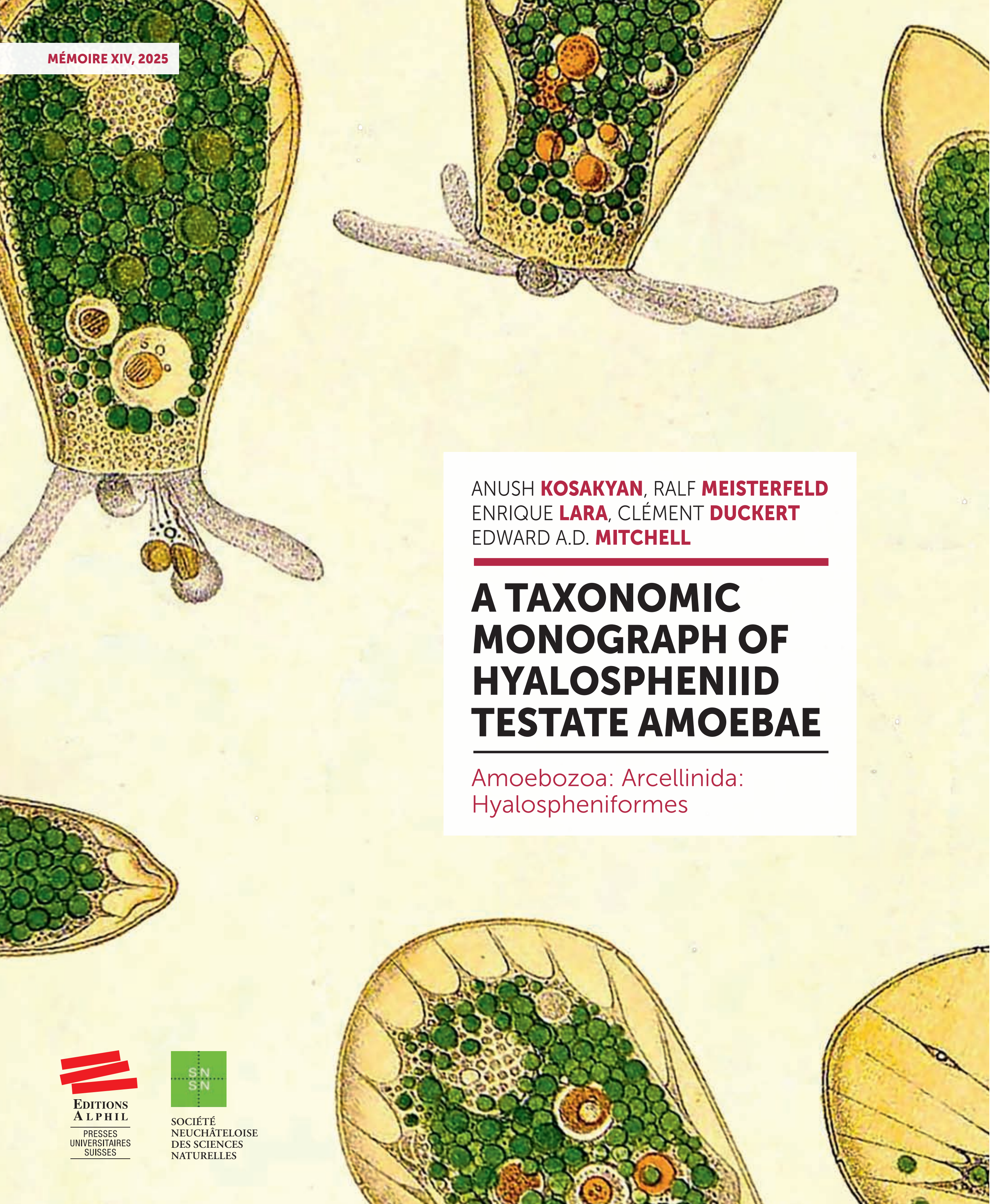

MÉMOIRE XIV, 2025

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Amoebozoa: Arcellinida: Hyalospheniformes

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A taxonomic monograph of hyalospheniid testate amoebae (Amoebozoa: Arcellinida: Hyalospheniformes)

Mémoire tome xiv, 2025

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A TAXONOMIC MONOGRAPH OF HYALOSPHENIID TESTATE AMOEBAE (AMOEBOZOA: ARCELLINIDA: HYALOSPHENIFORMES)

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Cover image : *Hyalosphenia papilio*, modified from Josef Leidy's 1879 Monograph *Fresh-water Rhizopods of North America*. Pictorial Press Ltd / Alamy Stock Photo

“*No other lobose rhizopod has more impressed me with its beauty than this one.*
From its delicacy and transparency, its bright color and form,
as it moves among the leaves of sphagnum*, desmids, and diatoms,*
I have associated it with the idea of a butterfly hovering among flowers.”

Joseph Leidy, 1879 writing about *Hyalosphenia papilio*.

ABSTRACT

In this monograph, we present a taxonomic revision of the infraorder Hyalospheniformes (Amoebozoa, Arcellinida). We recognize one family, 14 genera, and 97 species and infraspecific taxa. The monograph includes taxonomic keys; taxon descriptions; ecological, geographical, and taxonomical notes; annotated lists of dubious and *incertae sedis* species; a list of possible synonymous names; notes on molecular data; and detailed plates containing light and scanning electron microscopic pictures; and/or original line drawings for each species.

The following taxa are moved to Arcellinida incertae sedis: *Argynnia* Vucetich, 1974; *Geamphorella* Bonnet, 1959; *Jungia* Loeblich & Tappan, 1961; *Lamtoquadrula* Bonnet, 1974; *Leptochlamys* West, 1901; *Maghrebia* Gauthier-Lièvre & Thomas, 1960; *Pentagonia* Gauthier-Lièvre & Thomas, 1960; *Physochila* Jung, 1942; *Pontigulasia* Rhumbler, 1896; *Pseudawerintzewia* Bonnet 1959; *Schoenbornia* Decloitre, 1964; *Schwabia* Jung, 1942 and *Sexangularia* Awerintzew, 1906.

Family Padaungiellidae Luketa, 2015 is not recognized here, as we consider such an action premature.

This book is designed to benefit protistologists in general, and particularly ecologists and palaeoecologists, by assisting with the ease and accuracy of identification of hyalospheniid testate amoeba species, many of which are useful bioindicators. It will hopefully also serve as a useful basis for future work regarding the taxonomy, biogeography, and ecology of these organisms.

Supplementary keywords: testate amoebae; taxonomic revision; systematics; evolution

1. FOREWORD

The microbial world is unknown to most people, or rather they know it exists, but they have no connection to it. However, when we show a living testate amoeba or other microbial life under the microscope to people, many are fascinated. And for quite a few students, there is a magical moment when they suddenly know that this is what they want to study. The above-cited quote of Leidy illustrates this very well. To many protistologists, work is more than just work. We have passion for the organisms we study. We admire their beauty. We can see them hundreds of times and we are never bored. Somehow, we relate to them emotionally. We feel privileged to being able to live this life of passion. There are always open questions we want to study, no limit to our curiosity. Leidy expressed this very well "How could life be boring when there are still rhizopods to describe?". Beyond the cold scientific facts, this monograph is a way for us to share this passion, in the hope that it will be contagious…

2. INTRODUCTION

Quantifying global biodiversity is an age old, but unresolved question in biology. This holds particularly true for historically understudied organisms, such as protists, where the number of described species represents a small fraction of the true diversity. Indeed, the recent accumulation of new data based on modern morphological and molecular tools (e.g., high throughput sequencing of environmental DNA) has revealed just how incomplete our current knowledge of protist diversity is, indicating a great need for taxonomic revision of many taxa (FOISSNER, 1999a; ADL et al., 2007; PAWLOWSKI et al., 2012).

Traditional taxonomy was based on morphology alone, yet many descriptions date from a time when microscopic optical resolution was significantly lower than that in the present (e.g., prior to the development of oil immersion lenses), and contrast-enhancing options (e.g., phase contrast and differential interference contrast) did not exist. Furthermore, original descriptions are often either difficult to find, published in different languages, and/or lacking illustrations or proper morphometric data.

Studies combining molecular and morphological approaches are now shedding new light on the true diversity of many protist groups. Indeed, our vision of understanding of true diversity can be expanded by combining a barcoding approach with a careful morphological study. This has been demonstrated in several groups, including euglyphid testate amoebae (WYLEZICH et al., 2002; HEGER et al., 2010; CHATELAIN et al., 2013; GONZÁLEZ-MIGUÉNS et al., 2022), diatoms (KOOISTRA et al., 2010; MANN & VANORMELINGEN, 2013), radiolarians (AMARAL ZETTLER, 1998; DECELLE et al., 2012; BIARD et al., 2015), foraminiferans (MORARD et al., 2011), dinoflagellates (GOTTSCHLING et al., 2012), and chrysophytes (SCOBLE & CAVALIER SMITH, 2014).

The family Hyalospheniidae (Arcellinida, Amoebozoa) includes some of the most common, yet remarkable and well-studied species of testate amoebae. The first hyalospheniid testate amoeba was described by EHRENBERG (1848): *Difflugia collaris*, later renamed *Nebela collaris*. Hyalospheniids are widely used as bioindicators in palaeoecological studies and environmental monitoring (MITCHELL et al., 2008) and are a flagship group for studying protist biogeography (WILKINSON, 2001; FOISSNER, 2006; FOISSNER et al., 2008; SMITH et al., 2008). Mixotrophic hyalospheniid species (e.g., *Hyalosphenia papilio*) may even play a significant role in carbon sequestration at the global scale (JASSEY et al., 2015).

Despite the growing interest for Hyalospheniidae, current knowledge regarding their diversity, biology, taxonomy, and systematics remains limited. For most members of the family, existing data are in part unreliable or incoherent and confusing, making it difficult for most researchers' access to relevant information. We evaluated that 64% of the names (173 of 270) are *nomina nuda*, synonymous, dubious, or with uncertain position.

The most recent taxonomic monographs of this family date back to the mid-20th century (e.g., DEFLANDRE, 1936; GROSPIETSCH, 1965; CHARDEZ, 1967). Since then, three taxonomic reviews on all testate amoebae, including Hyalospheniidae, were published: a book chapter (MEISTERFELD, 2002) and an entire book with descriptions at species level (MAZEI & TSYGANOV, 2006) and a book with descriptions and keys to genus level (TSYGANOV et al. 2016). However, neither of the first two works included the results of barcoding and molecular phylogeny results. Furthermore, the first included only a selection of taxa, and the second was published in Russian, a language inaccessible to much of the scientific community, and the third was limited to the genus level.

Our goal here is to provide an up-to-date treatment of the taxonomy of family Hyalospheniidae (Amoebozoa, Arcellinida, Hyalospheniformes), combining all known data about the phylogeny, taxonomy and systematic of these organisms. We hope this monograph will be useful to all those interested in protist diversity (e.g., taxonomists, ecologists, and palaeoecologists), and will stimulate similar efforts across other groups making testate amoeba (and protist in general) species identification easier and more accurate.

3. SPECIES CONCEPT AND TAXONOMIC ACTIONS

3.1. Species concept

Our approach to the species concept is a compromise since molecular data are available only for a fraction of the species. In most cases, we follow the morphological species concept. The phylogenetic species concept is also applied when molecular data are available in addition to morphology (e.g., *Nebela tincta-collaris* complex). When only molecular data were available without any supporting morphometric studies (e.g., *Hyalosphenia papilio*), we simply indicated the number of phylotypes, strongly suggesting the existence of more species.

All species concepts are based on the existence of characteristics that make species a discrete and identifiable evolutionary entity. When isolated, species' populations can diverge, ultimately creating new species. During this process, one expects to see distinct populations representing "species in the process of formation". Taxonomists commonly describe these as different trinomial units, which can be divided into two major categories: subspecies and infra-subspecific taxa. Subspecies are commonly accepted as being a geographically or reproductively isolated race or population of a polytypic species; whereas, infra-subspecific representatives of a species are units based on variations occurring in individuals or groups and notably not necessarily confined to a single population. Infra-subspecific units can be caused by either genetic or environmental conditions. The treatments of these taxa are described below.

In this monograph, the rules of the International Code of Zoological Nomenclature (ICZN) have been followed; thus, we have separated binomial "species" (e.g., *Nebela tincta*) from trinomial "subspecies" (e.g., *Hyalosphenia papilio stenostoma*). We have further separated species names into five distinct categories:

1) Valid names with certain taxonomic positions: This category, however, includes several (10) problematic species which require further morphological and/or molecular data to fully confirm or refute their validity and/or position within a given group.
2) *Incertae sedis* names: Although we consider these 12 species, plus one species complex, as valid, their morphological characters correspond to more than one genus, and their taxonomic position is therefore unclear. Common and/or well-known incertae sedis species (e.g., *Nebela barbata*) were included

in the identification keys to facilitate the identification process. The list and notes to incertae sedis species can be found on p. 193

3) *Inquirenda* names: Species with doubtful identities, or when original species descriptions are insufficiently detailed or inaccurate. A list can be found on p. 209
4) Invalid (*nomen nudum*) or excluded names: A comprehensive list can be found on p. 229.
5) Varieties and forms described after 1960 were treated as infrasubspecific taxa (International Committee on Zoological Nomenclature—ICZN 45.6.3) and thus unavailable, and listed together with synonymous names. Varieties and forms described before 1961, and which were neither expressly given infrasubspecific rank by the authors nor subsequently adopted as valid species before 1985, were treated as subspecies. The key from LINGAFELTER & NEARNS (2013) was used for the most difficult cases.

3.2. Taxonomic actions

Numerous taxonomic actions were undertaken, including synonymizing, suggesting new combinations, providing descriptions for new taxa, defining types, type localities, or expanding/changing the taxonomic concept of species, genera, and the Hyalospheniidae family. Ultimately, the aim was to make future taxonomic work on this group easier by providing a curated list of taxa, illustrations, and identification keys.

The several taxa described as varieties after 1960 were deemed invalid under ICZN Art. 10.2. Here, for cases where we have validated these taxa as species, we can become the authority.

Another important action taken here was the neotypification of the majority of the taxa. Following recent molecular works on Hyalospheniformes, it became clear that the taxa described without using modern tools (e.g., high-resolution microscopy and DNA barcoding) were likely to represent a complex of closely related but distinct species that can often be differentiated only by small morphological differences (see KOSAKYAN et al. 2013 for *Nebela* and KOSAKYAN et al. 2016 for *Quadrulella*). This has one major practical impact: testate amoeba species should be represented using high-resolution microphotographs, as low-resolution pictures or drawings might not allow a clear distinction between closely related species, most of which could yet to be described. As most taxa were described prior to the existence of microphotography, the taxonomic identity of these "older species" is often unclear, and poses problems for the stability of nomenclature (see *Alabasta militaris*, where prevailing usage was at stake). As updating original descriptions based on the reinspection of the type material is often impossible owing to the generalized absence of Type specimen for older species, this remains one of the biggest issues for testate amoeba taxonomy, as also discussed in LARA et al. (2020).

The ICZN's position on neotypification is that it must be done only "when there is an exceptional need" for a neotype (Art. 75.3), and when "no name-bearing type specimen is believed to be extant, and an author considers that a name-bearing type is necessary to define the nominal taxon objectively" (Art. 75.1). Thus, to ensure that species can be reliably identified, and maintain the prevailing usage of their names, we have designated neotypes for older species that were re-characterized here using modern tools. ICZN Art. 75.3.4 requires that the designation of a neotype be justified by explaining "the reasons for believing the name-bearing type specimen(s) to be lost or destroyed, and the steps that had been taken to trace it or them". We assert here that no permanent materials which could be considered as the name-bearing type were found in either museum or private collections for any of the following designated neotype species; however, in the interest of space, we will not develop such further justifications for each step taken. As none of the original publications in which the neotypified species were originally described contained any indication of permanent materials, it is most likely that the type material was never preserved or was lost later on.

4. PRESENTATION OF THE TAXA

4.1. Iconography and Type specimen

Here, we present illustrations either taken from, or fitting the original descriptions, as well as any other relevant pictures available illustrating morphological details or other aspects (e.g., high-quality light microscopy and scanning electron microscopy images). Pictures of DNA-barcoded individuals were used whenever possible.

For most species described prior to 1999, the original drawings are considered as the type specimen (ICZN Art. 72.3). There are exceptions, however, where the preserved materials for a few species were isolated by Eugène Penard, and mounted on permanent slides deposited at the Natural History Museum of Geneva, Switzerland. We compared these slide images with the original descriptions and drawings of those species, and when the matches were exact, and the type localities were similar, we declared these slides as the type specimen; however, by doing so, we have inherently taken the risk of declaring neotype specimen that do not correspond to the same taxon as those observed by the original author. Pictures of the entire Penard's slide collection are available at: https://commons.wikimedia.org/wiki/Category:Testate_amoebae

4.2. Descriptions

Species descriptions are provided here either as direct quotes from the original publications, or as more general adaptations/translation to ensure a common style throughout the text. General dimensions are given as length, breadth in broad view (i.e., long axis), and pseudostome (i.e., test aperture) width in broad view, as these measurements are most easily recorded under routine light microscopy analysis (Fig. 1). The morphometrical data presented were derived from minimum and maximum measurements in the literature at hand. In cases where the provided measurements are based on our, or an individual author's observations, this clarification is mentioned parenthetically.

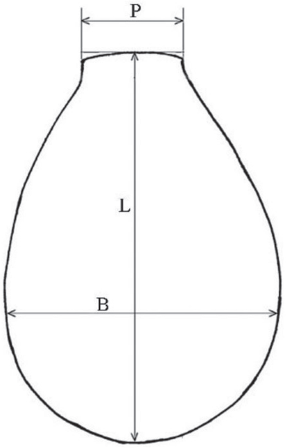

Fig. 1. Broad view sketch of a hyalospheniid test showing the positions of commonly measured dimensions. L: length, B: breadth, P: pseudostome (=aperture) maximum dimension.

4.3. Glossary of main key and diagnosis terminology

The most common hyalospheniid test shapes are illustrated in Fig. 2; however, various intermediate shapes also exist, including: ovoid; oblong ovoid; narrow ovoid; narrow-, broad-, or elongated-piriform; lageniform with short, long, or swollen neck; etc. Another term frequently mentioned in the species descriptions is the fundus, representing the aboral end of the test. When describing the shape of the test we used two terms: shape in broad and profile views (e.g., test piriform in broad view, compressed; elongated-piriform in profile view). Other morphological characteristics of the test are illustrated in Fig. 3. In addition to the test shapes, an often used, but commonly misspelled term in the

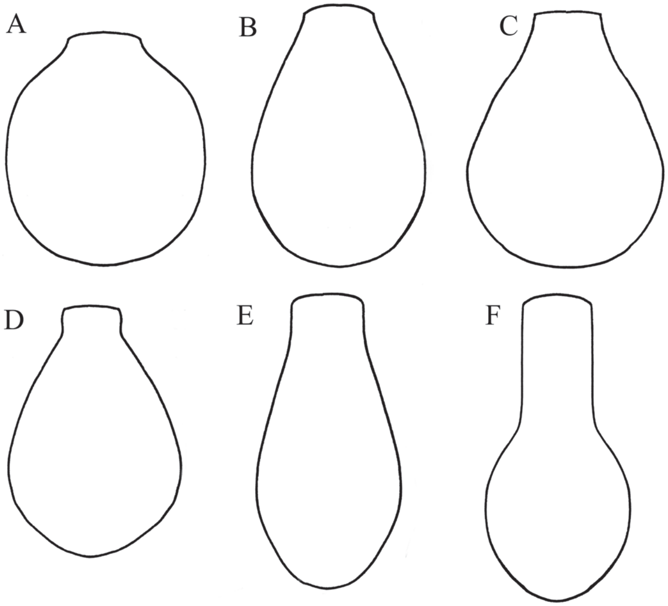

Fig. 2. Schematic outlines of the most common hyalospheniid test shapes: (A) Circular, (B) Piriform or pear-shaped, (C) Ovoid-piriform, (D) Drop-shaped, (E) Elongated-piriform, and (F) Lageniform or flask-shaped.

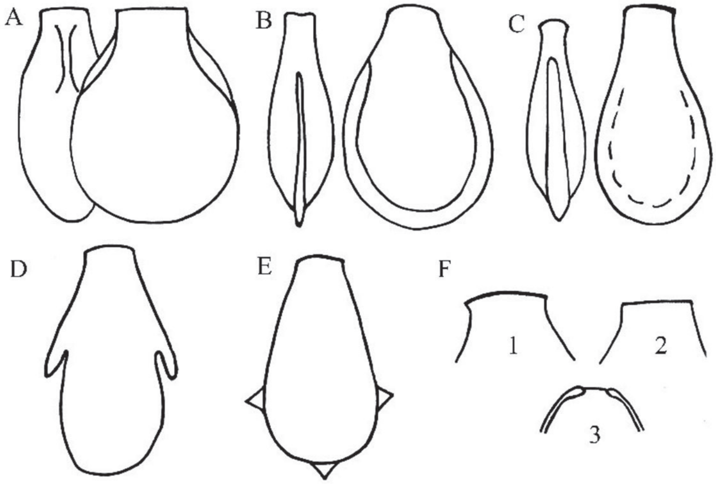

Fig. 3. Sketches of various morphological characteristics of hyalospheniid tests: (A) Test with a partial keel (profile and broad views), (B) Test with a complete lateral flat keel (profile and broad views), (C) Test with a complete lateral hollow keel (profile and broad views), (D) Test with two lateral hollow tubular protuberances—i.e., "horns" (broad view), (E) Test with conical protuberances. (F) Examples of pseudostomes: (1) curved, (2) linear, and (3) thickened inwards.

descriptions and discussions is "hyalospheniid" or "hyalosphenid testate amoebae". Although both versions can be found in the literature, we would like to state here that the correct term is the two "i" "hyalospheniid", in accordance with ICZN Art. 29.3, where "hyalospheni" is the stem of the name, and "id" is the suffix.

4.4. Abbreviations

The following abbreviations are used throughout the text: ***B***, breadth; ***L***, length; ***L/B***, length/breadth ratio; ***P***, pseudostome (aperture) major axis (i.e., width in broad view); ***LM***, light microscopy; ***SEM***, scanning electron microscopy.

4.5. Type locality, habitat, and geographical distribution

A general list of the type localities and habitats where each species was found is provided here. Although type localities and coordinates have been presented to the best of our ability, this information was limited for some species. Full details of the terra typica are given only for rare species. For more common and widespread species, the general distribution is presented as a list of regions and countries with a selection of corresponding references; however, for the majority of doubtful and problematic taxa, the true geographical distributions are likely uncertain, as these taxa have not been identified in many ecological studies.

The likely general distribution is suggested based on the following list of continents and geographical regions: **Africa**, **Europe** (including Iceland), **Asia**, **Australasia** (Australasian realm including New Guinea, Melanesia and Zealandia), **North America** (including Greenland), **Central America** (including the Caribbean), **South America**, **Indian Ocean**, **Pacific Ocean**, **Atlantic Ocean**, and **Antarctica** (including the peri-Antarctic islands south of the Antarctic convergence). Africa, Australia, South America, in addition to the Indian, Pacific, and Atlantic Oceans include islands north of the Antarctic convergence (as classified according to Wikipedia[1]), including: The Falkland/Malvinas Islands, Tristan da Cunha, Gough Island, Prince Edward Islands, Crozet Islands, Amsterdam Island, Saint-Paul Island, Macquarie Island, Campbell Island group, Auckland Islands, Snares Islands / Tini Heke', Bounty Islands, Antipodes Islands, Diego Ramírez Islands, Tierra del Fuego, and Isla de los Estados (i.e., Staten Island). The Kerguelen Island archipelago lies approximately on the Convergence and is thus included here within Antarctica. The South Shetland, South Orkney, South Georgia and the South Sandwich, Bouvet, Heard and McDonald, Balleny, Scott, and Peter I Islands all lie south of the Antarctic Convergence.

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[1] http://en.wikipedia.org/wiki/Antarctic_Convergence, accessed on 10/13/2015

5. HISTORICAL SURVEY OF INFRAORDER HYALOSPHENIFORMES

The classification of hyalospheniid testate amoebae has varied over time depending on the taxonomically relevant morphological traits considered:

LEIDY (1874a) was likely the first to notice the common characters between cells having a vase shaped test composed of "*discoid plates and minute rods, apparently siliceous and intrinsic to the structure of the animal*". Species were grouped according to these characters within the genus *Nebela*, differentiating them from the genus *Difflugia* Leclerc (1815), defined as "*those rhizopods with lobose pseudopods, which ordinarily possess a covering or test composed of extraneous bodies, such as particles of quartzose sand, and diatom cases*" (LEIDY, 1874a).

SCHULZE (1877) defined four testate amoeba families: Arcellidae, Difflugidae, Hyalospheniidae, and Quadrulidae. He placed genera according to an organic homogenous test, including: *Hyalosphenia* Stein, 1857 in the family Hyalospheniidae; genus *Nebela* Leidy, 1874 in the family Difflugidae; and genera with quadratic plates, such as *Quadrula* Schulze, 1875 (i.e., *Quadrulella* Cockerell, 1909 – became the replacement name for *Quadrula*) in the family Quadrulidae.

Based on the presence of siliceous plates, TARÁNEK (1882) first defined family Nebelidae by grouping genera *Nebela*; *Lesquereusia* Schlumberger, 1845; *Corythion* Taránek, 1881; and *Quadrula* (*Quadrulella*). Later, genus *Corythion* Taránek, 1881 was excluded, whereas the following genera were included: *Amphizonella* Greef, 1866; *Cochliopodium* Hertwig & Lesser, 1874; *Hyalosphenia* Stein, 1857; *Leptochlamys* West, 1901; and *Zonomyxa* (*Nusslin*) Taránek, 1882.

In 1942 Jung redefined the family Nebelidae and divided it into 13 genera: *Alocodera*, *Apodera*, *Argynnia*, *Deflandria*, *Nebela*, *Leidyella*, *Physochila*, *Porosia*, *Pterygia*, *Penardiella*, *Quadrulella*, *Schaudinnia* and *Umbonaria*. Unfortunately, Jung's classification lacked type designations; thus, all genera containing more than one species but lacking type designation were deemed invalid (ICZN Art. 13.3). Of the 13 new genera, only the three (then monospecific)—*Alocodera*, *Physochila*, and *Porosia*—were considered valid, while all other species were placed back within genus *Nebela*. LOEBLICH & TAPPAN (1961) subsequently validated *Apodera* and *Certesella* by selecting *A. vas* and

C. martiali as type species, and VUCETICH (1974) validated *Argynnia*, taking *A. schwabei* as a type species.

KORGANOVA (1987) described the genus *Apolimia* with *A. rotundistoma* as the type species, and included it within the family Hyalospheniidae based on the observation of its "*Nebela* like test composition such as round to oval plates"; however, the pseudostome is surrounded with oval-circular plates, and lacks the organic collar typical to hyalospheniids. This suggests that *Apolimia* is likely closely related to the genus *Argynnia*; thus, it was never reincluded in the family Hyalospheniidae or Nebelidae by any other author.

ŠTĚPÁNEK (1967) described the genus *Pseudohyalosphenia* with *P. prismatica* as the type species, although it was never included in the family Hyalospheniidae or Nebelidae by any other author. He separated this genus from *Hyalopshenia* based on the test structure built from small hexagonal prisms, as opposed to amorphous organic material. However, as the descriptions of *P. prismatica* and *Hyalosphenia punctata* Penard, 1891 overlap, the two species must be synonymized. As *H. punctata* was described first, this name takes priority (ICZN Art. 23, Principle of priority). The taxonomic position of this taxon however needs to be confirmed by molecular data.

In his review of the family, MEISTERFELD (2002) used only morphological data, as no molecular data existed at the time. He placed *Nebela* and closely related taxa into two families: taxa with rigid, chitinoid, organic, and non-areolar tests (namely *Hyalosphenia* Stein, 1857 and *Leptochlamys* West, 1901) were grouped in family Hyalospheniidae; whereas genera with tests composed of plates from small euglyphids or diatom fragments (*Apodera* Loeblich & Tappan, 1961; *Argynnia* Vucetich, 1974; *Certesella* Loeblich & Tappan, 1961; *Nebela* Leidy, 1874; *Physochila* Jung, 1942; *Porosia* Jung, 1942; *Schoenbornia* Decloitre, 1964) were grouped in family Nebelidae. MEISTERFELD did not include the genus *Quadrulella* Cockerell, 1909 in family Nebelidae, rather accepting OGDEN's (1979) classification of *Quadrulella* Cockerell, 1909 in family Lesquereusiidae Jung, 1942, with other taxa building tests from endogenous (self-secreted) siliceous elements (rod-like, nail-shaped, or rectangular) to which mineral particles may be added (e.g., *Netzelia* Ogden, 1979).

The first molecular studies of family Hyalospheniidae based on sequences of the gene coding for the small subunit of the ribosome (SSU rRNA) and actin, was conducted by NIKOLAEV et al. (2005), followed by a study on SSU rRNA by LARA et al. (2008). According to their research, Nebelidae sensu MEISTERFELD (2002) was paraphyletic, as *Argynnia dentistoma* Penard, 1890 appeared only distantly related to members of genus *Nebela* Leidy, 1874. A later study showed that genus *Physochila* Jung, 1942 did not belong to Hyalospheniidae either (GOMAA et al., 2012). Members of genera *Apodera* (JUNG, 1942); *Hyalosphenia* Stein, 1859; *Nebela* Leidy, 1874; and *Porosia* Jung, 1942 were intermingled in a robustly supported clade, informally called "core Nebelas". LARA et al. (2008) could not clearly show the phylogenetic relationships among members of the core Nebelas or other closely related taxa owing to a combination of under-sampling and the difficulty of discriminating closely related species based on the slow evolving SSU rRNA gene.

KOSAKYAN et al. (2012) studied the most common core Nebela species, using the more variable mitochondrial cytochrome oxidase subunit 1 (mt-COI) gene than the SSU rRNA gene. The study showed that: 1) genus *Nebela* is paraphyletic and can be split into two sub-clades: i) pear-shaped *Nebela* species—*N. carinata* (Archer, 1867), *N. tubulosa* Penard, 1902, *N. collaris* (Ehrenberg, 1848) sensu Kosakyan & Gomaa, 2012, and ii) the newly defined genus

Padaungiella Lara & Todorov, 2012, combining the "long necked" *Nebela* species, such as, *Padaungiella* (*Nebela*) *lageniformis* (Penard, 1890), *P. wailesi* (Deflandre, 1936), and *P. tubulata* (Brown, 1911). 2) Genus *Quadrulella*, one of the few arcellinid genera building its tests from self-secreted siliceous elements, and the mixotrophic *Hyalosphenia papilio* Leidy, 1879 branch together within the *Nebela* group, in agreement with: i) the general morphology of their test shape rather than composition, and ii) the presence of an organic collar around the pseudostome. The phylogenetic reconstruction showed that the genera *Argynnia* and *Physochila* formerly placed within Hyalospheniidae (MEISTERFELD, 2002) did not belong to this family. Interestingly, both these and subsequent molecular data have generally confirmed JUNG's (1942) treatment.

Although the organic collar around the pseudostome is generally considered as a synapomorphy for Hyalospheniidae, this criterion may not represent an absolute synapomorphy for the family. Indeed, in this monograph we discuss several exceptions, which mostly correspond to poorly studied taxa, some of which may prove not to belong to this family. However, several taxa which in other respect quite convincingly belong to this family also lack this feature.

Another study based on the SSU gene and including several common hyalospheniids— *Hyalosphenia* elegans Leidy, 1879, *H. papilio* Leidy, 1879, *Planocarina* (*Nebela*) *carinata* (Archer, 1867) Leidy, 1879, *Nebela flabellulum* Leidy, 1874, *Alabasta (Nebela) militaris* Penard, 1890, *Nebela tincta* s.l., *Longinebela (Nebela) tubulosa* Penard, 1902, and *Quadrulella symmetrica* s.l.— was published by OLIVERIO et al. (2014). Their results quite puzzlingly suggested that genera *Hyalosphenia* and *Nebela*, in addition to morphospecies *H. papilio* and *H. elegans*, were not monophyletic. A possible explanation for their derived pattern is the existence of paralogs for the SSU rRNA gene; however, no other study has supported these findings. Accordingly, such results illustrate the need for additional molecular studies to better understand the phylogenetic relationship among Hyalospheniidae members.

A few molecular based studies have focused in greater detail on individual Hyalospheniid testate amoeba genera or species complexes, including: the *Nebela collaris s.l.* (KOSAKYAN et al., 2013; SINGER et al., 2015), *Hyalosphenia papilio s.l.* (HEGER et al., 2013; SINGER et al., 2019), and *Quadrulella symmetrica s.l.* groups (KOSAKYAN et al., 2016).

