

# The relationships of *Eunotogramma frauenfeldii* (Bacillariophyta) I. An account of its structure and description of the new genus *Moralesonia*

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## Abstract

**Background and aims** – *Euodia frauenfeldii* has the characteristic ‘semi-circular’ or ‘crescent-shaped’ valves found in most species of *Euodia*, but as it also has a pair of conspicuous transapical costae, it was later transferred to *Eunotogramma*. Examination of the structure of its valves and girdle has led to a reassessment of its taxonomic position.

**Material and methods** – We discuss various aspects of terminology used for the parts of the valve, their abbreviations used throughout the literature and provide a detailed taxonomic background to both *Euodia* and *Eunotogramma*.

**Key results** – A new genus, *Moralesonia* is described and its relationships discussed.

## Keywords

Bacillariophyta, Eduardo Morales (phycologist), Novara Expedition, synapomorphy

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## INTRODUCTION

The species first described and named as *Euodia frauenfeldii* Grunow (1863: 158, pl. 14, fig. 19, “Habitat ad litus Africae australioris (Flugsand der Kalkbay am Cap der guten Hoffnung, von Herrn v. Frauenfeld auf der Novara-Expedition gesammelt)”) possesses the characteristic ‘semi-circular’ or ‘crescent-shaped’ valves found in most species of *Euodia* J.W.Bailey ex Ralfs (in A. Pritchard 1861: 852), but also has a pair of conspicuous transapical costae (‘transapical ribs’). As a consequence, it was later transferred to *Eunotogramma* Weisse: *Eunotogramma frauenfeldii* (Grunow) Grunow (in Van Heurck 1883: pl. 126, fig. 14, “Golfe de Carpentaria, Pernambuco, etc.”).

Most of the species placed in *Euodia* since its first description, have been transferred to *Hemidiscus* G.C.Wall. (Wallich 1860: 42), primarily due to reasons

of nomenclatural priority, as *Euodia* is a junior synonym of *Hemidiscus*. *Euodia* J.W.Bailey happens to also be a younger homonym of *Euodia* J.R.Forst. & G.Forst. (Forster and Forster 1776, Rutaceae) rendering the diatom name *Euodia* illegitimate for those two reasons.

Other species in *Euodia* were transferred to different genera, such as *Flexibiddulphia* Simonsen (= *Euodiella* P.A.Sims, see Williams and Sims 2022), *Leudugeria* Temp. ex Van Heurck, *Cymatotheca* Hendey, *Eunotia* Ehrenb., and *Eunotogramma* (see Table 1). In all, ca 12 species remain ‘unknown’ or ‘uncertain’ regarding their placement, making it clear that regardless of its convoluted nomenclature, the genus *Euodia* was an artificial assemblage to begin with (see also Table 1, ‘Current name’ column), whose species happened to simply share the possession of ‘crescent-shaped’ valves.

The genus *Eunotogramma* (Weisse 1855a [1854], 1855b) is similar, inasmuch as most of its included species (ca 40 names) have been dispersed to other, more appropriate genera based on morphological studies (Table 5, see ‘Current name’ column). It too is now being recognised as an artificial assemblage of species, which happen to have conspicuous transapical costae (‘transapical ribs’, see below) on the valves.

In this study, we have examined a number of herbarium specimens that have been named *Euodia frauenfeldii*, including relevant type specimens using LM and SEM. To provide context, as a prelude to a cladistic analysis of the relevant characters that will follow elsewhere, and to demonstrate that *Euodia frauenfeldii* is neither a species of *Euodia* nor a species of *Eunotogramma*, we outline the taxonomic histories of both genera and document the structure of the valves and girdle of *E. frauenfeldii*. Based on these observations including a putative synapomorphy, we propose a new genus to accommodate *E. frauenfeldii*, describe one new species, and suggest others that might be described and included in due course.

## MATERIAL AND METHODS

### Terminology

For the most part, the two standard valve and girdle terminology papers have been followed (Anonymous 1975 and its updated version Ross et al. 1979). Additional commentary can be found in Gogorev et al. (2018) and the glossaries in Diatoms of North America (see Spaulding et al. 2022) and Diatom Flora of Britain and Ireland (Jüttner et al. 2022). In many cases, there is no general agreement on the naming of particular valve and girdle parts. In these cases, we have either stated our source or if it is unique to us. In addition, problems with terminology can arise when the same term (name) is used for characters that are demonstrably non-homologous. For example, as Witkowski et al. (2020: 19) recently noted: “The presence of internal transverse costae across the ‘pennate/non-pennate’ diatom categories is hardly surprising, as it is part of a long list of ultrastructural features found in both generalized morphotypes along with apical pore fields, rimoportulae and marginal ridges”. Passing over what “generalized morphotypes” could mean, adopting a particular name for a feature without cladistic analyses does not (necessarily) imply it is homologous across all taxa that bear this character, nor should it be interpreted as such. To try and achieve some clarity, in this paper, we refer to the ‘internal transverse costae’ as ‘transapical ribs’. Nevertheless, our discussion of characters below is made with respect to proposing putative homologues, not simply to achieve terminological consistency, although both are obviously desirable. Most of that discussion will appear later in the companion paper (part II).

### Abbreviations

LM = light microscope; SEM = scanning electron microscope; herbarium acronyms are according to Index Herbariorum (Thiers 2024). The exclamation point (!) following material citation means ‘vidi’ (‘We have seen it’). No abbreviations are used for valve and girdle structures.

## TAXONOMIC BACKGROUND

We provide a reasonably detailed but succinct background (i.e. without swamping the text with every historical detail) for both *Euodia* and *Eunotogramma* with the aim of presenting evidence that they are artificial assemblages of unrelated taxa (i.e. polyphyletic).

### *Euodia* J.W.Bailey ex Ralfs

The name *Euodia* was first used for a diatom genus by Ralfs in Pritchard’s History of the Infusoria, it being attributed to J.W. Bailey, as was the only definitely included species, *Euodia gibba* J.W.Bailey ex Ralfs (Ralfs in Pritchard 1861: 852, “Recent. Gulf Stream”). Ralfs provided a relatively simple description of the genus: “Frustules cellulose or granulate; in lateral view lunate. *Euodia* agrees with the Eunotieae in the shape of its frustules which can scarcely be called angular; yet, notwithstanding that resemblance in form, its punctate or granulate surface induces us to place it here”. Alongside *E. gibba* – which was based on “a drawing by Professor Bailey” (Ralfs in Pritchard 1861: 852, pl. viii, fig. 22, see our Fig. 1A) – Ralfs included *Euodia brightwellii*, albeit with some reluctance (“*E? Brightwellii*”), suggesting it was a synonym of *Triceratium semicirculare* Brightw. (Brightwell 1853: 252, pl. IV, fig. 21, “Bermuda Earth”, see our Fig. 1B) and, possibly, of *Triceratium obtusum* Ehrenb. (Ehrenberg 1844: 88 [1841: 329, “Virginien, Richmond”]; in Ehrenberg 1854: pl. XVIII, figs 48, 49, see Fig. 1C, D). Under his description of *Hemidiscus*, Ralfs added: “We doubt whether *Hemidiscus* be distinct from *Euodia*, since the only distinction seems to be the marginal nodule of the former, - a character perhaps overlooked by Professor Bailey” (Ralfs in Pritchard 1861: 852–853).

The complex history of the name *Euodia* has been tackled a number of times (e.g. Hendey 1957 [1958]: 32; Simonsen 1987: 263; Sims 2000; Blanco and Wetzel 2016: 195–196; Gómez et al. 2017). It can be briefly summarised thus: after Ralfs’ initial account in Pritchard, a number of other species were added, all more or less with the ‘lunate’ valve outline (Table 1).

Hustedt transferred *Euodia gibba*, the generitype, to *Hemidiscus* under the name *H. cuneiformis* var. *gibba* Hust. (Hustedt 1930: 906, fig. 542g; see also Peragallo and Peragallo 1897) and later proposed a change of rank to *H. cuneiformis* f. *gibba* Hust. (Hustedt 1940: pl. 435, figs 4–6).

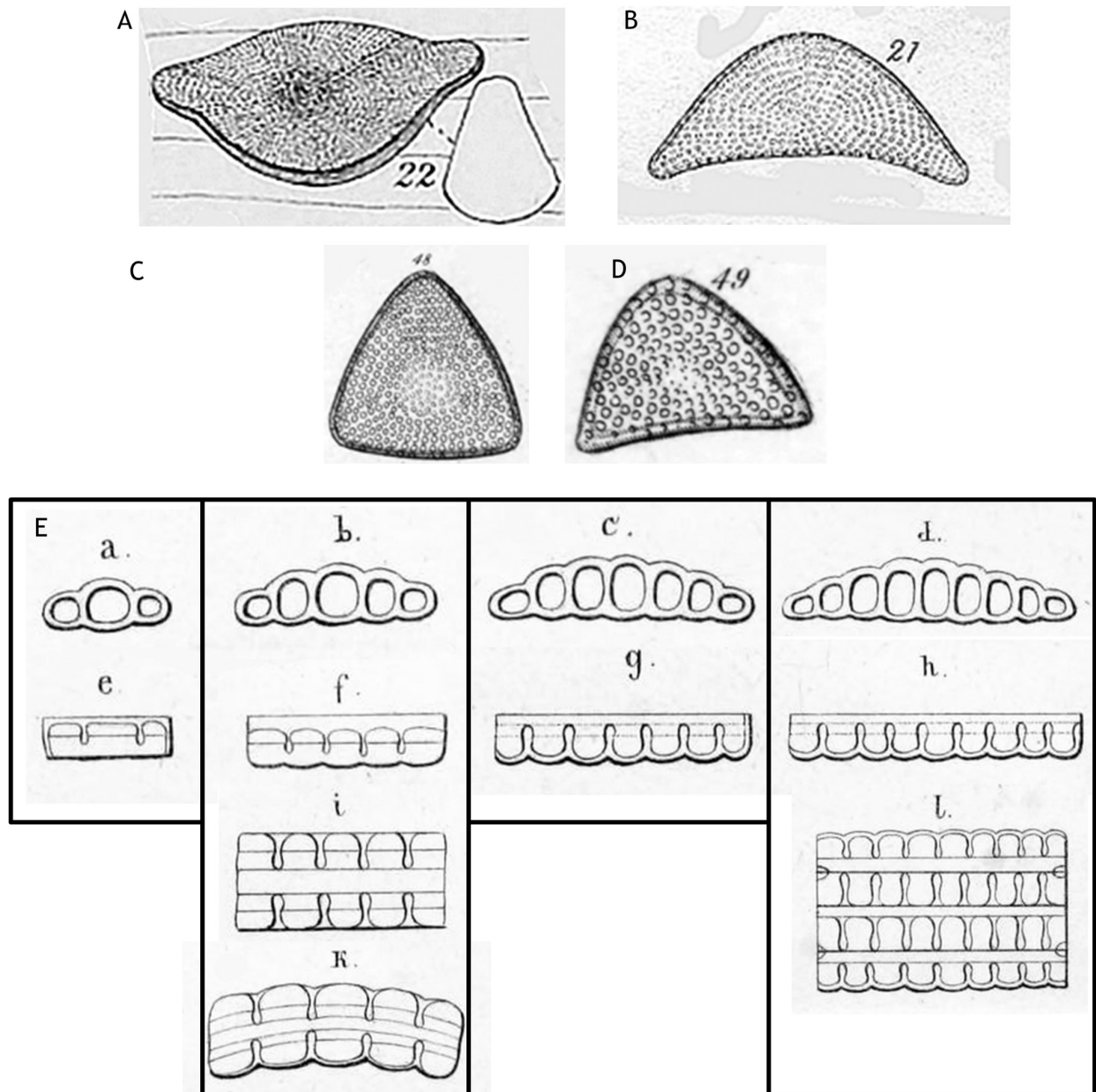
More recently, Gómez et al. (2017: 26) suggested that, using molecular evidence, “[...] *H. cuneiformis* should

be transferred to *Actinocyclus* Ehrenb. If *Hemidiscus* is retained as an independent genus, the current placement of *Hemidiscus* in the SSU rDNA phylogenetic tree makes *Actinocyclus* paraphyletic. Thus, either *Hemidiscus* is part of *Actinocyclus*, or *Actinocyclus* should be broken up into different genera” – this deserves comment, which is presented elsewhere (Williams in press).

