On the taxonomic identity of *Humidophila contenta* (Grunow) R.L.Lowe & al. and *H. biceps* (Grunow) Furey & al. (*Diadesmidaceae, Bacillariophyta*)

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Humidophila contenta (Grunow) R.L.Lowe & al. (2014: 357), originally illustrated by Grunow (in Van Heurck 1880: XIV [14], fig. 31 A, B, as *Navicula trinodis* f. *minuta* Grunow and *Navicula trinodis* f. *biceps* Grunow, respectively), named as *Navicula contenta* Grunow (in Van Heurck 1883: 46), and later described by Grunow (in Van Heurck 1885: 109), is one of the most frequently reported aerophilous diatoms, observed on every continent worldwide (e.g. Moser & al. 1998, Van de Vijver & al. 2002, Lange-Bertalot & al. 2017, Vouilloud & al. 2022). The species was first transferred in 1990 to the genus *Diadesmis* as *D. contenta* (Grunow) D.G.Mann (in Round & al. 1990: 666) and later to the newly erected genus *Humidophila* (Lowe & al. 2014: 357).
Despite this apparent worldwide distribution, its taxonomic identity is somewhat blurred following a series of incorrect interpretations of the original description and the original material, not least as a result of the confusion caused by Grunow and Van Heurck in the *Texte du Synopsis des Diatomées de Belgique* (Van Heurck 1885: 109) and the notes accompanying the exsiccata set *Types du Synopsis des Diatomées de Belgique* (Van Heurck 1883, n° 146). Table 1 gives an overview of all nomenclatural acts regarding *Navicula contenta* and the related name *Diadesmis biceps* Arnott, which remained a manuscript name.

The first indication of *Navicula contenta* (though not under that name) is found in Van Heurck (1880). Figure 31 in Van Heurck's *Atlas* (1880, plate XIV [14]) shows two valves, one (labelled 'a' in the figure legend) is named "*Navicula trinodis* W.Sm. forma *minuta* (nec *Achnanthes trinodis* [and not *Achnanthes trinodis*])," whereas the second drawing (labelled 'b' in the figure legend and next to the figure) bears the name "*Navicula trinodis* var. *biceps* Grunow (*Diadesmis biceps* Arnott)". Both drawings were made by Grunow, as indicated by the * behind the name in the figure legend. Unfortunately, no drawings could be found in the Grunow collection in the Natural History Museum of Vienna (**W**) where almost all original Grunow drawings are conserved (T.M. Schuster, pers. comm.). In the Van Heurck collection, kept in Meise Botanic Garden (**BR**), a slide made by Van Heurck from Delogne sample 97 is conserved (BR V-12-C7, Fig. 2) that most likely was used to make the drawing of fig. 31A, as this number is indicated, as an added label, on the slide (XIV, 31A, *N. trinodis*). Moreover, the original Delogne collection, containing several hundred raw samples, was rediscovered in the Van Heurck collection with one of the samples, labelled VH 97, Ardoisière de Hour (located in Rochehaut, Belgium, Van de Vijver, pers. obs.) containing two micas, together with a tube, also labelled 97 (Fig. 1). Analysis of this material and the slide mentioned earlier showed that they all represent the same material. Unfortunately, the only source for figure 31b is the citation by Grunow (in Van Heurck 1885: 109).

One of the two names, *N. trinodis* var. *biceps*, was used in Van Heurck (1883), the series of small taxonomic notes prepared by Grunow to accompany the *Types du Synopsis* exsiccata set. For Types

slide n° 146 from Groenendael (Belgium), labelled *N. contenta* Grun., "*Nav. trinodis* W.Sm. var. *biceps* Grun. in Atlas du Synopsis" is mentioned as the replaced name; the other name, *N. trinodis* f. *minuta*, is not listed. This small note is the first time the name *N. contenta* appears in the literature.

Table 1. Nomenclatural evaluation of names and nomenclatural acts related to *Navicula contenta* Grunow and *Diadesmis biceps* Arnott. *Publication date likely 1883 but not later than 1884, **used for the intended lectotype, published by Schoeman & Archibald (1978) and Moser & al. (1998). Taxon described as *Diadesmis simplex* by Reichardt (2004).