Families Hyalospheniidae and Nebelidae were originally described by SCHULZE (1877) and TARÁNEK (1882), respectively. According to their most recent revision (MEISTERFELD, 2002), the Nebelidae included genera with tests composed either of collected or predated circular or oval siliceous plates, fragments of diatoms, or mineral grains, including: *Alocodera* Jung, 1942; *Apodera* Loeblich & Tappan, 1961; *Argynnia* Vucetich, 1974; *Certesella* Loeblich & Tappan, 1961; *Geamphorella* Bonnet, 1959; *Jungia* Van Oye, 1949; *Nebela* Leidy, 1874; *Physochila* Jung, 1942; *Pseudonebela* Gauthier-Lièvre, 1953; *Porosia* Jung, 1942; and *Schoenbornia* Decloitre, 1964. Among these, MEISTERFELD (2002) considered genera *Geamphorella*, Jungia, *Pseudonebela* as *incertae sedis* and *Schoenbornia* as *sedis mutabilis*, despite their inclusion in the family key. Alternatively, the family Hyalospheniidae included genera with chitinoid, clear, completely organic, non-areolar tests, such as *Hyalosphenia* Stein, 1857 and *Leptochlamys* West, 1901. Considering that the molecular data unambiguously showed genus *Hyalosphenia* branching within the "core Nebelas" clade, and that the distinguishing characters of Hyalospheniidae (test transparent and entirely secreted) can also be found in some Nebelidae (e.g., *Alocodera* Jung, 1942), the two families were synonymized. The name Hyalospheniidae Schulze, 1877 takes precedence according to the principle of priority

(Art. 23 ICZN, as cited in KOSAKYAN et al., 2012).

LUKETA (2015a) described the family Padaungiellidae—including genera *Alocodera* Jung, 1942; *Apodera* Loeblich & Tappan, 1981; and *Padaungiella* Lara & Todorov, 2012—using *Padaungiella lageniformis* (Penard, 1890) as the type species. Although this would imply emending family Hyalospheniidae by formally excluding these taxa, this action was not taken by the author, nor there was any morphological synapomorphy to define both families provided; thus, this action was supported solely through the topology of the phylogenetic tree. Although all barcoded Padaungiellidae possess a lageniform shell, this test shape also occurs in Hyalospheniidae sensu Luketa, 2015, notably in genus *Certesella* (KOSAKYAN et al., 2012). Furthermore, many species remain to be barcoded, possibly creating further challenges to the proposed dichotomy. One such example can be found among the South American lageniform *Quadrulella* (*Q. vas*, *Q. lageniformis*, *Q. tubulata*), or by the equally lageniform *Hyalosphenia chardezi* sp. nov. Therefore, we have deemed premature the idea of splitting the Hyalospheniidae into two families and opted to maintain it as a single family until more genetic data are available.

In the latest comprehensive phylogeny of Hyalospheniidae based on mt-COI sequence data, KOSAKYAN et al. (2016) confirmed that the genus *Nebela* is paraphyletic and split it into six monophyletic genera based on the general test shape: *Nebela s.str.*, *Longinebela*, *Planocarina*, *Gibbocarina*, *Cornutheca*, and *Mrabella*. This resulted in a total 13 Hyalospheniidae genera, including: *Alocodera* Jung, 1942, *Apodera* Loeblich & Tappan, 1961, *Certesella* Loeblich & Tappan, 1961, *Hyalosphenia* (Stein, 1957) Schulze, 1877, *Padaungiella* Lara & Todorov, 2012, *Porosia* Jung, 1942, and *Quadrulella* Cockerell, 1909.

Recently, DUCKERT et al. (2018) created a new genus *Alabasta* based on mt-COI sequence data, by combining *Nebela militaris* and its closely related species. The current summary version of the phylogenetic tree is shown in Fig. 4.

The revised diagnosis of family Hyalospheniidae Schulze, 1877 emend. Kosakyan & Lara, 2012 was: "*The test is rigid, colourless or yellowish-brown, flask-vase shaped, oval or piriform, dorso-ventrally compressed. The shell is either entirely self-secreted (e.g.,* Hyalosphenia*) composed of an organic matrix, or reinforced through the inclusion of self-secreted siliceous plates (*Quadrulella*) or recycled shell plates of small euglyphids or other similar material such as diatom frustules incorporated in the test. The pseudostome is terminal and is bordered by a thin organic rim*". It should be noted, however, that several taxa lack a well-developed organic rim around the pseudostome.

As *Physochila* Jung, 1942 and *Argynnia* Vucetich, 1974 neither form a monophyletic clade with the Hyalospheniidae according to the molecular phylogenetic data (LARA et al., 2008, GOMAA et al., 2012), nor do they possess an organic rim around the pseudostome, we excluded these genera from the Hyalospheniidae, opting to transfer them to Arcellinida *incertae sedis*.

Similarly, *Leptochlamys* West, 1901 differs from all other Hyalospheniidae by its unique combination of characters, including: circular test in cross-section, circular pseudostome in frontal view, and possessing a unique hyaline pseudopod (CASH & HOPKINSON, 1909); thus, we therefore considered this genus as Arcellinida *incertae sedis* as well.

Family Lesquereusiidae must be invalidated, as *Quadrulella* was transferred to Hyalospheniidae, and recent molecular data showed that *Netzelia* Ogden, 1979 branched together with *Arcella* within infraorder Sphaerothecina (GOMAA et al., 2012; KOSAKYAN et al., 2016b), while *Lesquereusia* Schlumberger, 1845 branches close to elongated *Difflugia* within

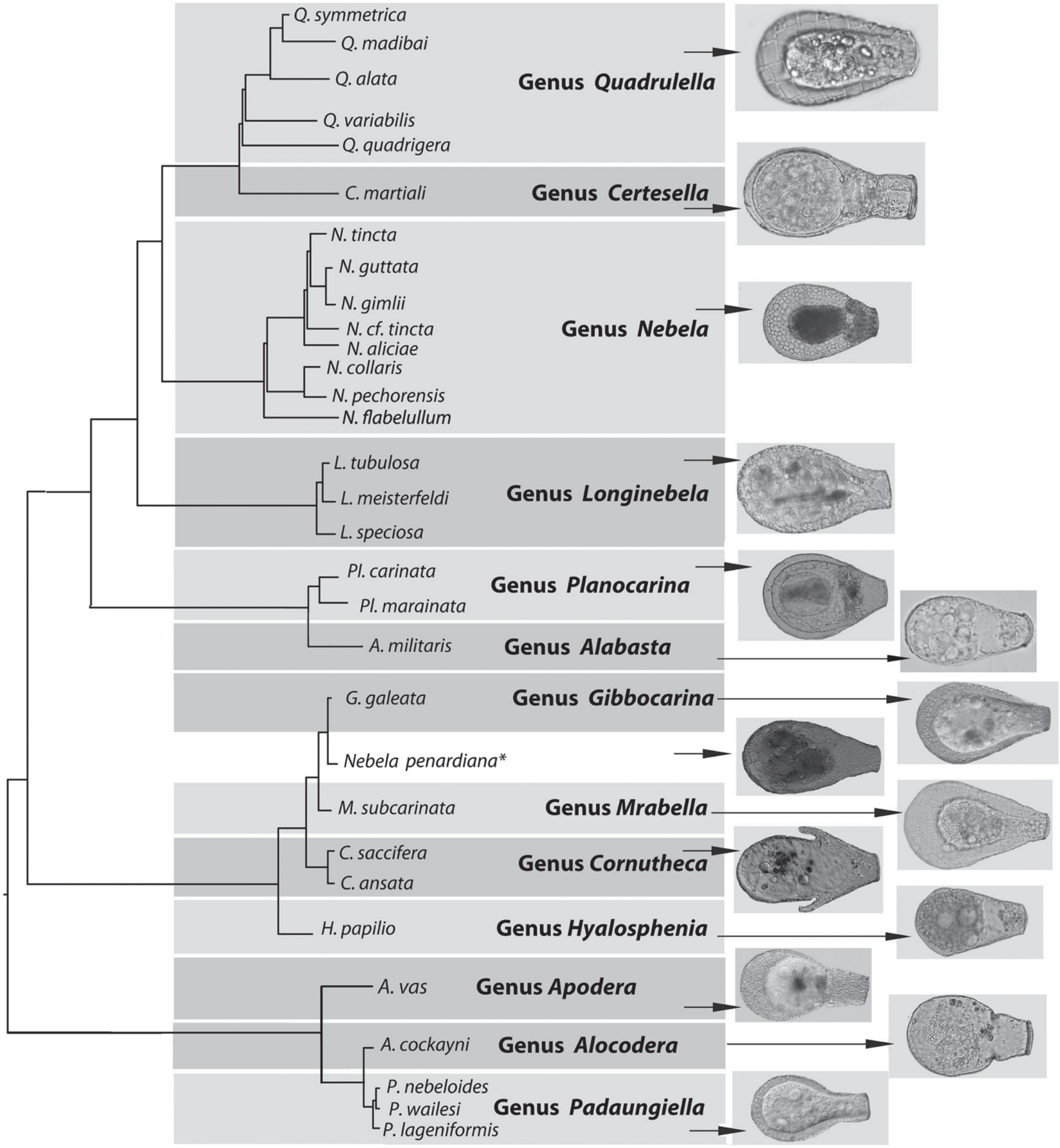

Fig. 4. Schematic phylogenetic tree of Hyalospheniidae based on mt-COI sequence data analysed by maximum likelihood (modified from KOSAKYAN et al., 2016) showing the position of the most common DNA barcoded hyalospheniid taxa. *The phylogenetic/taxonomic position of *Nebela penardiana* remains unclear. The tree topology suggests the possible misidentification or DNA extraction from several species, including one closely related to *Gibbocarina galeata*. See comments on this species for further detail.

infraorder Longithecina (LAHR et al., 2013, 2019), rather than *Netzelia*. Recent molecular data placed *Awerintzewia* Schouteden, 1906 within infraorder Excentrostoma, and *Lagenodifflugia* Medioli & Scott, 1983 together with *Zivkovicia* Ogden,1987 within infraorder Longithecina (RIBEIRO et al., 2023; GONZÁLEZ-MIGUÉNS et al., 2022). The status and phylogenetic position of *Microquadrula* Golemansky, 1968 and the marine supralittoral genus *Pomoriella* Golemansky, 1970 remain unclear, as both taxa currently lack molecular data. These two monospecific genera should therefore be considered as Arcellinida *incertae sedis*; however, based on their morphology alone, they likely belong to Hyalospheniidae or represent sister lineages to the rest of the group.

The most recent phylogenomic study based on transcriptomic data and 250 genes (LAHR et al., 2019), defined infraorder Hyalospheniformes with one family, Hyalospheniidae, and 14 genera: *Alabasta* Duckert, Blandenier, Kosakyan & Singer, 2018; *Alocodera* Jung, 1942; *Apodera* Loeblich & Tappan, 1961; *Certesella* Loeblich & Tappan, 1961; *Cornutheca* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell & Lara, 2016; *Gibbocarina* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell & Lara, 2016; *Hyalosphenia* (Stein, 1857) Schulze, 1877; *Longinebela* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell & Lara, 2016; *Mrabella* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell & Lara, 2016; *Nebela* (Leidy, 1874) sensu Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell & Lara, 2016; *Padaungiella* Lara & Todorov, 2012; *Planocarina* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell & Lara, 2016; *Porosia* Jung, 1942; and *Quadrulella* (Cockerell, 1909) sensu Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell & Lara, 2016. Accordingly, in this monograph, we recognize infraorder Hyalospheniformes with family Hyalospheniidae, including the 14 genera from LAHR et al. (2019).

6. TAXONOMIC COMPOSITION OF THE FAMILY HYALOSPHENIIDAE

Based on a critical investigation of the existing literature, we compiled a total of 270 hyalospheniid names. Of these, we consider 117 as synonymous (including 52 taxa currently do not belong to Hyalospheniidae), 17 (including one complex of five species) as *incertae sedis*, 26 (including one complex of three species) as *inquirenda* (doubtful), 13 as *nomen nudum*, and the remaining 97 as valid names with clear taxonomic positions. All names of species and infraspecific taxa in the monograph are provided in accordance to the ICZN; however, to aid readers' understanding of the taxonomic changes made by different authors, the species list in this section was prepared according to the style of the International Code of Nomenclature for algae, fungi, and plants. Notably, the primary difference is that, for taxa with revised names, in addition to the original author(s) in parentheses (as is the rule in the ICZN), the current authorities are included as well.

Currently, the family is composed of 14 genera and 97 valid species and subspecies (with certain taxonomic position). Ten of these 97 species are problematic species, having valid names but requiring additional morphological and/or molecular data to assess their validity and position within the group. We categorized hyalospheniid genera, species, and subspecies names as follows:

6.1. Valid names (* indicates "problematic species")

(In total 97 species and subspecies taxa)

Genus *Alabasta* Duckert, Blandenier, Kosakyan, & Singer, 2018
(3 species)
A. kivuense (Gauthier-Lièvre & Thomas, 1961) Duckert, Blandenier, Kosakyan, & Singer, 2018
* *A. longicollis* (Penard, 1890) Duckert, Blandenier, Kosakyan, & Singer, 2018
A. militaris (Penard, 1890) Duckert, Blandenier, Kosakyan, & Singer, 2018

Genus *Alocodera* Jung, 1942
(1 species)
A. cockayni (Penard, 1911) Jung, 1942

Genus *Apodera* Loeblich & Tappan, 1961
(4 species)

A. angatakere (Brehm, 1928) Mitchell, Blandenier, & Duckert, 2021
A. crenata (Jung, 1942) Loeblich & Tappan, 1961
A. vas (Certes, 1889) Loeblich & Tappan, 1961
A. wellingtonia (Decloitre, 1964) Loeblich & Tappan, 1961

Genus *Certesella* Loeblich & Tappan, 1961
(5 species)
C. australis (Vucetich, 1973) Loeblich & Tappan, 1961
C. certesi (Certes, 1889) Loeblich & Tappan, 1961
C. larai Bobrov, Duckert, & Mitchell, 2021
C. martiali (Certes, 1889) Loeblich & Tappan, 1961
C. murrayi (Wailes, 1913) Loeblich & Tappan, 1961

Genus *Cornutheca* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
(4 species)
C. ansata (Leidy, 1874) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
C. equicalceus (Leidy, 1874) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
C. jiuhuensis (Qin, Mitchell, & Lara, 2016) comb. nov.
C. saccifera (Wailes, 1913) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Genus *Gibbocarina* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
(2 species)
G. galeata (Penard, 1890) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
G. gracilis (Penard, 1910) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Genus *Hyalosphenia* (Stein, 1857) Schulze, 1877
(21 species and infraspecific taxa)
H. baliki sp. nov.
H. chardezi sp. nov.
H. elegans Leidy, 1874
H. gigantea De Graaf, 1952
* *H. humicola* Decloitre, 1973
* *H. insecta* Harnisch, 1938
* H. irregularis Decloitre, 1965
H. ligata (Tatem, 1870) Leidy, 1875
H. minuta Cash, 1892
* *H. ovalis* Wailes, 1912
H. papilio Leidy, 1874
H. papilio stenostoma Deflandre, 1931
H. penardi Lauterborn, 1908
H. platystoma West, 1903
* *H. punctata* Penard, 1891
* *H. rectangularis* Decloitre, 1965
H. savoiei Chardez, 1978
H. schoutedeni Van Oye, 1926
H. schoutedeni rotundata Van Oye, 1958
H. subflava Cash, 1909
H. tamdaoensis Balík,1995

Genus *Longinebela* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
(5 species)
L. ampulla Todorov, Bankov, & Ganeva, 2018
L. golemanskyi (Todorov, 2010) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
L. meisterfeldi (Heger & Mitchell, 2012) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
L. speciosa (Deflandre, 1936) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
L. tubulosa (Penard, 1890) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Genus *Mrabella* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
(2 species)
M. plicata (Hoogenraad & De Groot, 1940) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
M subcarinata (Gauthier-Lièvre, 1957) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Genus *Nebela* (Leidy 1874) sensu Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
(15 species)
N. acolla Cash, 1909
N. aliciae Mitchell & Lara, 2013
N. carinatella Beyens & Chardez, 1982
N. collaris (Ehrenberg, 1848) sensu Kosakyan & Gomaa, 2012
N. dydevallei Van Oye, 1953
* *N. fagni* Chardez, 1957
N. flabellulum Leidy, 1874
N. gimlii Singer & Lara, 2015
N. guttata Kosakyan & Lara, 2013
N. orbicularis (Deflandre, 1936) comb. nov.
N. pechorensis Kosakyan & Mitchell, 2013
N. pulchra Bartoš, 1938
N. rotunda Penard, 1890
N. subsphaerica Van Oye, 1956
N. tincta (Leidy, 1879) sensu Kosakyan & Lara, 2013

Genus *Padaungiella* Lara & Todorov, 2012
(10 species and infraspecific taxa)
P. americana (Taránek, 1882) comb. nov.
P. cordiformis (Heinis, 1914) comb. nov.
P. kenyana (Chardez, 1982) comb. nov.
* *P. lageniformis* (Penard, 1890) Lara & Todorov, 2012
* *P. longitubulata* (Gauthier-Lièvre, 1953) comb. nov.
P. magna (Van Oye, 1956) comb. nov.
P. nebeloides (Gauthier-Lièvre, 1958) Lara & Todorov, 2012
P. pulcherrima (Awerinzew, 1906) comb. nov.
P. tubulata (Brown, 1911) Lara & Todorov, 2012
P. tubulata spatha (Thomas, 1960) comb. nov.

Genus *Planocarina* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
(5 species)
P. carinata (Archer, 1867) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
P. marginata (Penard, 1902) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
P. maxima (Awerinzew, 1906) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
P. semimarginata (Van Oye, 1949) comb. nov.
P. spumosa (Awerinzew, 1906) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Genus *Porosia* Jung, 1942
(2 species)
P. biggibosa (Penard, 1890) Jung, 1942
P. paracarinata Bobrov & Kosakyan, 2015

Genus *Quadrulella* (Cockerell, 1909) sensu Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
(18 species and infraspecific taxa)
Q. acuminata Van Oye, 1958
Q. alata Gauthier-Lièvre, 1957
Q. camerounensis Gauthier-Lièvre, 1957
Q. constricta Lopretto & Vucetich, 1997
Q. deflandrei Bankov, Todorov, & Ganeva, 2021
Q. elegans Gauthier-Lièvre, 1953
Q. lageniformis Van Oye, 1949
Q. longicollis Taránek, 1882
Q. madibai Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
Q. quadrigera Deflandre, 1936
Q. scutellata Wailes, 1912
Q. symmetrica (Wallich, 1863) sensu Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
Q. symmetrica curvata Wailes, 1912
Q. texcalense Pérez-Juárez, Serrano-Vázquez, & Lara, 2017
Q. tropica Wailes, 1912
Q. tubulata (Gauthier-Lièvre, 1953) Gauthier-Lièvre & Thomas, 1961
Q. variabilis Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016
Q. vas Cerda, 1986

6.2. *Incertae sedis* names

(13 species and infraspecific taxa)
Hyalosphenia nobilis Cash, 1909
Hyalosphenia nobilis compressa Playfair, 1918
Hyalosphenia sinuosa Cash, 1909
Nebela barbata Leidy, 1876
Nebela barbata psilonota Jung, 1942
Nebela bicornis, bipes, triangulata, cornuta complex:
  Nebela bicornis West, 1905
  Nebela bipes (Carter, 1870) Murray, 1905
  Nebela triangulata (Lang, 1865) Cash & Hopkinson, 1909
  Nebela triangulata var. *bicornis* (West, 1905) Cash & Hopkinson, 1909
  Nebela cornuta Voronkoff, 1910
Nebela cylindrica Bonnet, 1979
Nebela penardiana Deflandre, 1936
Nebela penardiana elongata Gauthier-Lièvre, 1957
Nebela penardiana minor Gauthier-Lièvre, 1957
Quadrulella cordobensis Vucetich, 1983
Quadrulella elongata Van Oye, 1956
Quadrulella nunciae Vucetich, 1983

6.3. *Inquirenda* (*nomen dubium*) names

(24 species and infraspecific taxa)
Apodera vas recticollis Jung, 1942
Hyalosphenia angulata Schouteden, 1905
Hyalosphenia inconspicua West, 1903
Hyalosphenia insuetua Štěpánek, 1967
Hyalosphenia lucerna Štěpánek, 1967
Hyalosphenia mraconiae Godeanu, 1972
Hyalosphenia obliqua Decloitre, 1979
Hyalosphenia planctonica (Minkiewicz, 1900) Chardez, 1987
Hyalosphenia schönborni Štěpánek, 1967
Nebela bartosi Haager & Haagerova, 1970
Nebela carinulata Jung, 1942
Nebela deflandrei Decloitre, 1955
Nebela fabrei Certes, 1889
Nebela himalayana Chattopadhyay & Das, 2003
Nebela lageniformis elegans Štěpánek, 1963
Nebela parvula Cash, 1908
Nebela strangularia Decloitre, 1965
Nebela tincta galeata complex:
  Nebela tincta f. *galeata* Jung, 1936
  Nebela collaris var. *galeata* Hoogenraad & De Groot, 1952
  Nebela galeata var. *orbicularis* f. *minor* Tarnogradskij, 1959
Nebela varia Decloitre, 1966
Padaungiella wailesi (Wailes, 1912) Lara & Todorov, 2012
Padaungiella wetekampi (Jung, 1942) Lara & Todorov, 2012
Quadrulella scutellata vas Hoogenraad & De Groot, 1940
Quadrulella symmetrica irregularis Penard, 1911
Quadrulella symmetrica kivuensis Van Oye, 1958

6.4. Non-valid, *nomen nudum*, or excluded names

(13 species and infraspecific taxa)
Hyalosphenia baueri Schönborn, Dorfelt, Foissner, Krienitz, & Schafer, 1999
Hyalosphenia coogeana Playfair,1918
Hyalosphenia jiroveci Štěpánek, 1953
Hyalosphenia triquetra Imhof, 1895
Hyalosphenia turfacea Taránek, 1881
Hyalosphenia undans Coûteaux & Munsch, 1978
Nebela americana var. *falcata* Wailes, 1912
Nebela labiata Tarnogradskij, 1945
Nebela ciliata (mentioned without authority)
Nebela complanata Levander, 1900

Nebela militaris var. *penardina* (mentioned without authority)
Quadrulella symmetrica f. *major* Hoogenraad & de Groot (year unclear)
Quadrulella symmetrica f. *minor* Hoogenraad & de Groot (year unclear)

6.5. Synonymous names and new combinations

One hundred and seventeen synonymous names are listed at the end of the monograph. This list also includes new combinations and is therefore also relevant for taxa that do not belong to the current definition of family Hyalospheniidae.

7. IDENTIFICATION KEYS, DESCRIPTIONS, AND ILLUSTRATIONS

7.1. Family Hyalospheniidae (Schulze, 1877) sensu Kosakyan & Lara, 2012

Description of the family

Test rigid, colourless or yellowish-brown, circular, oval, or piriform, elongated-piriform, lageniform, often dorso-ventrally compressed. Test either entirely self-secreted and composed of either an organic matrix, with an addition of self-secreted siliceous plates, or recycled test plates of euglyphids, *Quadrulella*, or, more rarely, other similar siliceous material, such as diatom frustules. Pseudostome terminal, and in most species, bordered by an organic rim or lip, ranging from almost absent to very thick.

Currently, the family includes 14 genera. All valid names with a certain position are included in the keys, as well as some very characteristic *incertae sedis* species, such as *Nebela barbata*. Readers using this monograph for species identification are strongly encouraged to also check the list of *incertae sedis* and *inquirenda* species (see p. 193 and 209).

Key to the genera

1. Test piriform in broad view, with a lateral indentation of both sides at the junction of the main body to the neck (note: the neck is not deeply constricted, as in genus *Apodera*; the constriction is only lateral); test often organic, hyaline, or sometimes with a rough granulated structure (visible using SEM), or with siliceous plates (probably recycled from euglyphid testate amoebae) *Alocodera* (p. 41)
   – Test without lateral indentation, possibly with a constriction around the base of the neck (*cf. Apodera*), or a neck with slightly convex margins, but lacking a clear constriction (*cf. Padaungiella*) 2

2. Test rigid, chitinoid, totally transparent (clear to amber colored), completely organic without visible structure in LM; in broad view, wedge-shaped (e.g., *Hyalosphenia papilio*), some species oval (e.g., *H. subflava*), or flask shaped with a clear neck (e.g., *H. elegans*) *Hyalosphenia* (p. 79)

– Test composed of a different material, usually with self-secreted or recycled siliceous elements but occasionally lacking any incorporated recycled elements (most frequently in the *Nebela tincta-collaris* complex) 3

3. Test entirely composed of self-secreted square plates or made of small hexagonal units connected by an organic cement 4

– Test composed of usually oval to circular plates (recycled from small euglyphids, e.g., *Trinema*, *Corythion* or *Euglypha*), more rarely square plates (most likely recycled from *Quadrulella*), other similar materials (e.g., incorporated diatom frustules), or agglutinated particles (e.g., genus *Difflugia*) Plates sometimes covered by a thick organic layer, giving the impression of a chitinoid, clear, organic, and non-structured test 6

4. Test composed of small, organic, hexagonal prisms, giving a pitted impression *Hyalosphenia (Pseudohyalosphenia) punctata* (p. 97)

– Test composed of square plates 5

5. Hollow keel present (i.e., not a flat short keel, as in *Quadrulella alata*; note: the origin of the square plates is unclear, possibly recycled) *Mrabella* (p. 116)

– Hollow keel absent, although a flat keel may be present (*Quadrulella alata*), square plates interpreted as self-secreted *Quadrulella* (p. 166)

6. Test piriform or flask shaped in broad view, with two large (2–5 µm) and conspicuous pores in depressions connected by internal tubes, situated at the base of the neck (ca. 2/3rd from the aboral end of the test). Test composed of plates (idiosomes recycled from euglyphid testate amoebae) embedded in an unstructured organic cement, often covered with a thick layer of organic cement, giving a smooth appearance 7

– Test lacking such conspicuous large pores in broad view, either composed of siliceous plates or diatom frustules, sometimes covered with a thick organic layer giving the impression of either entirely self-secreted organic, hyaline, and unstructured test, or composed of agglutinated particles (as in the unique case of *Padaungiella nebeloides*) 8

7. Test flask-shaped in broad view, often with an elongated neck. In some species, internal side of the neck with conical protuberances pointing inwards, perpendicular to the test surface, visible in LM as lines of dots *Certesella* (p. 57)

– Test shape similar but generally less elongated (more piriform) in broad view. No pointed protuberance on the internal side of the neck *Porosia* (p. 162)

8. Test bottle-shaped in broad view, neck elongated, with parallel sides, possibly swollen and always very distinct 9

– Test elongated-piriform, piriform, or oval-elongated in broad view; neck either absent, short, or if long, tapering towards the pseudostome and never clearly separated from the base of the test 11

9. No circular constriction at the base of the neck 10

– Deep circular constriction present at the base of the neck (note: constriction rather oval in frontal view, as the test is not round in cross-section) *Apodera* (p. 45)

10. Test with an elongated neck and bearing numerous short, fine spines (easily broken) protruding from the plate junctions towards the exterior of the test at various angles. Test plates often with irregular shape rather than oval shaped. About eight tooth-like structures protruding from the inner margin

of the pseudostome towards its centre (visible in frontal view) *"Nebela" barbata* (see *incertae sedis* list, p. 196)

– Test with an elongated neck, but lacking spines. Tooth-like structures of the pseudostome absent. Test plates usually oval, similar to those of genera *Apodera* and *Padaungiella* (p. 139)

11. Test with a pair of lateral "horns" (hollow tubular protuberances) protruding on either side in broad view. Horns are either free or connected to the main part of the test by a flat extension of the shell (similar to the keel of genus Planocarina). When present, the keel is either limited to the horn region, or surround the aboral end of the test completely (i.e., horseshoe-shaped keel) *Cornutheca* (p. 63)

– Lateral "horns" absent 12

12. Keel absent (note: in some cases, the presence of a hollow keel may be hard to determine, careful observation at different focal planes or in profile view is necessary, cf. *Nebela orbicularis*). Test ovoid, drop-shaped, rounded-piriform, piriform, or elongated-piriform in broad view 13

– Hollow or flat keel present, sometimes narrow and barely visible (e.g., *Planocarina marginata*; see also genus *Nebela*, e.g., *N. aliciae*), test piriform to elongated-piriform in broad view 15

13. Test narrow piriform, pseudostome strongly curved in broad view, deeply notched in profile view *Alabasta* (p. 38)

– Pseudostome linear, or more or less curved, never strongly curved and notched in profile view, as in genus *Alabasta* 14

14. Test ovoid, drop-shaped, piriform to rounded-piriform in broad view (note: see the few exceptions of Nebela species with a keel below) *Nebela* (p. 121)

– Test elongated-piriform in broad view *Longinebela* (p. 105)

15. Keel very short, starting near the pseudostome and stopping shortly below, at approximately 1/3rd of the distance between the pseudostome and the fundus *Nebela carinatella* (p. 124)

– Keel surrounding the fundus (aboral end) of the test 16

16. Keel flat, not hollow; test piriform to elongated-piriform in broad view, sides tapering towards the pseudostome *Planocarina* (p. 154)

– Keel hollow 17

17. Test elongated-piriform in broad view *Gibbocarina* (p. 75)

– Test wide piriform to almost circular in broad view 18

18. Test wide-piriform to almost circular in broad view, with two small lateral pores (one on each side, Fig. 56). Hollow keel approximately 5 μm wide. Dimensions (based on seven individuals): Smaller species: L = 104–115 μm, B = 76–93 μm, P = 24–27 μm. *Nebela aliciae* (p. 123)

– Test wide-piriform, almost circular in broad view, except for the short neck and pseudostome. L = 166–208 μm, B = 140–170 μm (for L 135-150, see also *N. tincta galeata* complex on p. 221).

Nebela orbicularis (p. 133)

7.2. Genus *Alabasta* Duckert, Blandenier, Kosakyan, & Singer, 2018

Type species: *Alabasta militaris* (Penard, 1890)

2018 *Alabasta* gen. nov. Duckert, Blandenier, Kosakyan & Singer, in DUCKERT et al., 2018, Eur. J. Protistol. 66: 156-165 (new genus established based on molecular data).

The genus *Alabasta* was established by DUCKERT et al. (2018). A phylogenetic reconstruction based on mt-COI data showed that *Nebela militaris* does not belong to genus *Nebela* and should be placed in its own genus. Distinct morphological characters, such as a strongly curved pseudostome in broad view and a marked notch in profile view, also supported this taxonomic action. Based on morphological similarities, *Nebela kivuense* and *Nebela longicollis* were placed in this newly established genus as well.

Description (based on the original description): Test rigid, colourless, or yellowish, elongated in broad view with a maximal width approximately two-thirds of the distance from the pseudostome to the fundus. Sides taper from this broadest point towards the aperture. Test proteinaceous, often with incorporated silica scales taken from euglyphid preys. Pseudostome strongly convex with a flare (i.e., fan-shaped) in broad view and a deep notch in profile. Lateral pores usually present at approximately one-third of the distance from the pseudostome to the fundus.

Differential diagnosis: *Alabasta* can be distinguished from similar genera, such as *Nebela* and *Longinebela*, by its fan-shaped pseudostome (i.e., strongly curved with a flare) in broad view and a deep notch in profile.

Etymology: The name of the genus is derived from the Greek word "ἀλάβαστος" (alabaster), in reference to the diaphanous and yellowish aspect of the type species test, *Alabasta militaris*. Additionally, it appears that *Alabasta* is the name of a fictitious city established in the middle of a desert in the manga One Piece (ODA, 1999), reminiscent of the ecological preferences of *Alabasta militaris*, which is used as an indicator of dry conditions in ecological and palaeoecological studies of *Sphagnum* peatlands.

Three species were assigned to this genus:

Key to the species

1. Smaller species < 100 µm, test narrow piriform in broad view 2
– Larger species: L = 120–140 µm, test elongated-piriform in broad view, with a long neck *A. longicollis* (p. 40)

2. Wider species in broad view (L/B = 1.8–2), pseudostome wide (15–22 µm). *A. militaris* (p. 40)
– Narrow species, often laterally curved in broad view (L/B = 2.4–2.7), pseudostome narrow (12–16 µm) *A. kivuense* (p. 38)

Alabasta kivuense (Gauthier-Lièvre & Thomas, 1961) Duckert, Blandenier, Kosakyan, & Singer, 2018

1961 *Nebela kivuense* Gauthier-Lièvre & Thomas, Bull. Soc. d'Hist. Natur. D'Afrique du Nord. 52: 47.

2018 *Alabasta kivuense* Gauthier-Lièvre & Thomas, 1961 – Duckert, Blandenier, Kosakyan, & Singer, in DUCKERT et al., 2018, Eur.

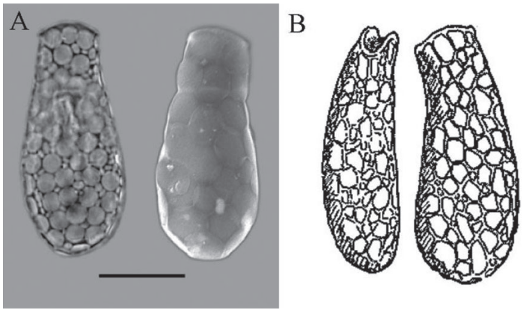

Fig. 5. *Alabasta kivuense*: (A) Light microscopy (LM) and scanning electronic microscopy (SEM) broad view images of individuals from Ontario, Canada (modified from NICHOLLS, 2015); (B) Original drawing by GAUTHIER-LIÈVRE & THOMAS (1961; profile and broad view). Scale bar = 20 µm.