It is worth noting that Ehrenberg’s name *Dichomenis* Ehrenb. (Ehrenberg 1862: 293; see also Ehrenberg 1873: 264–265) is another junior synonym of *Hemidiscus*. Only three species were ever transferred to *Dichomenis*

alongside Ehrenberg’s *D. subtilis* Ehrenb., and all are now in *Hemidiscus* with the exception of *D. janischii* (Grunow) Karst., which is *Leudugeria janischii* (Grunow) Temp. ex Van Heurck (Table 2). Ehrenberg’s *D. subtilis* may have nomenclatural significance for species in *Hemidiscus*.

In summary, of the 30+ names in *Euodia* (Table 1), most are now in *Hemidiscus*, others are in *Flexibiddulphia*, *Cymatotheca*, *Leudugeria*, or *Eunotia* Ehrenb., with ca 12 with relationships either ‘unknown’ or ‘uncertain’; *Euodia frauenfeldii* is of uncertain relationships, but is currently included in *Eunotogramma*.



**Figure 1.** A. *Euodia gibba*, reproduced from Pritchard (1861: pl. viii, fig. 22), based on “a drawing by Professor Bailey” (Ralfs in Pritchard 1861: 852). B. *Euodia brightwellii* reproduced from Brightwell (1853: pl. IV, fig. 21, “Bermuda Earth”). C–D. *Triceratium obtusum* reproduced from Ehrenberg (1854: pl. XVIII, figs 48, 49, “Virginien, Richmond”). E. *Eunotogramma* Weisse figure reproduced from Weisse (1855a [1854]: pl. III [‘Dritte Tafel’], fig. 37a–e [f–i, k, l] – the latter few figures are not mentioned in Weisse’s legend’s title but f–h are noted in the text; i, k, l are referred to as “Die übrigen [the remainder]”, Weisse 1855a [1854]: 278).

**Table 1.** Names of species placed in the genus *Euodia* J.W.Bailey ex Ralfs from 1861–1987) showing that this was an artificial assemblage composed of several species currently recognised as distinct; table excludes the varieties of *Euodia gibba* and those of other species. The column ‘Name’ refers to the original assigned to *Euodia*, followed by the column ‘Date’ when first described. The binomials given in the ‘Current name’ column are those currently accepted. The genus name *Hemidiscus* has been retained for *Hemidiscus cuneiformis* rather than *Actinocyclus* (after Gómez et al. 2017). Names in single quotes were invalidly published. Some notes on the names: Gómez et al. (2017: 26) considered *Euodia barbadensis* to be *Hemidiscus barbadensis* (Grev.) Kuntze, and a heterotypic synonym of *Actinocyclus cuneiformis* (G.C.Wall.) F.Gómez, Lu Wang & Senjie Lin. Greville’s figures (Greville 1861: pl. VIII, figs 6, 7) suggest otherwise, and Sims’s determination of *Euodia barbadensis* as a species of *Medlinia* seems more appropriate (Sims 2000: 406). Hustedt made all of Castracane’s species of *Euodia* taxonomic ‘forms’ of *Hemidiscus cuneiformis* (Hustedt in Schmidt 1940: pls 435–439), whereas Gómez et al. (2017: 26) made them all synonyms of *Hemidiscus cuneiformis* (see also Peragallo and Peragallo 1897). The identification of *Euodia minima* as *Cymatotheca weissflogii* follows Simonsen (1992: 19–20).

Name	Date	Current name [? = assumed]	Publication
<i>Euodia gibba</i> J.W.Bailey ex Ralfs	1861	[ <i>Hemidiscus cuneiformis</i> G.C.Wall.] <i>Hemidiscus cuneiformis</i> [var. <i>gibba</i> (J.W.Bailey ex Ralfs) Hust.]	Hustedt (1930)
<i>Euodia barbadensis</i> Grev.	1861	<i>Medlinia</i> P.A.Sims ?	Greville (1861)
<i>Euodia brightwellii</i> Ralfs	1861	<i>Euodiella semicircularis</i> (Brightw.) P.A.Sims = <i>Flexibiddulphia semicircularis</i> (Brightw.) Simonsen	Simonsen (1987)
<i>Euodia frauenfeldii</i> Grunow	1863	<i>Eunotogramma frauenfeldii</i> (Grunow) Grunow	Grunow (1863)
<i>Euodia chimmoana</i> O’Meara	1869	<i>Hemidiscus</i> G.C.Wall.	O’Meara (1869)
‘ <i>Euodia hardmaniana</i> (Grev.) H.L.Smith’	1877	<i>Palmerina hardmaniana</i> (Grev.) Hasle	Smith (1877)
<i>Euodia ceylanensis</i> Leud.-Fortm.	1879	<i>Hemidiscus</i> G.C.Wall. ?? <i>Actinocyclus</i> Ehrenb. ??	Leuduger-Fortmorel (1879)
<i>Euodia janischii</i> Grunow	1883	<i>Leudugeria janischii</i> (Grunow) Temp. ex Van Heurck	Van Heurck (1896)
<i>Euodia weissflogii</i> Grunow	1883	<i>Cymatotheca weissflogii</i> (Grunow) Hendey	Hendey (1957) [1958]
<i>Euodia producta</i> Grunow	1883	<i>Leudugeria</i> Temp. ex Van Heurck ?	Van Heurck (1896)
<i>Euodia inornata</i> Castrac.	1886	<i>Hemidiscus cuneiformis</i> G.C.Wall.	Castracane (1886)
<i>Euodia orbicularis</i> Castrac.	1886	<i>Hemidiscus cuneiformis</i> G.C.Wall.	Castracane (1886)
<i>Euodia radiata</i> Castrac.	1886	<i>Hemidiscus cuneiformis</i> G.C.Wall.	Castracane (1886)
<i>Euodia recta</i> Castrac.	1886	<i>Hemidiscus cuneiformis</i> G.C.Wall.	Castracane (1886)
<i>Euodia ventricosa</i> Castrac.	1886	<i>Hemidiscus cuneiformis</i> G.C.Wall.	Castracane (1886)
<i>Euodia striata</i> Grove & Sturt	1887	<i>Eunotia grovei</i> Desikachary & Sreel.	Grove and Sturt (1887)
<i>Euodia atlantica</i> Petit in Perag.	1888	<i>Hemidiscus</i> G.C.Wall.	Peragallo (1888)
<i>Euodia rotundus</i> Janisch	1888	?	Janisch (1888)
<i>Euodia margaritacea</i> Brun in Brun & Tempère	1889	<i>Hemidiscus cuneiformis</i> G.C.Wall.	Brun and Tempère (1889)
<i>Euodia capillaris</i> Brun	1891	<i>Palmerina</i> (Grev.) Hasle	Brun (1891)
<i>Euodia hungarica</i> Pant.	1892	?	Pantocsek (1892)
<i>Euodia cuneiformis</i> (G.C.Wall.) A.Mann	1893	<i>Hemidiscus cuneiformis</i> G.C.Wall.	Mann (1893)
<i>Euodia ratabouli</i> Brun in Leuduger-Fortmorel	1898	<i>Cymatotheca weissflogii</i> (Grunow) Hendey ?	Leuduger-Fortmorel (1898)
<i>Euodia arcuata</i> B.Schröd.	1900	<i>Hemidiscus</i> G.C.Wall. ?? <i>Actinocyclus</i> Ehrenb. ??	Schröder (1900)
‘ <i>Euodia gigantea</i> ’ Brun	1907	<i>Hemidiscus</i> G.C.Wall.	Tempère and Peragallo (1907)
<i>Euodia subrotundata</i> Azpeitia	1911	?	Azpeitia Moros (1911)
<i>Euodia caballeroi</i> Azpeitia	1911	?	Azpeitia Moros (1911)
<i>Euodia minima</i> Heiden & Kolbe	1928	<i>Cymatotheca weissflogii</i> (Grunow) Hendey ?	Heiden and Kolbe (1928)
<i>Euodia semicircularis</i> (Brightw.) Hust. in A.Schmidt	1940	<i>Euodiella semicircularis</i> (Brightw.) P.A.Sims = <i>Flexibiddulphia semicircularis</i> (Brightw.) Simonsen	Schmidt (1940)
<i>Euodia udiensis</i> Hust. ex Simonsen	1987	<i>Flexibiddulphia udiensis</i> (Hust. ex Simonsen) Simonsen	Simonsen (1987)

**Eunotogramma Weisse**

Weisse (1855a [1854], 1855b) offered the first description of the genus in the text of a detailed figure legend for the illustrations on his plate III (“Dritte Tafel”), fig. 37a–e [f–i, k, l] (the latter few figures are not mentioned in the legend’s title but f–h are noted in the text; i, k, l are referred to as “Die übrigen” [the remainder], and j is missing; Weisse 1855a [1854]: 278, 1855b: 244, see our Fig. 1E and Table 3). Weisse provided a possible choice of names for the different ‘kinds’ he illustrated: “Will man

aus den verschiedenen Formen besondere Abarten bilden, so wären die Beinamen *tri-quinque-septem* und *novem loculata* wohl die passendsten” [If one wanted to rank these forms as species, the epithets *tri-quinque-septem* and *novem loculata* would likely be the most appropriate] (Weisse 1855a [1854]: 278, 1855b: 244; Ralfs (in Pritchard 1861: 860) appears to accept all of these names).

Ehrenberg’s (1855: 302) own study of Weisse’s material accounted for eight taxa in *Eunotogramma*: *E. novemloculatum* Weisse, *E. quinqueloculatum* Weisse, *E. septemloculatum* Weisse, and *E. triloculatum* Weisse

**Table 2.** Names placed in *Dichomenis* Ehrenb.

Name	Date	Current name [? = assumed]	Publication
<i>Dichomenis subtilis</i> Ehrenb.	1862	<i>Hemidiscus cuneiformis</i> G.C.Wall. ?	Ehrenberg (1862)
<i>Dichomenis cuneiformis</i> (G.C.Wall.) Karst.	1928	<i>Hemidiscus cuneiformis</i> G.C.Wall.	Karsten (1928)
<i>Dichomenis janischii</i> (Grunow) Karst.	1928	<i>Leudugeria janischii</i> (Grunow) Temp. ex Van Heurck	Karsten (1928)
<i>Dichomenis ventricosa</i> (Castrac.) Skvortzov	1932	<i>Hemidiscus cuneiformis</i> G.C.Wall.	Skvortzov (1932)

**Table 3.** Names of taxa in *Eunotogramma* according to Ehrenberg (1856: 103, 1876: 48–51; in brackets: ‘proper’ names, see Ehrenberg 1855: 298–299); the names are partly derived from his interpretation of Weisse’s taxa (1855a [1854], 1855b). References to Weisse’s plate III are shown in the second column (see our Fig. 1E; where the figures have been re-arranged to correspond to the taxon listing below, so that drawings referring to the same ‘species’ are placed together and in a series for direct comparison). Some notes on the names: Ehrenberg implied that *E. weissei* is a new species (“[*Eunotogramma*] *Weissei* n.sp.”, Ehrenberg 1855: 302), but earlier in the same paper he has it as a synonym of *Biddulphia tridentata* (Ehrenberg 1855: 298) as, later, does Grunow (1884: 59). There is a complex synonymy yet to be disentangled around the name *Biddulphia tridentata*.

