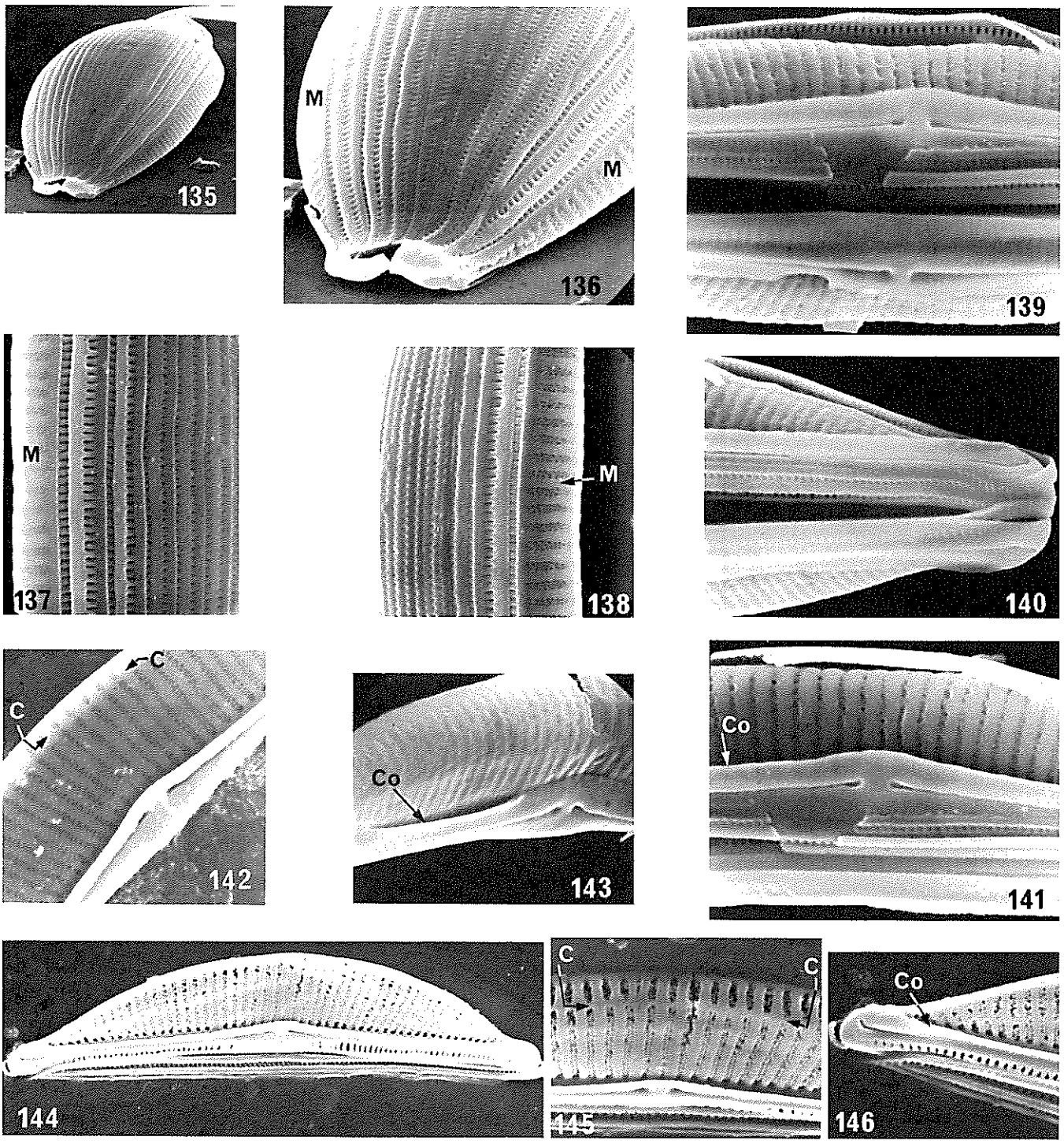
(b) Van Heurck slide No. 257 (S. Abbe Head, Angleterre) = NIWR 13/257

Grunow (in Van Heurck 1884–1887: 73) mentioned *A. aponina* (misspelt as *A. aponnia*) as the only *Amphora* species on this slide. Having examined this slide (*cf.* Figures 78, 79), we could only find specimens of *A. veneta* var. *capitata* (also see paragraphs 4.2(a) and 4.2(d).