J. Protistol. 66: 156-165 (transfer to new genus based on morphological data).

Icon.: GAUTHIER-LIÈVRE & THOMAS, 1961, Fig. 1e, f; BOBROV et al., 2013, Fig. 3A (as Nebela sp. 1); NICHOLLS, 2016, Figs. 2–21.

Description: Test narrow piriform in broad view (like a glove finger “doigt de gant”, as mentioned in the original description), compressed. Sides of the test subparallel, slightly tapering towards the pseudostome. Test colourless, composed of irregular polygonal plates. Test sizes vary among different authors L = (49) 58–63 (64) µm, B = 18–22 (26) µm, P = 12–16 µm. Pseudostome strongly curved with a clear notch in broad view and a thick organic lip.

Differential diagnosis: *Alabasta kivuense* and *A. militaris* both have similar narrow piriform tests, a deeply curved pseudostome, and overlapping test lengths (*A. kivuense*, L = 49–64 µm; *A. militaris*, L = 50–82 µm); however, *A. militaris* (B = 25–46 µm, P = 15–22 µm) has a wider fundus than *A. kivuense* (B = 18–26 µm, P = 12–16 µm), and the pseudostome of *A. militaris* is more curved.

Type locality: Kivu, between Lubero and Butembo, Democratic Republic of Congo. Likely coordinates: -0.027527°, 29.233861°.

Type specimen: Not provided. We declare Fig. 1 e, f by GAUTHIER-LIÈVRE & THOMAS (1961), here reproduced in Fig. 5B, as the type.

Etymology: The species was named after the place where it was found for the first time.

Habitat: Wet mosses, *Sphagnum* mosses (fens).

Geographical distribution: Africa: Democratic Republic of Congo (GAUTHIER-LIÈVRE & THOMAS, 1961); North America: Canada (NICHOLLS, 2015); Mexico (BOBROV et al., 2013, mentioned as *Nebela* sp. 1 in Fig. 3). Reported from Romania by Godeanu (1972a), although without proper description and illustration.

Remarks: *Alabasta (Nebela) kivuense* was described by Gauthier-Lièvre and Thomas (1961) from an area near Lake Edward, Democratic Republic of Congo. It was formally moved to genus *Alabasta* (DUCKERT et al., 2018) based on morphological characters (i.e., strongly curved pseudostome). *A. kivuense* was considered a very rare species, perhaps endemic to a small, local equatorial region of the African continent. The report from Romania by GODEANU (1972a) appeared doubtful, particularly considering that no illustration was provided. However, recently NICHOLLS (2015) rediscovered it in two wetland-coniferous forest ecosystems of southern Ontario, Canada, thus challenging previous perceptions of its restricted distribution. NICHOLLS (2015) highlighted the biogeography of *A. kivuense* as a clear example illustrating the danger of inferring endemism from rarity. *Alabasta kivuense* may potentially be mistaken for *A. militaris* (see differential diagnosis), but this does not appear to be a concern in NICHOLLS (2015), as both species were identified within the same ecosystem, with clear morphological and biometric differences. Molecular data are needed to clarify if *A. kivuense* represents an independent species, and if the African, Canadian, and possibly other (e.g., Romanian and Mexican populations) indeed belong to the same taxon.

Alabasta longicollis (Penard, 1890)

1890 *Nebela longicollis* Penard, Mem. Soc. Hist. Nat. 31(2): 158 (Pl. 6, Figs. 45–49, original drawings).

2018 *Alabasta longicollis* Penard, 1890 – Duckert, Blandenier, Kosakyan, & Singer, in DUCKERT et al., 2018, Eur. J. Protistol. 66: 156-165 (transfer to new genus based on morphological data).

Description: Test very elongated-piriform (L/B = 3), compressed, with a rounded fundus, in profile elongated elliptical with a slightly pointed end. Test transparent, composed of oval or circular, often overlapping plates. L = 120–140 µm, B = 40–45 µm. Pseudostome curved, with an organic lip.

Differential diagnosis: Differs from other *Alabasta* species by its larger size and elongated outline.

Type locality: Wiesbaden, Germany. Likely coordinates: 50.11619°, 8.234734°.

Type specimen: Not provided. We declare Pl. 6 Fig. 45 (PENARD, 1890), here reproduced in Fig. 6, as the type.

Etymology: The species name is derived from general morphology of the test (i.e., elongated neck).

Habitat: *Sphagnum* mosses.

Geographical distribution: Europe: Austria (AESCHT & FOISSNER, 1989), Bulgaria (GOLEMANSKY, 1968b), British Isles (BROWN, 1911), France (NECTOUX, 1956), Germany (PENARD, 1890), Romania (GODEANU, 1970), Switzerland (WAILES, 1912b); North America: Canada (WAILES, 1929), USA (PENARD, 1891; COCKERELL, 1909; WAILES, 1912a); South America: Colombia (PENARD, 1914); New Zealand (PENARD, 1911; WILKINSON, 1990).

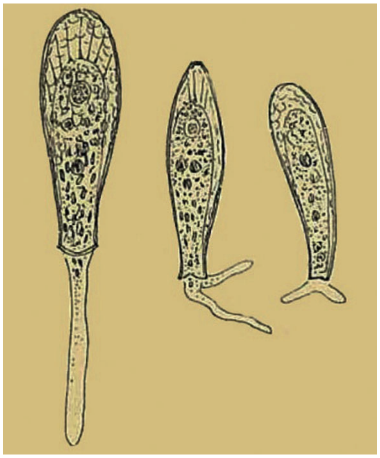

Fig. 6. Original drawing of *Alabasta longicollis* PENARD, 1890.

Remarks: This is very rarely reported and problematic species. PENARD (1980) noted that it could represent a variety of *Nebela collaris*, and mentioned some synonymous names, including *Nebela barbata* (Penard, 1890) or *Nebela americana* auct. non Taranek (Penard, 1902), which we do not believe to be appropriate for this species. Although the species name is reported from many geographical regions, considering the taxonomic confusion, the validity of these reports remains unclear. This species was placed into the genus *Alabasta* (DUCKERT et al., 2018) based on the strongly curved pseudostome.

Alabasta militaris (Penard, 1890)

1879 *Nebela collaris* (pars) in Leidy, Freshw. Rhiz. N. America, p. 147, Pl. 22 Figs. 11, 12, 16 (misidentification).

1881 *Nebela bursella* Vejdovsky in Taranek (1881) Sitzber. Böhm. Ges. Wiss. P. 230, Fig. 2 and Abh. Böhm. Ges. Wiss. (6) XI (1882), 8, p. 36, Pl. III, Figs. 7-14 (overlapping morphology).

1890 *Nebela militaris* Penard, Mem. Soc. Phys. Hist. Nat. Genève 31: 164.

1933 *Nebela americana bryophila* Van Oye, Arch. Naturgestch. Abt. B., N.F. 2 (overlapping morphology).

1962 *Nebela militaris* var. *curvata* Golemansky, Recherches Africaines, Études guinéennes (Nouvelle Série) 4: 33-60, Fig. 61 (Infrasubspecific [not available] name: var. published after 1960, ICZN Art. 45.6.3).

2018 *Alabasta militaris* Penard, 1890 – Duckert, Blandenier, Kosakyan, & Singer, in DUCKERT et al., 2018, Eur. J. Protistol. 66: 156–165 (transferring to a new genus based on morphological and molecular data).

Icon.: PENARD, 1890, Figs. 16–22; DEFLANDRE, 1936, Figs. 76–78; OGDEN & HEDLEY, 1980, Pl. 41.

Description: Test narrow, ovoid-piriform in broad view, compressed, with two small lateral pores, one on each side. Test colourless, composed of oval or circular test plates. Test sizes vary among different authors: L = 50–70 (82) µm, B = 25–41 (46) µm, P = 15–20 (22) µm. Pseudostome strongly curved with a clear notch in broad view and thick organic lip.

Differential diagnosis: See details under *Alabasta kivuense*.

Type locality: Two localities are mentioned: Tröllhattan, Rosersberg, Marstrand, Sweden; and Vallee de Joux, Switzerland. As we declare the specimen by PENARD (1890) to be the type, the type locality is then Vallee de Joux (Switzerland). Likely coordinates: 46.564913°, 6.172125°.

Type specimen: DUCKERT et al. (2018) declared specimen nr. 515-2 from the Penard collection deposited at the Natural History Museum of Geneva, Switzerland as name-bearing type.

Etymology: PENARD (1890) mentioned that its shape resembles that of an ancient short cannon.

Habitat: *Sphagnum* mosses (relatively drier microhabitats, such as hummocks), brown mosses, acidic forest litter, sediments (rare).

Geographical distribution: Apparently cosmopolitan.

Remarks: Combined molecular (single cell mt-COI barcoding) and morphological (detailed LM, SEM, and morphometry) revealed that *A. (N.) militaris* does not belong to genus *Nebela*. The phylogenetic reconstruction placed it as a sister clade to genus *Planocarina*; however, this position was weakly supported (bootstrap support, 48; posterior probability, 0.97). Moreover, the genetic distance between *A. (Nebela) militaris* sequences and those of the genetically closest species in genus *Nebela* (i.e., *N. flabellulum*, 18% dissimilarity) is well above the barcoding gap calculated for Hyalospheniidae and Amoebozoa (KOSAKYAN et al., 2012; SINGER et al., 2018). The studied isolates could not be ascribed to genus *Planocarina* either owing to: (1) an even higher genetic distance (ca. 20% of dissimilarity with *P. marginata*), or (2) the fact that *Planocarina* is characterized by the presence of a keel on the posterior margin of the test (KOSAKYAN et al., 2016), whereas it is absent in *A. militaris*. This justifies establishing a separate genus for *N. militaris* and morphologically similar species. Genus *Alabasta* incorporates species with an elongated test and strongly curved pseudostome with a flare and marked notch in profile view (DUCKERT et al., 2018).

Nomenclature: The history of the taxonomy and nomenclature of this species is presented in detail in DUCKERT et al. (2018) as follows:

"*The taxonomic history behind* Nebela militaris *is rather complicated as* N. militaris *is*

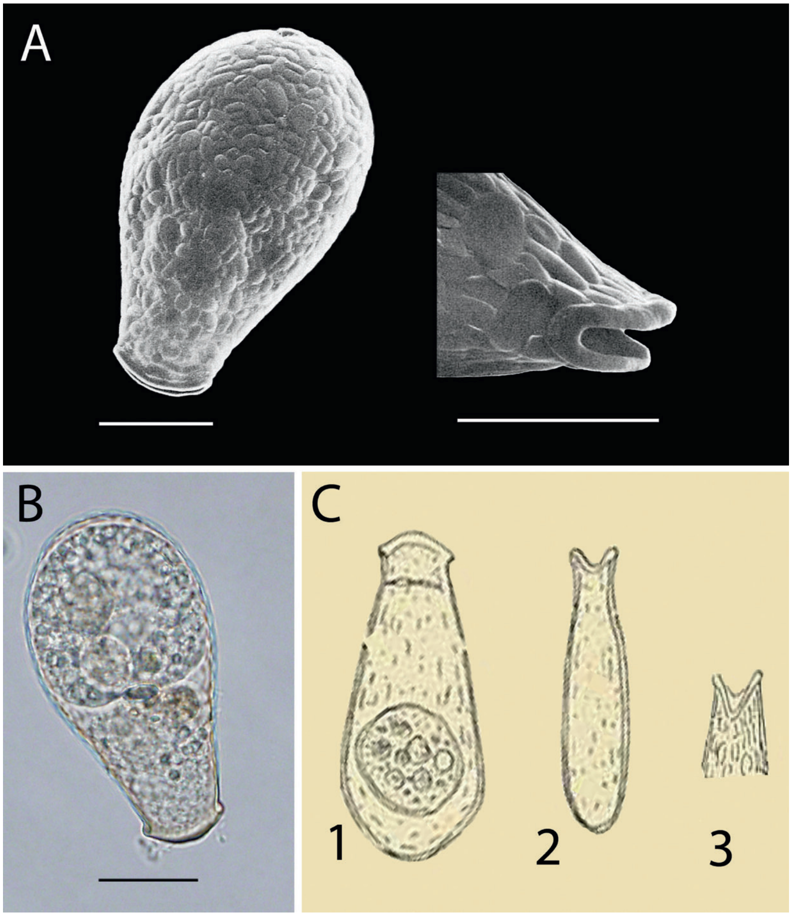

Fig. 7. *Alabasta militaris*: (A) SEM images of a specimen in broad view, and detailed side view of the pseudostome (modified from OGDEN & HEDLEY, 1980); (B) LM image of a living specimen from Switzerland (by Amandine Pillonel); (C) Original drawings of *A. militaris* modified from PENARD (1890): (1) lateral view of encysted specimen, (2) profile view of empty test, and (3) detailed broad view of the pseudostome). Scale bars = 20 µm.

morphologically similar to two other taxa: Nebela bursella *and* N. americana var. bryophila. *It is thus unclear whether* N. militaris, N. bursella, *and* N. americana var. bryophila *represent distinct taxa and the confusion encompassing those names comforts the idea that they are merely the same morphospecies.* Nebela bursella *was originally described by Vejdovsk´y (1882) and was later reported in Taranek's monograph (1882). The illustrations that Taranek includes in the description of* N. bursella *are confusing, since some of them clearly correspond to the original description of* N. bursella *made by Vejdovsk´y while other depicted specimens are ambiguous. Indeed, while two illustrations (Plate III Fig. 8 and 12 by Taranek 1882 (Supplementary material 1), Fig. 8 here reproduced as Fig. 1E) resemble Vejdovsk´y's original drawings of* N. bursella *with its characteristic curved pseudostome, the other illustrations correspond to specimens that are clearly broader. Based on modern knowledge of Hyalospheniidae systematics, these illustrated specimens should rather be assigned to another species within genus* Nebela *(Plate III Fig. 7 and Plate IV Fig. 16 by Taranek (1882) (Supplementary material 1), reproduced here as Fig. 1H, I respectively) or, possibly even, given the slit-like aperture, to genus* Heleopera *(Plate III Fig. 9–11 by Taranek (1882), reproduced here as Fig. 1F, G), resulting in one description possibly corresponding to three species. This situation led to the misinterpretation that* N. bursella *corresponded to the broader morphotype rather than to the cells illustrated by Vejdovsk´y. This error was not corrected and* N. bursella *was ultimately considered as a synonym to* Nebela tincta *(Awerintzev 1906). In his description of* N. militaris*, Penard (1890) states that his new species could be considered by some as mere aberrant specimens of* N. bursella*, thus suggesting that he too was misled. However, unfortunately Penard did not explain what features could be considered as aberrant. He actually based his concept of* N. bursella *on Taranek's erroneous lumping and thus confused it with* Nebela tincta *(see Penard 1902). Penard then described* N. militaris*, being certain that it was not only an aberrantly slender form* Nebela tincta*, resulting in the redescription of* N. bursella *(Vejdovsk´y) as* N. militaris *(Penard).* Nebela americana var. bryophila *Van Oye (1933) was described as a smaller morphospecies of* Nebela americana *(Taranek 1882). The dimensions and shape of the test are comparable to* N. militaris *but Van Oye (1933) noted the absence of lateral pores on his isolates. As the pores remain difficult to observe, we consider that the original description of* Nebela americana var. bryophila *is too lacunar to allow distinguishing it from* N. militaris *and we consider them as synonyms. For these reasons, we propose to synonymize* N. militaris, N. bursella *and* N. americana var. bryophila*. Although we are aware that the name* Nebela bursella *precedes the others and thus should prevail,* N. militaris *has been consistently used since Penard's description and is well known to the scientific community working on testate amoebae. Moreover, we performed an extensive literature search and found no report for* N. bursella*, after 1964 (Sudzuki 1964). For these practical reasons, we invoke Article 23.9.3 of the International Code of Zoological Nomenclature to keep* N. militaris *as the valid name even though it is technically a junior synonym*".

Other related species: DUCKERT et al. (2018) mentioned that *Hyalosphenia elegans* (LEIDY, 1879) and *H. insecta* (HARNISCH, 1938) also share several common morphological characteristics with *Alabasta militaris* (i.e., general outline of the test, curved aperture) and could potentially be included in genus *Alabasta*; however, two major differences between these species exist: 1) the inability of *H. elegans* and *H. insecta* to perform kleptosquamy (i.e. recycling of shell plates produced by other organisms, LAHR et al., 2015), as is commonly observed in *Alabasta militaris*, *A. longicollis*, and *A. kivuense*; and 2) the presence of circular to oval depressions on the surface of the test of *H. elegans* and *H. insecta*, that are not observed in *Alabasta* species.

GOLEMANSKY (1962) described *N. militaris* var. *curvata*, which differs from the type by its larger size (L = 90, B = 40 µm) and curved test. The author did not mention how many such curved individuals he observed. Accordingly, we considered it as infra-subspecific taxa (var. after 1960, ICZN Art. 45.6.3).

7.3. Genus *Alocodera* Jung, 1942

Type species: *Alocodera cockayni* (Penard, 1911)

1942b *Alocodera* gen. nov. Jung, 1942b, Arch. Protistenk. Bd. 95. H.3: 313–314 (redefinition of family Nebelidae, splitting it into 13 genera, including *Alocodera*).

The genus is monospecific and is only known from the southern hemisphere. JUNG (1942b) proposed this genus without type designation; this oversight is of little consequence owing to its monospecificity.

Description: Test piriform, compressed, with a well-developed neck separated from the fundus of the test by two lateral indentations. One to three lateral pores on each side of the neck, often difficult to observe, especially in LM. Test almost transparent, yellowish, or slightly brownish, with a smooth or slightly granulose surface. DEFLANDRE (1936) described the shape of this species as "*similar to a violin or more precisely the ancient viola d'amore*". This is indeed true for the characteristic constriction of the neck.

Differential diagnosis: The two lateral indentations at the base of the neck are characteristic for the genus and clearly separate it from other taxa with a swollen neck (e.g., *Apodera*, *Padaungiella lageniformis*, *Certesella certesi*).

Remarks: Although often believed to be only organic and self-secreted, it is relatively common to observe external material incorporated into the test (most likely recycled euglyphid shell plates, DEFLANDRE, 1936; JUNG, 1942b; HOOGENRAAD & DE GROOT, 1948; BONNET, 1966), see Fig. 9A & B.

Etymology: Not provided by JUNG (1942). It remains unclear what "aloco" refers to, but "dero (δέρη)" means "neck" in ancient Greek.

Alocodera cockayni (Penard, 1911)

1911 *Hyalosphenia cockayni* Penard, Brit. Ant. Exp.: 238 (Pl. 22, Fig. 5 original drawing).

1913 *Nebela cockayni* Penard, 1911 – Wailes, Journ. Lin. Soc. Zool. XXXII: 215 (re-description and transfer into a new genus based on the test structure).

1942b *Alocodera cockayni* Penard, 1911 – Jung, 1942b, Arch. Protistenk. Bd. 95. H.3: 313–314 (redefinition of the family Nebelidae, split into 13 genera, one of which was *Alocodera*, see notes directly below).

Icon.: PENARD, 1911, Pl. 22, Fig. 5; JUNG, 1942b, Fig. 49; DEFLANDRE, 1936, Fig. 107, 108; MEISTERFELD, 2002, Fig. 68; SMITH et al., 2007, Fig. 1c; KOSAKYAN et al., 2011, Fig. 6b–d.

Description: Test piriform in broad view, compressed with a well-developed neck, separated from the fundus by one indentation on each side. Two lateral (sometimes more) pores present approximately halfway between the pseudostome and the indentations, often difficult to observe in LM. Test almost transparent, yellowish, or slightly brownish. Surface generally smooth, sometimes appearing rough and granulose (Fig. 8A, B), or with embedded recycled plates (Fig. 9A, B). Test size according to PENARD (1911): L = 89–100 µm, B = 45–55 µm; WAILES (1913): L = 120–126 µm, B = 74–75 µm, P = 25–28 µm; Our observations (A.K., E.M., E.L.) from Tierra del Fuego (Argentina): L = 92–100 µm, B = 55–60 µm, P = 28–30 µm, with a thick organic rim; L up to 132 µm from New Zealand (E.M., C.D.).

Differential diagnosis: General shape similar to that of *Apodera* vas and *Padaungiella lageniformis* but differs by the characteristic indentations on either side of the base of the neck.

Type locality: The Auckland Islands, on epiphytic mosses growing on southern rātā (*Metrosideros umbellata*) trees. Likely coordinates: -50.628863°, 166.137271°.

Type specimen: As it has not yet been provided, we declare here Fig. 9 D as the type.

Etymology: The species was named after the famous botanist Dr. Leonard Cockayne (1855-1934) from New Zealand, who collected the moss samples where the species was found.

Habitat: *Sphagnum* mosses, other mosses.

Geographical distribution: South America: Argentina (KOSAKYAN et al., 2012), Chile (WAILES, 1913; JUNG, 1942; FERNANDEZ et al., 2015; MEISTERFELD unpubl.); Australia: (PENARD, 1911); New Zealand (Penard, 1911; Hoogenraad, 1948; VAN OYE, 1956a; MCGLONE & WILMSHURST, 1999, WILMSHURST et al., 2003); the Auckland Islands (PENARD, 1911). Probably circumaustral.

Remarks: *Alocodera cockayni* was first described by PENARD at 1911 as *Hyalosphenia cockayni*. He observed tests with a yellowish colour or almost transparent, with a homogenous structure. WAILES (1913) found tests with the same shape, but somewhat larger, in Chile, and observed a test structure fitting more to the description of genus *Nebela*, with small oval test plates embedded in an organic cement. We (E. Mitchell, C. Duckert) have also observed wider morphotypes from Avoca Valley, New Zealand (e.g., the individual illustrated in Fig. 9C, L = 123 µm, B = 82 µm, P = 30 µm).

JUNG (1942b) redefined family Nebelidae (13 genera) to include the new genus *Alocodera*, with *A. (Nebela) cockayni*. Molecular data (KOSAKYAN et al., 2012) showed that *A. cockayni* is closely related to *Padaungiella* species (*P. lageniformis*, *P. wailesi*, *P. nebeloides*). Single-cell COI sequences originating from the Valdivian Forest (Monumento Nacional Alerce Costero, Chile) and Fueguian peatlands (Parque Nacional Lapataya, Argentina) differed slightly, as did the corresponding test structures (Fig. 8; see also KOSAKYAN et al., 2012). These data clearly suggest that *A. cockayni* is a species complex. We, therefore, encourage researchers to carefully document the morphology and biometry of specimens from this genus and to sequence them.

7.4. Genus *Apodera* Loeblich & Tappan, 1961

Type species: *Apodera vas* (Certes, 1889)

1942b *Apodera* gen. nov. Jung, Arch. Protistenk. 95: 380 (invalid genus owing to lack of type designation).

1961 *Apodera* Jung, 1942 – Loeblich & Tappan, Proc. Biol. Soc. Wash., 74: 205 (validation of genus *Apodera* by assignment of *A. vas* as type species).

Description: Test composed of two clearly distinct parts: a subcircular, oval, or ellipsoidal compressed posterior (fundus) and a neck. The

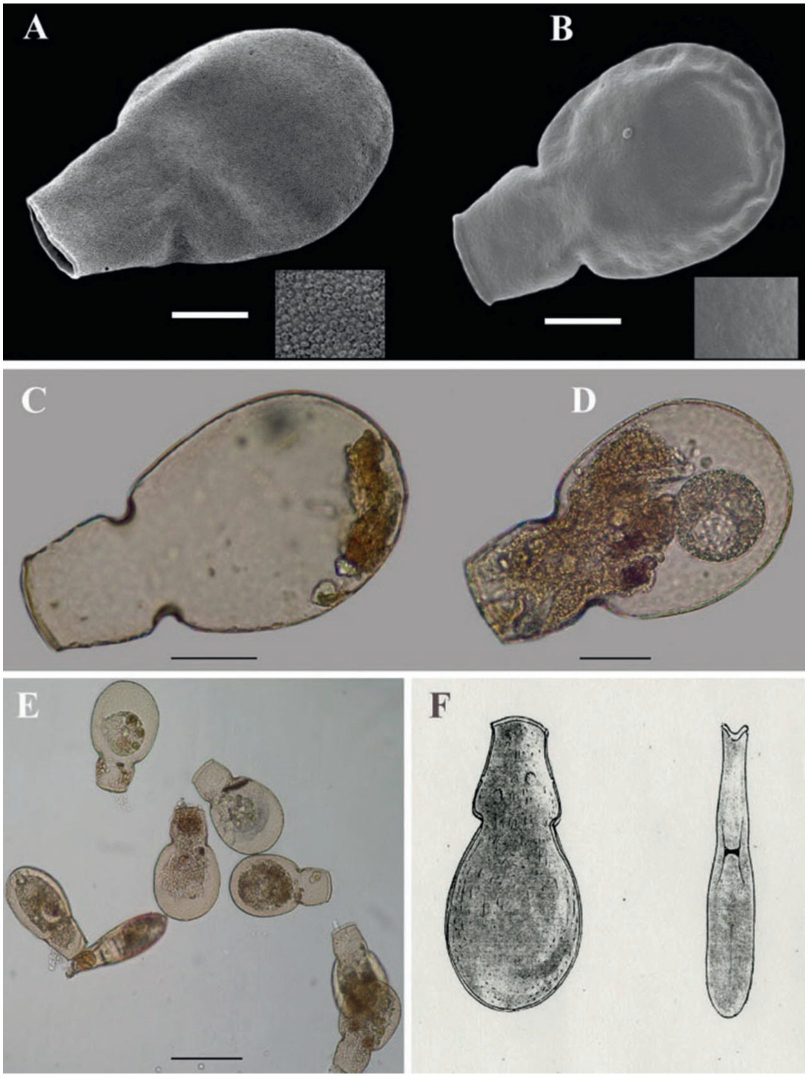

Fig. 8. *Alocodera cockayni*: (A) SEM image of a specimen from Tierra del Fuego, Argentina—a lateral pore is visible on the side of the neck, (inset) higher magnification view of the test surface's granular structure; (B) SEM image of a specimen from continental Chile (temperate rainforest near Valdivia), (inset) higher magnification view of smooth organic structure of the test; (C) LM image of an empty test from Tierra del Fuego, Argentina; (D) LM image of a specimen from Argentinian Patagonia. (E) Eight individuals—one in profile view—from the Chilean temperate rainforest; and, (F) Drawing of *A. cockayni* from the original description (PENARD, 1911), with broad and profile views. Scale bars: A–D = 20 µm, E = 60 µm. Images by: (A, C, D, E) Enrique Lara and (B) Anush Kosakyan.

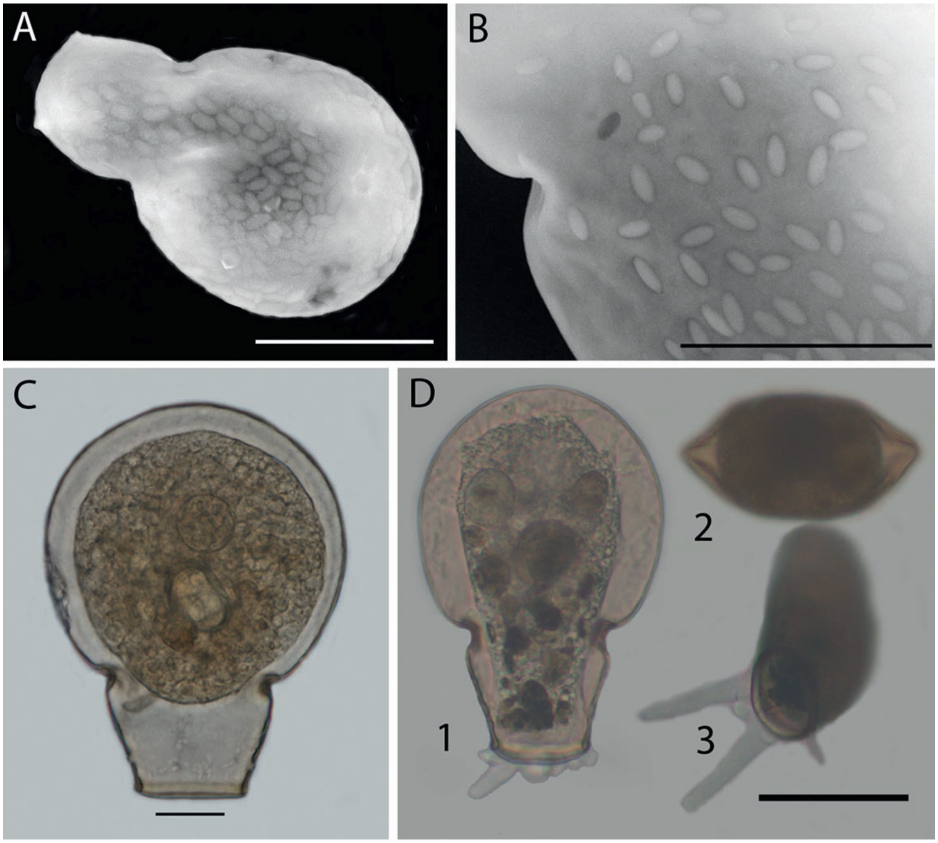

Fig. 9. *Alocodera cockayni*: (A) SEM image of specimen from NW of Dunedin, South Island, New Zealand, illustrating an individual with embedded recycled plates; (B) Higher magnification view of recycled plates embedded in the organic cement; (C) LM image of a wide morphotype from Avoca Valley, New Zealand; (D) LM image of a specimen from the type locality in the Auckland Islands, New Zealand, showing the test in: 1) broad view, 2) cross-section view, and 3) oblique apertural view. Scale bars: A & D = 50 μm, B = 30 μm, C = 20 μm. Images by: (A, B, D) Edward Mitchell and (C) Michelle McKeown.

two parts are separated by a deep constriction around the entire base of the neck. Sides of the neck more or less convex in broad view.

Differential diagnosis: The deep constriction around the entire circumference of the test at the base of the neck distinguishes this genus from other taxa with elongated necks (e.g., *Alocodera*, *Padaungiella*, *Certesella*, and *Hyalosphenia elegans*).

Remarks: This genus was proposed by JUNG (1942b) without type designation. It was subsequently validated by LOEBLICH & TAPPAN (1961). Test shape is similar to that of genera *Alocodera* and *Padaungiella*, with the presence of a distinct elongated neck; however, in genus *Apodera*, a deep constriction clearly separates the body from the neck around the entire circumference of the neck base.

Etymology: Not provided by JUNG (1942b). *Apodera* likely refers to the general morphology of the test—i.e., in ancient Greek "apo (απο)" means "separation", and "dero (δέρη)" means "neck".

Three species have been described:

Key to the species

1. Hollow keel present *A. angatakere* (p. 48)
– Hollow keel absent 2

2. Neck laterally bent in broad view, irregular ("crenulate") pseudostome margin, smaller species L = 93 µm, B = 39 µm *A. crenata* (p. 50)
– Neck straight in broad view 3

3. Smaller species, L = 130–170 µm, B = 55–103 µm *A. vas* (p. 51)
– Larger species, L = 185–220 µm, B = 125–130 µm *A. wellingtonia* (p. 55)

Apodera angatakere (Brehm, 1928) Mitchell, Blandenier, & Duckert, 2021

1928 *Nebela penardi* Brehm, Trans. N. Z. Inst. 59: 779 (Fig. 52 original drawing)

2021 *Apodera angatakere* Brehm, 1928 – Mitchell, Blandenier, & Duckert, Euk. Microbiol. E12867 (emended owing to insufficient description).

Description: Test composed of two clearly distinct parts: a subcircular, oval, or ellipsoidal, compressed posterior part (body) and a neck. The two parts are separated by a deep constriction around the entire base of the neck. Sides of the neck straight to slightly concave, with a bulge at the base in broad view. Neck margins sometimes compressed. Posterior part with a hollow keel starting near the constriction and surrounding the entire posterior end of the test. Body almost circular. Dimensions based on 63 individuals: L = 186–226 µm, B = 120–167 µm, P = 39–50 µm.

Differential diagnosis: Differs from other *Apodera* species by the presence of a hollow keel surrounding the main part of the test, as in genus *Gibbocarina*. *Padaungiella kenyana* comb. nov. is very similar, as it also bears a hollow keel, but the base of the neck is similar to that of Padaungiella and lacks the characteristic circular constriction of *Apodera*.

New type locality: Ahukawakawa swamp, on the saddle between Mt. Taranaki and Pouakai Hut, the North Island, New Zealand. Coordinates, -39.255058°, 174.043106°; Elevation, ca. 921 meters above sea level (m.a.s.l.).