Names in Ehrenberg	Reference to Weisse’s plate III
<i>3loculatum</i> ( <i>Eunotogramma triloculatum</i> Weisse)	Taf. III, fig. 37a, e
<i>5loculatum</i> ( <i>Eunotogramma quinqueloculatum</i> Weisse)	Taf. III, fig. 37b, f, i, k
<i>7loculatum</i> ( <i>Eunotogramma septemloculatum</i> Weisse)	Taf. III, fig. 37c, g
<i>9loculatum</i> ( <i>Eunotogramma novemloculatum</i> Weisse)	Taf. III, fig. 37d, h, l
[β [var.] <i>octonum</i> ] [Ehrenberg 1855: 302]	
<i>amphioxys</i> n.	Taf. III, fig. 36a–d [= <i>Biddulphia tridentata</i> Ehrenb.]
<i>elongatum</i> n.	Taf. III, fig. 21 [= ?]
<i>Weissei</i> n.	Taf. I, fig. 22a, b [= <i>Triceratium</i> Ehrenb. ?] [Ehrenberg 1855: 299]

**Table 4.** The six names of *Eunotogramma* according to Grunow (in Van Heurck 1883); the first three (*producta*, *laevis* and *debilis*) are new to Grunow, the two varieties of *variabilis*, although derived from Weisse’s taxa, are nomenclatural status changes made by Grunow, where he attributed the original name to Ehrenberg rather than Weisse. Finally, *Eunotogramma frauenfeldii* is derived from *Euodia frauenfeldii* Grunow. *Eunotogramma producta* and *E. variabilis* (and its varieties) are all from “Dépôt de Simbirsk, Sibérie”, the same locality as Weisse’s taxa (found in W0164932: Grunow sample 3090).

Names by Grunow (in Van Heurck 1883)	Locality
<i>Eunotogramma producta</i>	“Dépôt de Simbirsk, Sibérie”
<i>Eunotogramma laevis</i>	“Caroline du Nord, Floride [...]”
<i>E.[unotogramma]? debilis</i>	“Baie de Campèche [...] de l’île Bartolomé [...] d’Ostende (Belgique)”
<i>Eunotogramma variabilis</i> var. <i>septemloculare</i>	“Dépôt de Simbirsk”
<i>Eunotogramma variabilis</i> var. <i>quinqueloculare</i>	“Dépôt de Simbirsk”
<i>Eunotogramma frauenfeldii</i> (= <i>Euodia frauenfeldii</i> )	“Golfe de Carpentaria, Pernambuco, etc.”

plus four new taxa provided by Ehrenberg: *E. amphioxys* Ehrenb., *E. elongatum* Ehrenb., *E. septemloculatum* β [var.] octonum Ehrenb., and *E. weissei* Ehrenb. In 1856, this work was summarised again with a list of species names including those in *Eunotogramma* (Table 3 modified from Ehrenberg 1856: 103; also in Ehrenberg 1876: 48–51).

Ehrenberg published no illustrations for any of his new taxa (nor do any exist in his unpublished drawings as far as we are aware), but his references to Weisse indicate what he had in mind for each (summarised in Table 3). It is still not clear if any of these names have been validly published, by Weisse, Ehrenberg, or anyone else, for that matter.

**Table 5.** Selected list of names currently in, or that have been in, *Eunotogramma*; there are, roughly, three groups: \*Fossil = a distinct fossil group of species, \**Eunotogramma* = those species ‘similar’ to *Eunotogramma laevis* (‘laeve’) (the generitype according to Round et al. 1990: 288, see Amspoker 2011, also Amspoker 2016), and species in *Drepanotheca* H.-J.Schrad. ex Crawford, Round & D.G.Mann; many species named by Ehrenberg were never illustrated and their interpretation relies upon his comparisons with Weisse (Table 3), most here being interpreted as ‘\*Fossil’ (these will be dealt with in a subsequent contribution). Species names in single quotes are invalidly published. Some notes on the names: Boyer (1900: 737) noted that *E. amphioxys* is “equivalent to *Biddulphia ? lunata* E. [...]”. An illustration of *Biddulphia lunata* can be found in Ehrenberg (1844: 77, 1854: pl. XVIII, fig. 53, “Richmond”, see also Ehrenberg 1855: 302). ‘*Eunotogramma bicornigerum*’ is given in Chambers (1997, nom. inval.). The illustrations in Simonsen suggest that *Eunotogramma dubium* may be a species of *Ceratanaulus* Górecka et al. (Simonsen 1987: pl. 374, figs 1–6). ‘*Eunotogramma vittatum* De Toni (1894: 892)’ is an error for *Eunotogramma bivittata*. De Toni refers to “Grun. et Pant. Foss. Bacill. Ung. I, p. 48, t. XXVI, f. 247”, which is the original description and figure of *Eunotogramma bivittata* (Pantocsek 1886: 48), and to “Grove & St. J.Q.M.C. 1887, p. 77, t. 6, 24”, which is a drawing of ‘*Eunotogramma ?? bivittata*’ (Grove and Sturt 1887). De Toni notes the name ‘*Anaulus tenuis*’, an invalidly published name of Grove and Sturt (1887), which they refer to in their account of *Eunotogramma ?? bivittata*. There are two Grove slides in BM with specimens labelled ‘*Anaulus tenuis*’. Both are specimens of *Eunotogramma bivittata* (BM Adams G80 and BM Adams G111, “Oamaru”; Mills’s notebook for Grove’s slides has ‘*Anaulus tenuis* Gr.’ and also refers to ‘*Eunotogramma rigida*’, another unpublished name, from “Oamaru”).

Species	Current name or group (*Fossil/* <i>Eunotogramma</i> / <i>Drepanotheca</i> )
<i>Eunotogramma amphioxys</i> Ehrenb.	? *Fossil
‘ <i>Eunotogramma bicornigerum</i> ’	<i>Flexibiddulphia</i> Simonsen
<i>Eunotogramma bivittata</i> Grunow & Pant.	<i>Drepanotheca bivittata</i> (Grunow & Pant.) H.-J.Schrad.
<i>Eunotogramma cretacea</i> Streln.	*Fossil
<i>Eunotogramma debile</i> Grunow	<i>Anaulus debilis</i> (Grunow) Van Heurck
<i>Eunotogramma dubium</i> Hust.	? <i>Ceratanaulus</i> Górecka et al.
<i>Eunotogramma elongatum</i> Ehrenb.	? *Fossil
<i>Eunotogramma enorme</i> Krotov	*Fossil
<i>Eunotogramma frauenfeldii</i> (Grunow) Grunow	This study (see taxonomic section below)
<i>Eunotogramma fueleopi</i> Hajós	‘ <i>Drepanotheca</i> ’
<i>Eunotogramma fugei</i> Chenev.	*Fossil
<i>Eunotogramma gibbosa</i> Streln.	*Fossil
<i>Eunotogramma laevis</i> Grunow	* <i>Eunotogramma</i>
<i>Eunotogramma lunatum</i> Ashworth	* <i>Eunotogramma</i>
<i>Eunotogramma marginopunctatum</i> J.A.Long, Fuge & Js.Smith	‘ <i>Drepanotheca</i> ’
<i>Eunotogramma marinum</i> (W.Smith) Grunow	<i>Smithiella marina</i> (W.Smith) H.Perag. & Perag. [* <i>Eunotogramma</i> ]
<i>Eunotogramma novemloculata</i> Weisse	*Fossil
<i>Eunotogramma polymorpha</i> Streln.	*Fossil
<i>Eunotogramma productum</i> Grunow	*Fossil
<i>Eunotogramma quinqueloculatum</i> Weisse	*Fossil
<i>Eunotogramma rectum</i> Salah	?
<i>Eunotogramma rostratum</i> Hust.	* <i>Eunotogramma</i>
<i>Eunotogramma trioculata</i> Weisse	*Fossil
<i>Eunotogramma variabilis</i> (Ehrenb.) Grunow	*Fossil
‘ <i>Eunotogramma vittatum</i> ’	‘ <i>Drepanotheca</i> ’
<i>Eunotogramma weissei</i> Ehrenb.	*Fossil

Subsequently, however, Grunow (in Van Heurck 1883) published a further six names in *Eunotogramma*: *E. producta* Grunow, *E. laevis* Grunow, *E. variabilis* var. *quinqueloculare* Grunow, *E. variabilis* var. *septemloculare* Grunow, *E. frauenfeldii* Grunow, and the questionable “*E? debilis*” Grunow (Table 4). *Eunotogramma producta* and these two varieties of *E. variabilis* were recorded from fossil material, “Dépôt de Simbirsk, Sibirie”, the same locality as Weisse’s earlier study.

Witt (1885: 24, 1886: 160) recognised only *E. variabilis* and *E. weissei*.

No generic type was designated for the genus *Eunotogramma* until Boyer (1927: 143) chose *E. triloculatum* Weisse, which may still be unacceptable as it has yet to be validly described. Round subsequently designated *Eunotogramma laevis* Grunow as such, but, that too may be inappropriate as it is not associated with any material from the original publication (in Round et al. 1990: 288).

Table 5 is a selected list of taxon names in the genus *Eunotogramma* (from its creation in 1855 to the most recent addition in Witkowski et al. 2020; as in Table 1, for brevity’s sake, varieties have been omitted – but there are probably no more than four). Overall, there are roughly three groups: a distinct set of robust fossils, a distinct set of species that (probably) belong in *Drepanotheca* (Williams et al. in prep.; distinctions within *Eunotogramma* have previously been recognised by Sims 2000 and Witkowski et al. 2020: 21; a review of these species is in preparation), and a group of species ‘similar’ to *Eunotogramma laevis*, the generic type according to Round et al. (1990: 288; see Amspoker 2011, 2016), leaving only two species not fitting these broader categories: *Eunotogramma rectum* Salah (1955: 88) and, as in *Euodia*, *Eunotogramma frauenfeldii*.

With respect to both *Euodia* and *Eunotogramma*, *Eunotogramma frauenfeldii* belongs in neither, as both genera are not defined with respect to any unique character of their own. *Eunotogramma frauenfeldii* has a central area with radiating areolae (a putative generic synapomorphy), and hence a new genus is proposed for it (*Eunotogramma rectum* will be investigated in due course). In addition, this is also based on a cladistic analysis, which will be published separately. The relationships of *E. frauenfeldii*, in comparison to the other relevant genera where former species of *Euodia* and *Eunotogramma* are now placed, will be discussed in detail.

## TAXONOMIC TREATMENT

***Moralesonia*** D.M. Williams, Ts. Georgiev, T.M. Schust. & C.E. Wetzel, **gen. nov.**

**Type species.** *Moralesonia frauenfeldii* (Grunow) D.M. Williams, Ts. Georgiev, T.M. Schust. & C.E. Wetzel, **comb. nov.**

**Etymology.** Named for the late Eduardo Morales (1968–2023, <https://diatoms.org/news/in-memoriam-eduardo-a-morales>).

**Registration.** <http://phycobank.org/104544>

**Description.** Valves lunate, each with two transapical ribs dividing valve into three ± equal parts. Transapical ribs evident, extending to mantle, internally raised, tapering towards mantle edge. Areolae ± round, radiating from eccentric hyaline centre, sometimes elongated. Rimoportulae absent. Few simple pores on valve surface. Cribra with well-developed, complex volate structure. External surface of valve ornamented. Girdle composed of few bands, all (presumed) copulae. ‘Central area with radiating areolae’ is the proposed (putative) synapomorphy (diagnostic character) for this genus.

**Notes.** We have included all specimens from various parts of the African continent in *Moralesonia frauenfeldii* and omitted those from other localities for the time being, except from two samples from the Nicobar Islands as they present a similar morphology. These specimens may not be *Moralesonia frauenfeldii* but, as yet, detailed examination has not been possible (see below). Of these, we have documented them according to the details available to us. The specimens from Australia have been given a specific name, while the others are left without names as relevant characters have yet to be identified. We have SEM details for some specimens from Île Rodriguez, but no LM specimen, so are unable to assign a holotype other than the SEM stub, which we are reluctant to do at this time as their longevity cannot be established with any certainty (Fig. 10A–F).