4.7 *Amphora taylori* Grunow: Type slide

Although Van Heurck slide No. 13 (= NIWR 1/13) is a syntype slide for *A. taylori*, we are faced with the problem of its identification. According to Grunow (in Van Heurck 1884–1887: 4) the slide contains three species of *Amphora*. *A. arenaria* Donkin, one of the species mentioned, is easily identifiable, but the dilemma arises when trying to determine which is *A. taylori* and which is *A. lineata* Gregory var. Having thoroughly examined the slide in our collection we could recognize only one other *Amphora* taxon, which occurred fairly abundantly as a number of valves and numerous frustules (Figures 80–83). We could find nothing that would differentiate these specimens into two separate taxa. Notwithstanding this, it still remains a problem to decide whether these forms should be identified as *A. taylori* or as *A. lineata* var. This is apparently the only material from which both *A. taylori* and *A. lineata* var. have been recorded, so we are unable to formulate a concept of these taxa from other sources. None of the specimens measuring 27–57 μm long and 7,0–7,5 μm broad for valves (frustules 12–19 μm wide) observed on this slide agreed with the dimensions

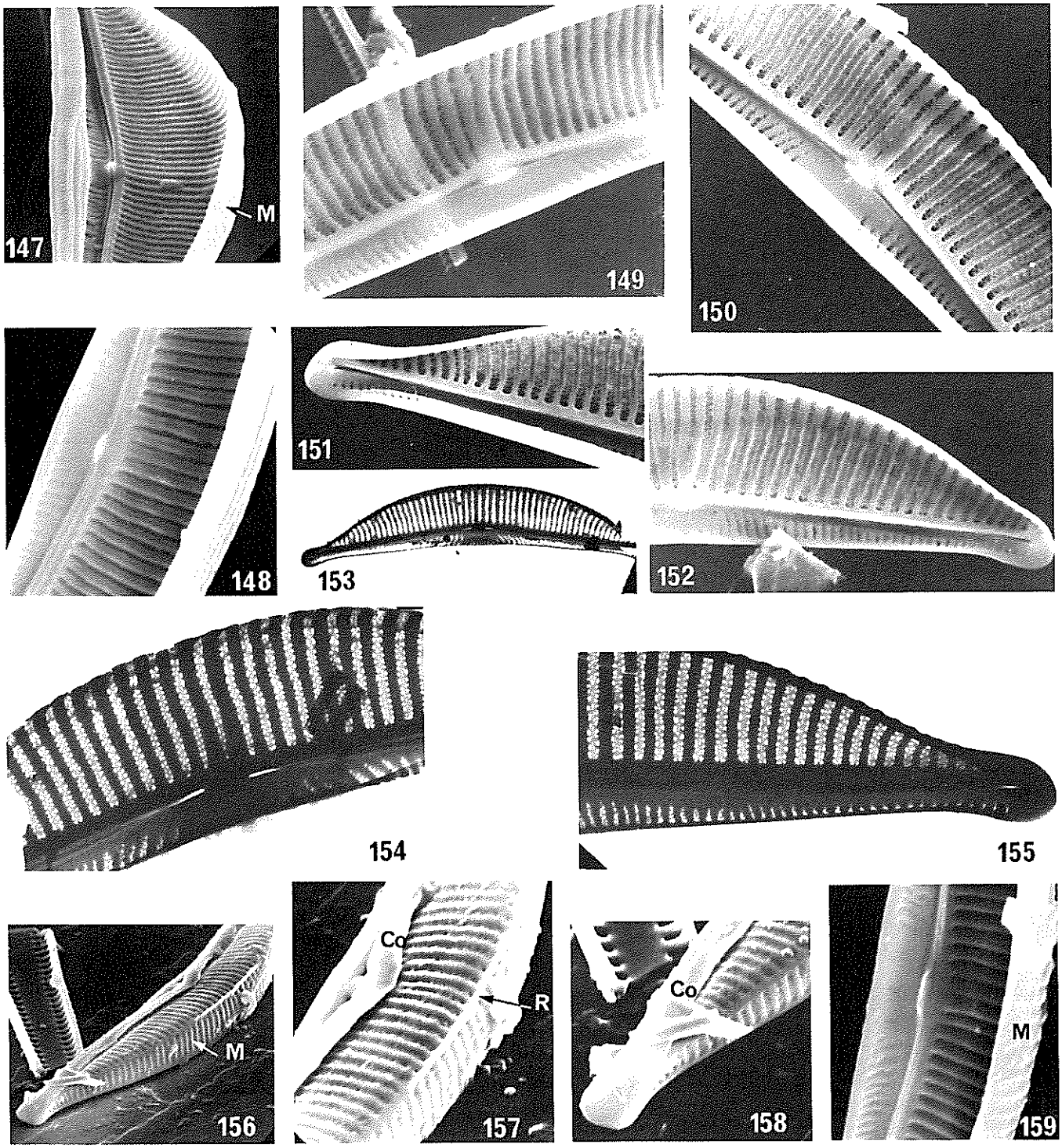
(58–70 μm long, valves 8,0 μm wide, frustules 20–24 μm wide) obtained by Grunow (*cf.* Van Heurck 1884–1887) for *A. taylori* from the same material (Van Heurck slide No. 13). Thus to identify these examples as *A. taylori* on the basis of their dimensions is open to criticism. Furthermore, Grunow's description of *A. taylori* is not sufficiently diagnostic to assist in reaching a positive identification of these specimens. On the other hand, to assign these specimens to *A. lineata* is equally difficult, since we have no idea of Grunow's concept of this variety. In addition we have no clear concept of what constitutes *A. lineata* Gregory, since the authenticity of Gregory's types in the British Museum (Natural History) has not been firmly establilshed. This point is discussed further under the comments on *A. lineata* (see paragraph 4.8