Neotype: Quoting from DUCKERT et al. (2021): "*Brehm did not preserve any specimen, and the original type material is only represented by two simple drawings without indication of size. Because small variation in the morphology of the test can be used to distinguish closely related species, only high magnification microphotographs can be used to accurately represent a species*

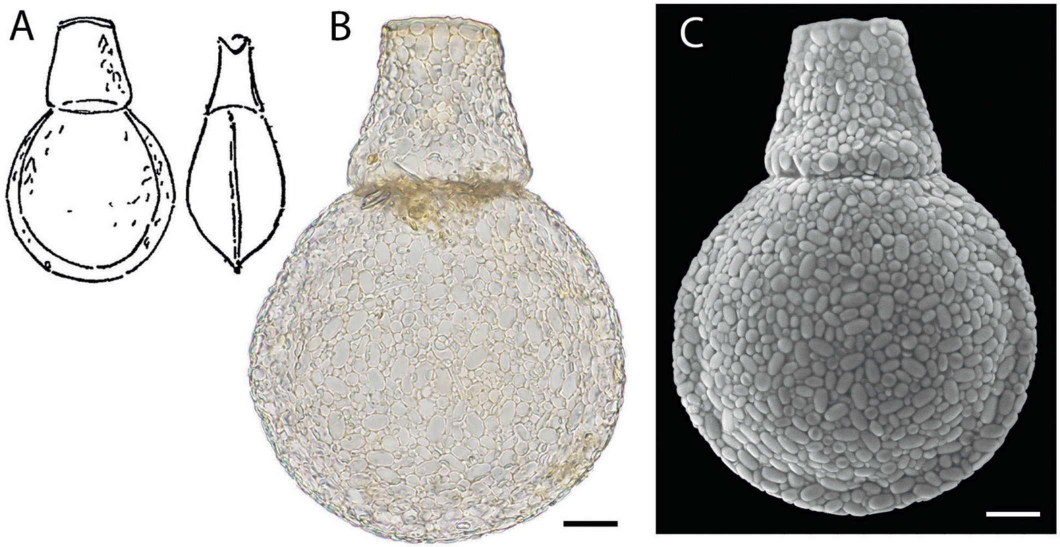

Fig. 10. *Apodera angatakere*: (A) Brehm's (1928) original drawing (lacking scale), described as *Nebela penardi* from Margaret's Tarn, Arthur's Pass, South Island, New Zealand; (B & C) Two individuals from Mt. Taranaki, North Island, New Zealand (extended depth focus (stacked) DIC image and SEM, respectively; images by Edward Mitchell). Note the presence of a ca. 10 µm wide keel. Scale bars = 20 µm.

and reliably distinguish it from taxa yet to be described (Kosakyan et al., 2016, Duckert et al., 2020). For this reason, we designate the specimen in pictures Figure 2E as the neotype. As we were unable to find unfractured tests at the previous type locality (Margaret's tarn, Mt. Rolleston near Arthur's pass, New Zealand South Island) the neotype has been designated among a population from Mt. Taranaki, New Zealand's North Island. However, tests from the previous type locality and the ones from Mt. Taranaki were in all point similar. A permanent slide/stub has been deposited at the Natural History Museum of Neuchâtel. Slide nr. ID 95-1. A COI gene sequence of Apodera angatakere (352-655 bp) was deposited in GenBank (no. MZ615186–MZ615188 and MZ615189–MZ615191)."

Etymology: The species name is derived from the Māori words: "anga" meaning "shell" and "takere" meaning "keel", in reference to the characteristic hollow keel of the species.

Habitat: *Sphagnum* and brown mosses in peatlands, as well as alpine wetlands and mosses in low *Metrosideros* forest (the Auckland Island).

Geographical distribution: Known from New Zealand's North, South, and Auckland Islands. Given the known distribution, we consider its occurrence also likely on Campbell and Chapman Islands. Notably, it was not observed in the single *Sphagnum* sample we observed from the Macquarie Island. We did not analyze any materials from Australia (including Tasmania), taking into account the prevailing winds

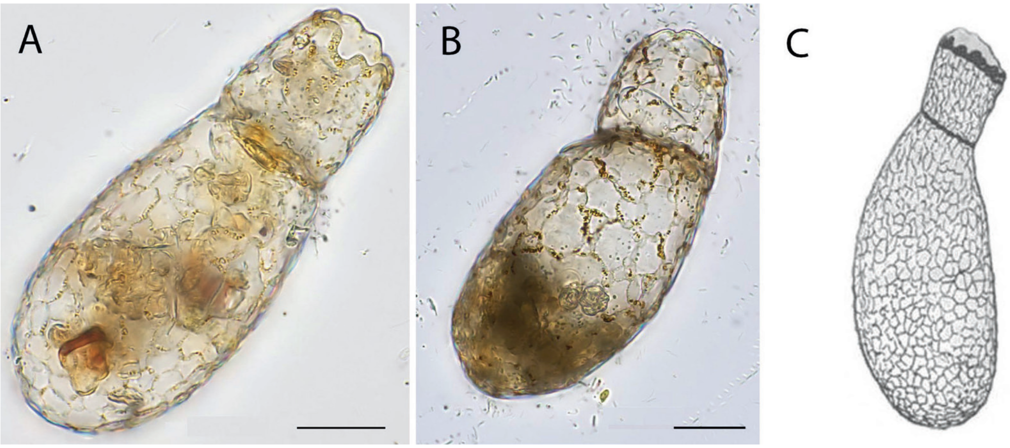

Fig. 11. *Apodera crenata*: (A & B) LM images of a specimen from Ecuador; (C) Original drawing from JUNG (1942). Scale bars = 20 µm. Images by: (A, B) Clément Duckert.

and the relatively large taxon size, we consider it unlikely to occur there.

Remarks: Originally described by BREHM (1928) as *Nebela penardi*. DUCKERT et al. (2021) note the following: "*We did not succeed in obtaining DNA sequences from material collected from the previous type locality (Margaret's tarn, Mt. Rolleston near Arthur's pass, New Zealand South Island) and found only fractured test unfit to be designated as the neotype. (…). Given that 13 distinct molecular clades were recorded within* Hyalosphenia papilio*, a common but smaller species commonly found in Holarctic* Sphagnum *peatlands (Heger et al., 2013, Singer et al., 2019), it is possible that several cryptic or pseudo-cryptic species exist within* A. angatakere *and that specimens from Margaret's tarn constitute a distinct species. If this were the case a new species would need to be described from Margaret's tarn, New Zealand South Island with its own type locality.*"

Apodera crenata Jung, 1942

1942a *Apodera crenata* Jung, Arch. Protistenk. 95: 314 (Fig. 55, original drawing).

Description: Test almost colourless or yellowish, subcircular or ellipsoidal, compressed, with a marked constriction between the body and the swollen neck. Neck curved or twisted on one side, tapering from its junction towards the pseudostome. Pseudostome irregularly lobed or wavy, surrounded with a thick rim. L = 93 µm, B = 39 µm, P = 20 µm (JUNG, 1942a). We (E.M. and C.D.) have observed six tests from Ecuador (Fig. 11A & B): L = 110–120 µm, B = 44–50 µm, P = 19–24 µm.

Differential diagnosis: Differs from other *Apodera* species by its smaller size, curved test, and crenate pseudostome.

Type locality: Calbuco Island, Southern Chile. Likely coordinates: -41.780682°, -73.136297°; Elevation: ca. 20 m.a.s.l..

Type specimen: Not provided. We thus declare Fig. 55 by JUNG (1942a), reproduced here in Fig. 11C, as the type.

Etymology: Not provided, but likely derived from the crenate (irregular) margin of the pseudostome.

Habitat: *Sphagnum* mosses.

Geographical distribution: Described from Chile (JUNG, 1942a). We report here a new finding from Ecuador (DUCKERT & MITCHELL, unpubl.).

Remarks: The crenate pseudostome is unusual for the family and disagrees with the general synapomorphy of a smooth pseudostome margin. Molecular data are needed to clarify the phylogenetic position of this species.

Apodera vas (Certes, 1889) Loeblich & Tappan, 1961,

1889 *Nebela vas* Certes, Mission Scientifique du Cap Horn, t. VI: 53 (Pl. I, Figs. 4–5, original drawings).

1932 *Nebela goudinii* Gericke, S. Afr. J. Sci.: 624–625 (overlapping morphology).

1942b *Apodera vas* Certes, 1889 – Jung, Arch. Protistenk., 95: 256 (invalid combination of genus *Apodera* because of the lack of type designation).

1961 *Apodera vas* Certes, 1889 – Loeblich & Tappan, Proc. Biol. Soc. Wash., 74: 205 (assignment of A. vas as type species).

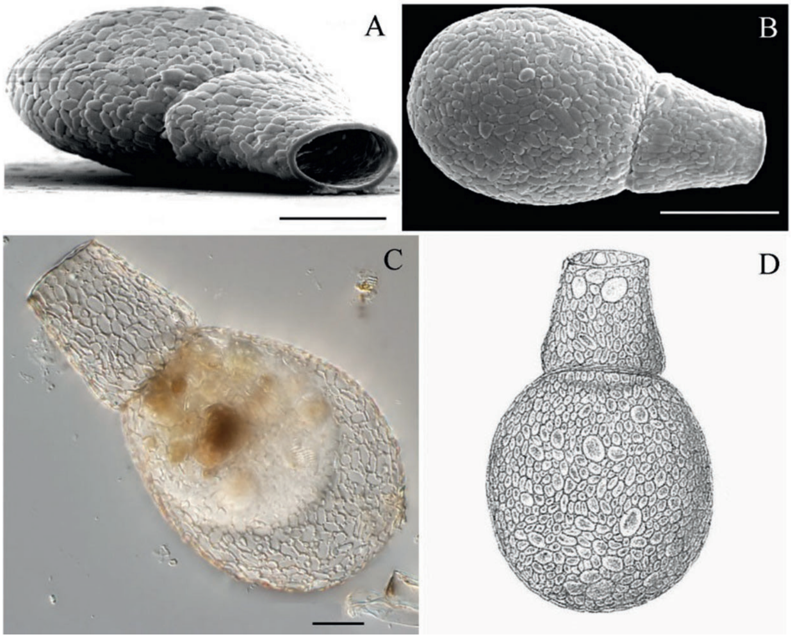

Fig. 12. *Apodera vas*: (A & B) SEM images of a specimen from Tanzania (oblique frontal and broad views, respectively); (C) LM image of a living specimen from Tierra del Fuego, Chile; (D) Original drawing from CERTES (1889). Scale bars: A & B = 50 µm, C = 20 µm. Images: (A & B) are modified from MITCHELL & MEISTERFELD, 2005, and (C) by Edward Mitchell.

1971 *Nebela vas* var. *longicollis* Grospietsch, Marion, and Prince Edward Islands. Report on the South African Biological and Geological expedition 1965/1966: 417, Fig. 89c (infra-subspecific [not available] name: var. published after 1960, ICZN Art. 45.6.3).

1971 *Nebela vas* var. *obliqua* Grospietsch, Marion, and Prince Edward Islands. Report on the South African Biological and Geological expedition 1965/1966: 417, Fig. 89b (infra-subspecific [not available] name: var. published after 1960, ICZN Art. 45.6.3).

Icon.: PENARD, 1911, Pl. XXIII, Fig. 10; WAILES, 1913 p. 127; DEFLANDRE, 1936, Figs. 109-111; GRACIA, 1987, Fig. 13; YEATES & FOISSNER, 1995, Figs. 1, 5, 15–18; SMITH et al., 2007, Fig. 1a.

Description: Test sub circular or ellipsoid, compressed, and with a constriction around the entire circumference of the neck base. Neck swollen at the base above the constriction, then tapering towards the pseudostome. Pseudostome ellipsoid in frontal view, slightly arched in broad view. Test composed of collected or predated euglyphid idiosomes. Average dimensions: L = 130–170 μm, B = 55–103 μm, P = 26–32 μm.

Differential diagnosis: A combination of a straight neck (in contrast with *A. crenata*) and smaller size (than *A. wellingtonia*), and lack of hollow keel (in contrast with *A. angatakere*) is characteristic within the genus.

Type locality: Cape Horn (Tierra del Fuego, Chile). Likely coordinates: -55.521438°, -68.100129°; Elevation: ca. 10 m.a.s.l..

Type specimen: Not provided. We declare Fig. 4 by CERTES (1889), here reproduced as Fig. 12D, as the type.

Etymology: Not provided. It is likely the name vas is related to the shape of the test, since the Latin “vas” means “vase” or “amphora”.

Habitat: Mosses (often *Sphagnum*), litter, and organic soils.

Geographical distribution: North America: Mexico (GOLEMANSKY, 1967; LAMINGER, 1973); South America: Bolivia (GRACIA, 1987), Brazil (WAILES, 1913; RHODEN & PITONI, 1999), Chile (WAILES, 1913; JUNG, 1942; BONNET, 1966; GRACIA & GADEA, 1982; GRACIA, 1987), Colombia (HEINIS, 1914), Ecuador (KRASHEVSKA et al., 2007), Malvinas/Falkland Islands (RICHTERS, 1908b), South Georgia (SMITH, 1982; BEYENS & CHARDEZ, 1995), Tierra del Fuego (CERTES, 1891; RICHTERS, 1908b; HOOGENRAAD & DE GROOT, 1951; VUCETICH, 1974); Venezuela (VAN OYE, 1956b); Central America: Costa Rica (LAMINGER, 1973; HEGER et al., 2011), Dominican Republic (BOBROV et al., 2021), Guadeloupe (BONNET, 1977a, 1977b), Guatemala (LAMINGER, 1973), Nicaragua (HEGER et al., 2011), Panama (HEGER et al., 2011), El Salvador (HEGER et al., 2011); Africa: Angola (BONNET, 1969), Congo (GAUTHIER-LIÈVRE, 1953; VAN OYE, 1956a, 1958, 1959), Guinea (GOLEMANSKY, 1963), Ivory Coast (BONNET, 1978), Kenya (CHARDEZ, 1990b), Madagascar (TODOROV & GOLEMANSKY, 2014), South Africa (GERICKE, 1932), Tanzania (MITCHELL & MEISTERFELD, 2005); Indian Ocean: Amsterdam Island (RICHTERS, 1908a), Iles Crozet (RICHTERS, 1908c), Marion Island (GROSPIETSCH, 1971; LARA et al., 2008); Asia: Java (HOOGENRAAD & DE GROOT, 1940a; VAN OYE, 1949), Philippines (BONNET, 1980b), Sumatra (HOOGENRAAD & DE GROOT, 1940a); Australasia: Australia (MEISTERFELD & TAN, 1998), Macquarie Island (PENARD, 1911), New Zealand (PENARD, 1911; HOOGENRAAD & DE GROOT, 1948; VAN OYE, 1956a; YEATES & FOISSNER, 1995; CHARMAN, 1997), Papua (BONNET, 1980a), Tasmania (SEAMER & GROOME, 2007); Pacific Ocean: Hawaii (RICHTERS, 1908a); Antarctica: Kerguelen Islands (BONNET, 1981a).

Table 1. *Morphometric characteristics of Apodera vas from beech (Nothofagus menziesii & N. truncata, now Lophozonia menziesii and Fuscopora truncata) forests in the Orongorongo Valley Field Station, southern North Island, New Zealand. Data are based on 23 randomly selected, empty tests. All measurements are given in µm. CV is given as % (M, median; Min, minimum; Max, maximum; from Yeates & Foissner,1995).*

Character	*Mean*	M	SD	CV	Min	Max
Length (total)	165.0	168	13.5	8.2	132	184
Length (posterior part or fundus)	104.0	104	6.7	6.5	88	120
Width of fundus (broader side)	92.3	93	7.0	7.6	79	110
Width at base of neck (broader side)	52.6	52	4.1	7.9	44	60
Width at pseudostome (broader side)	33.7	34	2.1	6.4	30	38
Width of fundus (narrower side)	60.5	64	7.9	13.1	44	72
Width at pseudostome (narrower side)	25.3	25	3.4	13.3	20	32

The record from Nepal (BONNET, 1977a, 1977b) is doubtful. Louis Bonnet (pers. comm. to E. Mitchell 11/13/2018) mentioned that this finding corresponds to a morphotype similar to *Padaungiella lageniformis*, with a constriction less clearly marked than that in the type ("*une forme atypique d'*A. vas *rappelant plus ou moins* lageniformis*, la constriction de la base du col étant moins nette que chez* vas *typique*.") Unfortunately, no sample or permanent slide exists from this record. In the collection deposited by Louis Bonnet at the Natural History Museum of Geneva; therefore, we consider this record as doubtful, possibly corresponding to *P. lageniformis* or to a yet undescribed closely-related species.

The record from mainland Antarctica (PENARD, 1911) is also highly doubtful. Murray reported seeing this species in Antarctica. Although the exact locality is unknown, Penard presumed it may have been collected from Blue Lake, near Cape Royds; however, he was unable to identify the species from the materials brought back by Murray and, thus, concluded that it was extremely rare, if present at all. Here, we consider this report as invalid. Although some shells could potentially be blown from the nearest known locality (Macquarie Island), the habitat seems too harsh for this species, as supported by a lack of reports from high alpine areas in locations otherwise known to be inhabited by the species (e.g., the South Island, New Zealand).

Remarks: Morphology similar in approximate shape and size to *Padaungiella lageniformis* (Penard) Lara & Todorov and *Alocodera cockayni* Penard, from which it differs mainly by the presence of a deep constriction around the entire circumference of the neck base (i.e., the junction between the main part of the test and the neck). Based on SSU rRNA data, LARA et al. (2008) confirmed that *Apodera vas* is closely related to *P. lageniformis*. For the comparison of *A. vas* with *A. wellingtonia*, see notes under the latter species. Despite being a large and distinctive species, *A. vas* displays highly variable shapes and dimensions. The test is lageniform and compressed. The colour varies from faint yellowish to dark brown. L/B can be variable, viz., 1:1.5-2.0. Likewise, the ratio between the inflated posterior part

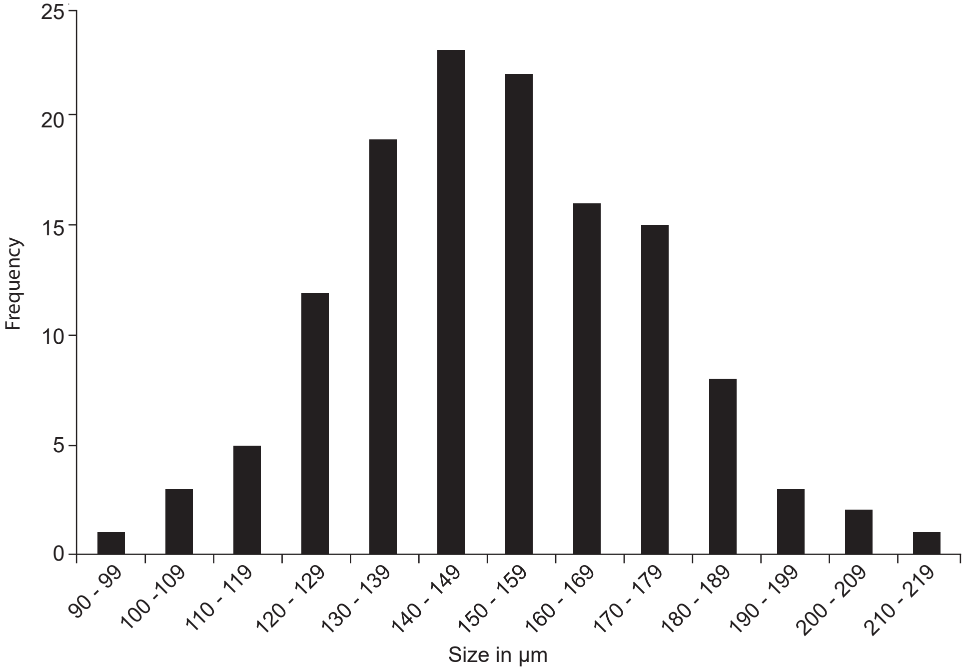

Fig. 13. Frequency distribution of *Apodera vas* test length based on 130 measurements from 22 publications (SMITH & WILKINSON, 2007).

and the neck can be rather variable, viz., 1:1.5-1.7 (YEATES & FOISSNER, 1995, see also Table 1 for the detailed morphometric characteristics).

The neck is variable in length, but never longer than the main, posterior part of the test, and always separated from it by a deep constriction. The neck attachment to the main posterior part can vary from straight to strongly oblique (YEATES & FOISSNER, 1995; ZAPATA & FERNANDEZ, 2008). In broad view, the sides of the neck can be parallel, or slightly to strongly swollen at the base. The aperture is always elliptic, with an unstructured rim and variable in size, although it is never larger than the base of the neck. Test is covered by circular, oval, or elliptical plates distributed more or less regularly.

The test dimensions vary considerably among studies. SMITH & WILKINSON (2007) summarized data from 130 individual measurements in 22 publications, revealing an observed test length from 90 to 210 µm (median of 150 µm; and a modal 63 percentiles between 130 µm and 170 µm). The frequency distribution of test length is shown in Fig. 13.

Ecology and distribution: *Apodera vas* is frequently cited as an example of a microorganism with restricted distribution (probability > 95%; FOISSNER et al., 2008). Absent from the mid- to high-latitudes of the Northern Hemisphere where most research on testate amoebae has been conducted, and appears mostly restricted to land masses corresponding to the former Gondwana

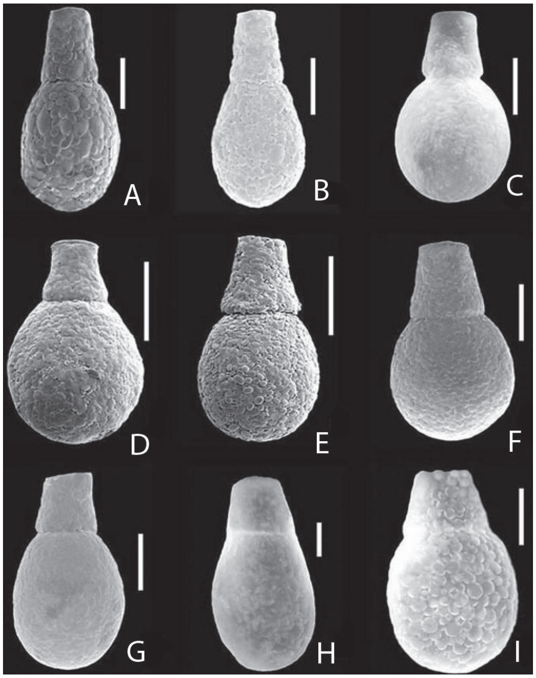

Fig. 14. SEM images illustrating the morphological variability of *Apodera vas*. Scale bars: A-C, F, G, & I = 50 μm; D & E = 100 μm; H = 25 μm. Modified from ZAPATA & FERNANDEZ (2008) with permission from the editor.

super-continent; however, it also occurs in adjacent, non-Gondwanian regions, such as the Caribbean, Central America, and Southeast Asia. The Tropic of Cancer belt seems to demarcate a border to its northward expansion (FOISSNER, 1999b; MITCHELL & MEISTERFELD, 2005; SMITH & WILKINSON, 2007; SMITH et al., 2008). *A. vas* was shown to prey on nematodes (YEATES & FOISSNER, 1994), but its overall feeding habits are unknown.

Nomenclature: GROSPIETSCH (1971) described two varieties of *Apodera vas*: var. *longicollis* and var. *obliqua*, which differ from the type mainly by their elongated and laterally bent necks, respectively. We have included these two varieties in the list of synonyms, as varieties described after 1960 should be considered as infra-subspecific taxa and are thus unavailable names according to ICZN Art. 45.6.3. Some authors believe that such forms fall within the natural variability of the species (DEFLANDRE, 1936; YEATES & FOISSNER, 1995). Whether these variations are due to phenotypic plasticity or should be assigned to independent species requires further detailed analyses. ZAPATA & FERNÁNDEZ (2008) reported polymorphism within *A. vas* (see Fig. 14) and identified two or three morphotypes. Accordingly, the taxonomy of *A. vas s.l.* must be studied further using molecular and morphometric methods. Given its size, described morphological diversity, and distribution range, it is likely that *A. vas* is a complex of species (ZAPATA & FERNANDEZ, 2008), and each of these species is likely to have a more restricted distribution than that of the overall complex (as observed for *Hyalosphenia papilio*; HEGER et al., 2013; SINGER et al. 2019).

Another problematic taxon is *A. vas recticollis* described by JUNG (1942a). The identification criterion (less swollen neck) is not wholly convincing based on the author's illustrations. We have therefore included this taxon in the list of *inquirenda* names (see p. 209).

Apodera wellingtonia (Decloitre, 1964) Chardez, 1994

1964b *Nebela wellingtonia* Decloitre, Expéditions Antarctique Françaises en Terre Adelie (Missions Paul-Emile Victor) 259: 41 (Fig. 44, original drawing).

1994 *Apodera wellingtonia* Decloitre, 1964 – Chardez, Trav. Lab. Unit. Zool. Fac. Sc. Agr. Gembloux 15: 2 (re-evaluation of morphology and transfer to the genus *Apodera*).

Fig. 15. *Apodera wellingtonia*: Original drawing from DECLOITRE (1964b).

Description: Test lageniform, compressed, with a deep constriction between the posterior part and the neck (as in *A. vas*). Sides of the neck approximately parallel, tapering from the junction of the neck constriction to the pseudostome (notably not or less swollen than in *A. vas*). Test composed of recycled, collected, or predated euglyphid idiosomes. Large species: L = 185–220 µm, B = 125–130 µm, thickness of the main body part = 34–40 µm, L_{neck} = 55-63 µm, B_{neck} base = 67-74 µm, P = 51–55 µm x 10–15 µm.

Differential diagnosis: Differs from *Apodera vas* by its larger dimensions and smaller neck (cf. remarks).

Type locality: Summit area of Mount Wellington, Tasmania. Likely coordinates: -42.896344°, 147.230518°; Elevation, ca. 1240 m.a.s.l..

Type specimen: Not provided. We declare Fig. 44 by DECLOITRE (1964b), reproduced here as Fig. 15, as the type.

Etymology: The name of this species is derived from the name of Mount Wellington, from where the original species-containing samples were collected.

Habitat: Meltwater puddles; also mentioned from temperate rain forests along the mountain slopes, in wet, rotten wood of a tree stump, and cortical lichens.

Geographical distribution: Tasmania (DECLOITRE, 1964b).

Remarks: DECLOITRE (1964b) separated this species from *Apodera vas* based on the larger test dimensions (L = 130–170 µm, B = 55–103 µm in A. vas vs. L = 185– 220 µm, B = 125–130 µm in *A. wellingtonia*) and an allegedly more swollen neck; however, several authors reported a larger size range for *A. vas* (L = 90–234 µm), without referring it to as possibly *A. wellingtonia* (YEATES & FOISSNER, 1995; SMITH & WILKINSON, 2007; ZAPATA & FERNANDEZ, 2008). Accordingly, the validity of the taxon *A. wellingtonia* is questionable, and further detailed taxonomic work is required to assess the range, as well as morphological and genetic variability within the species of this genus. The original drawing resembles Fig. 14 (I). Thus, if future studies showed that *A. vas* indeed represents a species complex, then *A. wellingtonia* will likely be confirmed as one of the valid taxa within this complex.

7.5. Genus *Certesella* Loeblich & Tappan, 1961

Type species: *Certesella martiali* (Certes, 1889)

1942 *Penardiella* gen. nov. Jung, Arch. Protistenk. 95: 381 (invalid genus owing to lack of type designation).

1961 *Certesella* Jung, 1942 – Loeblich & Tappan, Proc. Biol. Soc. Wash., 74: 216 (validation of genus *Penardiella* under the new name *Certesella* by assignment of *C. martiali* as the type species).

Description: Test piriform, elongated, or lageniform in broad view. The development of the neck varies among species, from slightly- to well-differentiated. The two primary genus characteristics are: 1) the presence of two depressions with large pores located on the broad side of the test near the margin, approximately 2/3rds of the distance between the fundus of the test and the pseudostome. Which do not open into the test but are instead connected by short tubes, (as in genus *Porosia*); and 2) The presence of protuberance "teeth" on the inner surface of the neck of most species, visible as punctuations in LM. Tooth number and distribution appear to have a taxonomic value.

Remarks: This genus was proposed by JUNG (1942b) as *Penardiella*, without type designation. It was later validated under a new name by LOEBLICH & TAPPAN (1961). The genus was believed to be restricted to the Southern Hemisphere (MEISTERFELD, 2002) but has recently been reported from Central America (HEGER et al., 2011a; BOBROV et al., 2013) and the Caribbean (BOBROV et al., 2021). Like genera *Apodera* and *Alocodera*, it does not seem to have crossed the subtropical desert belt around the Tropic of Cancer (SMITH et al., 2008).

Etymology: The genus is named in honour of the French naturalist Adolph-Adrien Certes (1835–1903).

Five species have been described:

Key to the species

1. Large test without distinct neck in broad view, the main body tapering gradually towards the pseudostome. A single line of teeth situated parallel to the edge of the pseudostome, giving a punctuated impression. Keel present. Largest known species in the genus; indeed, one of the largest Hyalospheniidae: L = 199.5–277.5 µm, B = 119-140 µm *C. australis* (p. 58)

– Test generally < 200 µm (but see *C. martiali*), with a distinct neck in broad view. Internal teeth organized differently or absent 2

2. Neck short, only moderately compressed, subcylindrical (oval in cross-section), sharply differentiated from the rest of the test. Presence of internal teeth unclear (described as "granules"); but, if indeed teeth are present, these are scattered with no apparent organization. Short hollow keel: L = 120–136 µm, B = 95–100 µm *C. murrayi* (p. 67)

– Limit between the neck and the main part of the test less abrupt. Test gradually tapering from the two large pores towards the neck in broad view 3

3. Internal teeth clearly visible on either side of a narrow longitudinal internal ridge, or a broad central part without internal teeth, more or less elongated species, L/B mostly < 2, but see *C. certesi* 4

– Internal teeth absent or very rare, no narrow longitudinal internal ridge in the neck region, elongated species (L/B = 2.03–2.58) *C. larai* (p. 62)

4. Internal teeth randomly scattered along the entire neck area, separated by a narrow longitudinal internal ridge. Narrow keel present. Smaller species: L = 80–157 µm, B = 70–90 µm, rather elongated (L/B = ca. 1.75–2.9, median ca. 2) *C. certesi* (p. 58)

– Neck divided into three parts of approximately equal width: A broad central part without longitudinal ridge and two areas on either side with internal teeth. Keel absent. Larger species: L = 147–238 µm, B = 77–130 µm, somewhat less elongated (L/B = ca. 1.5–2, median ca. 1.75) *C. martiali* (p. 65)

Certesella australis (Vucetich, 1973)

1973a *Nebela australis* Vucetich, Neotropica 19: 80 (Figs. 1–2, original drawing).

1973b *Certesella australis* (Vucetich, 1973a) – Vucetich, Obra del Museo de La Plata IV: 310 (re-evaluation of morphological characters and transfer to a new genus).

Icon.: VUCETICH, 1973a, Figs. 1–2; VUCETICH, 1973b, L. III.

Description: Test elongated-piriform in broad view, gradually tapering towards the pseudostome, without a distinct neck. Test compressed, with a distinct hollow keel covering the entirety of its lateral margin, except for the neck region. According to the original description, two small pores are present on the lateral margin but are very difficult to observe. Two lateral depressions are located close to the margin of the test, approximately in the longitudinal middle, somewhat below the level where the neck begins. In each of these depressions, a short pore connects the two sides of the test. Test transparent to yellowish-brown, composed of circular or oval test plates that are sometimes hard to observe, as they are covered with a thick organic layer. Largest species in the genus: L = 199.5–277.5 µm, B = 119–140 µm, P = 40–46 µm. Pseudostome curved in broad view, with a thick organic lip. One single line of teeth (ca. 10 in total) situated parallel to the edge of the pseudostome, giving a punctuated impression in SEM (Fig. 16).

Differential diagnosis: Differs from other *Certesella* species by its larger dimensions, elongated-piriform test shape, and the absence of a distinct neck. It may be confused with *Porosia paracarinata* from which it differs by its larger dimensions and the presence of internal teeth parallel to the pseudostome.

Type locality: Lapataia, Tierra del Fuego, Argentina. Likely coordinates: -54.832504°, -68.560833°.

Type specimen: Not provided. We declare Fig. 1 by VUCETICH (1973a), reproduced here as Fig. 16D1, as the type.

Etymology: From Latin, “auster” means the “south”.

Habitat: *Sphagnum* mosses, wet green mosses.

Geographical distribution: South America: Chiloe Island (Chile) (MEISTERFELD unpubl.), Southern Chile in the region of Puerto Montt (FERNANDEZ et al., 2015), Tierra del Fuego (Argentina and Chile, KOSAKYAN et al., this work)

Remarks: This species has not been found outside of the southern part of South America and, thus, may be endemic to this region.

Certesella certesi (Certes, 1889)

1889 *Nebela collaris* var. a, b, Certes, Cap Horn VI: 13–14 (misapplied name), (Pl. II. Figs. 2–3, 5, original drawings).

1911 *Nebela certesi*, Penard, Brit. Ant. Exp. 1907–9, I, Biology I: 241.