Scientific name	Van Heurck (1880)	Van Heurck (1883*)	Van Heurck (1885)
Navicula trinodis f. *minuta* Grunow	Validly published as pl. 14: fig. 34a according to Turland & al. (2018: ICN, Art. 38.8 (original material: Specimen depicted as pl. 14: fig. 31a).	[not mentioned]	[not explicitly cited]
Navicula trinodis var. *bi[c]eps* Grunow	Validly published as fig. pl. 14: 34b according to ICN, Art. 38.8 (original material: Specimen depicted as pl. 14; fig. 31b)	Replaced synonym for *Navicula contenta* Grunow	Publication of the type locality "Rochehaut"
Navicula contenta Grunow		New name for *Navicula trinodis* var. *biceps*. A new name on species rank was necessary to avoid a later homonym for *Navicula biceps* Bory 1827 and Ehrenberg 1843, *nom. illeg.* (The taxon concept was added to the nomenclatural act, not being original material, see below)	Emending description of the taxon depicted as pl. 14: fig. 31(a?, i.e. *N. trinodis* f. *minuta*) in Van Heurck (1880)
Navicula contenta var. *biceps* (Grunow) Grunow		[not mentioned]	Superfluous combination for *Navicula contenta* var. *contenta*; citing pl. 14: fig. 31b in Van Heurck (1880).
"*Diadesmis biceps*" Arnott	Unpublished designation mentioned as conspecific with *Navicula trinodis* var. *biceps*	[not mentioned]	[not mentioned]
Taxon in Sample 146**		Preparation "Groenendael" including an undescribed taxon, cited for *Navicula contenta* but not being original material, thus not appropriate for selection as a lectotype	Specimens in preparation "Groenendael", cited for both taxa are in serious conflict to the original material used for pl. 14: fig. 31a, b in Van Heurck (1880).

In 1885, Van Heurck presented a written description for *N. contenta* in the *Texte du Synopsis* on page 109 with the following words: "*Valve linéaire, renflée à la partie médiane et aux extrémités. Raphé entouré d'une zone hyaline notable, à peine un peu dilatée près du nodule médian. Stries*

très-délicates, à peu près parallèles, environ 36 en 1 c.d.m. Longueur 0,7 à 1 c.d.m. Largeur 0,2 à 0,025 de c.d.m." [Valve linear, inflated in the middle part and at the apices. Raphe bordered by a distinct hyaline zone, hardly widened near the central nodule. Striae very delicate, more or less parallel, around 36 in 10 µm. Length 7–10 µm, width 2–0.25 µm]. Van Heurck added that the species was found on moist places and as type locality mentioned a quarry in Rochehaut (near Bouillon, Belgium), based on a sample collected by Charles-Henri Delogne (Del., 1834–1901). This sample is without doubt the above-mentioned sample 97.

Interestingly, but confusingly, Van Heurck added that the species was found in his exsiccata slide *Types du Synopsis* 146, and referred to his Atlas plate XIV [14], fig. 31, under the name of *N(avicula) trinodis* (Figs 4, 5).

Together with the nominate variety of *N. contenta*, Grunow also discussed a variety *biceps*, referring to *Atlas* pl. XIV [14], fig. 31b) using the words: "*diffère du type par le renflement median qui est nul ou très-faible*" [differs from the type by the middle inflation that is absent or very weak]. As type locality, Grunow indicated Groenendael (near Brussels, Belgium), also a sample collected by Delogne (Van Heurck 1885, p. 109). This sample may very well be Types n°146.