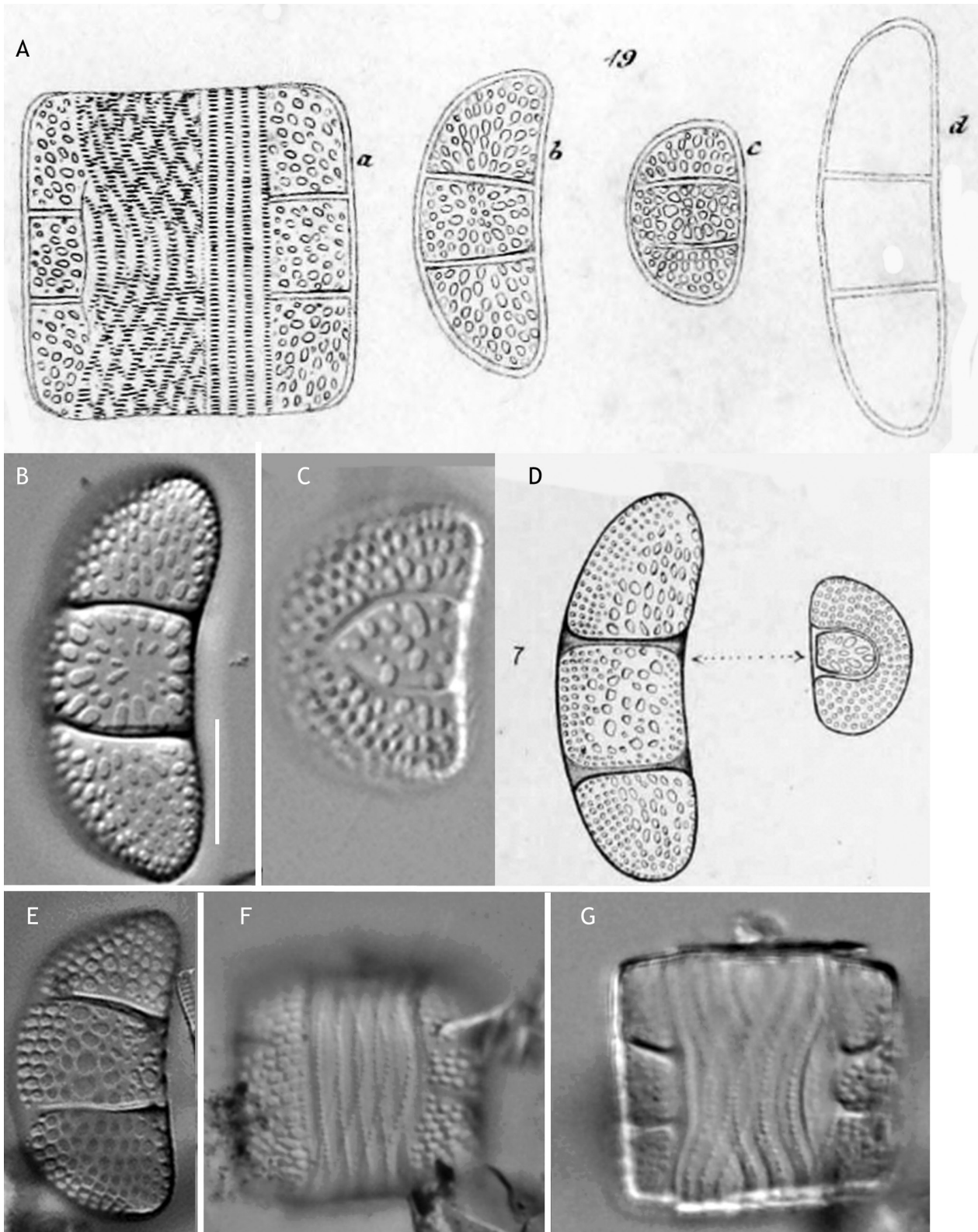
***Moralesonia frauenfeldii*** (Grunow) D.M. Williams, Ts. Georgiev, T.M. Schust. & C.E. Wetzel, **comb. nov.**

Figs 2–6

*Euodia frauenfeldii* Grunow (**basionym**), Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 13: 158, pl. 14, fig. 19a–d (= our Fig. 2A) (Grunow 1863). Also described in Grunow (1864: 119) and Grunow (1878: 24).

*Eunotogramma frauenfeldii* (Grunow) Grunow (in Van Heurck 1883: pl. 126, fig. 14, reproduced here as Fig. 4J–K).

**Type locality.** South Africa, Kalk Bay [Kalkbaai] (“Habitat ad litus Africae australioris [occurs on the South African coast] (Flugsand der Kalkbay am Cap der guten Hoffnung, von Herrn v. Frauenfeld auf der Novara-Expedition gesammelt [airborne sand from Kalkbay at the Cape of Good Hope, collected by Mr. von Frauenfeld during the Novara Expedition]”), (Grunow 1863: 158; “Im Flugsande der Kalkbai am Cap der guten Hoffnung, Frauenfeld [in airborne sand from Kalkbaai at the Cape of Good Hope, Frauenfeld].” “Auch im Strandsande der Nikobaren-Insel Kamortha beobachtete ich neuerdings diese Art [I have recently also observed this species in coastal sand from the Nicobar island Kamortha] (Sandstrand von Kamortha), (Sandstrand von Kamortha,



**Figure 2.** A. ‘*Euodia Frauenfeldii* Grunow’ (= *Moralesonia frauenfeldii*) reproduced from Grunow (1863: pl. 14, fig. 19a–d). B–C, E–G. *Moralesonia frauenfeldii*, specimens from Grunow sample 790 [2 slides, W0164898 (lectotype), W0164899, scale bar = 20 μm for all images]. D. ‘*Eunotogramma Frauenfeldii*’ (= *Moralesonia frauenfeldii*) reproduced from Leuduger-Fortmorel (1898: pl. V, fig. 7, “Congo”).



Nicobaren I.”) (Grunow 1867: 24; for the Nicobar Island specimens, these refer to two separate slides, see below); see Leuduger-Fortmorel 1898: 26, pl. V, fig. 7, [“Congo”] = our Fig. 2D), W: Grunow sample 790 (W0164898!, W0164899!) [Grunow kept two slides, which still exist: “Kalkbay”, cream-coloured original label, round cover slip (W0164898) and “Kalkbai”, green original label, square cover slip (W0164899), see Fig. 3B].

**Lectotype (designated here).** Slide “Kalkbay” of Grunow sample 790 (W0164898!) lectotype designated here (= Fig. 2B, C, E–G, Grunow’s drawings, catalogue notes, and slides: Fig. 3A–C); BR [VI-41-B10 = Grunow sample 790 duplicate from W].

**Isolectotypes (designated here).** SEM in Fig. 5A from subsample of the Kalk Bay raw material (Grunow sample 790 in BR); BM 57572! (Wynne Baxter 2943 = Grunow sample 790, duplicate from W = Fig. 4A–F), W [W0164899! = Grunow sample 790 “Kalkbai”], BRM HB-20 and BRM 24460, BM 10889! (“Kalkbai Cap d. g. Hoffn.”; L. H.[ardman] | 1132” (= Fig. 4G–I), BM 55989! (“Kalkbay”, ex Wynne Baxter 1361), BM 26220! (H.L.

Smith, Diat. spec. typ. No. 659, “Cape of Good Hope original”; “In mare”), ANSP Febiger 3099, H.L.S.O A-98, H.L.Sm. EX 659 (Mahoney and Reimer 1997: 146).

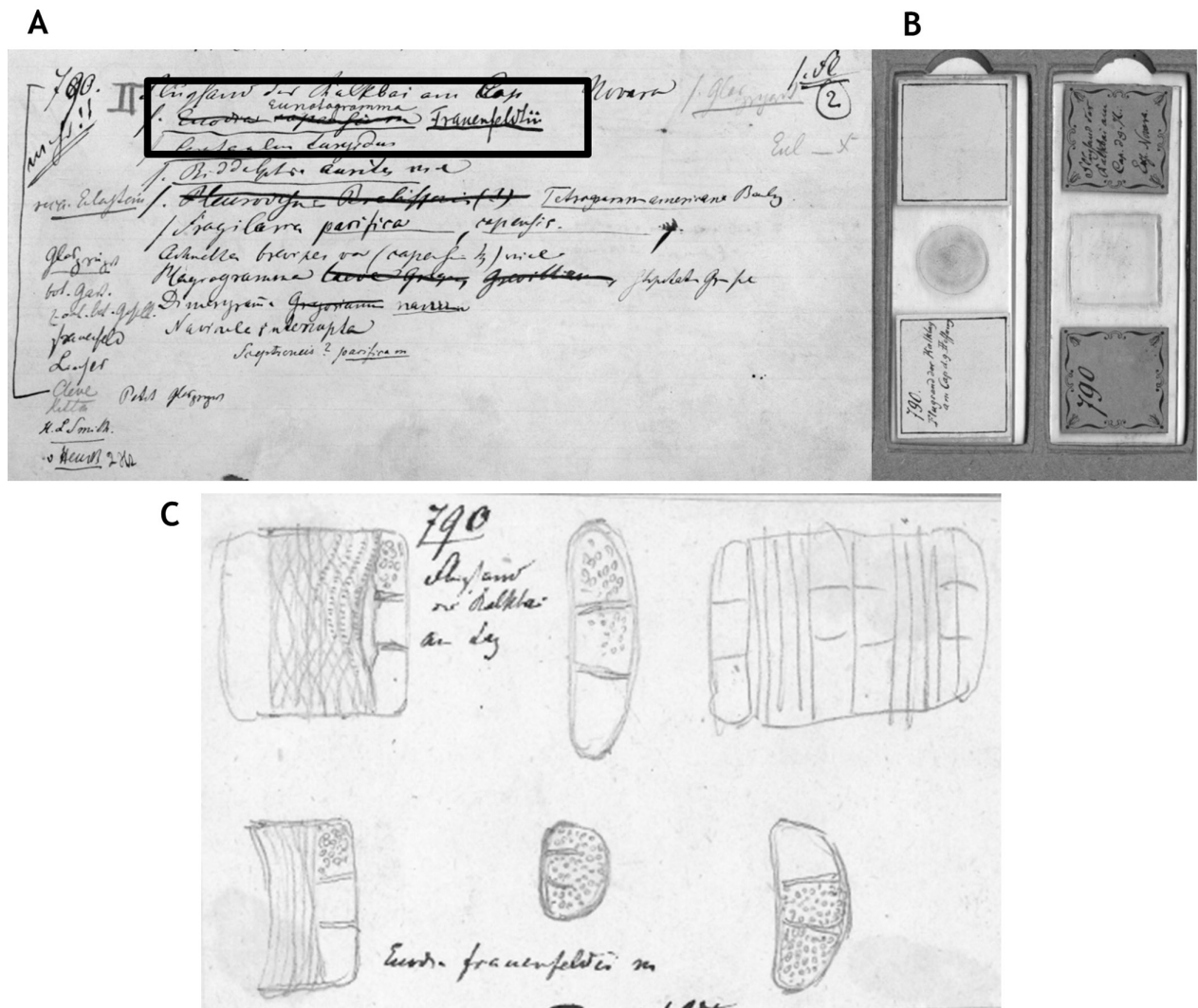
**Registration.** <http://phycobank.org/104545>

**Analysed material.** MOZAMBIQUE • Lourenço Marques [Maputo]; BM Adams TS 751! (figured in Desikachary 1988: pl. 583, fig. 8).