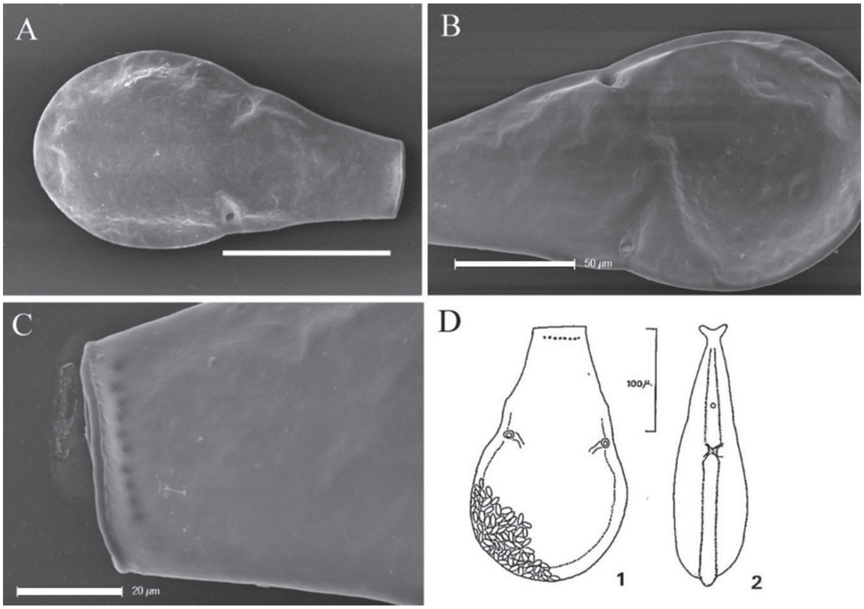

Fig. 16. *Certesella australis*: (A) SEM image of a specimen from Tierra del Fuego, Argentina; (B) Higher magnification view of another specimen from the same sample showing lateral depressions with pores and a hollow keel; (C) Further higher magnification view of specimen in image B showing the line of teeth (approximately ten) situated parallel to the edge of the pseudostome, giving a punctuated impression; (D) Line drawings from the original description, broad and profile views showing the hollow keel, and two large pores situated on the lateral margin. Note the presence of a lateral pore between the large pores and the pseudostome (from VUCETICH, 1973b). Scale bars: A & D = 100 µm, B = 50 µm, C = 20 µm. Images (A–C) by Anush Kosakyan and Enrique Lara.

1942b *Penardiella certesi,* Jung Arch. Protistenk. 95: 21 (invalid genus, lack of type species).

1961 *Certesella certesi*, Loeblich & Tappan, 1961, Proc. Biol. Soc. Wash. 74: 213–234 (validation of the genus *Certesella* by assigning a type species).

Icon.: CERTES, 1889, Pl. II, Figs. 2–3, 5; PENARD, 1911, Pl. XXIII, Fig. 7; JUNG, 1942, Fig. 56; VUCETICH, 1973a, Pl. II; MEISTERFELD, 2002, Fig. 70.

Description: Test elongated to piriform in broad view, with a distinct elongated neck, giving the test a bottle shape in broad view. The original description (PENARD, 1911) indicated the presence of a “faint keel”, although this is not visible in the illustrations. Test composed of circular or oval plates, sometimes hard to observe, as they are covered with a thick organic layer. L = 80–157 µm, B = 70–90 µm, P = 30–45 µm. Pseudostome curved in broad view, with a thick organic lip. Two lateral depressions with large

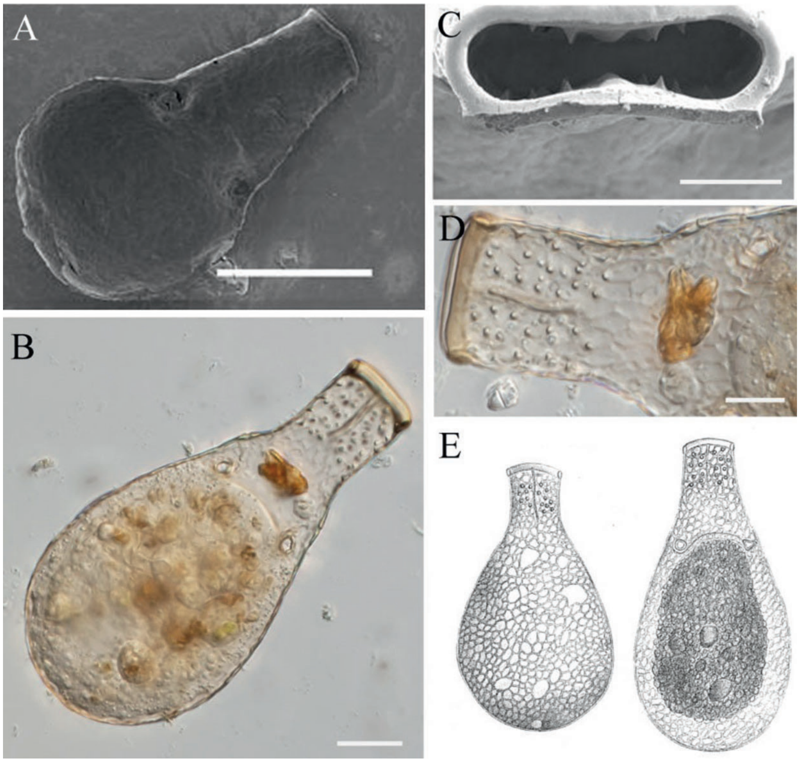

Fig. 17. *Certesella certesi*: (A & C) Broad and frontal view (respectively) SEM images of a specimen from Marion Island, South Africa, possibly corresponding to the original description of *C. certesi* showing conical teeth and longitudinal thickening (note that the specimen on image A appears to be collapsed); (B & D) Broad view LM images of a living specimen from Tierra del Fuego, Chile, detailing the neck, showing the groove and punctuations, as well as the lateral pores and localized thickening of the test (top of the image); (E) Line drawings (right) from the original description from CERTES (1889). Original names: left: *N. collaris* va r. a, right: *N. collaris* var. b. Scale bars: A = 50 µm, B = 20 µm, C & D = 10 µm. Note that the sides of the neck for the specimen illustrated in the SEM images are not parallel, in contrast to the specimens illustrated in the LM images and drawings. Accordingly, the specimen illustrated in A & C may represent another closely related species. Images: (A & B) modified from SMITH et al. 2008, and (B & D) by Edward Mitchell.

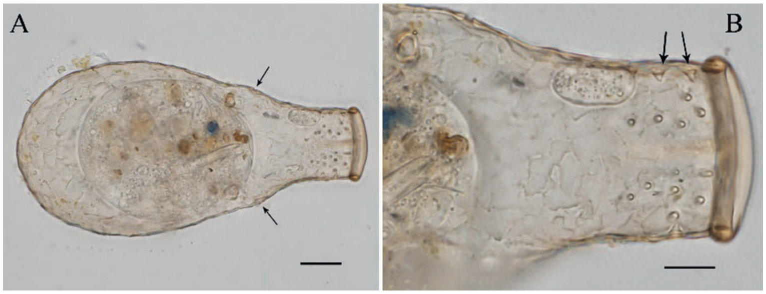

Fig. 18. (A) LM images of the same specimen of *Certesella* sp. from New Zealand illustrating the punctuations on the neck. The images show intermediate characters between *C. certesi* and *C. martiali*, depicting the morphological diversity, and likely existence of several non-described species within this group. Test length (ca. 150 µm) is slightly below the lower range of *C. martiali*, but within the range of *C. certesi*. Arrows indicate two lateral pores. (B) Higher magnification view of the pseudostome region for the same individual. The arrows indicate the position of lateral teeth protruding from the internal sides of the neck. A lateral pore is also visible in the upper left of the image, with a thicker localized test, and producing a small bulge (also visible in image A.) Scale bars: A = 20 µm, B = 10 µm. Images (A & B) by Edward Mitchell.

central pores, connected to each other by internal tubes at the base of the neck, ca. 2/3rds from the fundus of the test to the pseudostome. Lateral pores clearly visible in LM ca. 10 µm towards the pseudostome from the position of the two large pores; here, the test is thickened and more or less swollen but less so than that in *C. martiali*. Longitudinal, central thickening present along most of the neck (Fig. 17C & D). A variable number (ca. 25–30) of conical tooth-like punctuations, well visible in LM, inserted without any apparent order on the inner surface of the neck, along either side of the central line (Fig. 17D), with a few more (2–3) inserted on the inner surface of the sides of the neck and which are therefore clearly visible in LM (Fig. 18).

Differential diagnosis: *Certesella certesi* is very similar in appearance to *C. martiali*. The two species differ mainly in size. *C. certesi* is smaller than *C. martiali* (L = 80–157 µm versus L = 147–238 µm, respectively), with only a limited size overlap. In his monograph on Hyalospheniidae, DEFLANDRE (1936) discussed the similarities between these two species and the possibility that they represented varieties or forms of the same species. DEFLANDRE (1936) also mentioned that the longitudinal groove present in the neck of *C. certesi* is lacking in *C. martiali*. Other differentiating characters mentioned by VUCETICH (1973a) include the presence of a faint keel in *C. certesi*, as well as the size and shape of pores situated in the lateral depressions. According to Vucetich, the pores are comparatively smaller, with irregular margins in *C. certesi* than the larger and more regular-margined pores in *C. martiali*; however, in the absence of detailed morphometry, the validity of these criteria remains unsupported. Accordingly, the most convincing and simple criterion regards the presence or absence of a groove in the middle of the neck, easily visible in LM (see Fig. 17B & D). Nevertheless, the respective taxonomic position of these two species mandates clarification using modern morphological and molecular methods.

Type locality: Hoste Island, Cape Horn, Chile. Likely coordinates: -55.521438°, -68.100129°; Elevation, ca. 10 m.a.s.l..

Type specimen: Not provided. We declare Pl. II, Fig. 5 by CERTES (1889), reproduced here as Fig. 17E (right image corresponding to the var. b), as the type.

Etymology: The species was named in the honour of the French naturalist Adrien Certes (1835-1903), who first reported this species as a new variety of *Nebela collaris* (see Remarks below).

Habitat: *Sphagnum* mosses.

Geographical distribution: South America: Tierra del Fuego (MITCHELL et al., unpubl.), Cape Horn (CERTES, 1889), Argentina (VUCETICH, 1973a), Chile (JUNG, 1942; FERNANDEZ et al., 2015), Colombia (HEINIS, 1914); Pacific Ocean: West Samoa, Tonga (KORGANOVA, 1985); Asia: Java (HOOGENRAAD & DE GROOT, 1940a); Australasia: Australia (PENARD, 1911; MEISTERFELD & TAN, 1998), Marion Island (GROSPIETSCH, 1971; SMITH et al., 2008), New Guinea (Irian Jaya) (BONNET, 1992), New Zealand (PENARD, 1911; CHARMAN, 1997; MCGLONE & WILMSHURST, 1999). Likely circumaustral.

Remarks: The species first was described by CERTES (1889) as a variety of *Nebela collaris*. Certes mentioned two varieties (a and b), which are very similar, save for the presence of two lateral depressions with large pores connected by tubes, as in genus *Porosia*, in var. b that are lacking in var. a, and a longitudinal line in the neck in var. a that is lacking in var. b. Therefore, the characteristic morphological traits of *C. certesi* represent a mixture of both illustrations (see Fig. 17E). In line with this, PENARD (1911) considered these characters (combining var. a and b) quite distinct from those of *N. collaris* and described a new species *Nebela certesi*. The range of morphologies illustrated in Fig. 17 suggests the existence of several species. JUNG (1942b) redefined family Nebelidae, including *Nebela certesi* into genus *Penardiella*. As Jung's classification lacked type designations, the genus was invalidated (ICZN Art. 13.3). LOEBLICH & TAPPAN (1961) validated it as genus *Certesella*. The authority for this taxon has been erroneously attributed to PENARD (1911), as he named the species; however, CERTES (1889) was the first to illustrate and describe its morphology, under the name "*Nebela collaris* var. a". According to ICZN Art. 50, Certes deserves recognition as the authority for this taxon.

Certesella larai Bobrov, Duckert, & Mitchell, 2021

2021 *Certesella larai*, Bobrov et al. 2021, Acta Protozool. 60: 61-75.

Icon.: BOBROV et al., 2021, Figs. 1–3.

Description: Shell elongated, pear-shaped, compressed with two large, rounded to irregular-elongated elliptical pores connected by tubes clearly visible in broad view. No visible lateral pore. Punctuations and inner teeth on the neck absent or rare. In broad view, shell outline ovoid, elongated at the fundus, then narrowing slightly towards the area of the two large pores where the sides are approximately parallel, and narrowing again at the neck base. Neck relatively short, with a slight bulge, and then again approximately parallel near the aperture. L = 138.2–153.4 µm, B = 56.8–63.9 µm, P = 24.0–29.8 µm, distance from the fundus to pores = 79.5–92.3 µm, distance from the fundus to the base of the neck = 109.3–125.0 µm, distance between pores =

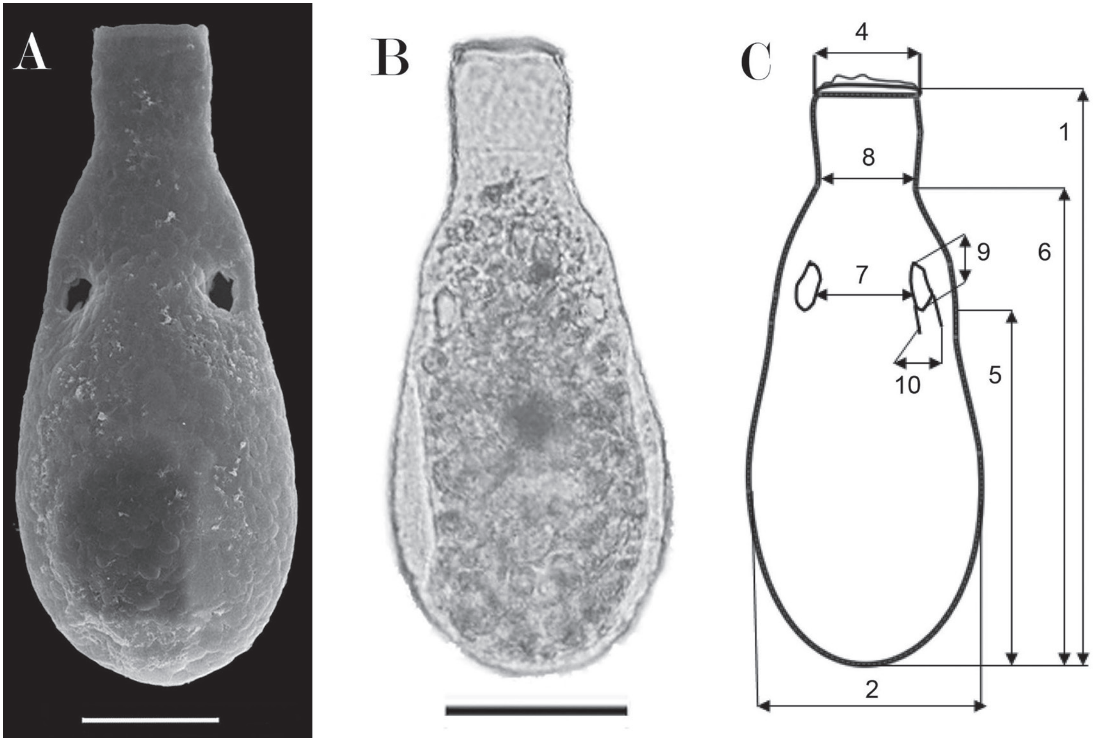

Fig. 19. *Certesella larai*: (A) SEM image of overall shape (modified from BOBROV et al., 2021, Fig. 3); (B) LM image of specimen from Dominican Republic, broad lateral view (modified from BOBROV et al. 2021, Fig. 2B); (C) General shape of *C. larai* and indication of the morphometrical measurements: (1) test length (L), (2) test breadth (B), (3) test length/breadth ratio (L/B, not illustrated), (4) aperture (long axis), (5) distance from fundus to the pores, (6) distance from fundus to the base of neck, (7) distance between the pores, (8) width of the neck at the narrowest point, (9) pore length, and (10) pore width (from BOBROV et al. 2021, Fig.1). Scale bars: A = 30 µm, B = 40 µm.

31.2– 34.1 µm, width of the neck at the narrowest point = 18.5–28.4 µm, pore length = 8.5–12.8 µm, pore width = 4.3–5.7 µm, shell L/B = 2.18–2.58. Shell colourless, covered with oval plates of different sizes and shapes, most likely recycled idiosomes from euglyphid testate amoebae. Pores surrounded by smaller recycled idiosomes than those of the main body. Pseudostome rim smooth and somewhat wavy, with lip 2–2.5 µm thick.

Differential diagnosis: *Certesella larai* stands out as the most elongated and narrowest species of the genus, thus making confusion unlikely.

Type locality: Parque Nacional Alerce Costero, Los Rios Region Chile, Small *Sphagnum* peatland, with Fitzroya trees, *Sphagnum* mosses, 40.171975°; 73.491841°, 1028m. a.s.l.. Sample code in the reference collection of the Laboratory of Soil Biodiversity, University of Neuchâtel, Switzerland: EM-1453. Note: in contrast to the original description, the type locality is here changed to match the sampling location of the type specimen

Type specimen: Type: (Chilean population) Natural History Museum of Neuchâtel, Rue des Terreaux 14, 2000 Neuchâtel, Switzerland, slide no. 95-2. Paratype: Laboratory of Soil Bioindication, Department of Soil Geography, Faculty of Soil Science, Lomonosov Moscow State University, slide no. 4-2020.

Etymology: The species was named in the honour of Enrique Lara, as a recognition for his major contribution to the molecular taxonomy and phylogeny of testate amoebae.

Habitat: Forest litter, fern litter, *Sphagnum* mosses.

Geographical distribution: South America: (Chile); Caribbean: Dominican Republic. Probably widespread in South America, Central America, and the Caribbean.

Remarks: The taxonomic position of this species is a bit confusing. Indeed, BOBROV et al. (2021) discussed it as: "*The taxonomic position of this new species is not crystal clear from morphology alone and indeed we shifted back and forth between placing this new species into genera* Certesella *or* Porosia. *The overall shape is most similar to* C. certesi, *but the absence of characteristic longitudinal groove is a clear distinguishing character. The range of illustrated morphotypes for* Certesella certesi *suggests this is a species complex but all share the characteristic longitudinal grove. Based on the absence of clear internal teeth (or near absence if the observed element indeed corresponds to such structures) it would be logical to consider it as an elongated species in genus* Porosia, *which would indeed be very different in shape from the other two species. Given the fact that this species was rare in the three samples, its specific habitat as well as companion species may not necessarily reflect its ecological optimum.* Certesella certesi, C. martiali, *and* C. australis *were all described from* Sphagnum *peatlands in South America (Certes 1889; Vucetich 1973; Wailes 1913). In Mexico, Bobrov et al. found* Certesella certesi *only in mountain cloud forests (Bobrov et al. 2013), while in New Zealand, Bamforth found it only in lowland podocarp forests (Bamforth 2015).* Certesella martiali *was reported from mosses in Guatemala (Laminger 1973). Heger et al. observed* Certesella sp. *in mosses in several locations across Central America (Heger et al. 2011a). By analogy,* Porosia bigibbosa *is a rare testate amoeba species in peatlands but is quite common in beech forests in Bulgaria (Todorov 2002) and a new species,* P. paracarinata, *was also found in forests in Japan (Bobrov et al. 2015). The discovery of* Certesella larai *suggests that the genus* Certesella *is also not restricted to peatlands. Thus, while hyalospheniids in general are most diverse in acidic and nutrient-poor habitats such as* Sphagnum *peatlands, this is not true for genus* Porosia *and possibly not either for* Certesella. *As the ecology and diversity of testate amoebae have been much more intensively studied in peatlands than in forests, the ecology of some species may not yet be fully understood. The fact that this new species was found in two very distant regions but was rare in the three samples and absent from ca. 100 other neotropical samples may reflect a sampling bias in favour of* Sphagnum *or other habitats which are a priori perceived as more favourable for testate amoebae. This can potentially cause interesting species to be overlooked. Another recent example is the discovery of a new* Quadrulella *species in a semi-desert environment in Mexico (Pérez-Juárez et al. 2017), which contrasts with the wetland habitats where species of this genus are usually found. The discovery of these new species illustrates that when under sampled habitats are studied, some surprising discoveries can be made. This should be a motivation for protistologists to continue exploring a broad range of habitats*".

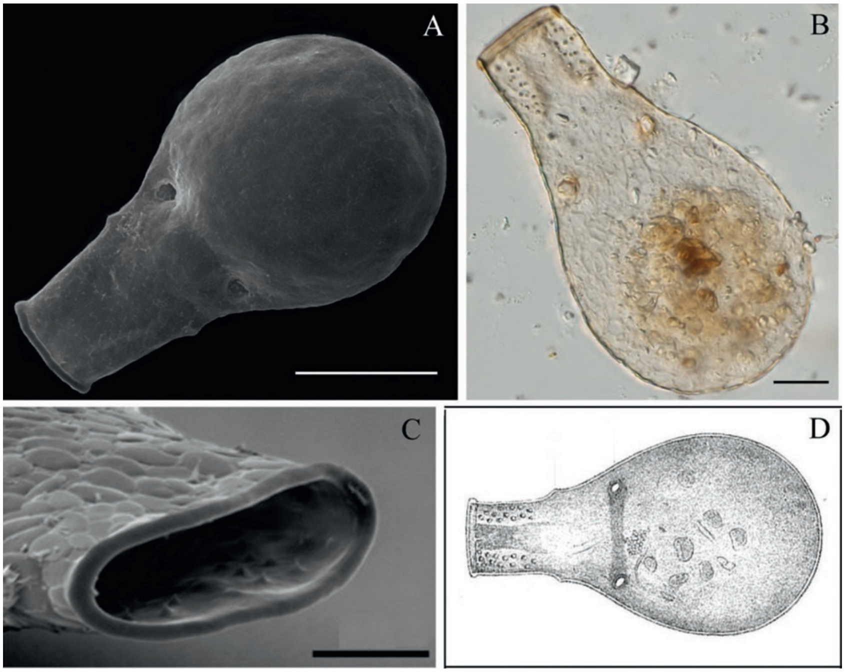

Fig. 20. *Certesella martiali*: (A & C) Broad view SEM image of a specimen from Argentina, (B) Broad view LM image of a specimen from Chile, (C) Close-up oblique-frontal view of the aperture showing the internal conical teeth (note the lack of a narrow internal ridge compared with Fig. 17C), (D) *C. martiali* broad view from the original description (CERTES, 1889). Scale bars: A = 50 µm, B = 20 µm, C = 10 µm. Images by: (A) Anush Kosakyan, (B) Edward Mitchell, and (C) Ralf Meisterfeld.

Certesella martiali (Certes, 1889) Loeblich & Tappan, 1961

1889 *Nebela martiali*, Certes, Mission Sci. Cap. Horn, T.VI: L14 (Pl. I, Fig. 3, original drawing).

1914 *Nebela penardi* Heinis, Mem. Soc. Sci. Nat. Neuchateloise 5: 687 (junior synonym).

1942b *Penardiella martiali*, Jung, Arch. Protistenk. Bd. 95. H.3: 381 (invalid genus, lack of type species), non Penardiella Kahl, 1930.

1961 *Certesella martiali*, Loeblich & Tappan, Proc. Biol. Soc. Wash. 74: 213–234 (validation of the genus *Certesella* by assigning a type species).

Icon.: CERTES, 1889, Pl. I, Fig. 3; DEFLANDRE, 1936, Figs. 142–144; VUCETICH, 1973a, Pl. I; KOSAKYAN et al., 2012, Fig. 7b.

Description: Test elongated-piriform (i.e., bottle-shaped) in broad view, with a distinct elongated neck. Test composed of circular, ovoid, or angular plates, covered with a thick organic layer and, therefore, sometimes difficult to observe. Dimensions according to the original description: L = 155–170 µm, B = 85–91 µm. VUCETICH (1973) provided a broader size range: L = 147–238 µm, B = 77–130 µm. Here, we (E.M.) present material from Argentina, Tierra-del-Fuego (Rancho Hambre peatland complex): L = 175–178 µm, B = 90–92 µm, P = 38–45 µm. Pseudostome curved in broad view, with a thick organic rim. Two lateral depressions located ca. 2/3rds of the distance from the fundus of the test to the pseudostome, each with a large central pore connecting the two sides of the test by an internal tube. Two triangular expansions of the test are often visible where lateral pores are located and corresponding to a thickening of the test ca. 10 µm towards the pseudostome from the position of the two large pores, as in *Nebela penardiana*, and to a lesser extent in *Certesella certesi* (Fig. 20A). Neck divided longitudinally into three parts of approximately equal width: Central part of the neck lacking any obvious structure (particularly visible for the characteristic groove of *C. certesi*) On either side of this central part, two rows of randomly arranged, conical tooth-like punctuations pointing towards the inside of the test (visible in LM, but not in SEM; Fig. 20B). A few conical tooth-like punctuations inserted on the sides of the neck and pointing towards the inside of the test.

Differential diagnosis: *Certesella martiali* is very similar to *C. certesi*. See differential diagnosis on *C. certesi* in p. 61.

Type locality: Hoste Island, Cape Horn, Chile. Likely coordinates: -55.521438°, -68.100129°, Elevation, ca. 10 m.a.s.l..

Type specimen: Not provided. We declare Pl. I, Fig. 3 by CERTES (1889), reproduced here as Fig. 20D, as the type.

Etymology: This species was named in honour of Louis-Ferdinand Martial, commander of the Romanche, a three-mast vessel of the French navy used for the 1882-1883 scientific expeditions to Tierra del Fuego.

Habitat: *Sphagnum* mosses.

Geographical distribution: South America: Tierra del Fuego (VUCETICH, 1973a; MITCHELL et al., unpubl.), Argentina (VUCETICH, 1973a), Cape Horn (CERTES, 1889), Chile (JUNG, 1942a; FERNANDEZ et al., 2015), Colombia (HEINIS, 1914), Ecuador (KRASHEVSKA et al., 2007); North & Central America: Mexico, Guatemala (LAMINGER, 1973), Guadeloupe (BONNET, 1977); Asia: Java (HOOGENRAAD & DE GROOT, 1940a); Sumatra (HOOGENRAAD & DE GROOT, 1940a); Australasia: New Guinea (Irian Jaya, BONNET, 1992), Tasmania (DECLOITRE, 1964; SEAMER & CROOME, 2007), New Zealand (HOOGENRAAD & DE GROOT, 1948), Macquarie Islands, Marion Island (GROSPIETSCH, 1971); Arctic Russia (misidentification, see Remarks). Probably circumaustral.

Remarks: Genus *Certesella* has a non-cosmopolitan distribution. As observed for genera *Apodera* and *Alocodera*, the genus *Certesella* does not appear to have crossed the subtropical desert belt around the Tropic of Cancer (SMITH et al., 2008). BEYENS et al. (2000) reported *C. martiali* from moss and aquatic habitats within Arctic Russia (Dikson Island and Eklips, Severnaya Zemlya, and Franz Joseph's Land archipelago); however subsequently, in accordance with YANG et al. (2010) and confirmed by Lous Beyens (pers. com.), this record was deemed invalid, and more likely a typographical error or mis-identification (perhaps *Porosia*).

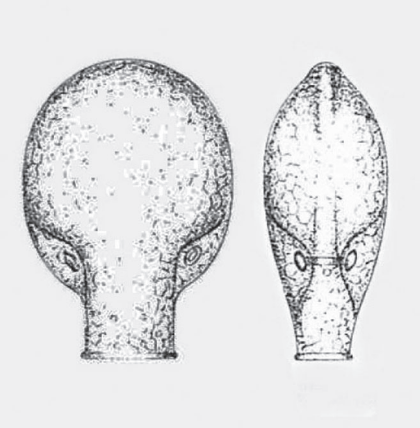

Fig. 21. *Certesella murrayi* (broad and profile views) according to the original description (from WAILES, 1913).

Certesella murrayi (Wailes, 1913)

1913 *Nebela murrayi* Wailes, Journ. Lin. Soc. Zool. XXXII: 201–218 (Figs. 18–19, original drawings).

1942 *Penardiella murrayi* (Wailes) Jung, Arch. Protistenk. Bd. 95. H.3: 381 (invalid genus, lack of type species).

1961 *Certesella murrayi* Wailes 1913 – Loeblich & Tappan, Proc. Biol. Soc. Wash. 74: 213–234 (validation of genus *Certesella* by assigning a type species).

Icon.: WAILES, 1913, Figs. 18–19; SMITH et al., 2007, Fig. 1b, d.

Description: Test wide piriform in broad view, compressed with a well-developed, but short subcylindrical (ovoid in cross-section) neck, and a short hollow keel at the base of the neck. L = 120–136 µm, B = 95–100 µm, P = 30–35 µm. Pseudostome with a thick organic rim. Two lateral depressions at the junction of the neck and the main part of the test, each with a large central pore connecting the two sides of the test by an internal tube. Conical teeth present on the inner surface of the neck (invisible on the illustration, but indicated in the original description).

Differential diagnosis: Differs from other *Certesella* species by the presence of a short hollow keel at the base of the neck and a neck sharply differentiated from the rest of the test, rather than gradually tapering toward the pseudostome as in *C. australis*, *C. certesi* and *C. martiali*.

Type locality: Two localities are mentioned in the original description: Puntas Arenas (Southern Chile), likely coordinates: -53.142121°, -71.003947°; and Mt. Papagaio (Rio De Janeiro, Brazil). **The locality corresponding to the illustrated specimen is unspecified.**

Type specimen: Not provided. We declare Figs. 18–19 by WAILES (1913), reproduced here as Fig. 21, as the type.

Etymology: The species was named after James Murray who collected the moss samples where the species was found.

Habitat: *Sphagnum* and other mosses. The material analysed by WAILES (1913) from Brazil was described as, "gatherings from moss (shore and inland), ponds, and *Sphagnum* collected on the slopes and near the summits of Mt. Papagaio (4000–5000 ft.) and Mt. Corcovada (2200 ft.)"; and the material from Punta Arenas as, "gatherings from *Sphagnum*, ponds, and streams".

Geographical distribution: South America: Argentina (VUCETICH, 1980), Brazil (WAILES, 1913), Chile (WAILES, 1913). Possibly a South American endemic, like C. australis.

7.6. Genus *Cornutheca* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Type species: *Cornutheca ansata* (Leidy, 1874)

2016 *Cornutheca* gen. nov. Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in Kosakyan et al., Cladistics 32: 622.

Description: Test elongated-piriform, with a distinct neck, and lateral margins tapering towards the aperture. Two lateral horns, pointing towards the fundus of the test, either free or connected to the main part of the test by a lateral hollow keel, and in some cases, surrounding the fundus. Test hyaline or slightly yellowish, composed of circular to elongated shell plates most likely recycled from euglyphid testate amoeba prey.

Remarks: This genus was proposed by KOSAKYAN et al. (2016), when they split genus *Nebela* into six monophyletic groups based on molecular data and general test shapes. The genus *Cornutheca* includes all *Nebela* species bearing two hollow, lateral conical expansions of the test (referred to as "horns") extending from the sides of the test at an angle towards the posterior end and starting at ca. 1/3rd of the distance from the pseudostome to the posterior end. The existing data suggest that these morphologically distinct species all share narrow geographical distributions (HEGER et al., 2011b; QIN et al., 2016); however, all are associated with *Sphagnum* in wet microhabitats from poor fens.

Etymology: The name of the genus derives from the Latin words "cornus" and "theca", meaning "horns" and "shell", respectively, the characteristic traits of the genus.

Four large species (L = 195-270 µm) are known:

Key to the species

1. Keel present, at least between the horns and the lateral side of the test 2
– Keel absent: LHorns = 25–59 µm long, L = (195) 220–264 (270) µm, B (main body) = 90–125 µm *C. ansata* (p. 68)

2. Keel surrounding the lateral margins, as well as the fundus of the test. Keel horseshoe-shaped, starting from the base of the "horns". Width of the keel corresponding to the distance between the main part of the test and the tip of the horn: L = 252–260 µm, B = 140–160 µm *C. equicalceus* (p. 70)
– Keel only present on the lateral margins, does not extend to the fundus of the test 3

3. "Horns" 35–60 µm long and extending to approximately half of the length of the keel. Test dimensions: L = 203–240 µm *C. saccifera* (p. 73)
– "Horns" shorter, extending to approximately 1/3rd of the length of the keel. Test dimensions: L = 198–226 µm *C. jiuhuensis* (p. 72)

Cornutheca ansata (Leidy, 1874)

1874 *Difflugia ansata* Leidy, Pr. Ac. Nat. Sc.: 156.

1876 *Nebela ansata* Leidy, 1974 – Leidy, Pr. Ac. Nat. Sc.: 118, Fig. 14 (redefinition of genus *Difflugia* and transfer to genus *Nebela*).