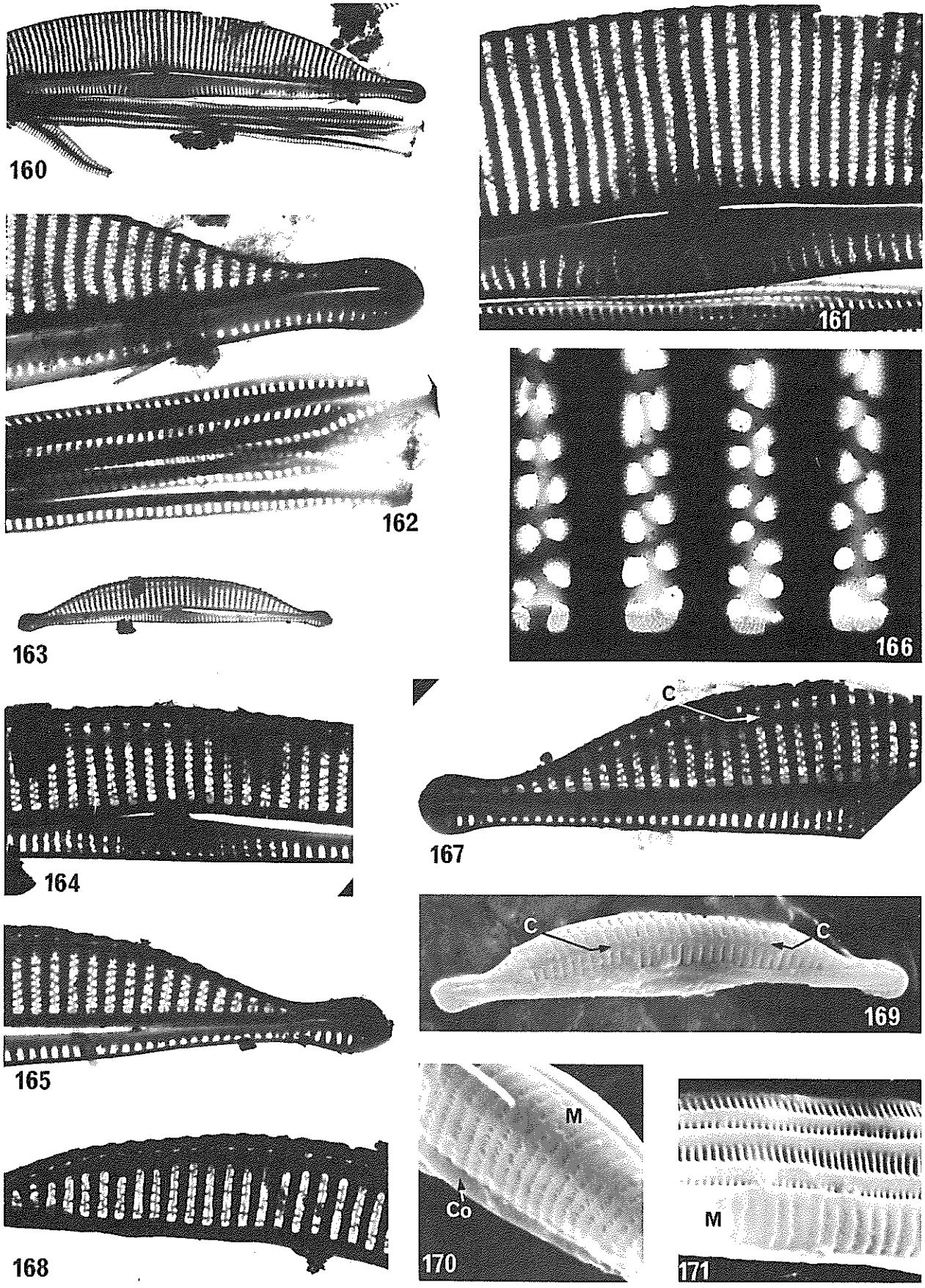
Figures 135 – 146 Figures 135–146: *A. coffeaeformis* — Sundays River, South Africa (sample SUN 37). SEM, external views. Figures 135, 136: a complete frustule viewed from the dorsal side with one pole enlarged (Figure 136); note dorsal mantles (M) of the two valves with the connecting girdle bands. Figures 137, 138: portions of the mantle (M) and accompanying girdle bands from the left and right hand valves respectively of the specimen in Figure 135 to show girdle band structure. Figures 139–141: various aspects of a frustule from the ventral side; Figure 141 at same position as Figure 139 but tilted to show conopeum (Co) more clearly. Figures 142, 143: enlargements of valve centres to show longitudinal costa (C) in Figure 142 and conopeum (Co) in Figure 143. Figures 144–146: an etched valve (Figure 144) with enlargements of the centre and pole to show longitudinal costa (C) in Figure 145 and conopeum (Co) and external raphe ending at the pole in Figure 146. Figure 135: × 2 880. Figures 136–143, 145, 146: × 6 600. Figure 144: × 4 000.