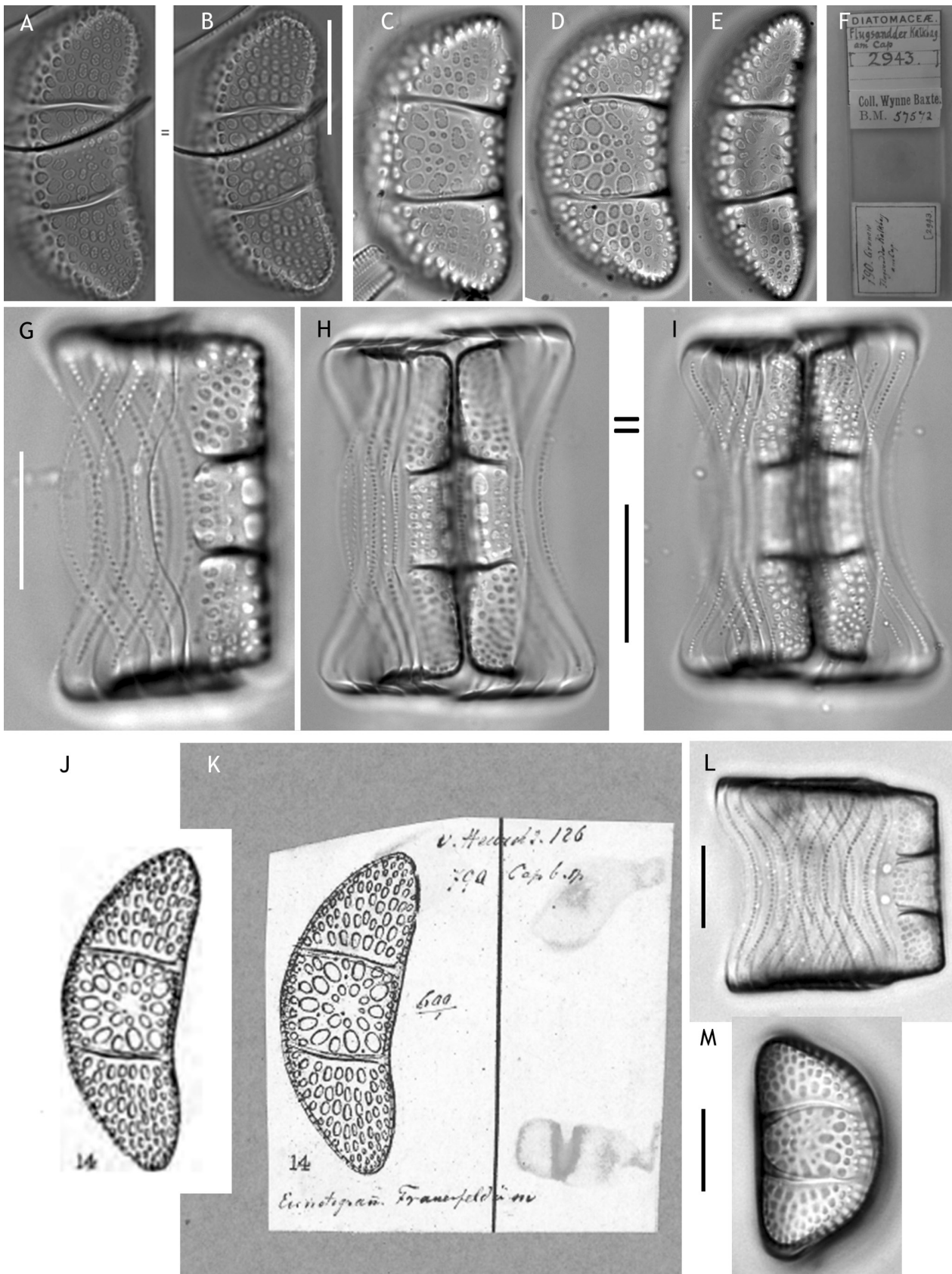
SIERRA LEONE • ‘Freetown’ (“The site at Freetown was in Fura Bay, which is on the south side of the estuary at a point where it is about 10 km wide”, Hendey 1957 [1958]: 29; one micrograph exists in the Hendey collection (specimen dimensions: 80 × 27 µm, Fig. 7G), slide not identified).

CONGO • Leuduger-Fortmorel (1898: 26, pl. V, fig. 7 = Fig. 2D; [“Cette petite Diatomée, très commune de la côte du Congo, a été déterminée et nommée par M. le professeur Brun”, Leuduger-Fortmorel 1898: 24].

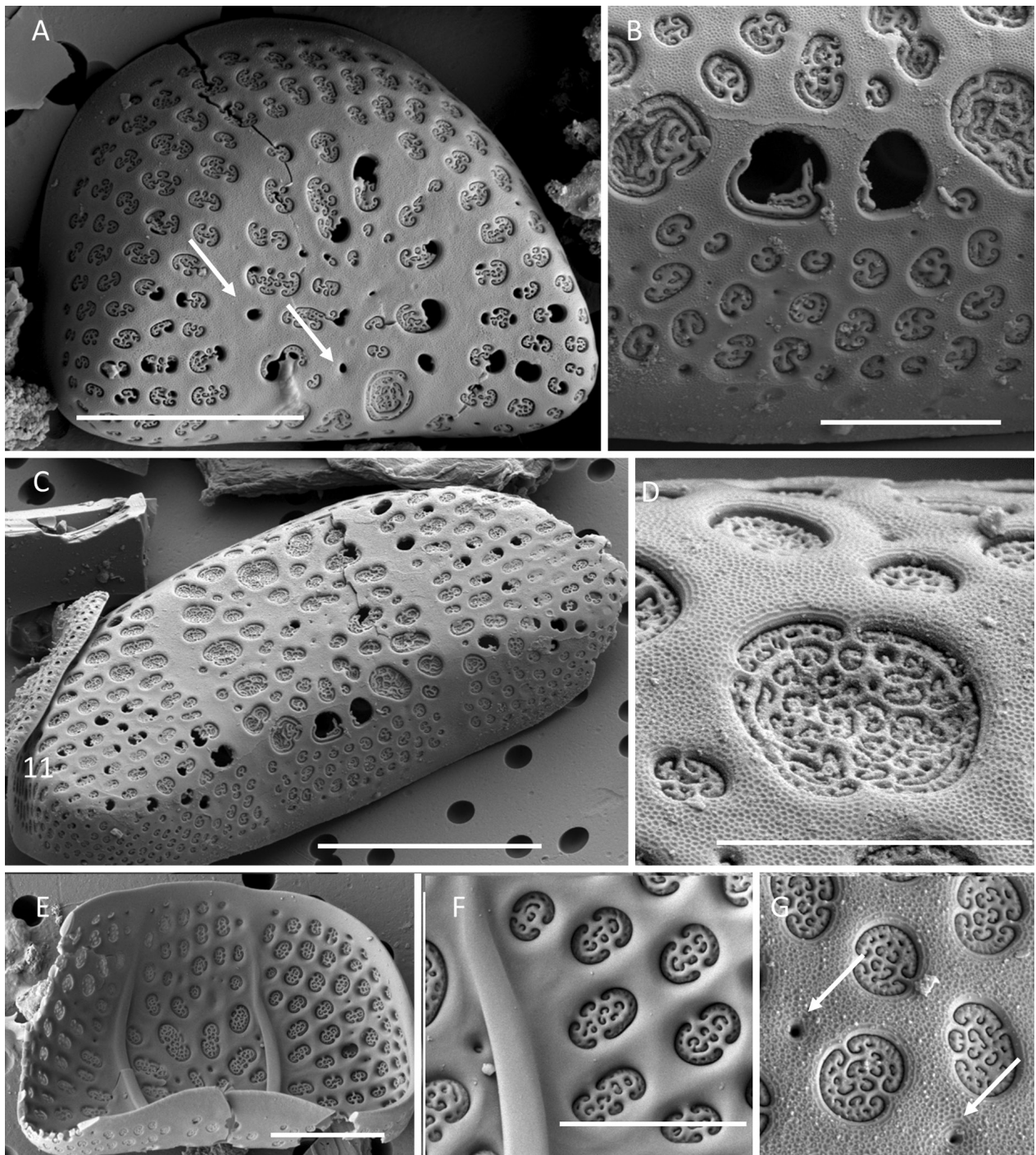
NICOBAR ISLANDS • Kamorta Island; “Auch im Strandsande der Nikobaren-Insel Kamortha beobachtete ich neuerdings diese Art [I have recently also observed this species in coastal sand from the Nicobar island



**Figure 3.** ‘*Eunotogramma Frauenfeldtii* [sic]’ (= *Moralesonia frauenfeldii*), reproductions from Grunow’s drawings (C), notes in his catalogue (A), and slides in W for his sample 790 (B).



**Figure 4.** A–F. *Moralesonia frauenfeldii*, specimens from BM 57572, isolectotype (scale bar = 20 μm); note that it is a slide made from Grunow sample 790. G–I. *Moralesonia frauenfeldii*, specimens from BM 10889 (“Kalkbai Cap d. g. Hoffn., L. H. [ardman] | 1132” (scale bar = 20 μm), isolectotype. J–K. *Moralesonia frauenfeldii* reproduced from Van Heurck (1883: pl. 126, fig. 14) and a reproduction in Grunow’s drawing collection for his sample 790 in W. L. M. specimens from BM Adams D875 (“Fundort? [locality?]”).



**Figure 5.** *Moralesonia frauenfeldii*, specimens from isotype material, a subsample of the Kalk Bay raw material (Grunow sample 790) from BR (none available any longer at W). **A.** Whole external view of valve, arrows indicate 'unadorned' holes, scale bar = 10  $\mu\text{m}$ . **B.** Detail of external view of valve (as in Fig. 5A), scale bar = 5  $\mu\text{m}$ . **C.** External view of valve with ribs evident by clear area, extending through to entire mantle, indicating it as part of valve, dividing valve into three  $\pm$  equal parts, scale bar = 20  $\mu\text{m}$ . **D.** Detail of cribra with well-developed, complex volute structure, usually with 2–4 pegs supporting complex (contorted) closing plate, scale bar = 5  $\mu\text{m}$ . **E.** Internal view showing ribs, with detail in Fig. 5F, scale bar = 5  $\mu\text{m}$ . **G.** Detail of valve surface with 'unadorned' holes (arrows), scale bar = 4  $\mu\text{m}$ .

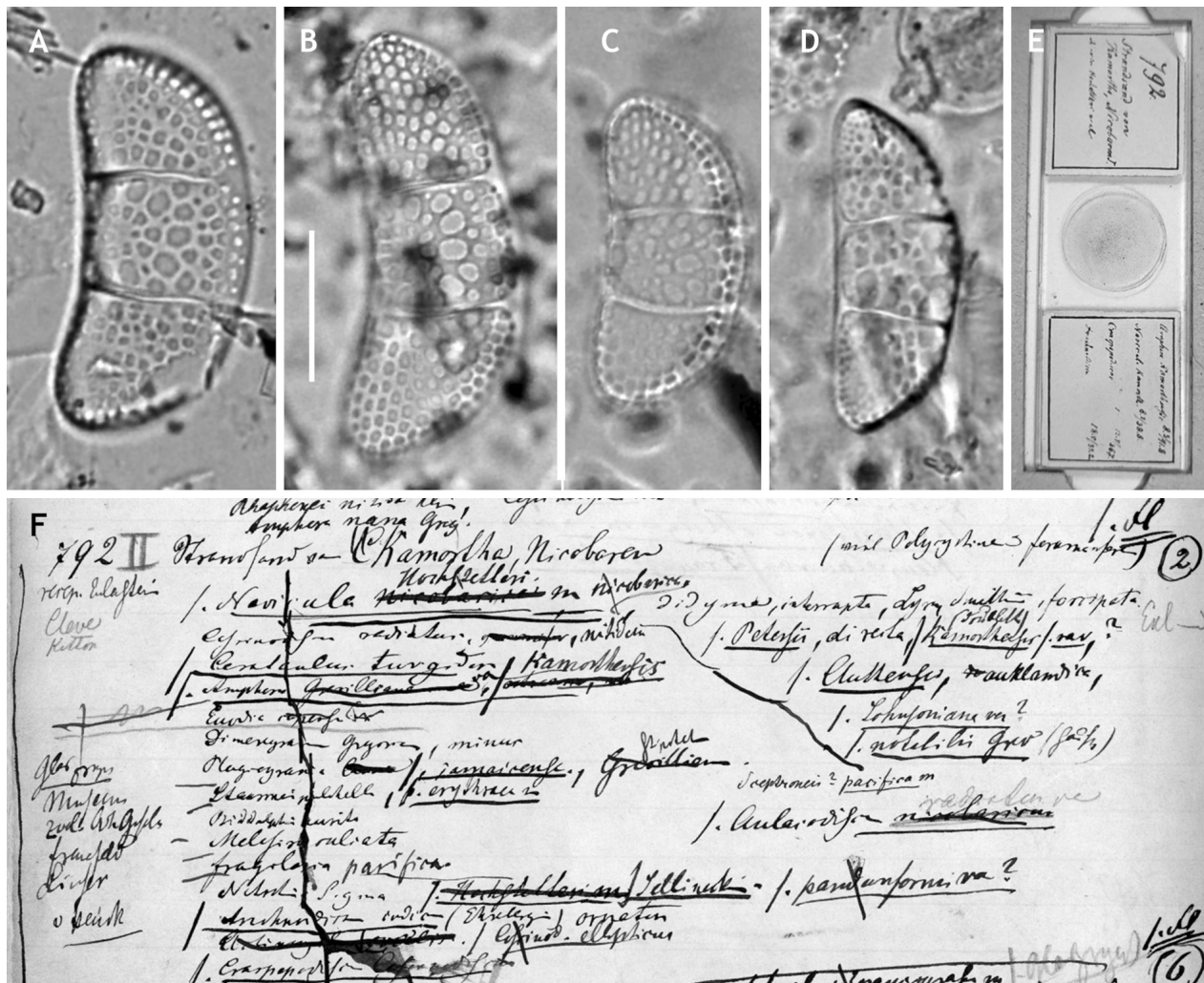
Kamortha”], W0164901! (“Sandstrand von Kamortha”), W0164902! (“Sandstrand von Kamortha, Nicobaren I.”), where the latter two designations in parentheses regarding locality refer to the two slides kept by Grunow for his sample 792 and are labeled as such; Grunow 1867: 24).