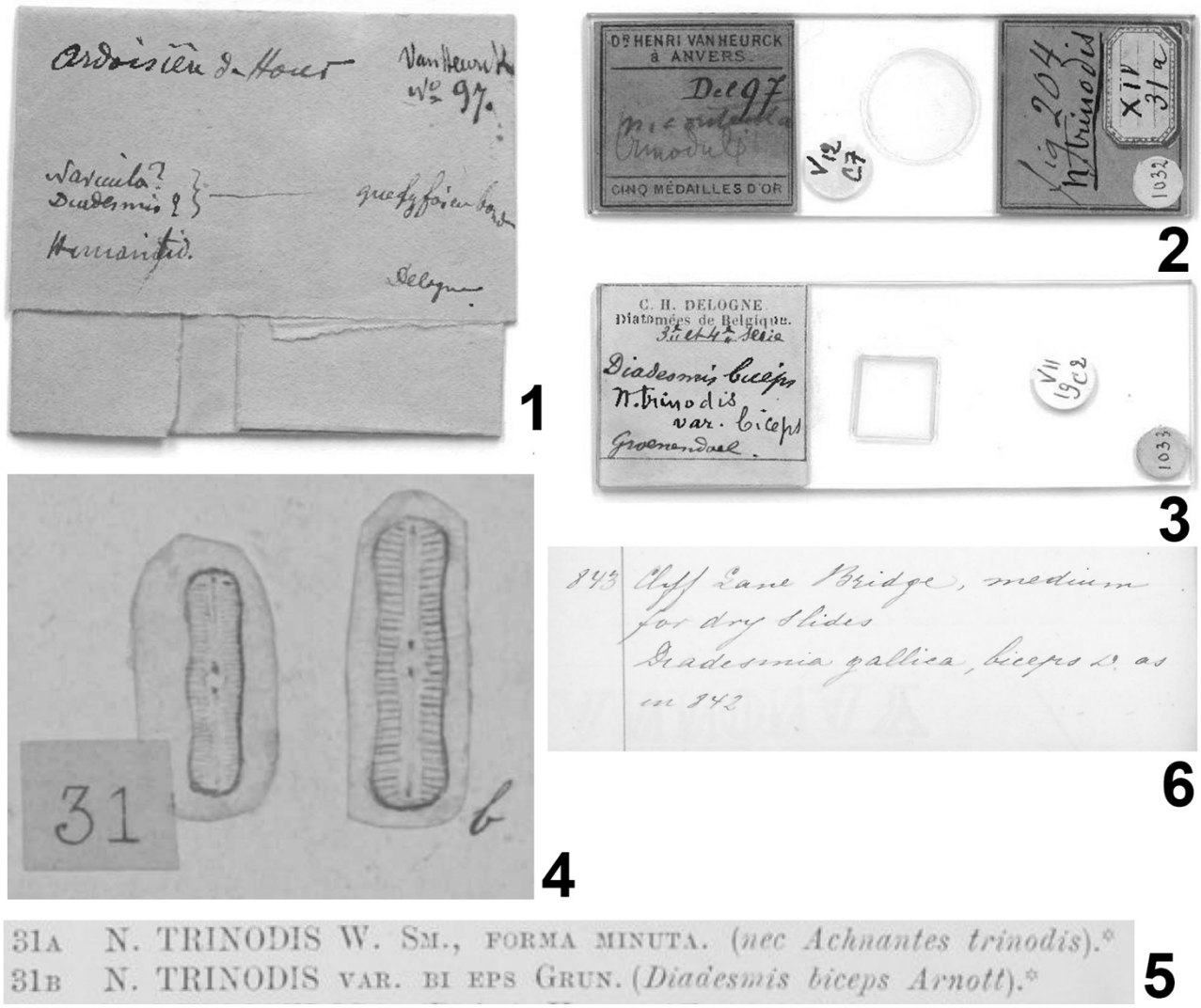

Fig. 1. Original Delogne sample 97. Ardoisière de Hour. Package found in the Delogne collection, part of the Van Heurck collection kept in **BR**. **Fig. 2**. Slide V-12-C7 prepared from Delogne

sample 97, labelled as *N. trinodis*, XIV 31a. **Fig. 3**. Slide VII-19-C2, original Delogne slide containing *Diadesmis biceps/N. trinodis* var. *biceps* – Groenendael. **Fig. 4.** Original handmade drawings by Grunow used on Van Heurck plate XIV [14], fig. 31. One drawing marked as b. **Fig. 5**. Legend from plate XIV, fig. 31 in Van Heurck (1880). **Fig. 6**. Scan of Walker Arnott sample 843 (Cliff Lane Bridge [i.e. Warrington, UK]) containing a population of *Diadesmis gallica* and *D. biceps*, scan made from the original hand-written Walker Arnott catalogue kept in **BR**.

In 1978, Schoeman & Archibald discussed the morphology and identity of *Navicula contenta*, and introduced the concept of *N. contenta* used today. Prior to that publication, Hustedt (1962) provided an illustration (p. 210, fig. 1328 a–d) of *Navicula contenta* that closely resembled the original Grunow drawing and description of Figure 31. However, the first four drawings were taken from the Schmidt Atlas, plate 402, figs 12–15; figures 12 and 13 are based on a sample from Iceland and the other two on material from Ranu Lamongan (Java, Indonesia). It is possible that the Icelandic specimens represent *Humidophila eldfjallii* Furey, Manoylov & R.L.Lowe, a species described in 2020 from Iceland showing a comparable valve outline but different ultrastructure (Furey & al. 2020, fig. 8 A–H). Hustedt also added three drawings showing *N. contenta* var. *parallela* J.B.Petersen (1928: 15, fig. 2) and two valves of the var. *biceps* "(Arnott)" Grunow in Van Heurck.

Schoeman & Archibald (1978) discussed the taxonomic history of *Navicula contenta*, basing their analysis entirely and solely on slide 146 from Groenendael (including the confusing note Grunow had added for the slide), but ignoring the original description and original locality (Rochehaut) given by Grunow (Van Heurck 1885: 109). Schoeman & Archibald (1978) finally concluded that *Navicula contenta* should be based on *Navicula trinodis* var. *biceps* (=*Diadesmis biceps* Arnott), despite the entry in VanLandingham (1975: 2479).