2016 *Cornutheca ansata* Leidy, 1876 – Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in Kosakyan et al. (2012), Cladistics 32: 606–623 (redefinition of genus *Nebela* and establishment of genus *Cornutheca* based on molecular data).

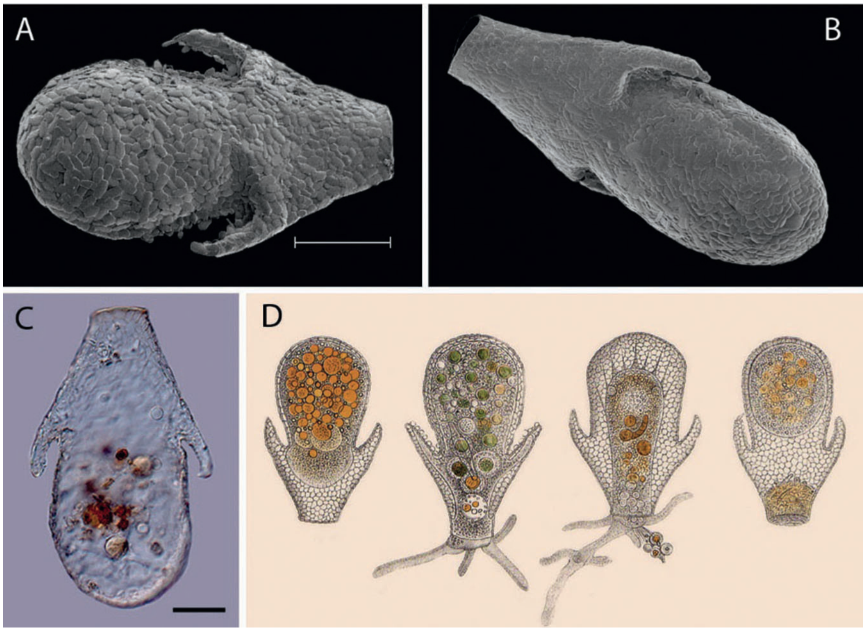

Fig. 22. *Cornutheca ansata*: (A & B) SEM images of a specimen from Peggy's Cove, Nova Scotia, Canada; lateral and oblique side views, respectively. (C) LM image of a specimen from the same location. (D) Original drawings from LEIDY (1879). Scale bars = 50 µm. Images (A–C) by Thierry Heger.

Icon.: LEIDY, 1874, Fig. 14; LEIDY, 1879, Pl. XXV, Figs. 1-8; HEGER et al., 2011b, Figs. 3–4; KOSAKYAN et al., 2012, Fig. 3.

Description: Test piriform in broad view, compressed, with a pair of hollow horns protruding on either side of the neck at 1/3rd of the distance from the pseudostome to the fundus (Fig. 22). Test almost transparent or slightly yellowish-brown, composed of small ovoid particles likely predated from small euglyphids. Dimensions: L = (195) 220–264 (270) µm, B (between the ends of the lateral horns) = (110) 130–150 (169) µm, B (main body) = 90–125 µm, P = 40–55 µm, horn length = 25–59 µm. Pseudostome slightly curved in broad view.

Differential diagnosis: *Cornutheca ansata* has a remarkable morphology and cannot be mistaken for any other species. The general shape is comparable to that of C. equicalceus (syn. *Nebela hippocrepis*), and indeed, LEIDY (1879) described *Nebela ansata* as follows: "It gives the impression of *Nebela hippocrepis* devoid of the horseshoe-like body, which is the striking peculiarity of the latter. The general shape of the shell is like that of *N. hippocrepis*, and it is also about the same size". Other closely related species are *C. saccifera*, and the recently described species *C. jiuhuensis* (Qin, Mitchell & Lara, 2016) comb. nov., which has a hollow keel like *C. equicalceus*; however, in *N. saccifera* and *C. jiuhuensis*, the keel is only present between the "horns" and the lateral part of the test and does not cover the entire fundus of the test (as in *C. equicalceus*).

Type locality: Absecom, New Jersey, USA. Likely coordinates: 39.426909°, -74.512855°.

Type specimen: Not provided. We declare Pl. XXV Fig. 4 by LEIDY (1879), which illustrates the first test found in 1874, reproduced here as Fig. 22D (the individual on the far right), as the type.

Etymology: The name of this species refers to the general morphology of the test, in Latin "ansatus" means "having handles".

Habitat: *Sphagnum* mosses in wet, poor fen.

Geographical distribution: North America: East coasts of Canada (HEGER et al., 2011b) and the USA (LEIDY, 1879; STOKES, 1882; HOOGENRAAD & DE GROOT, 1952).

Remarks. There are very few records for *Cornutheca ansata*: It was first reported by LEIDY in 1874, 1876, and 1879 in *Sphagnum* samples collected at Absecom, New Jersey, USA, then by STOKES (1882), and later by HOOGENRAAD & DE GROOT (1952) at a site near the original locality. It has also been recorded in two Canadian localities, near Lanoraie in southern Quebec (FANTHAM & PORTER, 1945), and in Nova Scotia (HEGER et al., 2011b). Detailed notes about the natural history and geographical distribution of the species are provided in HEGER et al. (2011b). *Cornutheca ansata*, *C. saccifera*, and *C. jiuhuensis* branch together robustly in the mt-COI sequence-based phylogenetic tree (QIN et al., 2016). No molecular data are yet available for *C. equicalceus*.

Cornutheca equicalceus (Leidy, 1874)

1874 *Difflugia equicalceus* Leidy, Proc. Ac. Nat. Sc.: 156.

1876 *Nebela equicalceus* Leidy, Proc. Ac. Nat. Sc.: 156 (redefinition of genus *Difflugia* and transfer to genus *Nebela*).

1879 *Nebela hippocrepis* Leidy, Rep. US Geol. Surv. Terr. 12: 156 (ICZN § 33.2.3 unjustified emendation).

2016 *Cornutheca equicalceus* Leidy, 1876 – Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., Cladistics 32: 606-623 (redefinition of genus Nebela and establishment of genus *Cornutheca* based on molecular data).

Icon.: LEIDY, 1879, Pl. XXV, Figs. 9-14; DEFLANDRE, 1936, Fig. 135; KOSAKYAN et al., 2012, Fig. 3C and D represent *C. saccifera*, mislabeled as *N. hippocrepis* (= *N. equicalceus*).

Description (based on the original description): Test elongated-piriform in broad view, compressed sides gradually taper towards the pseudostome. The fundus and lateral margins of the body of the test are surrounded by a thick, horseshoe-like keel, the ends of which project towards the pseudostome and inward into the cavity (Fig. 23). The entirety of this peculiar appendage occupies ca. 2/3rds of the test length. Its horns divide off from the general cavity of the test, as a pair of elongated conical recesses extending towards the fundus of the test and outward along the lateral border. Test pale yellowish, composed of circular or ovoid plates. Relatively large: L = 252–260 µm, B = 140–160 µm, P = 40–45 µm. Pseudostome linear or slightly curved in broad view.

Differential diagnosis: Can be confused with *C. saccifera* and *C. jiuhuensis*, from which it differs by the presence of the keel that covers the entire fundus of the test, not only between the "horns" and the lateral part, like in *C. saccifera* and *C. jiuhuensis*. For further details, see differential diagnosis under *C. ansata*.

Type locality: Absecom, New Jersey, USA. Likely coordinates: 39.426909°, -74.512855°.

Type specimen: Not provided. We declare Pl. XXV, Fig. 9 by LEIDY (1879), illustrating the individual found for the first time in 1874, reproduced here as Fig. 23A, as the type.

Etymology: The name of the species refers to the general morphology of the test and the

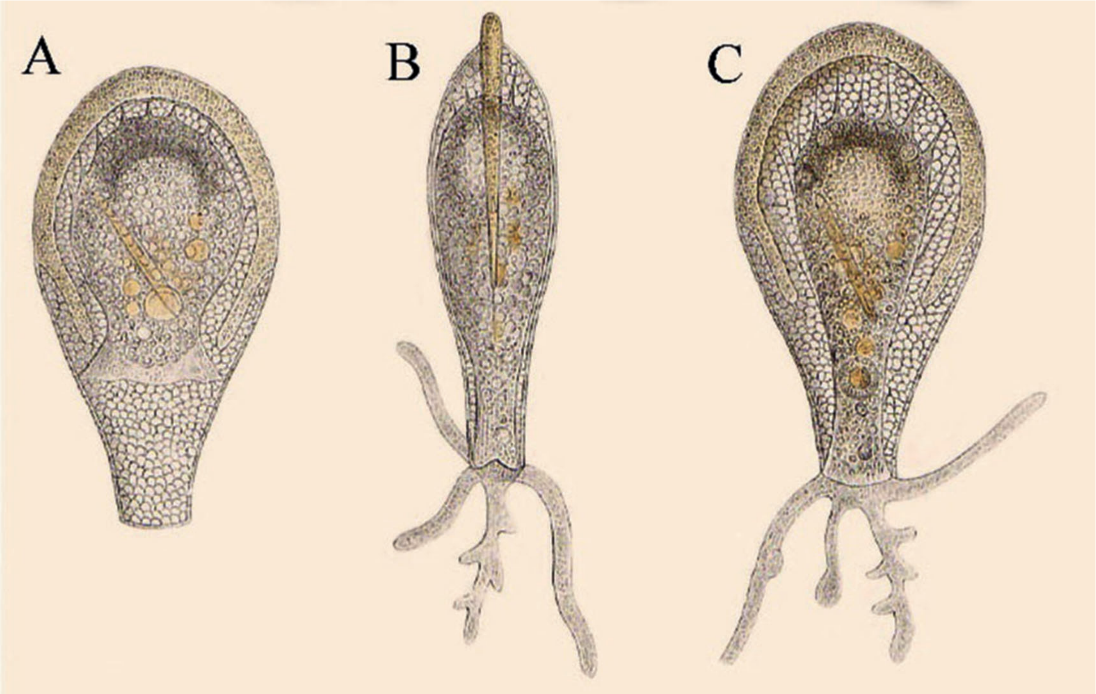

Fig. 23. *Cornutheca equicalceus*: Original drawings of active individuals (labelled as *N. hippocrepis*) from LEIDY (1879): (A & C) broad view, (B) profile view.

presence of the horseshoe-like keel; i.e., in Latin "hippocrepis" means "horseshoe vetch", while "equi" refers to horse and "calceus" to shoe.

Habitat: Wet *Sphagnum* mosses, edge of pond.

Geographical distribution: North America: Canada (KOSAKYAN et al., 2012), USA (LEIDY, 1879); Europe: UK (WEST, 1901; doubtful); Asia: Nepal (Bonnet 1977 – but most likely another yet undescribed taxon, see QIN et al., 2016 for further discussion), Korea (CHUNG et al., 1992 – now attributed to C. jiuhuensis).

Remarks: LEIDY (1879) considered *C. equicalceus* (named *N. hippocrepis* in the original publication) as related to *Planocarina carinata*, likely owing to the presence of a keel; however, if the original illustrations are trusted, the very edge of the keel in *C. equicalceus* is not as flat as in *P. carinata*, but hollow. The same applies to *C. saccifera* (in this case LM and SEM images are available). In addition, this keel has a typical horseshoe-like shape extending towards the center of the test, between the main body and the interior edge of a pair of hollow elongated conical recesses (i.e., horns). These horns extend towards the fundus of the test and outward along the lateral border; thus, it cannot be mistaken for the keel of *P. carinata*. Further information available under *Cornutheca ansata* (p. 69) regarding *C. equicalceus* and closely related species.

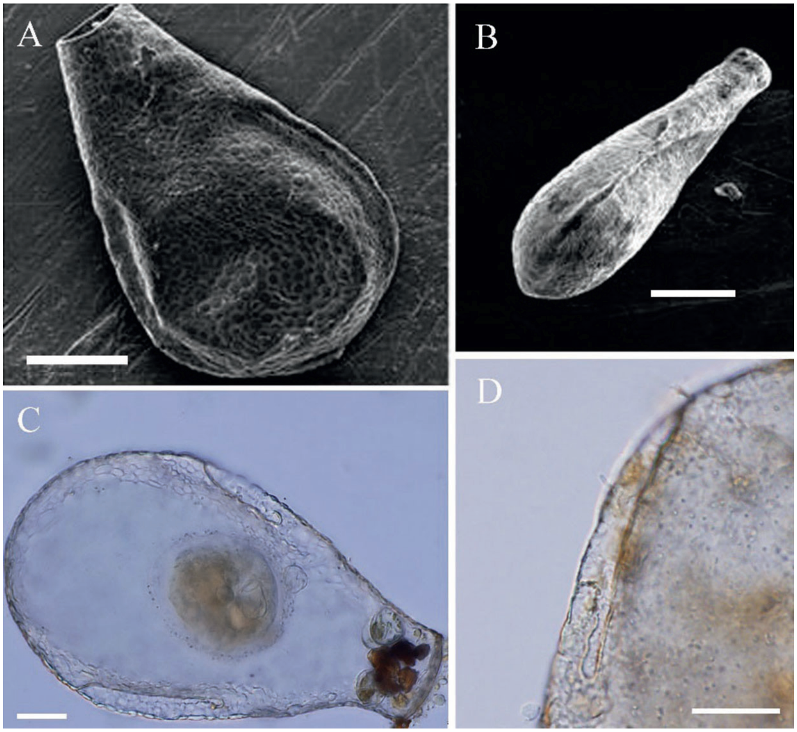

Fig. 24. *Cornutheca jiuhuensis*: (A & B) SEM broad and profile view (respectively) images of a specimen from China, showing the keel (modified from QIN et al., 2016); (C & D) Broad view LM images of a specimen from China showing one of the lateral extensions and the keel. Scale bars: A & B = 50 µm, C & D = 20 µm. Images by: (A & B) Yangmin Qin and (C & D) Anush Kosakyan.

Cornutheca jiuhuensis (Qin, Mitchell & Lara, 2016) comb. nov.

1992 *Nebela equicalceus* Chung, Kang, & Choi,1992 Kor. J. System. Zool. (Plate 2, Figs. A–B)

2016 *Nebela jiuhuensis* Qin, Mitchell, & Lara, J. Eukaryot. Microbiol. 63: 558–566 (Figs. 3–4, original images).

Icon.: CHUNG, 1992, Pl. 2, Fig. A–B, *N. equicalceus*; QIN et al., 2016, Figs. 3–4.

Description (based on the original description): Test piriform in broad view, tapering from the middle of the body towards the pseudostome region, compressed, and colourless. Two short, hollow horn-like extensions, one on each side, are visible in broad view, beginning from approximately the middle of the test. Keel present on each side, beginning from the base of the lateral extensions to the posterior end of the test. Test composed of ovoid and polygonal materials, presumably recycled euglyphid scales derived from prey. Test relatively large, L = 176–229 (mean = 199 ± 16.3 µm; n = 31); B = 101–130 (mean = 118 ± 7.9 µm; n = 31), P = 30–46 µm (average = 37 ± 3.8; n = 31). Lateral extension of the keel (±SD) = 77 ± 15.9 µm. Pseudostome ovoid in frontal view, with an organic rim.

Differential diagnosis: *Cornutheca jiuhuensis* is morphologically most similar to *C. saccifera*. The main difference between the two species resides in the length of the horns, which occupy 30% of the total keel length in *N. jiuhuensis*, and 50% in *C. saccifera*. The horns are also slenderer in *C. jiuhuensis* than in *C. saccifera*.

Type locality: Dajiuhu peatland in the Shennongjia Mountains, south-central China. Coordinates: 31.480851°, 110.008411°.

Type specimen: A type specimen mounted in Canada balsam on a microscopy slide was deposited in the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Wuhan, China, under catalogue number D2010-54.

Etymology: The Latin word "jiuhuensis" refers to the peatland "Dajiuhu", where this species was found. "Jiuhu" means "nine lakes" in Mandarin.

Habitat: *Sphagnum* mosses in relatively minerotrophic and wet habitats.

Geographical distribution: Asia: South Central China (QIN et al., 2016), South Korea (CHUNG et al., 1992, misnamed as *Nebela equicalceus*).

Remarks: The relatively large size and its hollow horn-like lateral extensions suggest that *Cornutheca jiuhuensis* is related to *C. saccifera*, *C. equicalceus*, and *C. ansata*. COI sequencing and subsequent phylogenetic analyses confirmed this relationship, placing *C. jiuhuensis* in a basal position with respect to *C. ansata* and *C. saccifera* (QIN et al., 2016).

Cornutheca saccifera (Wailes, 1913)

1879 *Nebela hippocrepis* pars Leidy, U.S. Geol. Surv. XII: 156, Pl. 24, Fig. 13.

1913 *Nebela saccifera* Wailes, J. Linn. Soc. Zool. 32: 206-207 (Pl. 15, Figs. 7–9, original drawings).

2016 *Cornutheca saccifera* Wailes, 1913 – Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 606–623 (redefinition of genus *Nebela* and establishment of genus *Cornutheca* based on molecular data).

Icon: WAILES, 1913, Pl. 15, Figs. 7–9; KOSAKYAN et al., 2012, Fig. 3C, D (misnamed as *Nebela hippocrepis*).

Description (based on the original description): Test in broad view narrowly piriform, compressed, with a hollow keel around the fundus and two lateral hollow curved horns extending from the middle of the test. Two flat "internal keels" (similar in structure to the large keel of *Planocarina [Nebela] carinata*) form a narrow, arched, finger-shaped band starting from the base of the "horns" and extending almost to the edge of the test. Test edge is as thick as the "horns" and thus undistinguishable from them in profile view (as illustrated in the original line drawing and SEM image, reproduced here as Fig. 25C-2 and Fig. 25A, respectively). It opens with a narrow, longitudinal slit-like orifice positioned beyond the tip of the horn, at the external end of the flat part of the keel (see Fig. 25, original drawing – C2). Test colourless, reinforced with euglyphid scales, L = 230–240 µm, B = 126–145 µm, P = 38–45 µm. Pseudostome elliptical in frontal view, Lhorns = 35–60 µm.

Differential diagnosis: For discussion on *C. saccifera* and its closely related species, see the Differential diagnosis section under *C. ansata* (p. 69), *C. equicalceus* (p. 70), and *C. jiuhuensis* (p. 73).

Type locality: Good Ground, Long Island, NY, USA. Likely coordinates: 40.87914°, -72.52427°.

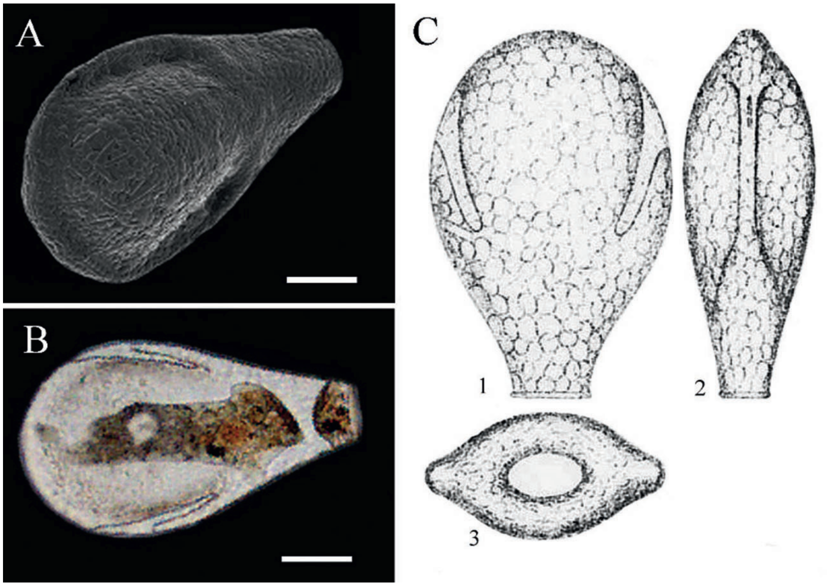

Fig. 25. *Cornutheca saccifera*: (A & B) SEM and LM images of two specimens from Nova Scotia, Canada (mislabelled as *N. hippocrepis* in KOSAKYAN et al., 2012); (C) Original drawings of an empty test from WAILES (1913): (1) broad view, (2) profile view, and (3) frontal view of pseudostome. Scale bars = 50 μm.

Type specimen: Not provided. We declare Pl. 15, Figs. 7-9 (representing the same individual) by WAILES (1913), reproduced here as Fig. 25C, as the type.

Etymology: Not provided. It may be related to the general shape of the test; i.e., in Latin “saccifera” means “sac-bearing”.

Habitat: *Sphagnum* mosses, in wet poor to intermediate fens.

Geographical distribution: Canada (Nova Scotia; KOSAKYAN et al., 2012 misnamed as *N. hippocrepis*), USA (Lakehurst, New Jersey by LEIDY, 1879; Long Island, New York by WAILES, 1912).

Remarks: Wailes (1912) stated that, “*Leidy found only two empty tests of* N. saccifera*, and realized that they were distinct from* Nebela equicalceus*, from which it could be distinguished by the absence of horseshoe-shaped keel around the fundus, by the horns not being solid, and the shorter neck. The small openings at the base of the horns are very narrow slits usually indistinguishable but readily detected tests are removed from water and placed into clove oil, which can penetrate through. Although it is not uncommon in samples and many living individuals were seen, none of these were active. No specimens of* N. equicalceus *were found. It may perhaps be more than coincidence that if the space occupied by the horns were vacant, the test would then be similar to that of* N. ansata*, and the small discs often attached to the horns of that species may represent the discarded material*”. It remains unclear what Leidy was referring to by “the horns not being solid”, as the horns of all species in this group are apparently hollow.

7.7. Genus *Gibbocarina* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Type species: *Gibbocarina galeata* (Penard, 1890)

1942b *Umbonaria* gen. nov. Jung, Arch. Protistenk. 95: 382 (invalid genus owing to lack of type designation).

2016 *Gibbocarina* gen. nov. Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 621.

Description: Test elongated-piriform in broad view, with a hollow tuberous keel surrounding the entire fundus, hyaline or slightly yellowish, composed of circular to elongated shell plates likely recycled from euglyphid testate amoeba prey.

Etymology: The name of this genus derives from the Latin words “gibba” and “carina”, meaning “tuberous” and “hollow keel”, respectively, the characteristic traits of the genus.

Remarks: KOSAKYAN et al. (2016) established genus *Gibbocarina* by splitting genus *Nebela* into six groups based on molecular data and the general test shape. The species included in genus *Gibbocarina* have elongated-piriform shells in broad view, with a hollow keel. The difference between *Gibbocarina* and *Planocarina* can be readily observed in profile view; while both genera possess a keel, that of *Gibbocarina* is hollow, whereas that of *Planocarina* is flat. A molecular phylogenetic analysis showed that “*Nebela*” *penardiana*, a species without keel, was closely related to *Gibbocarina galeata* in an mt-COI-based phylogenetic tree (with high support; 100/1.00 B and PP, KOSAKYAN et al., 2016; see also Fig. 4); however, *N. penardiana* has all the morphological characteristics of genus *Longinebela*. Furthermore, given the fact that only one mt-COI sequence is available for *N. penardiana* (which was based on DNA extraction of several cells), it is possible that a species closely related to *Gibbocarina galeata* was included in the DNA extraction, and that the obtained sequence actually corresponds to this species. Members of this genus are typically found in minerotrophic fens and are not necessarily associated with *Sphagnum*.

Two species were assigned to this genus:

Key to the species

1. Larger species (L = 180–283 µm), internal keel margin smooth *G. galeata* (p. 75)

– Smaller species (L = 90–140 µm), internal keel margin irregular *G. gracilis* (p. 77)

Gibbocarina galeata (Penard, 1890)

1890 *Nebela galeata* Penard, Mémoires de la Société de Physique & d’Histoire Naturelle de Genève 31: 161 (Pl. VI, Figs. 64-78, original drawings).

2016 *Gibbocarina galeata* Penard, 1890 – Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 621 (redefinition of genus *Nebela* and establishment of genus *Gibbocarina* based on molecular data).

Icon.: PENARD, 1890, Pl. VI, Figs. 64-78; DEFLANDRE, 1936, Figs. 112, 123; OGDEN & HEDLEY, 1980, Pl. 39; KOSAKYAN et al., 2012, Fig. 3E; LUKETA, 2017b, Fig. 1.

Description: Test elongated in broad view, compressed, with sides gradually tapering towards the pseudostome. Lateral margins distinctly compressed, giving the impression of a thick keel (Fig. 26). Accordingly, the test is elongated, elliptical, and with a pointed aboral end in profile. Two small lateral pores are present,

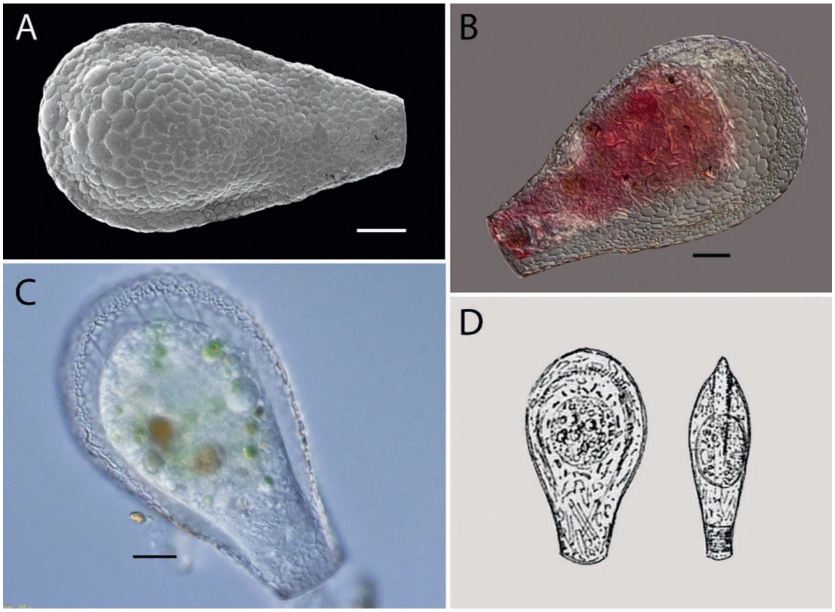

Fig. 26. *Gibbocarina galeata*: (A) SEM image of a specimen from Canada, (B) LM image from the Eugène Penard collection, no. 755-2 (Natural History Museum of Geneva, Switzerland), (C) LM image of an active individual from Switzerland, (D) Original drawings of *G. galeata* modified from PENARD (1890; broad and profile views). Scale bars: A = 25 μm, B & C = 20 μm. Images by: (A) Thierry Heger, (B) Thierry Arnet (Wikimedia), and (C) Anush Kosakyan.

one on each side of the test (sometimes hard to observe), almost at the point where the keel begins. Test colourless, reinforced with siliceous plates, probably recycled from prey. Test relatively large, L = 180–283 μm, B = 94–190 μm, P = 26–51 μm. Pseudostome linear or slightly curved in broad view, with a thick organic rim.

Differential diagnosis: Can be confused with members of *Planocarina* (i.e., *P. carinata*, *P. marginata*); however, *Planocarina* has a flat keel, while the keel in *Gibbocarina* is hollow.

Type locality: Vallée de Joux, Jura, Switzerland. Likely coordinates: 46.58987°, 6.252446°.

Type specimen: Not provided. We declare the specimen from the E. Penard slide collection, no. 755-2 (Natural History Museum, Geneva, Switzerland), reproduced here as Fig. 26B, as the type.

Etymology: Not provided. The term “galeata”, Latin for “helmeted” or “covered by a helmet”, likely refers to the thick, hollow keel.

Habitat: Wet *Sphagnum* mosses, wet forest litter. In relatively minerotrophic environments.

Geographical distribution: North America: Canada (FANTHAM & POTER, 1948), USA (INGHAM & MASSICOTTE, 1994); South America: Argentina (VUCETICH, 1975), Brazil (LANSAC-TOHA et al., 2001), Chile (JUNG,

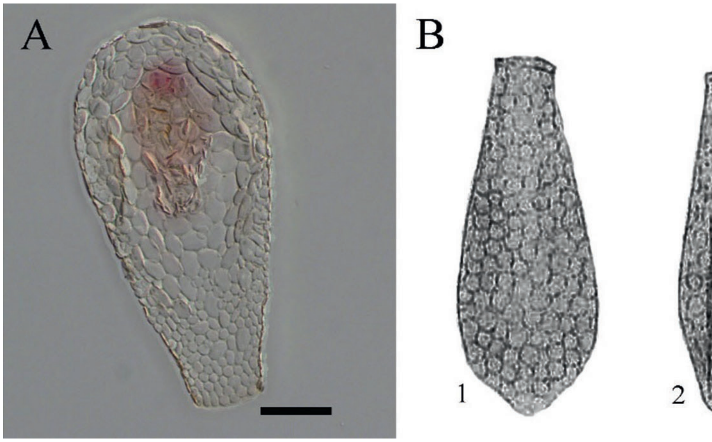

Fig. 27. *Gibbocarina gracilis*: (A) LM image of a specimen from the Eugène Penard slide collection, no. 504-5 (Natural History Museum of Geneva, Switzerland); (B) Original drawings from PENARD (1910): (1) lateral and (2) profile views. Scale bar = 20 µm. Image (A) by Thierry Arnet (Wikimedia).

1942a; FERNANDEZ et al., 2015), Ecuador (KRASHEVSKA et al., 2010); Africa: Republic of Congo (CHARDEZ, 1964); Asia: Azerbaijan (ALEKPEROV & SNEGOVAYA, 2000), Java (HOOGENRAAD, 1946), Nepal (BONNET, 1977), North Korea (GOLEMANSKY & TODOROV, 1991), Thailand (BONNET, 1981), Russia (AWERINZEW, 1906; MAZEI et al., 2016); Australasia: New Guinea (Irian Jaya (BONNET, 1992); Europe: Austria (AESCHT & FOISSNER, 1989), Belgium (CHARDEZ, 1987), Bulgaria (TODOROV, 1993; TODOROV & GOLEMANSKY, 1995; TODOROV & BANKOV, 2019), British Isles (CASH & HOPKINSON, 1909; OGDEN & HEDLEY, 1980), Czech Republic (BARTOŠ, 1949), France (DEFLANDRE, 1927), Germany (FRANKEN, 1933; HARNISCH, 1937; JUNG & SPATZ, 1938), Greenland (DECLOITRE, 1956), Herzegovina (LUKETA, 2017b), Hungary (VARGA, 1956), Ireland (WAILES & PENARD, 1911), Italy (MAZEI et al., 2016), the Netherlands (HOOGENRAAD, 1934, 1935), Romania (GODEANU, 1972a), Spain (MARGALEF, 1948), Sweden (SCHÖNBORN, 1975), Switzerland (PENARD, 1890; KOSAKYAN et al., unpubl.).

Remarks: The wide size variability and seemingly cosmopolitan distribution suggest that *Gibbocarina galeata* might represent a species complex. More data are however required to test this hypothesis.

Gibbocarina gracilis (Penard, 1910)

1910 *Nebela gracilis* Penard, Revue Suisse de Zoologie 18: 934 (Figs. 6–7, original figures).

1912 *Nebela gracilis* var. *stomata* Wailes, J. Linn. Soc. Zool. 32: 157 (assigned to the type with insufficient morphological differences, see Notes below).

1935 *Nebela galeata* f. *minor* Hoogenraad & De Groot 1935, Arch. Neerl. Zool. 1, p. 457–461,

Fig. 8a–d (assigned to the type with insufficient morphological differences, see Notes).

1971 *Nebela tubulosa* var. *adami* Laminger, Zool. Anz. 187, p. 379 (overlapping morphology with *G. gracilis*, see Notes).

2016 *Gibbocarina gracilis* Penard 1910 – Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 621 (redefinition of genus *Nebela* and establishment of genus *Gibbocarina* based on molecular data).

Icon.: PENARD, 1910, Figs. 6–7; DEFLANDRE, 1936, Pl. XXIV, Figs. 8, 11; Pl. XXV, Figs. 1–3.

Miss-applied icon.: LEIDY, 1879, Pl. XXIII, Figs. 4–6 (as *N. collaris*, but corresponds to G. gracilis); PENARD, 1902, Figs. 4–5 (as *N. galeata*, but corresponds to *G. gracilis*).

Description: Test elongated-piriform in broad view, compressed, with a rounded, sometimes slightly pointed fundus and a hollow keel laterally surrounding the fundus of the test. Sides gradually taper towards the pseudostome, with two lateral pores, one on each side (often difficult to observe). Irregular internal margin of the keel visible on empty tests (see Fig. 27). In profile, test elongated-elliptical, with a pointed tip corresponding to the keel. Test transparent or slightly yellowish, composed of circular or elongated plates: L = 90–140 µm, B = 50–60 µm. Pseudostome curved in broad view, with a thin (sometimes thick) organic rim, Brim = 19–25 µm.

Differential diagnosis: Resembles *Gibbocarina galeata*, which has a similar keel. Can be distinguished by its much smaller size, and the irregular internal margin of the keel.

Type locality: La Trélasse peatland (formerly referred to as “La Pile”), Canton Vaud, Jura Mountains, Switzerland, coordinates: 46.446279°, 6.094322°.

Type specimen: Not provided. We declare the specimen from the E. Penard slide collection, no. 504-5 (Natural History Museum, Geneva, Switzerland), reproduced here as Fig. 27A, as the type.