COUNTRY UNKNOWN • s.loc.; BM 59207! (I.[J.]D. Möller slide, Wynne Baxter 4591).

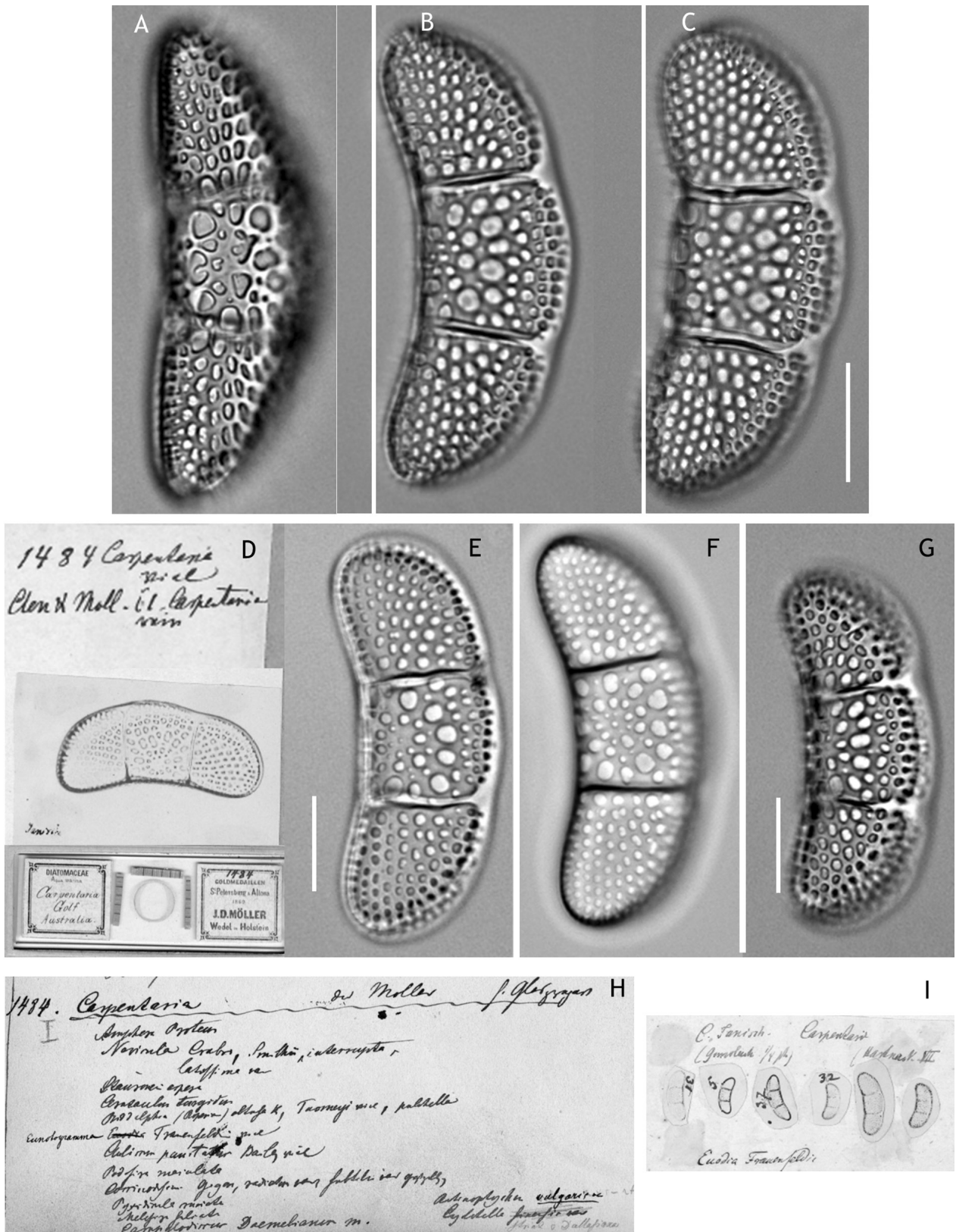
**Description.** Valves lunate, occasionally fusiform, length 32–62 µm, width 20–22 µm [measurements of type specimens from Grunow sample 790 (W0164898)], smaller valves tending towards ca 30 µm, width ± constant, forming less convex ventral margin. Each valve with two transapical ribs dividing valve into three ± equal parts. Ribs evident externally by clear area, extending through to entire mantle, indicating it as part of valve. Internally raised by 2–3 µm tapering towards mantle edge. Areolae ± round, radiating from eccentric hyaline centre, sometimes elongated. Rimoportulae absent. Few simple pores observed, randomly distributed on valve, notably near hyaline centre, absent elsewhere. Cribra

with well-developed, complex volate structure, usually having 2–4(–6) pegs supporting complex (contorted) closing plate. External surface of valve finely ornamented. Girdle composed of few bands (3–4?), valvocopula and copulae, each with one curved row of areolae. Species synapomorphy: denser striation, less ornamented areolae.

**Notes.** In Grunow’s later description he notes that aside from the Kalk Bay locality (Grunow 1863: 158), “Auch im Strandsande der Nikobaren-Insel Kamortha beobachtete ich neuerdings diese Art” (Grunow 1867: 24). Those specimens have been examined and, for the moment, are considered *Moralesonia frauenfeldii* (W0164901 & W0164902, slides for Grunow sample 792, Fig. 6A–F). Although not examined in detail here, *Euodia gibba* var. *africana* M.Perag. (in Tempère and Peragallo 1908: 83, nos 152–153, sample from ‘Algérie, Village-Nègre, Oran, Terre fossile tertiaire’), the specimens are fragmented, but might possibly be interpreted as a species of *Hemidiscus*.



**Figure 6.** *Moralesonia frauenfeldii*. A–D. Specimens from Kamorta Island, Nicobar Islands, W0164902 (“Sandstrand von Kamortha, Nicobaren I.”). E. Slide W0164902 from W. F. Grunow’s catalogue notes on slides W0164901 & W0164902 (Grunow sample 792).



**Figure 7.** *Moralesonia australis*. A–C. *Moralesonia australis*, BM 26837 (as “*Eunotogramma frauenfeldii* Grun. | Australie.”, Van Heurck 1885: 118, sér. XXII, no. 526), scale bar = 20  $\mu$ m. D, H, I. Grunow’s drawings, catalogue notes on his sample 1484 (W0164933), and slides. E, F. BM 12829 (Australia, Carpentaria Bay (Arafura Sea), holotype (= Cleve and Möller *Diatoms* [no.] 61, “Carpentaria Bay”, as *Euodia Fraunfeldii* Grun.)), scale bar = 20  $\mu$ m. G. BM 6481 (“*Euodia Fraunfeldii* Grun. | Australien | J.D. Möller”), scale bar = 20  $\mu$ m.

**Moralesonia australis** D.M. Williams, Ts. Georgiev, T.M. Schust. & C.E. Wetzel, **sp. nov.**

Fig. 7

**Type locality.** Australia, Carpentaria Bay (Arafura sea), BM 12829! (= Fig. 7E–F), holotype (= Cleve & Möller Diatoms [no.] 61, “Carpentaria Bay”, as *Euodia Fraunfeldii* Grunow), and BM Adams ‘Cleve & Möller [no.] 61’, isotype. BM 31718! [Comber 927], “Carpentaria Golf”, Australia, J.D. Möller [no. 896, 1889]; BM 6481! (*Euodia Fraunfeldii* Grun. | Australien | J.D. Möller, Fig. 7G), BM 60070! (J.D. Möller ex Wynne Baxter 6992); BM 74090! (J.D. Möller ex Wise [no.] 1918, “Australie”); BM 26837! (as “*Eunotogramma frauenfeldii* Grun. | Australie”, Van Heurck 1885: 118, sér. XXII, no. 526 = Fig. 7A–E) and BM Adams HVH 526!; W0164933! (Grunow sample 1484) (J.D. Möller, “Carpentaria Golf, Australia”), isotype, Fig. 7D, H–I, Grunow’s drawings, catalogue notes, and slide; BRM HB-19–20.

**Registration.** <http://phycobank.org/104548>

**Description.** Valves lunate, occasionally fusiform, length 55–65 µm, width 20–25 µm, width ± constant, forming less convex ventral margin. Each valve with two transapical ribs dividing valve into three ± equal parts. Ribs evident externally by clear area, extending through to entire mantle, indicating it as part of valve. Internally raised by 2–3 µm, tapering towards mantle edge. Areolae ± round, radiating from eccentric hyaline centre. Rimoportulae absent. Cribra detail not visible or preserved. Girdle unknown. Species synapomorphy: large and diffuse areolae.

**Notes.** It is quite possible that all the material cited above is from the same source: Carpentaria Bay (Arafura Sea), Australia, which is a reasonably large area. The notes on the material for Cleve and Möller slide no. 61 simply state “Comm.[unicavit] I.D. Möller [= Johann Diedrich Möller]” (Cleve and Möller 1878: 2).

### *Moralesonia* sp.

Figs 8, 9A–I

**Analysed material.** ECUADOR • Galápagos Islands, Punta Espinosa, beach from Fernandina (Narborough) Island; 27 Jan. [19]67; I.L. Wiggins in Hendey (1971: 385, figs 16–18, CAS 211014–6, hypotypes 20032–20034, acc. no. 40287); BM 105488! (= Hendey 6702), BM 105494! (= Hendey 6708 = Fig. 8E, F), BM 105495! (= Hendey 6709), BM 105516! (= Hendey 6730) (Fig. 8C, D) • “Galápagos Islands, Santa Cruz [...] 16<sup>th</sup> Aug. 1986, J.A. Broadhead” in Stidolph et al. (2012: pl. 24, fig. 58 = our Fig. 8B, [https://pubs.usgs.gov/of/2012/1163/pages/Plates/24\\_Galapagos.pdf](https://pubs.usgs.gov/of/2012/1163/pages/Plates/24_Galapagos.pdf) and [https://planktonnet.awi.de/index.php?contenttype=image\\_details&itemid=60816#content](https://planktonnet.awi.de/index.php?contenttype=image_details&itemid=60816#content)).

BRAZIL • Pernambuco; J.D. Möller no. 893 [Möller 1889]; BM 31716! (Fig. 9A–C, one specimen), BRM HB-21.

PHILIPPINES • Cebu (“Zebu”); L. H. [ardman] no. 4001 (Fig. 9G, one specimen); BM 10790!.

SOUTHERN PACIFIC OCEAN • J.D. Möller no. 24 [Möller 1892: 139: “Südllicher Stiller Ocean”] • J.D. Möller no. 832 [Möller 1897: 17].

PACIFIC OCEAN • Bahía Magdalena, sediments (BMS) [López Fuerte et al. 2010: pl. 14, figs 1, 2, smaller valves with two bars, not quite joining at centre].

COUNTRY UNKNOWN • s.loc.; BM Adams D875! (“Fundort? [locality?]”); many selected specimens, valve and girdle views, Fig. 4L, M); BM 104871! (Hendey 6060, 3 specimens).

**Analysed fossil material.** UNITED STATES • California, ‘Patos guano’; BM 41317! (Payne 7818) (Fig. 9D, H–I).

UNITED KINGDOM • Nottingham; BM Adams GC1451! (Tempère) (Fig. 9E).