Subsequently, Schoeman & Archibald (1978) analysed three slides made of Walker Arnott material (BM 3615 Maryhill Bridge, Glasgow, Scotland; BM 11222 Cheshire, England; BM 24640 Warrington, Cheshire) and Van Heurck slide Type 146 (Groenendael, Brussels, Belgium), the latter borrowed or analysed from the Vienna collection (most likely from the Grunow collection where a complete Van Heurck exsiccata set *Types du Synopsis des Diatomées de Belgique* is present (Van de Vijver, pers. obs.) and the Natural History Museum in London (slide **BM** 26457). All illustrated valves (Schoeman & Archibald 1978, figs 46–56) show concave valve margins and a clear hyaline fascia forming the entire central area, two morphological features in clear contrast with the original description (see above). The findings in Schoeman & Archibald (1978) were further discussed in Moser & al. (1998:133–134, 137). The notion that '*Navicula contenta* is an extremely polymorphic taxon', as claimed by Schoeman & Archibald (1978), was contradicted. Slide Van Heurck 146 from Groenendael was proposed as lectotype for *Navicula (Diadesmis) contenta,* but only the drawings 1–8 in Schoeman & Archibald (1978: 134) were included. The other four drawings represent *Navicula lepida* Grunow, as our own analysis of sample Van Heurck Type 146 shows (Van de Vijver, unpubl. res.). Despite a renewed, thorough analysis of several copies of Van Heurck slide 146 present in the Van Heurck collection (**BR**), no other *Humidophila* species could be found (Van de Vijver, pers. obs.). Many of the other illustrated valves were excluded from conspecificity (Moser & al. 1998). Moreover, "*Diadesmis biceps"* Arnott was separated from *Diadesmis contenta* by designating one of the above-mentioned Walker Arnott slides (BM 3615 Maryhill Bridge, Glasgow, Scotland, UK) as lectotype for "*D. biceps"*. Curiously, both drawings in Van Heurck (1880, plate 14, fig. 31) were added as synonyms to "*D. biceps"*, although the authors in Moser & al. (1998: 137) raised some doubts about fig. 31b adding a question mark to the synonyms.

These morphological ideas were later adopted in almost all references mentioning *Navicula contenta* (e.g. Van de Vijver & al. 2002: 34 as *D. contenta*, Lange-Bertalot & Werum 2001, figs 58 & 59 as *D. contenta*, Lange-Bertalot & al. 2017: 344 as *Humidophila contenta*), all showing valves with a clear fascia and concave to straight valve margins. Valves with a slightly gibbous centre lacking a fascia (conforming to the original description) were only illustrated in Krammer & Lange-Bertalot (1986, pl. 75, figs 2 & 3), but in later publications disappeared completely.

The rediscovery of the original Delogne material in the Van Heurck collection, together with a reanalysis of all original information requires a revision of our current ideas on the taxonomic identities of *Humidophila contenta* and *Humidophila biceps* (Table 1). Delogne sample 97 (Ardoisière de Hour in Rochehaut, Belgium, Figs 1, 2) is believed to be the original material for *Humidophila contenta* and should therefore be designated as lectotype for *Navicula contenta*, instead of the intended lectotypification in Moser & al. (1998: 134) choosing Van Heurck sample 146 (Groenendael, Belgium) as intended lectotype. A new slide and SEM stub were made from the original Delogne 97 material from Rochehaut and investigated using light and scanning electron microscopy. The slides contained a very large population of a *Humidophila* species, showing a high similarity to the drawing 31a and fitting entirely into the description Grunow made (Figs 7–31).

The designation "*Diadesmis biceps"* Arnott has not been validly published and only appears in the species lists for several samples in the handwritten catalogue of the Walker Arnott collection (part of the Van Heurck collection in **BR**) (for instance Fig. 6 shows the entry for Walker Arnott sample 843, Cliff Lane Bridge, Warrington, UK). The first time the name *Diadesmis biceps* appears in print is in the Cleve & Möller exsiccata set "Diatoms" as '*Diadesmis biceps* Arn. Mscpt var. *subundulata* Grun." (Cleve & Möller 1879, p. 23, no. 175). Grunow mentioned the designation in the figure legend of Van Heurck pl. XIV [14]: fig. 31b, probably indicating that it represents the same taxon as his *Navicula trinodis* var. *biceps* (Fig. 5). Cleve (1894:132) names the taxon *Navicula contenta* var. *biceps* Arnott Ms. It is only in Moser & al. (1998) that the species (not variety) "*Diadesmis biceps"* Arnott appears in the published literature for this taxon, probably based on the figure legend in Van Heurck (1880).