below).

Although it is still a matter of speculation as to what these specimens should be called, for convenience of comparison with similar forms observed elsewhere in this study, we designate them as '*A. taylori*'. Whether we are correct in doing this or not, the forms now called '*A. taylori*' do not fully accord with the concept of *A. coffeaeformis* as outlined above and differ from the latter in a number of respects. In valve view the valves are more elliptical with a slightly flattened dorsal margin around the centre and narrowing abruptly at the ends to form narrow elongated subcapitate to capitate poles, which are characteristically somewhat dorsally deflected (Figures 54–56, 76, 77, 82, 83). The raphe branches of '*A. taylori*' are parallel to and lie very close to the ventral



Figures 147–159 Figures 147–152: *A. coffeaeformis* — Sundays River, South Africa (sample SUN 37). SEM, internal views. Figures 147–150: centres of various valves enlarged to show tongue-like projection of the central nodule, mantle (M) in Figure 147 and internal striae structure. Figures 151, 152: poles of two valves enlarged to show distal endings of the internal raphe fissures. Figures 153–159: *A. salina* W. Smith — Iford, England (Syntype) = *A. coffeaeformis*. Figure 153: TEM. A more or less complete valve. Figures 154, 155: TEM. Centre and pole of two specimens enlarged to show striae structure. Figures 156–158: SEM, external views of a valve with centre and pole enlarged; note mantle (M) in Figure 156, conopeum (Co) in Figures 157 and 158, and the ridge (R) in Figure 157. Figure 159: SEM, internal view showing tongue-like projection of the central nodule. Figures 147–152, 157–159: × 6 600. Figure 153: × 2 200. Figures 154, 155: × 7 525. Figure 156: × 3 240.



Figures 160–171 Figures 160–162: *A. coffeaeformis* — Etosha National Park, South West Africa (NIWR mat. No. SWA 227). TEM. Valve and girdle bands with centre (Figure 161) and pole (Figure 162) enlarged. Figures 163–171: *A. aponina* Kützing — Abano (Kützing mat. No. 393), Type = *A. coffeaeformis* var *aponina comb. nov.* Figures 163–166: TEM. A valve with centre (Figure 164), pole (Figure 165) and striae (Figure 166) enlarged. Figure 167: TEM. Portion of another valve showing longitudinal costa (C). Figure 168: TEM. Fragment of valve to show unusual striae structure. Figure 169: SEM. Whole valve showing longitudinal costa (C). Figures 170, 171: SEM. Portion of valve to show valve face and dorsal mantle (M) in Figure 170 and strongly tilted to show dorsal mantle (M) and adjoining girdle bands in Figure 171. Figures 160, 163: × 2 200. Figures 161, 162, 164, 165, 167, 168: × 7 550. Figure 166: × 45 000. Figure 169: × 4 950. Figures 170, 171: × 7 200.

margin, ending in small terminal nodules situated at the apex of the capitate poles. Because of these differences we are hesitant in accepting '*A. taylori*' as synonymous with *A. coffeaeformis* (*cf.* VanLandingham 1967: 202 and 273).

4.8 *Amphora lineata* Gregory: Type slide?

The proper identity of *A. lineata* Gregory is difficult to ascertain. From his own comments (*cf.* Gregory 1857a: 71; 1857b: 512) it is obvious that Gregory himself had a somewhat confused concept of the taxon. Reference to type slides is of little help, since, as far as we are aware, there are no slides in the British Museum (Natural History) that have been positively verified as Gregory's original type slides. There are, however, a number of slides prepared from Gregory material (Glenshira) in the Greville Collection at the British Museum. On two of these (BM 955 and BM 956) there are rings labelled as containing *A. lineata* Gregory. Slide BM 955 bears two ringed frustules (ring Nos 1 and 3), but they are unfortunately poor specimens making it difficult to establish their morphological characteristics. On the other hand the single frustule ringed on slide BM 956 (Figure 84) is in somewhat better condition. This frustule resembles *A. coffeaeformis* in general shape and structure but the striation of the valves is coarser (15–16 dorsal striae in 10 μm near the centre) than we have observed in *A. coffeaeformis*.

According to VanLandingham (1967), modern interpretation of *A. lineata* still follows Cleve (1895) in viewing *A. lineata* from the Glenshira deposit (Gregory 1857a: 71, Plate 1, Figure 33) as *A. coffeaeformis*, while *A. lineata* from the Firth of Clyde and Loch Fine (Gregory 1857b: 512, Plate 4, Figure 70) is considered synonymous with *A. coffeaeformis* var. *acutiuscula* (= *A. acutiuscula*). Having examined the Glenshira material, we believe that *A. lineata* may form part of the range of variation in *A. coffeaeformis*, but at this stage we would hesitate to state categorically that *A. lineata* is a synonym of *A. coffeaeformis*.