HUNGARY • Castel; BM Adams H885! (F. Adams) (Fig. 9F).

**Notes.** Hendey’s unpublished drawings of the specimens found in the Galápagos Islands are reproduced here as Fig. 8A and some of the specimens are illustrated in Fig. 8C–F. Again, these have a superficial ‘similarity’ to the African specimens but, as yet, no specific character has been identified to associate them with *Moralesonia frauenfeldii* or to describe these specimens as a separate taxon. The three unpublished drawings are said to be from slides ‘Hendey 6701’ (= BM 105487), ‘Hendey 6708’ (= BM 105493), and ‘Hendey 6730’ (= BM 105516). Slide ‘Hendey 6701’ (= BM 105487) must be an error for 6702 (6701 is from San Diego; 6702 is labelled *Eunotogramma frauenfeldii*). In addition to the notebook, there are a series of unpublished Icones Diatomacearum documenting the Galápagos Islands study (Hendey 1971).

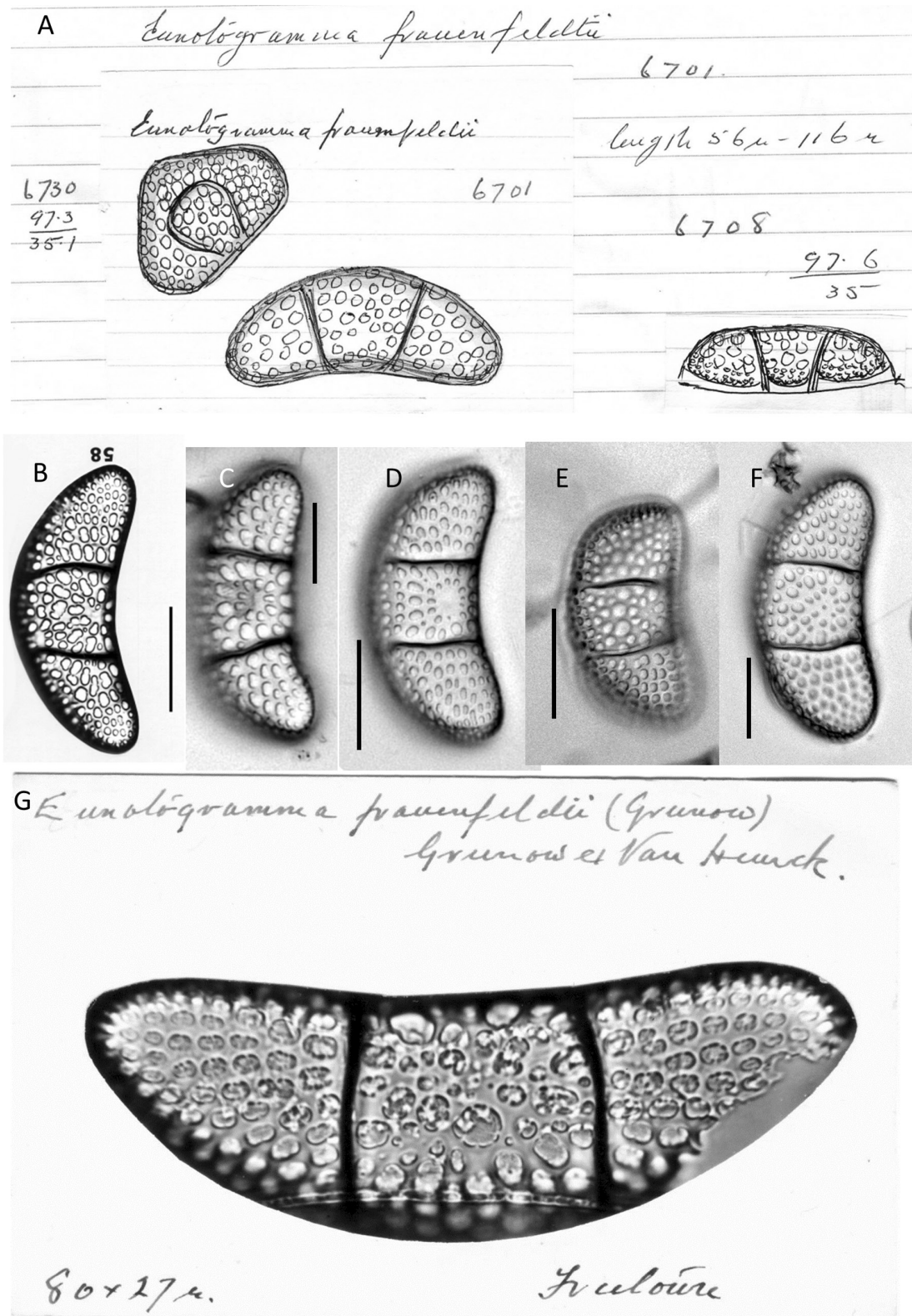
### *Moralesonia ? frauenfeldii*

Figs 9J, 10

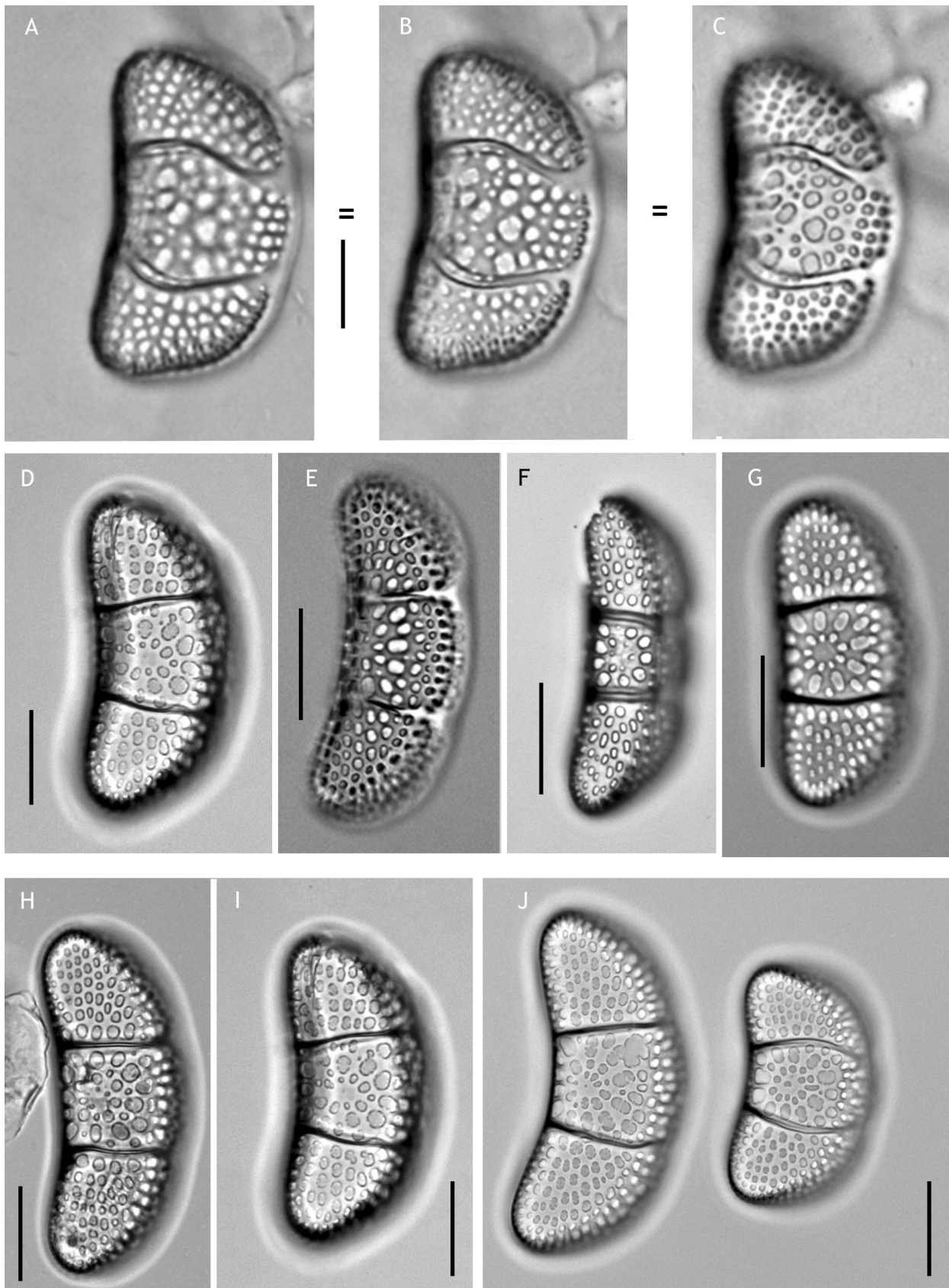
**Analysed material.** MOZAMBIQUE • East Africa, Ibo; BM Adams TS 457! (E. Leonard, no. 7); BM Adams TS 459! (E. Leonard, two specimens) (figured in Desikachary 1988: pl. 583, figs 2–4, 6, 7); BM Adams F16! (ex W.A. Firth) (figured in Desikachary 1988: pl. 583, fig. 1); BM Adams GC 1450! (ex W.A. Firth) (Fig. 9J).

MAURITIUS • Rodriguez (Île Rodriguez); Stub NHM I6 (see Fig. 10A–F).

**Description.** Valves lunate, occasionally fusiform, length 60–65 µm, width 20–25 µm, width ± constant, forming less convex ventral margin. Each valve with two transapical ribs dividing valve into three ± equal parts. Ribs evident externally by clear area, extending through to entire mantle, indicating it as part of valve. Internally raised by 2–3 µm tapering towards mantle edge. Areolae ± round, radiating from eccentric hyaline centre. Rimoportulae absent. Cribra detail not visible or preserved. Girdle unknown.



**Figure 8.** *Moralesonia* sp. **A.** Hendeý's unpublished drawings of the specimens found in the Galápagos Islands. **B.** Reproduced from Stidolph et al. (2012: pl. 24, fig. 58 [inverted], Ecuador, "Galápagos Islands, Santa Cruz [...] 16<sup>th</sup> Aug. 1986, J.A. Broadhead"), scale bar = 30  $\mu$ m. **C–F.** Some of Hendeý's specimens. **C–D.** Ecuador, Galápagos Islands, Punta Espinosa, beach from Fernandina (Narborough) Island, 27<sup>th</sup> Jan. [19]67, I.L. Wiggins, BM 105516 (Hendeý 6730). **E–F.** BM 105494 (Hendeý 6708). **G.** "*Eunotogramma frauenfeldii*", image from Hendeý ms collection; specimen dimensions: 80  $\times$  27  $\mu$ m, scale bar = 20  $\mu$ m.



**Figure 9.** A–I. *Moralesonia* sp. A–C. BM 31716, Brazil, Pernambuco, J.D. Möller [no. 893, 1889], one specimen, scale bar = 20  $\mu$ m. D, H, I. Fossil material, BM 41317, Payne 7818, United States, California, “Patos guano”, specimen 71  $\times$  25  $\mu$ m, scale bar = 20  $\mu$ m. E. BM Adams GC1451, Tempère, Nottingham, specimen 64  $\times$  29  $\mu$ m, scale bar = 20  $\mu$ m. F. BM Adams H885, F. Adams, Hungary, Castel, specimen 72  $\times$  23  $\mu$ m, scale bar = 20  $\mu$ m. G. BM10790, L. H.[ardman] no. 4001, Philippines, Cebu [“Zebu”], one specimen, specimen 64  $\times$  29  $\mu$ m, scale bar = 20  $\mu$ m. J. *Moralesonia frauenfeldii*, BM Adams GC 1450, East Africa, Ibo, ex W.A. Firth, scale bar = 20  $\mu$ m.