As the origin of the drawing in Van Heurck (1880, plate XIV: fig. 31b) is unclear, initially it was difficult to find the specimen illustrated by Grunow as *Navicula trinodis* var. *biceps*. Delogne (1880–1881) published an exsiccata set containing 100 slides with diatoms from Belgium (*Diatomées de Belgique*, Fascicules I–IV). One of the slides (Delogne 81) is made from material collected in Groenendael and labelled *Navicula trinodis* var. *biceps*. The same material was used by Van Heurck for slide Types n°146 in his exsiccata set *Types du Synopsis des Diatomées de Belgique*, this time, however, probably erroneously labelled *Navicula contenta*. In the Van Heurck collection, several slides with hand-written labels (probably made by Delogne) were found, one labelled "*Diadesmis biceps"*, *N. trinodis* var. *biceps* – Groenendael (Fig. 3). Unfortunately, unmounted material for the Delogne slides could not be found (Van de Vijver, pers. obs.) but material for Van Heurck slide 146 was found and prepared. The results of the analysis of the Groenendael material using light and scanning electron microscopy is represented by Figs 32–53. In the material, a large population of a small *Humidophila* was observed with weakly concave margins and a clear fascia. As this is the only *Humidophila* present in the sample and given its similarity to a population identified by Walker Arnott as "*Diadesmis biceps"* (Walker Arnott sample 843, Cliff lane Bridge, Warrington, England, Figs 6, 54–81, material found in the Walker Arnott collection, part of the Van Heurck collection in **BR**), we assume these populations are conspecific. However, all (= Groenendael and Warrington) observed valves show little resemblance to the original drawing Grunow published in Van Heurck (1880, pl. 14: fig. 31b), as all valves in both observed populations possess a clear fascia whereas the drawing clearly lacks a fascia. These differences

make the use of the name *Navicula trinodis* var. *biceps* Grunow, as mentioned by Furey & al. (2020:190) for the taxon with concave valve outline, not appropriate.
Due to the invalidity of "*Diadesmis biceps"* Arnott, the name can no longer be used for the concave taxon. Reichardt (2004: 432, pl. 6: figs 21–22; pl. 8: figs 12–20) described a small-celled *Humidophila* species as *Diadesmis simplex* E.Reichardt, later transferred to the genus *Humidophila* as *H. simplex* (E.Reichardt) R.L.Lowe & al. (2014: 359). Although Reichardt (2004, 2006, 2018) only compared his new taxon with the confusing interpretation of *H. contenta*, it is clear that all illustrated populations (see for instance Reichardt (2018: pl. 133: figs 18–33) are conspecific with the investigated populations in the current contribution. The name *H. simplex* should therefore be used for this concave valve form.

Humidophila simplex can be easily separated from *H. contenta* based on its concave valve outline, the presence of a clear rectangular fascia, the continuous mantle striae at the apices (interrupted in *H. contenta*) and the shorter striae with rounded, almost never transapically elongated areolae.
The morphological concept of *Humidophila contenta*, however, has to be adjusted as our current analysis clearly showed that the populations of valves with a linear, concave to straight outline, T-shaped central and terminal raphe endings and the possession of a central fascia represent *H. simplex*.

Humidophila contenta (Grunow) R.L.Lowe & al. 2014 (Figs 7–31)
Basionym: *Navicula contenta* Grunow in Van Heurck, *Types du Synopsis des Diatomées de Belgique*, Séries VI: p. 46, 1883.
≡ *Navicula trinodis* var. *bi[c]eps* Grunow in Van Heurck, *Synopsis des Diatomées de Belgique Atlas* I(2): pl. XIV [14], fig. 31B, 1880.
= *Navicula trinodis* f. *minuta* Grunow in Van Heurck, *Synopsis des Diatomées de Belgique Atlas* I(2): pl. XIV [14], fig. 31A, 1880
To be excluded as a synonym: *Humidophila biceps sensu* Furey & al. (2020).
Lectotype (here designated): **BR** slide V-12-C7, slide prepared from Delogne sample 97 (Ardoisière de Hour, Rochehaut, Belgium), leg. C.-H. Delogne, original material present in the Van Heurck collection (**BR**). A typical specimen from the lectotype slide is illustrated in Fig. 12.
Comment: The intended lectotype in Moser & al. (1998) does not refer to original material and cannot be considered without formal conservation.
PhycoBank registration (of lectotypification): http://phycobank.org/103397
Synonym: *Diadesmis contenta* (Grunow in Van Heurck) D.G.Mann in Round & al. 1990
Description: Frustules in girdle view rectangular, solitary or in loose aggregates. Valves linear with distinctly inflated central part. Apices weakly inflated, broadly rounded. Valve dimensions (n=25): valve length 10–16 µm, valve width 3.0 µm. Axial area wide, linear. Central area formed by widening of the axial area, bordered by shortened, almost rounded, central striae. Presence of a fascia at present not observed. Raphe short, straight, filiform. Central raphe endings simple to very weakly inflated, straight. Terminal raphe fissures absent, terminal endings simple to very weakly inflated. Shallow markings present next to central and, occasionally also, terminal raphe endings. Striae composed of one transapically elongated areola, 35–40 in 10 µm, discernible in LM. Areolae in the central area rounded. Internally, central nodule clearly raised. Mantle striae composed of one, slit-like areola, shortly interrupted at the apices. Girdle composed of several open, perforated bands.

Grunow (in Van Heurck 1880, 1883, 1885) intended to differentiate two taxa taxonomically but failed because the protologues included only a figure and a name. All taxonomical treatments link back to his initial publication from 1880. This is an example where it is difficult to harmonise taxonomy and nomenclature. The taxonomic history since was characterised by uncertainties, and,

extremely confused with regard to name usage. Our proposed treatment resolves the nomenclatural-taxonomical problems. However, identifications and occurrence data for *Humidophila contenta* should always be accompanied by a reference to the taxonomic treatment used.