4.9 Other materials under the name *Amphora lineata*

(a) Tempère & Peragallo (1st Ed.) slide No. 161 (Barre de la Biddasoa) = NIWR 36/712

This slide is supposed to contain *A. lineata*, but nothing resembling *A. lineata* as seen in the Glenshira material, discussed above, could be found. Neither could we find anything that we could relate to *A. coffeaeformis* or *A. acutiuscula*. Examination of the slide enabled us to identify all except four of the *Amphora* valves, with the three species listed as occurring with *A. lineata* in this material. The four specimens (Figures 85, 86 illustrate two examples), which we could not assign to any of these species, may have been what Tempère & Peragallo intended as *A. lineata*, but we have no means of confirming this assumption.

(b) Tempère & Peragallo (1st Ed.) slide No. 292 (Saint Lunaire) = NIWR 43/843

Five species of *Amphora* are listed as being present on this slide. Of these *A. marina*, *A. proboscidea* and *A. proteus* cannot be associated with the most abundant *Amphora* taxon in this material. Thus, *A. lineata* and *A. salina* (= *A. coffeaeformis*) remain as the only two possible names for this taxon. However, it (Figures 87–91) cannot be identified with either of these two species, but appears to be almost identical to the most commonly observed form of *Amphora* on the type slide of *A. acutiuscula* Kützing (BM 18173 = Kützing material No. 252 from Genoa).

(c) Cleve & Möller slide No. 155 (Balearic Islands, Spain) = NIWR 67/1331

There are numerous *Amphora* species listed from this material. Having examined the slide carefully we could find nothing identical to *A. lineata* as represented on slide BM 956 (see paragraph 4.8 above) or to *A. coffeaeformis*. Only two forms on this slide approach the example of *A. lineata* on slide BM 956 (Figure 84). These are illustrated in Figures 92–94 and Figures 95 and 96 respectively. The first form (Figures 92–94) does not agree with *A. lineata* on account of the presence of a distinct conopeum and a characteristic dorsal extension of the central pores forming an inverted V-shaped marking over the central nodule. The second form (Figures 95, 96) also differs from *A. lineata* owing to the presence of a very distinct conopeum and to its much coarser striation. We have not been able to identify these two forms with any taxa known to us at present.

(d) Cleve & Möller slide No. 210 (Rovigno, Adriatic Sea) = NIWR 70/1386

The situation on this slide is similar to the previous one. *A. lineata* is indicated as one of a large number of *Amphora* species occurring on this slide. We were unable to find any specimens that could be equated with the Glenshira examples of *A. lineata* mentioned above, nor could we find any that could be identified as *A. coffeaeformis*. Of the two forms closest to our concept of *A. lineata*, one (Figures 97, 98) is identical to the specimens having the inverted V-shaped extension of the central pores (Figures 92–94) seen on the slide discussed immediately above, while the other (Figure 99) is similar to the form illustrated in Figures 95 and 96 but is more finely striate.

4.10 Misconceptions of *Amphora coffeaeformis* (Agardh) Kützing in the literature

On examining the literature on *A. coffeaeformis*, we again find several misconceptions of the species. In southern Africa there are numerous records of *A. coffeaeformis* from all over the region. On re-examining some of those materials still available to us, we discovered that in most cases the specimens identified as *A. coffeaeformis* were in actual fact *A. veneta* var. *capitata* Haworth (*cf.* Schoeman & Archibald 1978). This misconception also appears to be fairly common in the literature (Begin *et al.* 1974: Pl. 5, Figures 8–10; Hirano 1974: Pl. 5, Figure 12; Mayer 1946: Pl. 11, Figure 8). Hirano (1971: Pl. 5, Figures 22–25) recorded some specimens under the name *A. coffeaeformis* var. *transcaspica* Boye Petersen, but these appear to be a mixture of *A. veneta* and its var. *capitata*. Meister (1932: 8, Pl. 1, Figure 4) described a new variety, *A. coffeaeformis* var. *asiatica*, which bears little resemblance to *A. coffeaeformis* but is rather similar to *A. veneta* var. *capitata* except for its coarser straition.