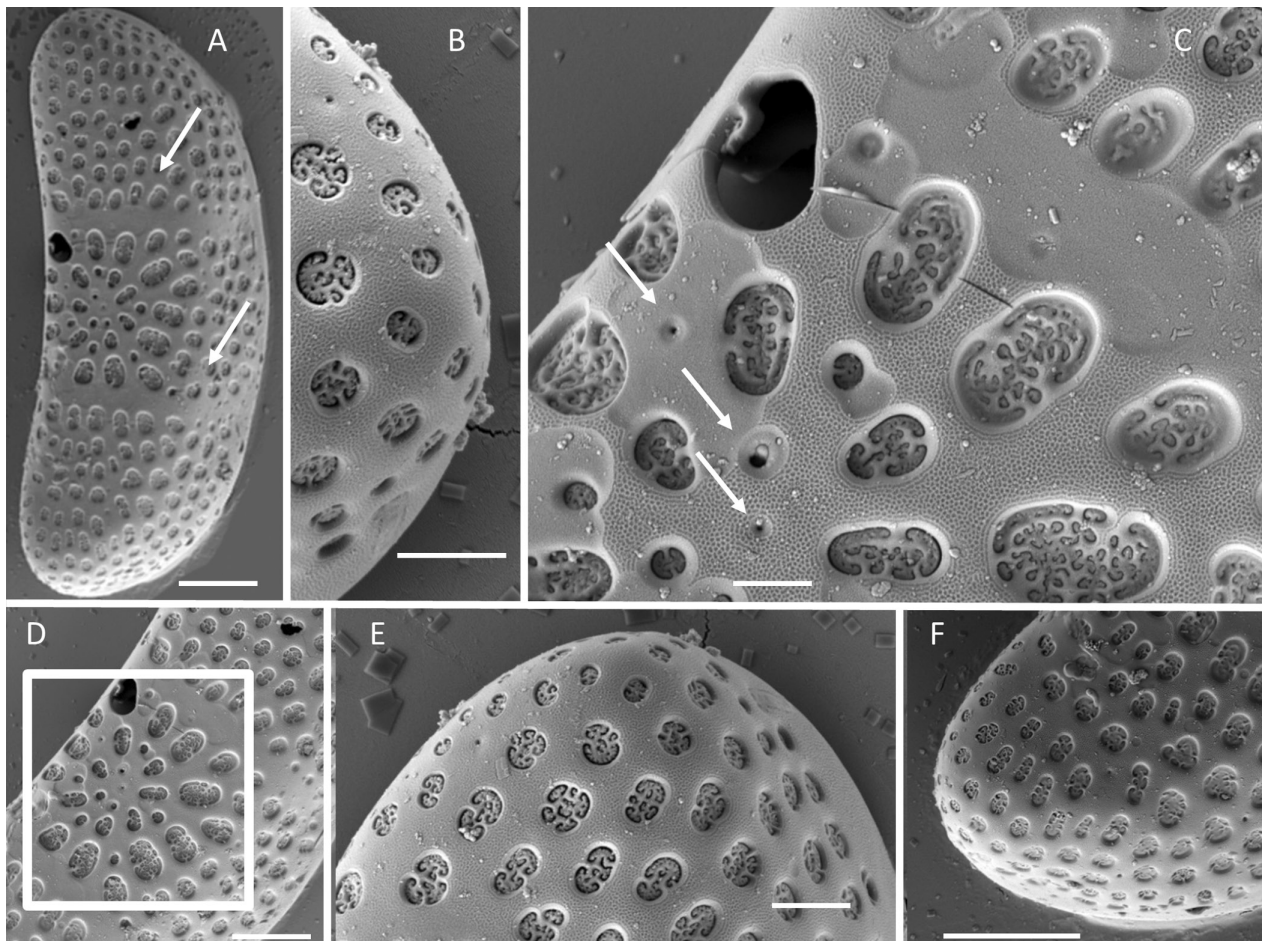
## DISCUSSION

With the description of *Moralesonia* and a preliminary estimate of its included species (ca 4–5), the relationships of the genus can be explored and the higher-level classification expanded, if applicable. As a starting point, the short history of the ‘Biddulphiées’ is worth recalling.

With the publication of the text accompanying his Atlas, Van Heurck (1885) revised his view on the status of *Eunotogramma*. None of the taxa described and noted in 1883 were discussed, with the exception of *E. debilis* Grunow (Grunow in Van Heurck 1883: pl. 126, figs 17–19; Van Heurck 1885: 202), for which Grunow had originally appended the name with a question mark. In 1885, Van Heurck’s order ‘Biddulphiées’ included a total of eight genera, of which *Anaulus* Ehrenb. was but one (Van Heurck 1885: 201; our Table 6, column 1). By 1896, Van Heurck’s classification appeared more complex than his earlier effort, the later version having four sub-families and numerous additional genera (Van Heurck 1896: xvi–xvii; our Table 6, column 2).

At first, *Anaulus* included only *A. debilis* (Grunow) Van Heurck (= *Eunotogramma debile* Grunow in Van Heurck 1883: pl. 126, figs 17–19). This species was assigned to the sub-genus (‘sous-genre’) *Eunotogramma*, but no other subgenera were recognised (or named) at that time (Van Heurck 1885: 202). This arrangement was modified in Van Heurck’s later book in which he explained: “I divide this genus [*Anaulus*] into the sub-genera *Eu-Anaulus* and *Eunotogramma* Auct., the latter being distinguished by the form of the valve being lunate (more or less crescent-shaped)” (Van Heurck 1896: 454). He included an illustration of *Anaulus birostratus* (Van Heurck 1896: 454, fig. 179, “California, Peru, Oamaru, the Balearic Islands, &c”), as an example of a “true *Anaulus*” (a member of *Eu-Anaulus*) and some illustrations of *Anaulus debilis* (from Ostend, Van Heurck 1896: pl. 19, fig. 626, pl. 34, fig. 892).

*Anaulus debilis* has many cross-members, similar to that seen in *E. laevis*, which was placed in *Anaulus* by Boyer (1901 [1900]: 737), now the type of the genus *Eunotogramma* (Amspoker 2011). Within the genus *Eunotogramma*, Boyer (1901 [1900]: 735) excluded all



**Figure 10.** *Moralesonia* sp., SEM images, specimens from Mauritius, Rodriguez (Île Rodriguez), stub NHM I6. **A.** Whole external view of valve, arrows indicate ribs, evident by clear area, extending through to entire mantle, indicating it as part of valve, dividing valve into three  $\pm$  equal parts, scale bar = 10  $\mu$ m. **B.** External view of pole, detail with absence of any pore-field, etc., scale bar = 1  $\mu$ m. **C.** Detail of centre of valve, arrows indicating ‘unadorned’ holes, scale bar = 1  $\mu$ m. **D.** Centre of valve with radiating ‘annulus’ (shown within white box), scale bar = 2  $\mu$ m. **E.** External view of pole, with detail of cribra with well-developed, complex volate structure, scale bar = 1  $\mu$ m. **F.** Additional external view of pole, with detail of cribra with well-developed, complex volate structure, scale bar = 2  $\mu$ m.

**Table 6.** Composition of Biddulphiaceae in Van Heurck (1885: 202), Van Heurck (1896: xvi–xvii; those genera marked \* are subdivided further, but these divisions are not discussed separately by Van Heurck) and Simonsen (1979: 50).

Biddulphiées (Van Heurck 1885)	Biddulphiaceae (Van Heurck 1896)	Biddulphioideae (Simonsen 1979)
	I. Isthmieae	
<i>Isthmia</i> C.Agardh	<i>Isthmia</i>	<i>Isthmia</i>
	II. Hemiaulidieae	
<i>Terpsinoë</i> Ehrenb.	<i>Terpsinoë</i> *	<i>Terpsinoë</i>
<i>Anaulus</i> [ <i>Eunotogramma</i> ]	<i>Anaulus</i> [ <i>Eunotogramma</i> ]*	<i>Anaulus</i> [ <i>Eunotogramma</i> ]
<i>Hemiaulus</i> Heib.	<i>Hemiaulus</i> *	<i>Hemiaulus</i>
	+ seven other genera	
	III. Eucampieae	
<i>Lithodesmium</i> Ehrenb.	<i>Lithodesmium</i>	
<i>Eucampia</i> Ehrenb.	<i>Eucampia</i> *	
<i>Bellerochea</i> Van Heurck	<i>Bellerochea</i>	
	+ two other genera	
	IV. Eubiddulphieae	
<i>Biddulphia</i> S.F.Gray	<i>Biddulphia</i> *	<i>Biddulphia</i>
	+ eight other genera	+ 7 other genera

the larger species (those recognised above as ‘\*Fossil’ in Table 5), suggesting that *E. amphioxys* is “equivalent to *Biddulphia ? lunata* E. [...]” (another member of the ‘\*Fossil’ group) and he divided *Anaulus* into two groups, one with “Valves elliptical” and the other “Valves lunate”, the latter equivalent to *Eunotogramma*. Van Heurck’s key appears more perplexing than his classification, but is illuminating with respect to characters used (Van Heurck 1896: 450, and page 510 regarding his concept of *Euodia* and *Leudugeria*, where he uses valve shape and the kinds of ‘puncta’ for *Leudugeria*, and shape and ‘a small pseudonodule’ for *Euodia*).

Simonsen’s classification differs little from Van Heurck’s (Table 6, column 3). His family Biddulphiaceae has three subdivisions. One of them, sub-family b, Biddulphioideae, includes 12 genera in all, *Isthmia* C.Agardh, *Terpsinoë* Ehrenb., *Anaulus* [*Eunotogramma*], *Hemiaulus* Heib., and *Biddulphia* S.F.Gray being amongst them (Simonsen 1979: 50).

Recent classifications are not much help. For example, Cox (2015) includes a number of redundant categories (following Round et al. 1990: 127), but still resulting in a classification similar to that of Van Heurck. The Order Anaulales has but one family, Anaulaceae, which has three genera: *Anaulus*, *Eunotogramma*, and *Porpeia* J.W.Bailey ex Ralfs (in Pritchard 1861: 850, 6–10 species, fossil). Nikolaev and Harwood proposed much the same, with the family Anaulaceae (placed within the order Biddulphiophycidae) composed of four genera: *Anaulus*, *Eunotogramma*, *Porpeia*, and *Terpsinoë* (Nikolaev and Harwood 2000: 52; Nikolaev et al. 2001: 41; Nikolaev and Harwood 2002: 78; *Terpsinoë*: Ehrenberg 1843: 402, with 20–30 species, fossil and extant). More recently, Anaulaceae has been modified in some online resources:

both DiatomBase and AlgaeBase (19 Oct. 2023) include in Anaulaceae, along with *Anaulus* and *Eunotogramma*, *Ceratanaulus* Górecka et al. (in Witkowski et al. 2020: 14, a monotypic genus erected for *Ceratanaulus creticus* (Drebes & Schulz) Górecka et al., basionym: *Anaulus creticus* Drebes & Schulz (Drebes and Schulz 1981: 166); it is possible that *Eunotogramma dubium* maybe a second species of *Ceratanaulus*, see Table 5). Yet, the cladogram in Witkowski et al. (2020) places *Ceratanaulus* as sister to some species of *Biddulphia* (which divides into two separate groups, for further details see Sims et al. 2022 [2023]), and *Terpsinoë* plus *Neocalyptrella* Hern.-Becerril & Maeve, with other species of *Biddulphia* sister to *Attheya* T.West. *Anaulus australis* and *Eunotogramma lunatum* are sister to the Thalassiosirales.

Although not all major classifications have been discussed here, those from the 19<sup>th</sup>, 20<sup>th</sup>, and 21<sup>st</sup> century, more or less, follow one another (with the exception of the molecular cladograms) and base their relationships on the possession of ‘transapical ribs’ (‘costae’) and valve shape. In terms of formulating hypotheses of relationships, the data are limited, except to note that the genera *Euodia*, *Eunotogramma*, and *Anaulus* are all at present clearly non-monophyletic (as earlier noted for *Anaulus* by Drebes and Schulz 1981, and for *Euodia* and *Eunotogramma* by Sims 2000) and (most) monophyletic higher taxa are seemingly either non-existent or inconsistent. Thus, somewhat unsurprisingly, for *Moralesonia*, the currently most informative classification is still that of Van Heurck (1896). By informative, we mean, accounts for the potential synapomorphies of the included taxa at whatever rank. This will be explored in more detail in Part II of a series of papers around these taxa.

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