Etymology: Not provided. The name likely refers to the general morphology of the test, as in Latin “gracilis” means “slender”.

Habitat: *Sphagnum* mosses.

Geographical distribution: North America: USA (WAILES, 1912a), Canada (FANTHAM & POTER, 1948); South America: Bolivia (CERDA, 1986), Brazil (WAILES, 1913; PINTO, 1925), Chile (JUNG, 1942a; WILKINSON, 1990), Colombia (HEINIS, 1914), Ecuador (KRASHEVSKA et al., 2007), Peru (WAILES, 1913); Europe: British Isles (MITCHELL et al., 2000), Finland (MITCHELL et al., 2000), France (DEFLANDRE, 1936; BONNET, 1953; VAUCHER & BENIER, 1988), Germany (MEISTERFELD, unpubl.), the Netherlands (HOOGENRAAD & DE GROOT, 1940, MITCHELL et al., 2000), Russia (TARNOGRADSKIJ, 1961; KASIMOV, 1972), Sweden (MITCHELL et al., 2000), Switzerland (PENARD, 1910; MITCHELL et al., 2000); Asia: Java (BONNET, 1985; HOOGENRAAD & DE GROOT, 1940a; 1946), Nepal (BONNET, 1977), Philippines (BONNET, 1980b), Sulawesi (BONNET, 1992), Thailand (BONNET, 1981, 1987); Indian Ocean: Seychelles (WAILES, 1912); Africa: Congo (GAUTHIER-LIÈVRE, 1957); Australasia: New Guinea (Papua New Guinea BONNET, 1980a).

Remarks. WAILES (1912a) described var. stomata based on the presence of lateral pores (one per side) as a differentiating taxonomic character from the type; however, as shown in several descriptions (DEFLANDRE, 1936) and in the discussion on synapomorphies of the Hyalospheniidae (KOSAKYAN et al., 2012), lateral pores are often present, but difficult to observe, and thus easily overlooked. Thus, we here follow DEFLANDRE (1936) and synonymize *Gibbocarina (N.) gracilis* var. *stomata* with

G. gracilis. HOOGENRAAD & DE GROOT (1935) described *N. galeata* f. *minor* as differing from the type only by its smaller size (L = 118–140 µm, B = 62–78 µm). In their original drawing (HOOGENRAAD & DE GROOT, 1935, Fig. 21d–h), the internal margin was wavy, exactly as in the nominal form of *G. gracilis*; thus, we consider *N. galeata* f. *minor* as a synonym of *G. gracilis*, pending molecular data confirmation.

7.8. Genus *Hyalosphenia* (Stein, 1857)

Type species: *Hyalosphenia ligata* (Tatem, 1870) Leidy, 1875

1857 *Hyalosphenia* gen. nov. Stein, Sitzungsb, Bohem. Akad. Wissens (without specific name, see Remarks below).

1875 *Hyalosphenia* gen. nov. Schulze, Archiv Mikr. Anat. XI: 335.

**Hyalosphaenia* misspelled (i.e., Daday, 1905; Scheffelt, 1920; Augustin et al., 1985; Jahnk et al., 2020)

Description: Test in broad view rounded, ovoid, elongated elliptical, or lageniform, in most cases compressed (exception: *H. savoiei* which has a circular cross-section). Pseudostome ranging from linear to strongly curved in broad view. Rim either thickened inwards or not. Test hyaline or slightly yellowish, with a smooth organic surface.

Remarks: The story behind the nomenclature of genus *Hyalosphenia* is rather complicated. LOEBLICH & TAPPAN (1964) discussed this in detail:

"*Seemingly a type species has not been selected previously for this genus, since it has commonly but erroneously been regarded as fixed by monotypy. Stein's original description of* Hyalosphenia *contains no mention of a specific name. The type reference has been cited both as a publication in the Transactions of the Czechoslovakian Academy for 1857 and as published in the Bericht of the Academy in 1859. Some bibliographies have listed these as two separate publications of differing date but with identical titles and pagination. In January 1857, Stein orally presented a classification of fresh-water Rhizopoda before the Academy in Prague, describing several genera, including* Hyalosphenia*. No formal paper was published, and the transactions of the meetings of this academy were first published in 1859 (including those of 1857 and other years), in the Bericht. Stein's only published reference to* Hyalosphenia *was in the transactions of the Academy meeting of 1857, published in 1859. No specific name was given to the form described; hence, the genus remained without valid species. About 20 years later, Schulze found a species in Germany, which he believed to fit the description of Stein's still unnamed and unfigured species of* Hyalosphenia *from Prague. Schulze and Stein exchanged illustrations of their respective forms, believed by both workers to represent distinct species, and Schulze, 1875 described his Hyalosphenia lata comparing it in publication to* Hyalosphenia cuneata *Stein. The latter name must have been included on Stein's unpublished sketches of the unnamed species that he had earlier described but was first introduced into the literature by Schulze in 1875. Owing to the rarity of the publication containing Stein's description, later workers have referred only to Schulze's publication, and all subsequent texts and treatises have cited H. cuneata Stein, although Stein gave only the description and generic name, without any mention of the specific name cuneata.* Hyalosphenia *dates from 1859 (date of publication of transactions of the 1857 meeting) but remained without included species until 1875, when the specific name* H. cuneata *was published, and* H. lata *was described by*

Schulze. Either of these nominal species is thus available for selection as type of genus. In the intervening years, Tatem (1870) had described Difflugia ligata*, which was made the basis for the genus* Catharia *Leidy, 1874. After Schulze's paper appeared, Tatem stated that* Hyalosphenia lata *Schulze was a junior synonym of* D. ligata. Catharia *Leidy was also a homonym of* Catharia *Lederer, 1863. Leidy, 1879 stated that he had not seen Stein's publication, but the description quoted by Schulze from Stein did not give sufficient differences to distinguish two species and added that "the specific names of* caudata*,* ligata *and* lata *are expressive of characters common to any or all the examples described by Stein, Tatem, Schulze, and myself''. Leidy recognized the species as* H. cuneata*, but this name was not published until 1875 by Stein in Schulze, which posted Tatem's publication. Hence, the valid name for the type species is* Hyalosphenia ligata *(Tatem), and* H. cuneata *Stein in Schulze and* H. lata *Schulze, 1875 are both junior synonyms*".

Here, we follow LOEBLICH & TAPPAN (1964) and MEISTERFELD (2002), considering *Hyalosphenia ligata* (Tatem, 1870) Leidy, 1875 as the valid type species of the genus, whereas *H. cuneata* Stein in Schulze, 1875 and *H. lata* Schulze, 1875 are junior synonyms.

Molecular data: The two species for which SSU rRNA gene data are available (*H. papilio* and *H. elegans*) do not branch together in the phylogenetic tree of LARA et al. (2008). This suggests that the genus is paraphyletic, and a new genus should be established for *H. elegans* (likely also including the closely-related species *H. insecta*); however, Oliverio et al. (2014) found that: (1) Both species, although relatively morphologically homogeneous, are actually paraphyletic; and (2) Both species shared identical SSU rRNA gene sequences, suggesting that the two forms belong to the same paraphyletic species complex. This topology, however, has not been confirmed by any other study. Further studies on other members of the genus are thus needed to clarify this rather complex situation prior to taking any taxonomic action.

Etymology: The name of the genus derives from Greek "hyalos", meaning "crystal", and "sphen", which means "a wedge".

Twenty taxa are considered valid; however, many of these are problematic, and detailed morphological and molecular data are required to clarify their status:

Key to the species

1. Test circular in cross-section *H. savoiei* (p. 100)
– Test more or less compressed 2

2. Test bottle-shaped or lageniform, with an elongated distinct neck in broad view 3
– Test rounded, ovoid, elongated elliptical, or piriform in broad view, possibly with a wavy outline; neck short, indistinct, or totally absent 5

3. Outline of test in broad view wavy owing to the presence of circular to ovoid depressions on the test surface, L <130µm 4
– Outline of test in broad view smooth (not wavy). Neck gradually tapering towards the pseudostome, L > 130 µm (130–145 µm) *H. chardezi* (p. 83)

4. Main part of test with circular to ovoid depressions (either not or only marginally present on the neck), giving an irregular-wavy outline, larger species: L = (68) 85–110 (130) µm, B = 40–65 µm; Pseudostome curved in broad view, P = 15–20 µm wide *H. elegans* (p. 83)

– Circular to ovoid depressions present across the entire test, including the neck, smaller species: L = 68–84 µm, B = 29–42 µm *H. insecta* (p. 87)

5. Pseudostome thickened inwards (readily visible in LM) 6

– Pseudostome not thickened inwards 12

6. Test very elongated in broad view, "dorsal" side vaulted, "ventral" side depressed, kidney shaped in cross-section: L = 107–115 µm, B = 31–36 µm, P = 9–11 µm *H. tamdaoensis* (p. 89)

– Test ovoid, oval-elliptical, or rounded in broad view, lacking all above-mentioned feature 7

7. Lateral margins of the test form right angles at the junction with the pseudostome in broad view: L = 45–55 µm, B = 30–32 µm *H. rectangularis* (p. 84)

– Lateral margins do not form right angles at the junction with the pseudostome 8

8. Posterior end of the test pointed in broad view, giving test an irregular shape: L = 60–70 µm, B = 45–50 µm *H. irregularis* (p. 73)

– Posterior end of the test rounded in broad view 9

9. Test circular in broad view, except for the neck and pseudostome. L = 20 µm, B = 17 µm *H. schoutedeni rotundata* (p. 87)

– Test ovoid to elliptical in broad view, possibly with a wavy outline 10

10. Test with a pronounced bulge around the pseudostome: L = 40–65 µm, B = 23–40 µm *H. schoutedeni* (p. 86)

– Bulge around the pseudostome less pronounced or absent, outline smooth or wavy 11

11. Outline egg-shaped, smooth: L = 45–87 µm, B = 30–53 µm *H. subflava* (p. 102)

– Outline wavy in broad view as well as in profile view: L = 58–81 µm, B = 36–52 µm, P = 14–28 µm *H. baliki* (p. 82)

12. Smaller species (L < 50 µm), heterotrophic species (i.e., lacking endosymbiotic algae) 13

– Intermediate to larger species (L > 50 µm), hetero- or mixotrophic (i.e., with endosymbiotic algae) 14

13. Test ovoid in broad view. Pseudostome narrow. P/B < 0.5; L = 26–43 µm, B = 16–27 µm, P = 13 µm *H. minuta* (p. 89)

– Test very wide ovoid in broad view, sides almost straight in broad view. Pseudostome wide: P/B > 0.5. Length almost equal to breadth, pseudostome linear: L = 40–42 µm, B = 28–32 µm, P = 28–32 µm *H. platystoma* (p. 82)

14. Test composed of small organic building units as in *Arcella*. L = 35–90 µm, B = 16–54 µm, P = 15-32 µm *H. punctata* (p. 97)

– Small organic building units absent 15

15. Intermediate-sized species (50–80 µm) 16

– Larger species (L > 85 µm), 17

16. Pseudostome narrow (P/B = ca. 1/3). Test slightly elongated in broad view, with relatively straight sides converging towards the pseudostome: L = 52–76 µm, B = 44–60 µm. Keel present, although difficult to observe, visible only in profile view *H. ligata* (p. 88)

– Test ovoid-rounded in broad view, pseudostome comparatively wider (P/B > 0.5): L = 65–70 µm, B = 50 µm, P = 15–23 µm *H. humicola* (p. 86)

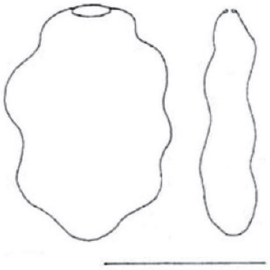

Fig. 28. Original drawing of *Hyalosphenia baliki* from BALIK (1994): broad and profile views. Scale bar = 50 µm.

17. Mixotrophic species, endosymbiotic green algae (Trebouxiophyceae, primarily genus *Chlorella*) always present 18

– Heterotrophic species, endosymbiotic green algae absent 19

18. Test wide piriform in broad view, sides gradually tapering towards the wide pseudostome (P/B = ca. 0.5): L = 90–175 µm, B = 60–155 µm, P = 30–40 µm *H. papilio* (p. 92)

– Sides of the test strongly tapering towards the narrower pseudostome (P/B = ca. 0.3–0.4): L = 110–127 µm, P = 23 µm *H. papilio stenostoma* (p. 95)

19. Test wide ovoid in broad view: L = 130–180 µm, B = 90–140 µm. Hollow keel present *H. ovalis* (p. 91)

– Test very elongated ellipsoid in broad view. Hollow keel absent 20

20. Very large species: L = 204–272 µm, B = 65–96 µm *H. gigantea* (p. 85)

– Large species: L = 180 µm, B = 70 µm *H. penardi* (p. 96)

Hyalosphenia baliki sp. nov.

1994 *Hyalosphenia subflava* var. *undulata* Balik, Cas. Slez. Muz. Opava (A) 43: 250, Fig. 6. – Infrasubspecific (not available) name: var. published after 1960, ICZN Art. 45.6.3.

Description (based on 10 individuals): Test ovoid in broad view, compressed, wavy sides, pseudostome small. Test colorless or yellowish, very smooth. L = 58–81 µm, B = 36–52 µm, P = 14–28 µm. Pseudostome straight in broad view, thickened at the edges, as in *Hyalosphenia subflava*.

Differential diagnosis: The only ovoid hyalospheniid species with a wavy irregular outline and lacking a neck.

Type locality: Velký Děd Mountain in the Hrubý Jeseník Mountain range of the Eastern Sudeten Mountains, Czech Republic. Coordinates: 50.0804058°, 17.2089856° (BALIK, 1994).

Type specimen: We declare the original drawing (Fig. 6) by BALIK (1994), reproduced here as Fig. 28, as the type.

Etymology: We name this species in honor of Vladimir Balik who described it.

Habitat: Conifer forest (plantation), humus, and litter.

Geographical distribution: Europe: Czech Republic (BALIK, 1994).

Remarks: Initially, this species was described as a variety of *Hyalosphenia subflava* (*H. subflava* var. *undulata*), differing from the type by its irregular wavy outline (BALIK, 1994). Morphometric data based on 10 individuals suggest that this is likely an independent taxon. As the name *H. subflava* var. *undulata* is not available and cannot be used according ICZN Art. 45.6.3 (variety described after 1960), we establish this taxon as a separate species: *Hyalosphenia baliki* sp. nov. To the best of our knowledge, this species has not been reported since its initial description.

Hyalosphenia chardezi sp. nov.

1962 *Hyalosphenia elegans* var. *cylindricollis* Chardez, Bull. Inst. Agro. Stat. Rech Gembloux 30 (1-2): 84, Figs. 1–4. – Infra-subspecific (not available) name: var. published after 1960, ICZN 45.6.3

Description: Test transparent to yellowish-brown, entirely organic, lageniform in broad view, sometimes with a slightly irregular outline. Long neck only slightly compressed, almost cylindrical, tapering towards the pseudostome. Two small pores visible, one on each side on the neck base. L = 130–145 µm, B = 60–70 µm, P = 20–27 µm. Pseudostome curved in broad view, with an organic rim.

Differential diagnosis: The test of *H. chardezi* is similar to that of *H. jiroveci* in general shape; but *H. jiroveci* is notably smaller (L = 84 µm, B = 49 µm) and characterized by a widening of the neck near the pseudostome. *H. chardezi* also resembles *H. elegans* in general shape but differs by: 1) The absence of hemispherical depressions, 2) A less compressed neck (nearly cylindrical), 3) a larger size (*H. elegans*: L = (68) 85–110 (130) µm), and 4) Ecology, as *H. chardezi* occurs in wetter and less acidic habitats (pH = 5.5–6 for H. chardezi vs. pH = 4.1 for *H. elegans*).

Type locality: Hautes-Fagnes, Belgium (CHARDEZ, 1962). Likely coordinates: 50.565832°, 6.084382°.

Type specimen: We declare Fig. 1 by CHARDEZ (1962), reproduced here as Fig. 29 (drawing of an active individual), as the type.

Etymology: We name this species in honor of the Belgian protozoologist Didier Chardez (1924-2000), who first described it, in recognition for his significant contribution to the study of testate amoebae.

Habitat: *Sphagnum* mosses (very humid, pH = 5.5–6).

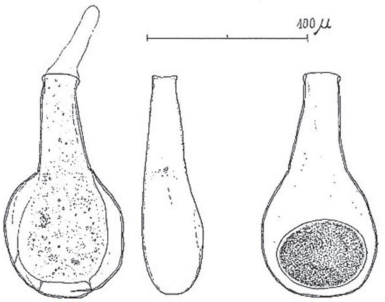

Fig. 29. Original drawing of *Hyalosphenia chardezi* from CHARDEZ (1962). Left to right: broad view of a living individual (declared as the type), profile view, and broad view of encysted individual. Scale bar = 100 µm.

Geographical distribution: Europe: Belgium (CHARDEZ, 1962), Romania (BUNESCU, 1979), Spain (GRACIA, 1972); North America: Canada (COSTAN & PLANAS, 1986).

Remarks: A large population of this species was found in the Hautes-Fagnes region of Belgium and was described as a variety of *H. elegans*—*H. elegans* var. *cylindricollis* (CHARDEZ, 1962). As the name *H. elegans* var. *cylindricollis* is neither available, nor can it be used according to ICZN Art. 45.6.3 (variety described after 1960), we rename it here *Hyalosphenia chardezi* sp. nov.

Hyalosphenia elegans Leidy, 1874

1874 *Difflugia (Catharia) elegans* Leidy, Proc. Ac. Nat. Sc.: 156.

1879 *Hyalosphenia elegans* Leidy, 1874 – Leidy, Rep. US Geol. Surv. Terr. 12: 140, Figs. 19-29 (original drawings). Figs. 19-21 represent individuals collected in 1874 (re-evaluation of

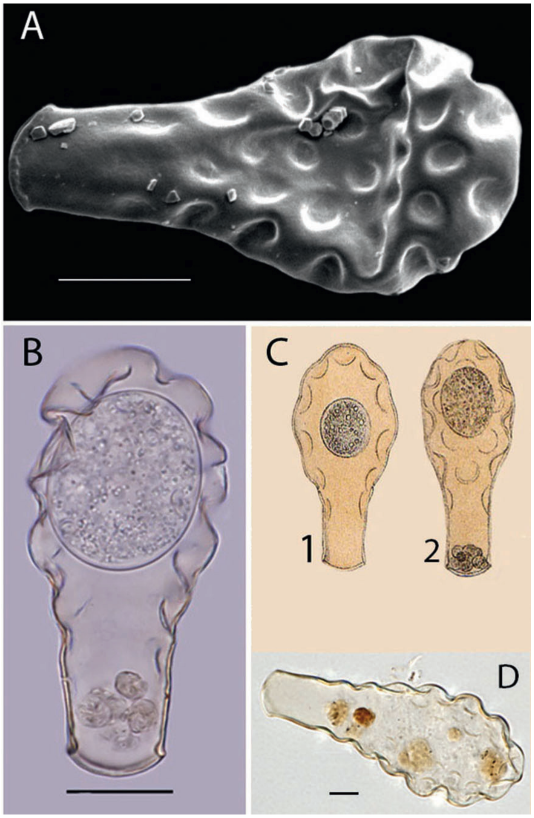

Fig. 30. *Hyalosphenia elegans*: (A) SEM broad view image of a (partly collapsed) individual from Switzerland; (B) LM broad view image of an encysted specimen from Shennongjia Mountains, central China (note the shell is slightly bent on the left side of the image); (C) Drawings of encysted individuals from the original description of LEIDY (1879): (1 & 2) living individuals in broad view; (D) LM image of a specimen in broad view from the Eugène Penard slide collection, no. 462-1-1 (Natural History Museum, Geneva, Switzerland). Scale bars: A & B = 20 μm, D = 10 μm. Images by: (A & B) Anush Kosakyan and (D) Thierry Arnet (Wikimedia).

morphological characters and transfer to new genus).

1964b *Hyalosphenia elegans* var. *major* Decloitre, Publ. Expéd. Polair. Franc. 259: 35 (Infra-subspecific [not available] name: var. published after 1960, ICZN Art. 45.6.3).

Icon.: LEIDY, 1879 Pl. XX, Figs. 19-29; PENARD, 1890 T. 7, Figs. 36–39; PENARD, 1902, Figs.1–3; VAN OYE, 1933, Fig. 4; GROSPIETSCH, 1965, Fig. 16; CHARMAN et al., 2000, Fig. 24a.

Description: Test compressed, lageniform in broad view, with a long neck tapering towards the pseudostome. Two small pores, one on each side approximately in the middle of the neck, very often difficult to observe. Test almost transparent or slightly yellowish-brown, totally organic without any visible structure in LM. Many hemispherical or oval depressions on the main part of the test, especially visible near the margin, giving a wavy impression. L = (68) 85–110 (130) μm, B = 40–65 μm, P = 15–20 μm. Pseudostome curved in broad view, with a thin organic rim.

Differential diagnosis: *Hyalosphenia elegans* resembles *H. insecta* and *H. chardezi*. See the section "Differential diagnosis" and "Remarks" under these two species.

Type locality: Absecom, New Jersey, USA. Likely coordinates: 39.426909°, -74.512855°.

Type specimen: Not provided. We declare the Pl. XX Fig. 28 (LEIDY, 1879), reproduced here as Fig. 30 C1, as the type.

Etymology: The name "elegans" is related to the graceful shape of the test.

Habitat: *Sphagnum* mosses, especially in open bogs, often in association with *Hyalosphenia papilio*, but usually most abundant deeper in the moss carpet (e.g., 3-6 cm depth; SCHÖNBORN, 1962; MITCHELL & GILBERT, 2004).

Geographical distribution: Africa: Congo (ŠTĚPÁNEK, 1963), Madagascar (DECLOITRE, 1956, MITCHELL, unpublished), Seychelles (WAILES, 1912a); South America: Argentina (VUCETICH, 1975), Cape Horn (Chile; CERTES, 1888; JUNG, 1942a), Colombia (HEINIS, 1914); North America: Canada (ODELL, 1905), USA (LEIDY, 1879); Asia: China (LI et al. 2010, QIN et al., unpubl.), Indonesia (VAN OYE, 1922; HARNISCH, 1951), Japan (YAMAMOTO, 1981), Java (BONNET, 1992), Russia (Siberia) KORGANOVA, 1985), Sri Lanka (DADAY, 1898); Australasia: New Guinea (Papua New Guinea, ENTZ, 1897), Europe: Austria (LAMINGER, 1971), Bulgaria (TODOROV & GOLEMANSKY, 1995), Belgium (CHARDEZ, 1987a), Czech Republic (TARÁNEK, 1881; BARTOŠ, 1954), Finland (LEVANDER, 1900; TOLONEN et al., 1994), France (DEFLANDRE, 1927), Germany (GREEF, 1888; JUNG, 1936; GROSPIETSCH, 1958; MEISTERFELD, 1977), Iceland (DECLOITRE, 1965), Italy (RAMPI, 1947, 1950), the Netherlands (HOOGENRAAD, 1908), Russia (AWERINZEW, 1899), Spain (GRACIA, 1964), Sweden (PENARD, 1890), Switzerland (PENARD, 1902; MITCHELL et al., 2000; KOSAKYAN et al., unpubl.), UK (WAILES, 1912b; HEAL, 1964; OGDEN 1984a; HENDON et al., 2001). Possibly cosmopolitan.

Remarks: LEIDY (1879) noted that *Difflugia spirigera* described by EHRENBERG (1853) is very similar and likely synonymous to *H. elegans*, if, when describing "the four internal longitudinal lines", the author was referring to the same as Leidy's "series of hemispherical inflections" on the body of the test; however, EHRENBERG's description (1853), together with his later illustration (EHRENBERG, 1871, Pl. 3, Fig. 4), appear insufficiently detailed to determine if *Difflugia spirigera* should indeed be considered synonymous to *H. elegans*. SSU rRNA data (OLIVERIO et al., 2014) have suggested that *H. elegans* is not monophyletic, and more data are needed to clarify its phylogenetic position, in addition to evaluating its relationships with other species of the genus especially *H. papilio* and *H. insecta* (if the latter can indeed be considered a valid species).

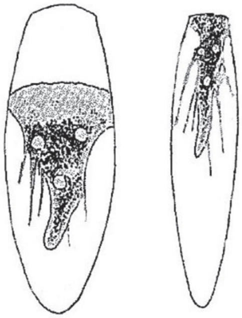

Fig. 31. Original drawing of *Hyalosphenia gigantea* from DE GRAAF (1952): broad and profile views.

Hyalosphenia gigantea De Graaf, 1952

1952 *Hyalosphenia gigantea* De Graaf, Beaufortia 23: 1–4, Fig. 1a–c.

Description: Test large, ovoid, or ellipsoid in broad view, narrow ellipsoid in profile. Lateral pores absent. Test almost transparent or slightly yellowish-brown, totally organic, without any visible structure in LM. L = 204–272 µm, B = 65–96 µm, P = 52–57 µm. Pseudostome ovoid in frontal view.

Differential diagnosis: *Hyalosphenia gigantea* is very similar to *H. penardi* (see Figs. 31, 40), from which it differs by its larger size (*H. gigantea*, L = 204–272 µm, *H. penardi*, L = 180 µm); however, as this size gap is relatively small (i.e., ca. 10% of the length—180 vs. 204 µm), the two species may be synonymous. Still, a careful examination of the original drawings shows that *H. gigantea* is more compressed in profile view, especially near the pseudostome. Further morphological and molecular data are thus needed to clarify the taxonomic status of these two species.

Type locality: Loenerveense Polder, the Netherlands. Likely coordinates: 52.210447°; 5.046124°.

Type specimen: Not provided. We declare Fig.1a–b by DE GRAAF (1952), reproduced here as Fig. 31, as the type.

Etymology: Species name is related to the large ("gigantic") size of the test.

Habitat: Freshwater, plankton, or benthos of neutral to alkaline water bodies (pH = 8).

Geographical distribution: Europe: Hungary (TOMAS & GELLERT, 1960; BERECZKY, 1973; TÖRÖK, 1998), the Netherlands (DE GRAAF, 1952).

Remarks: Rarely reported and possibly a rare species, although large species such as this one may never reach high densities and, thus, may remain difficult to find. This apparent rarity may also be partly due to the fact that planktonic testate amoebae have been much less studied in recent decades compared to those living in soils and (especially) peatlands.

Hyalosphenia humicola Decloitre, 1973

1973 *Hyalosphenia humicola* Decloitre, Extraits des Annales de la S.S.N.A.T.V. (25): 149–156, Fig. 2.

Description (based on the original publication): Differs from all other *Hyalosphenia* species in shape and size. Test ovoid, rounded in broad view, with a very short and compressed neck. Test transparent, colorless, with some foreign elements attached. L = 65–70 µm, B = 50 µm, depth of the test = 10 µm, P = 23–25 µm. At the short neck-level, pseudostome margin appearing shiny in some parts under LM. Shell lacking structure in LM, appearing amorphous.

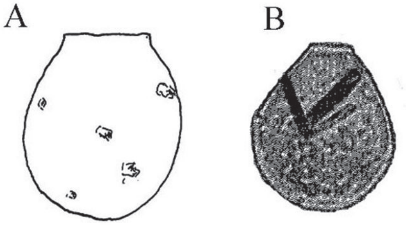

Fig. 32. *Hyalosphenia humicola*: (A) Original drawing from DECLOITRE (1973), and (B) Drawing from CHARDEZ (1990). Note the differences in shape between the two images (see species description for more details).

Differential diagnosis: Test shape differing from that of all other *Hyalosphenia* species when considering the original drawing, being ovoid, much closer to circular in outline than *H. subflava*. Lacks the characteristic pointed end of *H. irregularis*, as well as a clear neck.

Type locality: Méounes-lès-Montrieux, France. Likely coordinates: 43.284114°, 5.962147°.

Type specimen: Not provided. We declare Fig. 2 by DECLOITRE (1973), reproduced here as Fig. 32A, as the type.

Etymology: The species name refers to the habitat where it was found; i.e., in Latin "humicolous" means "organism that thrives on or in litter".

Habitat: Pine forest litter.

Geographical distribution: Europe: France (DECLOITRE, 1973), Sweden (CHARDEZ, 1990a, see Remarks).

Remarks: A problematic species. It was found only once by DECLOITRE (1973), in a single pine forest litter sample from south-eastern France. The author mentioned that the test did not resemble that of any other *Hyalosphenia* species by size or shape and, therefore, described it as a new species. The species has been reported only once since its description, by CHARDEZ (1990) from Sweden, but the illustration (Fig. 32B) is notably different from the original description, appearing similar to *H. ligata* and thus bringing uncertainty into this report. More data are thus needed to confirm the validity, taxonomic position, and geographical distribution of this species.

Hyalosphenia insecta Harnisch, 1938

1938 *Hyalosphenia insecta* Harnisch, Zool. Anz. 124: 138–150.

1964 *Hyalosphenia insecta* var. *megastoma* Decloitre (infrasubspecific [unavailable] name: var. published after 1960, ICZN Art. 45.6.3).

Icon.: HARNISCH, 1938, Fig. 1b; CASH et al., 1909, T. 31, Figs. 13–14; BONNET & THOMAS, 1955, Fig. 3.

Description: Test lageniform in broad view, closely resembling that of *H. elegans*. The only difference is that the hemispherical indentations are present on the entire test in *H. insecta*, including the neck. L = 68–84 μm, B = 29–42 μm.

Differential diagnosis: Likely often confused with *H. elegans*. The main difference between the two species is believed to be the extension of the indentations on the test. The number and density of indentations can, however, be rather subjective and may be dependent upon the observation method. Furthermore, as indentation size and depth are also rather variable, their density can be a subjective criterion, as interpretations can vary among researchers.

Type locality: Lappland, Sweden. Likely coordinates: 66.747463°, 20.590961°.

Type specimen: We declare Fig. 33 as the type.

Etymology: The species name refers to the test morphology; i.e., in Latin "insectare" means "to cut into". Additionally, in Latin "animal insectum" refers to an "animal with notched or divided body".

Fig. 33. *Hyalosphenia insecta*: LM broad view image from the Netherlands (by Ferry Siemensma). Scale bar = 20 μm.

Habitat: *Sphagnum* mosses, wet green mosses, soil.

Geographical distribution: Europe: Austria (SEIS, 1971; LAMINGER, 1975), Belgium (CHARDEZ, 1960), Bulgaria (TODOROV, 2001, 2002b), France (BONNET & THOMAS, 1955, 1960; CHARDEZ, 1960; BONNET, 1961), Germany (GROSPIETSCH, 1982), Poland (SCHÖNBORN, 1984); Romania (BUNESCU, 1979; BUNESCU et al., 1979), Sweden (HARNISCH, 1938; GROSPIETSCH, 1954); North America: USA (BOVEE, 1983); Caribbean: Cuba (GOLEMANSKY, 1968a); Asia: Java (HARNISCH, 1951; BONNET, 1992), Sulawesi (BONNET, 1992), Vietnam (BALIK, 1995). The report from Sunda Islands (Southeast of Asiatic mainland) by HARNISCH (1938) is doubtful, as HARNISCH (1932) reported *H. elegans* only from Indonesia. In their manuscript on Swedish Lapland testate amoebae, HARNISCH (1938) described *H. insecta* mentioning one empty test observed in the 1932 Sunda Island material.

Remarks: This is a problematic species, which we hesitated to consider as *inquirenda*. Apparently widespread, this species has rarely been reported. Unfortunately, HARNISCH (1938) did not provide any original illustrations to clarify the differences between *H. insecta* and *H. elegans*; however, their distinct ecological habitats advocate rather for two different species, as *H. insecta* has also been reported in soils, while *H. elegans* appears restricted to *Sphagnum*. A detailed systematic study, including morphological and molecular data, as well as neotypification, is thus needed to clarify the relationship between these two species.

Hyalosphenia irregularis Decloitre, 1965

1965 *Hyalosphenia irregularis* Decloitre, Bull. I.F.A.N., Ser. A1: 171, Fig. 4.

Description (based on the original description): Test ovoid, narrow elliptical in broad view, with a pointed posterior end, giving it an irregular shape. Test transparent with a yellowish tinge. L = 60–70 µm, B = 45–50 µm, P = 10–15 µm. Pseudostome elliptical, narrow, thickened inwards.

Differential diagnosis: Differs from other *Hyalosphenia* species by its pointed posterior end.

Type locality: Mvouti, Kouilou Region, Congo, Africa. Likely coordinates: -4.314049°, 12.378544°.

Type specimen: Not provided. We declare Fig. 4 by DECLOITRE (1965), reproduced here as Fig. 34, as the type.

Etymology: Not provided. The species name likely refers to the irregular margin of the test; i.e., its pointed posterior end, as opposed to round aboral outline of all other congeneric members.

Habitat: Unknown. No detail was provided in the original description.

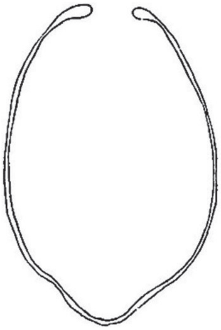

Fig. 34. *Hyalosphenia irregularis*: Original drawing from DECLOITRE (1965): broad view.