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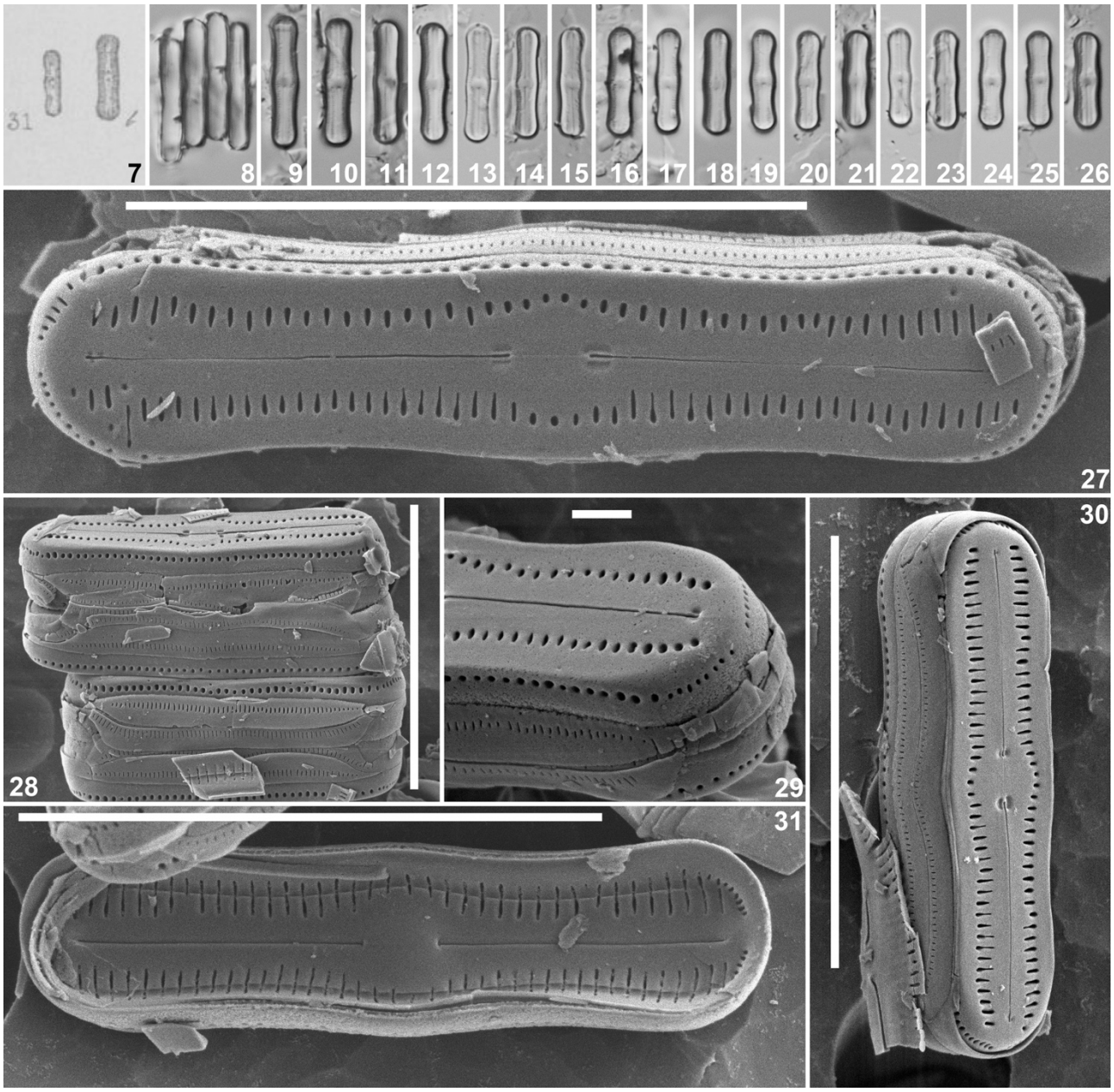