Another misconception of this species is portrayed in the identification of some marine forms as *A. coffeaeformis* (Anderson 1975: Figure 1; Lewin & Lewin 1960: Pl. 1, Figures 9–11). This error most probably originates from Helmcke &

Krieger's (1953: Pl. 76) interpretation of *A. coffeaeformis*. However, the identity of these forms is not clear to us at present.

One of the most frequently consulted reference books on diatom taxonomy is Hustedt's (1930) 'Bacillariophyta' in Pascher's 'Die Süsswasser-Flora Mitteleuropas'. It is therefore unfortunate that Hustedt's illustration (his Figure 634) does not accurately portray *A. coffeaeformis* (see paragraph 4.2(f). Hustedt's drawing depicts the raphe as having arcuate branches whereas *A. coffeaeformis* has straight branches, albeit inclined gently upwards from the poles to the central nodule, where the central pores are slightly deflected to the dorsal side. Furthermore there is usually a central area on the ventral side formed as a result of the interruption of the ventral striae either partially or wholly. Despite the inaccuracies of the illustration, Hustedt's (1930: 345) description of *A. coffeaeformis* seems to agree with our definition of the species based on the type material. The only point of discord concerns the number of striae on the girdle bands where Hustedt recorded 21 striae in 10 μm in contrast to our counts of 37–45 in 10 μm.

Van Der Werff & Huls (1957–74) retained *A. salina* as a separate species, but their illustrations of this taxon incline us to believe that it is more closely akin to our concept of '*A. taylori* Grunow' (see paragraph 4.7).

The observations of the various slides and of the literature discussed above indicate clearly that the concept of *A. coffeaeformis* and its supposed synonyms (VanLandingham 1967) is subject to great variation. This is highly significant since this species is frequently reported in the literature. Having discovered the wide range in interpretation of the various forms in this species complex and the inconsistency

Table 3 Summary of the material examined in the investigation of *A. coffeaeformis* (Agardh) Kützing

Slide/material No.	Taxa stated to occur	Present authors' identification	LM figures	EM figures
Agardh No. 4600 (LD)	*Frustulia coffeaeformis*	*A. coffeaeformis*	1–4, 11–14	100–115
BM 18945 (Kütz. Mat. No. 467)	*A. coffeaeformis* & var. *fischeri*	*A. coffeaeformis*	5, 15–18	116
BM 78009	*A. coffeaeformis*	*A. coffeaeformis*	6–8, 19–24	
NIWR 383/7644 (SUN 37)	*A. coffeaeformis*	*A. coffeaeformis*	9, 10, 25–29	117–152
BM 23126 (W. Smith, Iford)	*A. salina*	*A. coffeaeformis*	30–34	153–159
NIWR SWA 227	*A. acutiuscula*	*A. coffeaeformis*		160–162
Cleve & Möller No. 86	*A. coffeaeformis* var. (= *A. salina*)	*A. veneta* & var. *capitata*	35, 36	
Cleve & Möller No. 91	*A. coffeaeformis* var. (= *A. salina*)	*A. coffeaeformis*		
Cleve & Möller No. 204	*A. coffeaeformis* var. *salinarum*	*A. acutiuscula* ?	37	
Cleve & Möller No. 262	*A. coffeaeformis*	*A. veneta* var. *capitata*	38	
Hustedt U1,29	*A. coffeaeformis*	*A. coffeaeformis*	39	
Hustedt U1,30	*A. coffeaeformis*	*A. coffeaeformis sensu* Hustedt 1930	40	
Hustedt U1,54	*A. coffeaeformis*	?	41	
BM 23125	*A. salina*	?	42–44	
Eulenstein No. 96	*A. salina*	*A. coffeaeformis*	45, 46	
Van Heurck No. 11	*A. salina*	*A. hybrida*	47, 48	
Van Heurck No. 12	*A. salina* v.v.v	*A. coffeaeformis* e.p.	49, 50	
		A. coffeaeformis var.?	51–53	
Van Heurck No. 116	*A. salina*	'*A. taylori*'	54–56	
Temp. & Per. (1st) No. 415	*A. salina*	*A. coffeaeformis* var.?	57, 58	
	A. acutiuscula	*A. hybrida*	59, 60	
Temp. & Per. (1st) No. 422	*A. salina*	*A. coffeaeformis*	61–64	
Temp. & Per. (1st) No. 520	*A. salina*	*A. coffeaeformis* e.p.	65, 66	
		A. hybrida e.p.	67	
Cleve & Möller No. 218	*A. salina*	?		
Cleve & Möller No. 255	*A. salina* var.	*A. acutiuscula* ?	68, 69	
BM 18944 (Kütz. Mat. No. 393)	*A. aponina*	*A. coffeaeformis* var. *aponina*	70–75	163–171
H.L. Smith No. 29	*A. aponina*	'*A. taylori*'	76, 77	
Van Heurck No. 257	*A. aponnia* Kütz. = *A. aponina*	*A. veneta* var. *capitata*	78, 79	
Van Heurck No. 13	*A. taylori* & *A. lineata*	'*A. taylori*'	80–83	
BM 955	*A. lineata*	?		
BM 956	*A. lineata*	*A. coffeaeformis* var. ?	84	
Temp. & Per. (1st) No. 161	*A. lineata*	?	85, 86	
Temp. & Per. (1st) No. 292	*A. lineata* & *A. salina*	*A. acutiuscula* ?	87–91	
Cleve & Möller No. 155	*A. lineata*	?	92–94	
		?	95, 96	
Cleve & Möller No. 210	*A. lineata*	?	97–98	
		?	99	

of their identification by many of the older diatomists in the various well-known 'type slide collections', it becomes a matter of speculation as to what many modern diatomists accept as *A. coffeaeformis*. Undoubtedly in many cases the species has been correctly identified but there are also many instances in which the illustrations leave room for suspicion as to the accuracy of identification. On these grounds one should guard against blind acquiescence of what is written in the literature about *A. coffeaeformis* and become more discerning as to what can be accepted as pertaining to the true *A. coffeaeformis*.

5. Conclusions

Having examined a large number of materials, namely the type and other old but apparently well authenticated material of European origin, as well as local samples, it is clear that the species *Amphora coffeaeformis* (Agardh) Kützing has been widely misinterpreted (Table 3). It has been confused with a number of closely related taxa as well as with some that do not bear any close relationship to *A. coffeaeformis*.

We therefore examined the type material (Agardh No. 4600 — Lund, Sweden) carefully and have compared it with a number of other materials. Using the type specimens and some selected examples, identical to the types, from other samples, we have presented a new and more comprehensive concept of the species by describing it with the aid of the light and electron microscopes.

To a certain degree we have re-assessed a number of taxa that have in the past been considered synonymous with *A. coffeaeformis*. We have confirmed some as conspecific with *A. coffeaeformis* whereas others still require further research. *A. salina* W. Smith is identical to *A. coffeaeformis* and is therefore confirmed as a synonym. In contrast, taxa such as *A. aponina* Kützing, *A. lineata* Gregory and *A. taylori* Grunow, while bearing many features in common with *A. coffeaeformis*, do not quite agree with our revised concept of the latter species. In this regard we consider *A. aponina* to be a variety of *A. coffeaeformis*.

Owing to the wide range of misinterpretation of *A. coffeaeformis* we would advise a great deal of circumspection in the use of information obtained from the literature with regard to this species. This comment applies both to data in respect of its morphology and dimensions as well as to assessments of its autecology.

The true *A. coffeaeformis* does occur in southern Africa but a large number of the present records of this species need careful revision. Most of them refer to *A. veneta* var. *capitata* Haworth. Furthermore, the true *A. coffeaeformis* has been recorded either in part or totally under other names with no consistency in its identification. This makes the determination of its distribution in this region extremely difficult without recourse to laborious re-examination of many samples.

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