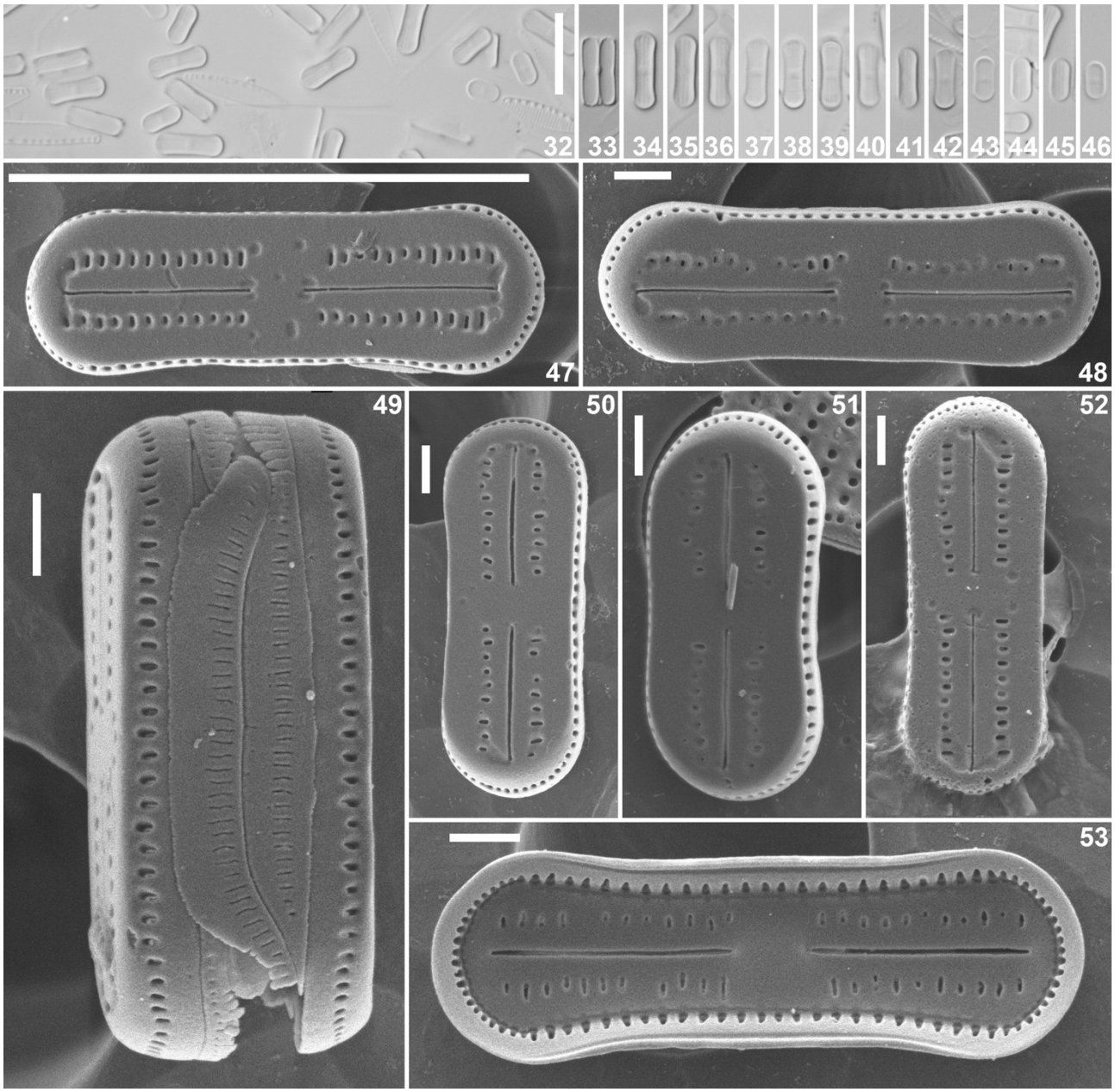
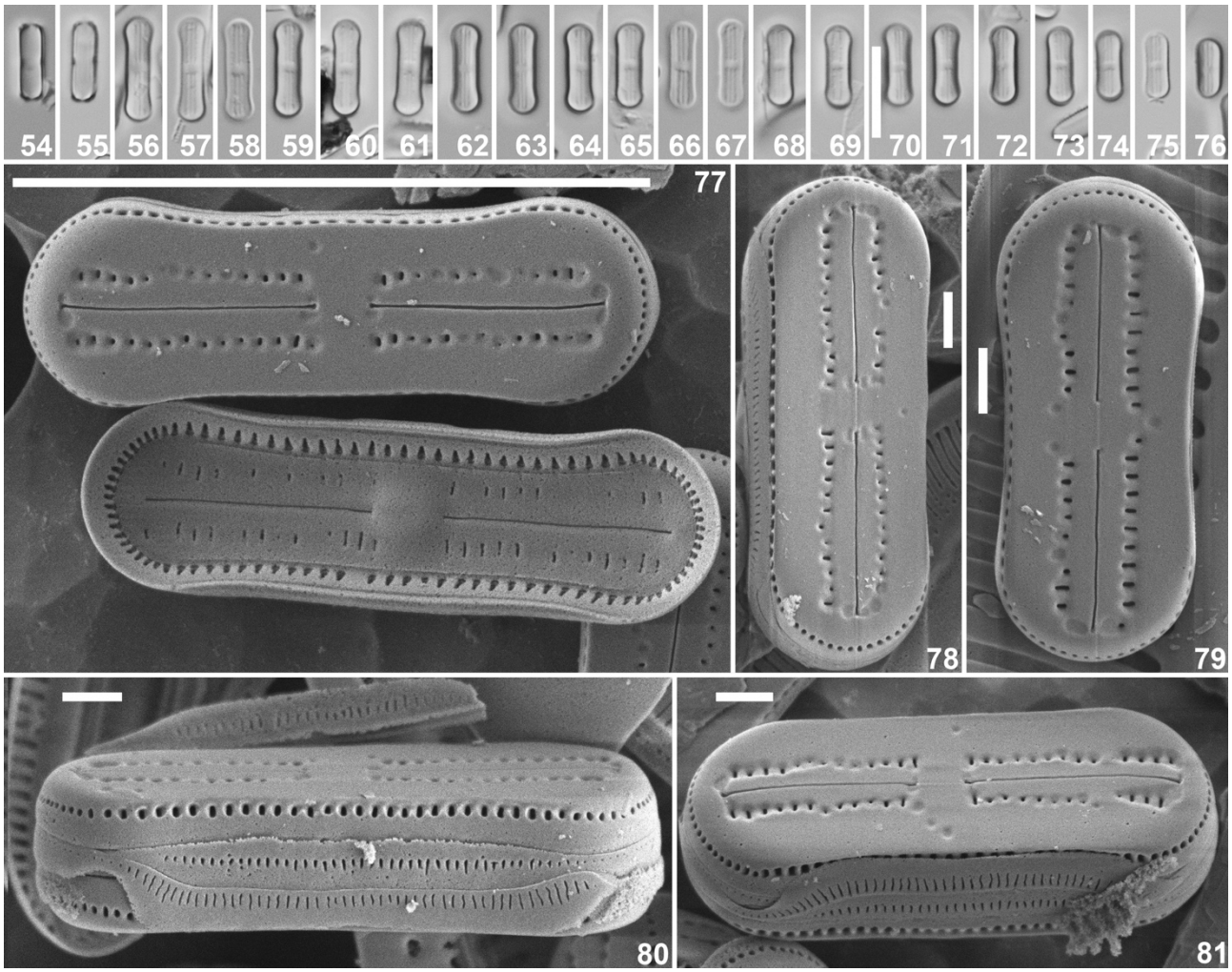


Figs 7–31. *Humidophila contenta* (Grunow) R.L.Lowe & al. LM and SEM pictures taken from the lectotype material (**BR** V-12-C7, Ardoisière de Hour, Rochehaut, Belgium, Delogne sample 97). **Fig. 7**. Original drawing taken from Van Heurck (1880, plate XIV, fig. 31). **Fig. 8.** Several frustules aggregated in girdle view. **Figs 9–26**. LM pictures of valves in decreasing length series. **Fig. 27**. SEM external view of an entire valve. Note the small central area and the gibbous valve center. **Fig. 28**. SEM girdle view of two superposing frustules. Note the open, perforated copulae. **Fig. 29**. SEM external view of the valve apex showing the interruption in the mantle areolae at the apex, the short areolae and the small, irregular markings next to the short terminal raphe fissures. **Fig. 30**. SEM external view of an entire frustule. **Fig. 31**. SEM internal view of an entire valve. Scale bars = 10 µm except for Fig. 29 where scale bar = 1 µm.



Figs 32–53. *Humidophila simplex* (E.Reichardt) R.L.Lowe & al. LM and SEM pictures taken from Delogne slide **BR** VII-19-C2, Groenendael, Belgium (leg. C.-H. Delogne) and **BR** Van Heurck Types du Synopsis sample 146, Groenendael, Belgium. **Fig. 32**. Overview picture showing the large population in the slide. **Fig. 33.** Two connected frustules in girdle view. **Figs 34–46**. LM pictures of valves in decreasing length series. **Figs 47–48, 50–52**. SEM external views of an entire valve. Note the large fascia in the central area and the straight to weakly concave valve outline. Note the continuous series of smaller mantle areolae at the apices. **Fig. 49**. SEM external view of an entire frustule. **Fig. 43**. SEM internal view of an entire valve. Scale bars = 10 µm except for Figs 48–53 where scale bar = 1 µm.



Figs 54–81. *Humidophila simplex* (E.Reichardt) R.L.Lowe & al. LM and SEM pictures taken from Walker Arnott sample 843 (Cliff Lane Bridge, Warrington, UK). **Figs 54–55**. Two frustules in girdle view. **Figs 56–76**. LM pictures of valves in decreasing length series. Fig. 77. SEM external and internal view of an entire valve. Note the continuous series of mantle areolae at the apices and the clear fascia. **Figs 78–79**. SEM external views of an entire valve. Note the large fascia in the central area and the straight to weakly concave valve outline. Note the continuous series of smaller mantle areolae at the apices. **Figs 80–81**. SEM external views of an entire frustule. Scale bars = 10 µm except for Figs 78–81 where scale bar = 1 µm.