Geographical distribution: Africa: Congo (DECLOITRE, 1965).

Remarks: This is a problematic species, which has not been reported since its description. Furthermore, the author did not mention on how many individuals the original description was based. Because we consider the original drawing and description of sufficient quality, we deemed the species as valid.

Hyalosphenia ligata (Tatem, 1870)

1857(1859) *Hyalosphenia cuneata* Stein, Sitzungsb. Bohm. Akad. Wissens 1859: 42 (junior synonym; see remarks on p. 79).

1870 *Difflugia ligata* Tatem, Month. Micros. Jour. IV: 313.

1874 *Catharia ligata* Leidy, Proc. Ac. Nat. Sc.: 79

1875 *Hyalosphenia ligata* Tatem,–1870, Leidy, Proc. Ac. Nat. Sc.: 415.

1875 *Hyalosphenia lata* Schulze, Archiv Mikr. Anat. VI: 335 (junior synonym; see remarks on p. 79).

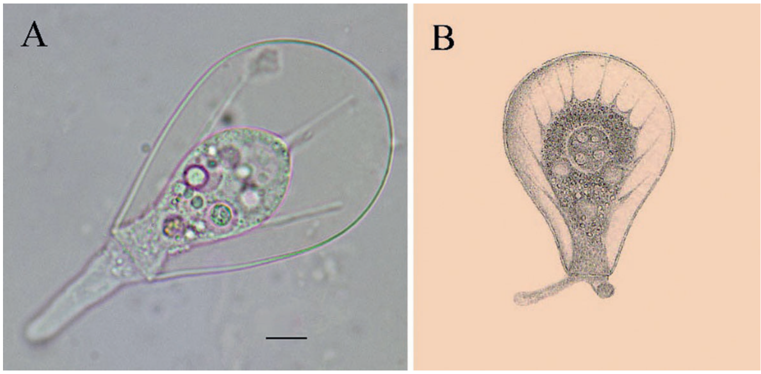

Fig. 35. *Hyalosphenia ligata*: (A) LM broad view image from the Netherlands (by Ferry Siemensma), (B) Original drawing of *H. ligata* from LEIDY (1879): broad view, declared here as the type. Scale bar = 10 μm.

Icon.: TATEM, 1870, Pl. lxviii, Fig. 1; SCHULZE, 1875, Pl. xviii, Figs. 15–18; LEIDY, 1879, Pl. XX, Figs. 1-10; PENARD, 1902, Figs. 1–7; CASH et al.,1909, T. 31, Figs. 1-4.

Description: Test ovoid, slightly elongated in broad view, gradually tapering towards the pseudostome, with a narrow hollow keel visible in profile view. No symbiotic algae. Similar in shape to *Hyalosphenia papilio*. Test very transparent and without any structure. Pores absent. L = 60–76 μm, B = 44–60 μm. Pseudostome linear in broad view (see Remarks below).

Differential diagnosis: Shape like *H. papilio*, but smaller and without symbiotic algae.

Type locality: Carlshof, Germany. Likely coordinates: 53.702793°, 12.554414°.

Type specimen: Not provided. We declare Pl. 22, Fig. 1 by TATEM (1870), reproduced here as Fig. 35B, as the type.

Etymology: Not provided. The name likely refers to the Latin word "Ligatum" which means "being connected".

Habitat: Reported from freshwater, peatlands among *Sphagnum* mosses, ponds, the sandy shore of a deep lake, on watercress in natural spring, and humus.

Geographical distribution: Possibly cosmopolitan.

Remarks: As FERRY SIEMENSMA (unpubl. data, www.arcella.nl) observed smaller tests (L = 52–64 μm), the updated length range has been revised to 52–76 μm. Despite its broad geographical distribution, *H. ligata* is rarely reported. Further notes on nomenclature are provided on p. 79.

Hyalosphenia minuta Cash, 1892

1892 *Hyalosphenia minuta* Cash, Trans. Ann. Rept. Manchester Microsc. Soc.: 49–50, Figs. 3–4.

Icon.: CASH, 1892, Figs. 3–4 (non CASH, 1891 Fig. 10); CASH et al., 1909, T. 24, Figs. 5–11; WAILES, 1928, T. 7, Fig. 40.

Description: Test transparent, hyaline, ovoid in broad view; in profile, narrow elliptical, compressed. Pseudostome straight in broad view,

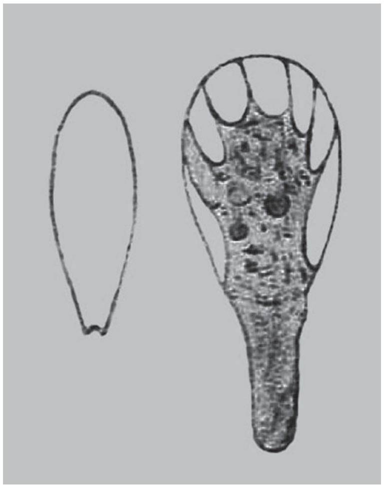

Fig. 36. *Hyalosphenia minuta*: Original drawing from CASH (1891): profile and broad views.

slightly rounded at the edges. In his description, Cash mentioned, "The slightly convex sides sloping gradually downward to the mouth, which forms a shallow notch. Great care is needed in order to see this owing to the delicate transparency of the shell membrane". Test small. L = 26–43 µm, B = 16–27 µm, P = 13 µm.

Differential diagnosis: The general species shape resembles *H. papilio* but differs by its smaller size (*H. papilio* is always at least twice as large, ≥ 90 µm) and lacks symbiotic algae (*H. papilio* has, to the best of our knowledge, only been observed with *Chlorella* symbionts). Can be distinguished from the very similar *H. ligata* by its smaller size.

Type locality: Dunham, England, UK. Likely coordinates (closest bog to Dunham, the original type locality is likely destroyed): 53.451034°, -2.465269°. Later found also near the sea at Perwick Bay, Isle of Man.

Type specimen: Not provided. We declare Figs. 3–5 (representing the same individual) by CASH (1892), reproduced here as Fig. 36, as the type.

Etymology: The name of this species refers to its "minute", small size.

Habitat: *Sphagnum* and wet green mosses.

Geographical distribution: Africa: Congo (VAN OYE, 1958), Morocco (DECLOITRE, 1965), Senegal (DECLOITRE, 1947); Europe: Austria (LÜFTENEGGER & FOISSNER, 1989), British Islands (CASH, 1891), Czech Republic (BALIK, 1990), France (DECLOITRE, 1976), Germany (WANNER, 1991), Italy (GRANDORY, 1934), the Netherlands (VAN OYE, 1936; MITCHELL et al., 2003), Norway (SANDON, 1924), Switzerland (MITCHELL et al., 2003), Sweden (SCHÖNBORN, 1966); Asia: China (YANG et al., 2005), India (MISHRA et al., 1977), Java (BONNET, 1992), Vietnam (NGUYEN-VIET et al., 2007); North America: Canada (LOUSIER & PARKINSON, 1981), Greenland (MATTHEEUSSEN et al., 2007), USA (LOUSIER & BAMFORTH, 1990), Central America: Puerto Rico (BAMFORTH, 2007); South America: Venezuela (DECLOITRE, 1955).

Remarks: The species is widespread, but infrequently reported, possibly because of its relatively small size. Furthermore, its small and transparent characteristics make it difficult to obtain high-quality LM images; therefore, it is rarely illustrated in publications. Hence, it is impossible to evaluate the accuracy of identifications in most studies, and as a result, its true geographical distribution remains uncertain. Such small and rather inconspicuous taxa deserve more detailed attention by taxonomists and ecologists alike.

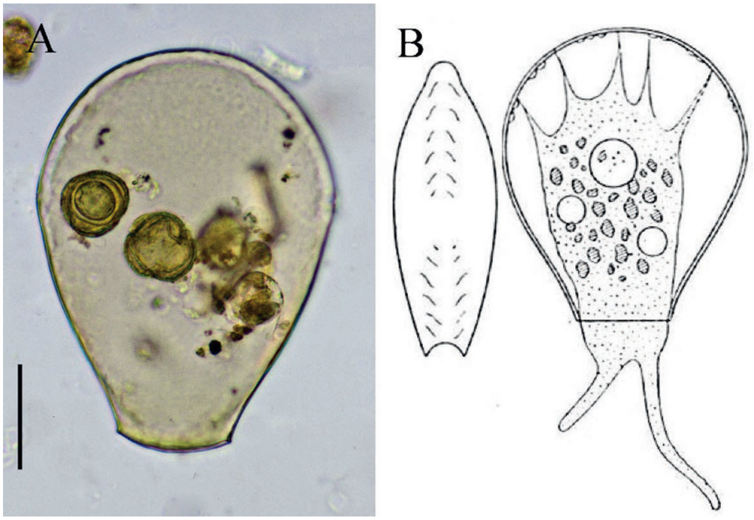

Fig. 37. *Hyalosphenia ovalis*: (A) LM image of a dead specimen from the Netherlands (by Ferry Siemensma), (B) Original drawing of H. ovalis from WAILES (1912): profile and broad views. Scale bar = 50 µm.

Hyalosphenia ovalis Wailes, 1912

1912 *Hyalosphenia ovalis* Wailes, Scott. Naturalist: 59–65.

Icon.: WAILES, 1912b, Fig.1; Cash et al.,1919, T.62, Figs. 3–4; JUNG, 1936, Fig. 25; CHARMAN et al., 2000, Fig. 24c (note: the latter illustration shows *Nebela tincta s.l.* lacking recycled idiosomes, not *H. ovalis*).

Description: Test wide piriform to wide-ovoid in broad view, compressed in the oral part, starting from the transition between the main body to the neck as in *Hyalosphenia papilio*. In profile, test elliptic with a narrow hollow keel, as in *Gibbocarina galeata*. Test transparent, with 2–12 pores on the lateral margin. L = 130–180 µm, B = 90–140 µm, P = 50–56 µm. Lacks symbiotic microalgae.

Differential diagnosis: The best discriminating character separating *H. ovalis* from *H. papilio* is that the latter is always mixotrophic (i.e., always observed with symbiotic *Chlorella*); whereas *H. ovalis* is strictly heterotrophic. Based on the original descriptions and illustrations, *H. ovalis* is generally less elongated: L/B < 1.5 for H. ovalis, and >1.5 for *H. papilio*. See Remarks below.

Type locality: Dumfries, Scotland, UK. Likely coordinates: 55.016677°, -3.683083°.

Type specimen: Not provided. We declare Fig. 1 by WAILES (1912b), reproduced here as Fig. 37B, as the type.

Etymology: Not provided. The name “ovalis” likely relates to the ovoid test shape.

Habitat: *Sphagnum* mosses.

Geographical distribution: Europe: Austria (SEIS, 1971; AESCHT & FOISSNER, 1989), Estonia (CHARMAN et al., 2004), Finland (TOLONEN et al., 1992), France

(MORACZEWSKI & BONNET, 1969), Germany (JUNG, 1936; GROSPIETSCH, 1965), Hungary (SCHNITCHEN et al., 2006), Poland (JUNG, 1936), Romania (SCHNITCHEN et al., 2006), Russia (BOBROV, 2003), Switzerland (BUTTLER et al., 1996), UK (WAILES, 1912b; CASH et al., 1919; WOODLAND et al., 1998; DAVIS & WILKINSON, 2004); North America: Canada (TOLONEN, 1985; CHARMAN & WARNER, 1992; WARNER et al., 2007), USA (TOLONEN, 1985; CHARMAN & WARNER, 1992); Australasia: New Zealand (MCGLONE & WILMSHURST, 1999).

Remarks: The validity of *Hyalosphenia ovalis* is questionable, as has been discussed in BOOTH & MEYERS (2010), "Considerable confusion exists regarding the identification of *H. papilio* and *H. ovalis* in recent peatland studies. Although early descriptions separated *H. ovalis* from *H. papilio* by its larger size, more oval shape, and rounded keel, some recent peatland work has focused more on the pronounced convex tapering of the pseudostome in *H. ovalis* (Charman et al. 2000). However, using this criterion, tests identified as *H. ovalis* are generally smaller than *H. papilio*, which is inconsistent with early descriptions. In fact, even specimens of *H. ovalis* in Penard's slides at the British museum would be classified as *H. papilio* if the convex tapering of the pseudostome were used as the primary diagnostic feature (Charman et al. 2000). To add to the confusion, individuals of *Nebela tincta* sometimes lack plates, as is common in some modern samples and most fossil samples, yet these would be identified as *H. ovalis* using the approach of Charman et al. (2000). *N. tincta* is generally smaller than *H. papilio*, and confusion between these taxa may help explain the smaller size of tests identified as *H. ovalis* in recent studies (Charman et al. 2000)".

The species is problematic. According to the original description, the it differs from *H. papilio* by the number of pores, its smaller size, and the presence of a hollow keel; however, as shown in recent studies, pore number is not a valid taxonomical criterion (BOOTH & MEYERS, 2010; KOSAKYAN et al., 2013; GOMAA et al., 2014; SINGER et al., 2015; MULOT et al., 2017), nor can size be used as a convincing discriminating character, as their ranges overlap (L = 130–180 µm, B = 90–140 µm for *H. ovalis* vs. L = 90–175 µm, B = 60–155 µm for *H. papilio*). Accordingly, the optimal discriminating character separating *H. ovalis* from *H. papilio* is that the latter is always mixotrophic (i.e., always observed with symbiotic *Chlorella*), while *H. ovalis* is heterotrophic. Further, the test of *H. ovalis* is characterized by the presence of a narrow hollow keel, while Leidy notes for *H. papilio*, "*in the narrow view…the fundus [is] angularly rounded and the oral end notched*". In this respect, the two species are rather similar, and further molecular studies are thus needed to determine if *H. ovalis* and *H. papilio* are indeed separate species.

Hyalosphenia papilio (Leidy, 1874)

1874b *Difflugia (Catharia) papilio* Leidy, 1874, Proc. Acad. Philad.: 156.

1879 *Hyalosphenia papilio* Leidy, 1874 – Leidy, Rep. Unit. Stat. Geol. Surv. 12: 324.

1936 *Hyalosphenia papilio* f. *multiporifera* Jung, Abh. Landesmus. Provinz. West., Mus. Fur Naturkd. 7: 1–87 (insufficient morphological differences from the type, see notes).

Icon.: LEIDY, 1879, T. 21; PENARD, 1902, Figs. 1–4; CASH et al., 1909, T. 24, Figs. 1–4; DEFLANDRE, 1931, Figs. 1–2; OGDEN & HEDLEY, 1980, Pl. 25; MEISTERFELD, 2002, Fig. 61; BOOTH & MEYERS, 2010, Fig. 1; HEGER et al., 2013, Fig 1.

Description: Test in broad view narrow, oblong ovoid, or occasionally narrow piriform

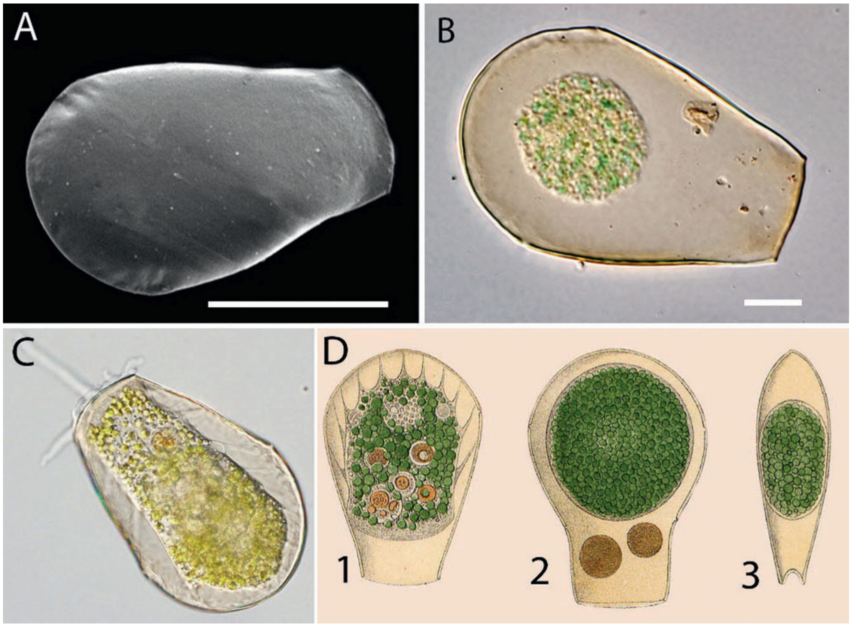

Fig. 38. *Hyalosphenia papilio*: (A) SEM image of an individual from Switzerland; (B) LM broad view image of a specimen from the Eugène Penard slide collection, no. 464-2-2 (Natural History Museum, Geneva, Switzerland); (C) LM image of an active cell from Switzerland showing the pseudopods; (D) Original drawings from LEIDY (1879): (1) active cell, (2) encysted cell, and (3) profile view of the test. Scale bars: A = 50 µm, B = 20 µm. Images by: (A) Anush Kosakyan, (B) Thierry Arnet (Wikimedia), and (C) Thierry Arnet (Wikipedia).

with a convex fundus; test sides gradually tapering to the slightly convex or linear pseudostome, or with piriform outline. In profile, fundus angularly rounded and pseudostome notched. In frontal view, pseudostome oval, with rounded commissures. Test composed of a transparent to yellowish chitinoid membrane, with usually two but up to ten pores on the lateral margin of the posterior end of the test. Size: according to LEIDY (1879): L = 108–140 µm; B = 68–84 µm, "thick" = 32–40 µm, P = 32–40 µm x 8 µm; including subsequent observations: L = 90–175 µm, B = 60–155 µm, P = 30–40 µm. Pseudostome bordered by a thin margin.

Differential diagnosis: *Hyalosphenia papilio* is similar to *H. minuta* and *H. ovalis* in general test shape, differing by its dimensions and the presence of symbiotic algae. For more details, see Differential diagnosis under these two species.

Type locality: Absecom, New Jersey, USA. Likely coordinates: 39.426909°, -74.512855°.

Type specimen: Not provided. We declare Pl. XXI, Fig. 5 by LEIDY (1879), reproduced here as Fig. 38D1, as the type.

Etymology: In Latin, the name "papilio" means "butterfly". LEIDY (1879) explained the choice of the species name as, "*No other lobose* *rhizopods has more impressed me with its beauty than this one. From its delicacy and transparency, its bright color and form, as it moves among the leaves of sphagnum, desmids, and diatoms, I have associated it with the idea of a butterfly hovering among flowers*". Leidy was obviously charmed by the beauty of this species, which led him to study testate amoebae in greater depth and ultimately leading to the publication of his famous 1879 monograph "It was the rediscovery of this beautiful form which impelled me to pursue the investigations which constitute the material of the present work." (LEIDY, 1879, footnote p. 133).

Habitat: Upper (living) parts of *Sphagnum* mosses, typically most abundant in poor fens and relatively wet habitats, such as lawns along the sides of pools.

Geographical distribution: Africa: Guinea (CHARDEZ, 1963), Marion Island (GROSPIETSCH, 1971), Tanzania (SCHAUDINN, 1898); South America: Argentina (VUCETICH & LOPRETTO, 1955), Brazil (WAILES, 1913; LANSAC-TOHA et al., 2001), Columbia (HEINIS, 1914),; North America: Canada (HEGER et al., 2013), Greenland (MATTHEEUSSEN et al., 2005), USA (LEIDY, 1879; BOOTH & ZYGMUNT, 2005; NIKOLAEV et al., 2005; HEGER et al., 2013); Asia: China (LI et al. 2010), Japan (SUDZUKI, 1971; YAMAMOTO, 1981), Sri Lanka (DADAY, 1898), Russia (MAZEI & CHERMYSHOV, 2011[EM2]; HEGER et al., 2013); Europe: Austria (SEIS, 1971), Belgium (CHARDEZ, 1965; BEYENS, 1985), Bulgaria (GOLEMANSKY & TODOROV, 1993; HEGER et al., 2013; TODOROV & BANKOV, 2019), Czech Republic (BARTOŠ, 1954), Estonia (HEGER et al., 2013), Finland (TOLONEN, 1966; MITCHELL et al., 2000), France (DECLOITRE, 1970; HEGER et al., 2013), Germany (JUNG, 1936; GROSPIETSCH, 1958; SCHÖNBORN, 1962; MEISTERFELD, 1979), Hungary (SCHNITCHEN et al., 2006), Iceland (DECLOITRE, 1965), the Netherlands (DE GRAAF, 1956; SCHROEVERS, 1966), Poland (LAMENTOWICZ & MITCHELL, 2005; HEGER et al., 2013), Romania (SCHNITCHEN et al., 2006), Russia (BOBROV, 2003; BOBROV & MAZEI, 2004; HEGER et al., 2013), Slovakia (OPRAVILOVA & HAJEK, 2006), Spain (HEGER et al., 2013), Sweden (GROSPIETSCH, 1954; LARA et al., 2008; HEGER et al., 2013), Switzerland (PENARD, 1902; MITCHELL et al., 2000, 2001; HEGER et al., 2013), UK (CASH & HOPKINSON, 1909; DAVIS & WILKINSON, 2004; HEAL, 1961; OGDEN & HEDLEY, 1980; MITCHELL et al., 2000; CHIVERRELL, 2001; HEGER et al., 2013); Australasia: New Guinea (Papua New Guinea, ENTZ, 1897).

Remarks: KIREEV et al. (2011) studied the spatial and temporal morphological variability of *H. papilio* based on 700 individuals from 14 populations within the Penza Territory (Russia), concluding that individuals from wet habitats are larger than those from dry ones. Furthermore, in dry habitats, shell length increased with *Sphagnum* depth; whereas in wet biotopes, the inverse trend was observed.

Molecular data: HEGER et al. (2013) and SINGER et al. (2019) investigated the genetic diversity and phylogeography of *H. papilio* in Holarctic *Sphagnum*-dominated peatlands using the mt-COI gene, revealing 12-14 different genetic lineages (depending on the statistical test used), with often non-overlapping geographical distributions. This strongly suggests that *H. papilio* represents a complex of species. SINGER et al. (2019) further showed that the origin of this species is in western North America, and that the pattern of diversification was congruent with expansion and contractions of *Sphagnum* peatland areas during the Quaternary glaciation/interglacial cycles. These different lineages of *H. papilio* are impossible to distinguish morphologically, at least in Europe. They are extremely variable in size, and experimental evidence suggests that this results from strong phenotypic plasticity, with test size increasing under colder climates and wetter conditions and decreasing in warmer and drier conditions (MULOT et al., 2018).

A phylogenetic study based on the SSU rRNA gene (OLIVERIO et al., 2014) also suggested that *H. papilio* is not a single species and is possibly paraphyletic, as the sequences intermingle with those of other hyalospheniids in the derived phylogenetic tree. Moreover, *H. papilio* and *H. elegans* could be conspecific, possibly even different phases of a complex life cycle. Until more data can corroborate this controversial hypothesis, we favour the more conservative and parsimonious view that *H. papilio* and *H. elegans* both represent monophyletic species complexes.

JUNG (1936) described *Hyalosphenia papilio* f. *multiporifera*, which differs from the type by the presence of more than two lateral pores. It was subsequently suggested (BOOTH & MEYERS, 2010; GOMAA et al., 2013; MULOT et al., 2017) that the number of pores is not genetically determined and thus cannot be used as a valid taxonomic criterion. Therefore, we included this variety into the list of synonyms.

We are listing one subspecies here:

Hyalosphenia papilio stenostoma Deflandre, 1931

1931 *Hyalosphenia papilio stenostoma* Deflandre, Ann. de Protistologie 3: 81–95, T. 14, Figs. 2, 6.

Description and differential diagnosis: Test shape differs from the type, gradually tapering towards the pseudostome in broad view, similar to the shape of *Alabasta militaris* for the anterior end, and by the narrower pseudostome. L = 110–127 µm.

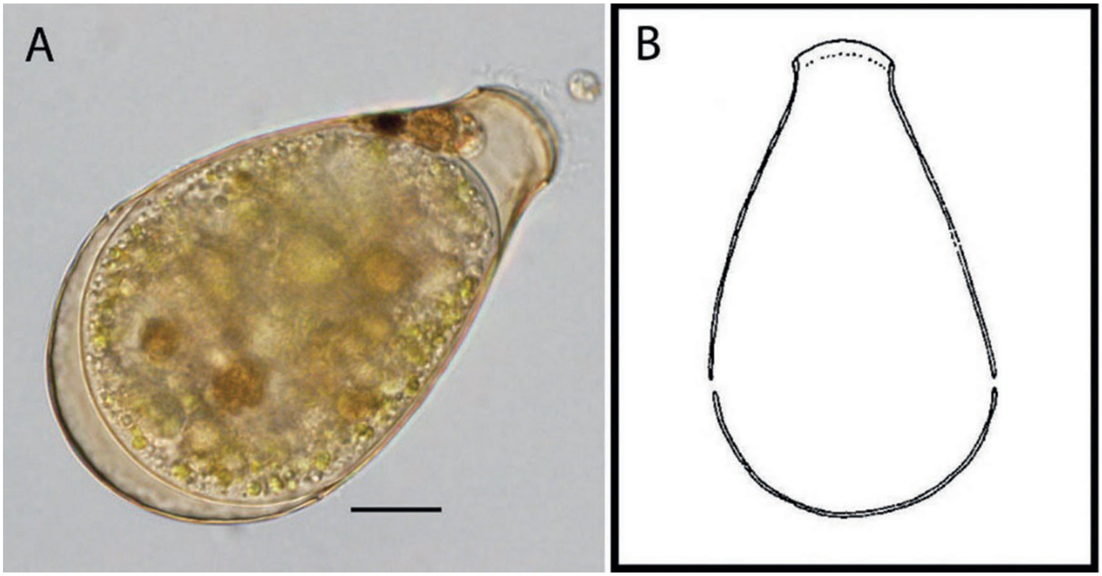

Fig. 39. *Hyalosphenia papilio stenostoma*: (A) LM image of a living cell from Switzerland (by Anush Kosakyan), (B) Original drawing modified from DEFLANDRE (1931). Scale bar = 20 µm.

Type locality: Joux Plane pass above Morzine Haute-Savoie, France. Likely coordinates: 46.129173°, 6.707276°.

Type specimen: Not provided. We declare Fig. 2 by DEFLANDRE (1931), reproduced here as Fig. 39B, as the type.

Etymology: The species name refers to the general shape of the test; i.e., in Greek "stenosis" (stɪˈnoʊ sɪs) means "narrowing", and "stoma" (stō′mə) means "mouth".

Habitat: *Sphagnum* mosses.

Geographical distribution: Europe: Belgium (CHARDEZ, 1957, 1987), France (DEFLANDRE, 1931), Germany (GROSPIETSCH, 1965; MEISTERFELD, 1973), Switzerland (A. KOSAKYAN, unpubl.).

Remarks: The original description of *H. papilio* by Leidy (1874) includes a general piriform outline among the possible outlines, perhaps corresponding to *H. papilio stenostoma*. In general, *H. papilio* is now known to correspond to at least 13 genetically distinct species (HEGER et al., 2013; SINGER et al., 2018), although no molecular data for *H. papilio stenostoma* are currently available.

Hyalosphenia penardi Lauterborn, 1908

1908 *Hyalosphenia penardi* Lauterborn, Z. Wiss. Zool. 90: 645–699, T. 41, Figs. 1–2.

Description (based on the original description): Test transparent, colourless, or yellowish-brown, elliptical in broad view, strongly laterally compressed. Rounded fundus and a strongly curved pseudostome. Pores absent. L = 180 µm, B = 70 µm.

Differential diagnosis: Morphologically very similar to *H. gigantea*. For further detail, see Differential diagnosis under *H. gigantea*.

Type locality: Upper Rhine, Germany. Likely coordinates: 48.237628°, 7.688538°.

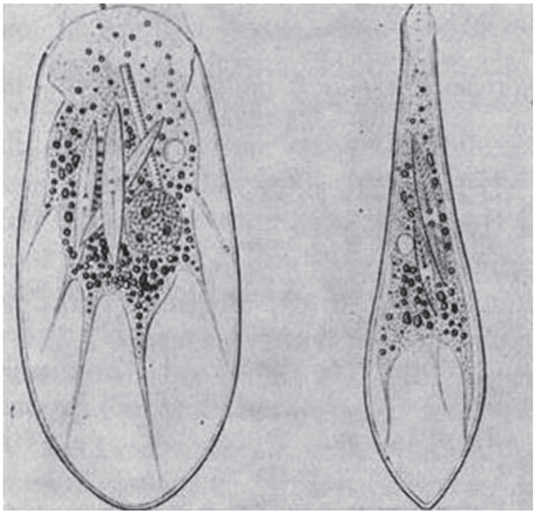

Fig. 40. *Hyalosphenia penardi*: Original drawing from LAUTERBORN (1908): broad and profile views.

Type specimen: Not provided. We declare Figs. 1–2 (representing the same individual) by LAUTERBORN (1908), reproduced here as Fig. 40, as the type.

Etymology: It is named in honour of the Swiss protozoologist Eugène Penard (1855-1954).

Habitat: Freshwater, among diatoms.

Geographical distribution: Germany (LAUTERBORN, 1908).

Remarks: This species has been recorded only once.

Hyalosphenia platystoma West, 1903

1903 *Hyalosphenia platystoma* West, J. Linn. Soc. 29: 108–117, T. 13, Figs. 3–6.

Icon.: WEST, 1903, T. 13, Figs. 3–6; CASH et al., 1909, T. 31, Figs. 7–8.

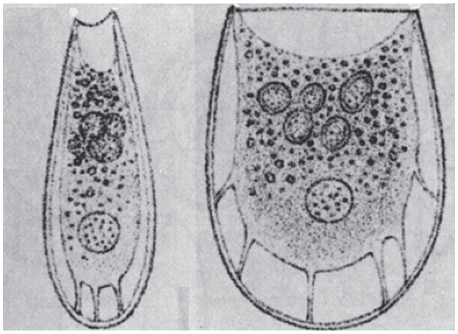

Fig. 41. *Hyalosphenia platystoma*: Original drawing from CASH et al. (1909): profile and broad views.

Description (based on the original description): Test transparent, wide ovoid in broad view, barely longer than wide, and slightly narrowing towards the pseudostome. In profile, elongated elliptical with a notched pseudostome. L = 40–42 µm, B = 28–32 µm, P = 28–32 µm. Pseudostome linear, nearly as wide as the test.

Differential diagnosis: Differs from other small sized *Hyalosphenia* species by the very wide and linear pseudostome.

Type locality: Tarbert, Scotland, UK. Likely coordinates: 55.876978°, -5.435341°.

Type specimen: Not provided. We declare Figs. 3–4 (likely representing the same individual) by WEST (1903), reproduced here as Fig. 41, as the type.

Etymology: The name of this species refers to the morphology of the pseudostome; i.e., in Latin, “platystoma” means “flat mouth”.

Habitat: *Sphagnum* mosses.

Geographical distribution: Europe: Austria (SIEMENSMA, www.arcella.nl accessed on Aug. 25, 2018), Belgium (SCHOUTEDEN, 1905), France (BONNET & THOMAS, 1955), UK (WEST, 1903; CASH et al., 1909); South America: Argentina (VUCETICH, 1980).

Remarks: This species has rarely been reported, and it’s unclear if it has been overlooked in the many studies of peatland testate amoebae, misidentified (although this seems unlikely), if it is rare, or possibly its ecological optimum is not in *Sphagnum*, but rather some other, less intensively studied habitat.

Hyalosphenia punctata Penard, 1891

1891 *Hyalosphenia punctata* Penard, Arch. Sci. Phys. Nat. Genève 26: 134–156, T. 2, Figs. 1–3.

1967 *Pseudohyalosphenia prismatica* Štěpánek, Hydrobiologia 29: 49, Fig. 4.

Icon.: PENARD, 1891, T. 2, Figs. 1–3; PENARD, 1899, T. 4, Figs. 20–29; PENARD, 1902, Figs. 1–7; ŠTĚPÁNEK, 1967, Fig. 4; TÖRÖK, 2001, Figs. 1–14.

Description: Test wide ovoid in broad view, compressed, tapering towards the pseudostome. Test wide piriform in broad view, greyish-brown. In profile, the fundus is narrowly elliptical, tapering towards the pseudostome. Test transparent, colourless, yellow or brownish, composed of small organic building units, similar to the structures observed in genus *Arcella*. L = 35–95 µm, B = 16–54 µm, P = 15–32 µm—wide range provided by TÖRÖK (2001). Pseudostome linear, with a thin lip. Does not contain symbiotic algae.

Differential diagnosis: Differs from other *Hyalosphenia* taxa (primarily *H. papilio*, *H. ovalis*, and *H. minuta*) by its punctuated test structure (see Remarks for more detail).

Type locality: Lake Geneva, Switzerland. Likely coordinates: 46.409111°, 6.708905°.

Type specimen: Not provided. We declare the specimen in broad view from the E. Penard slide collection, no. 468-1-1 (Natural History

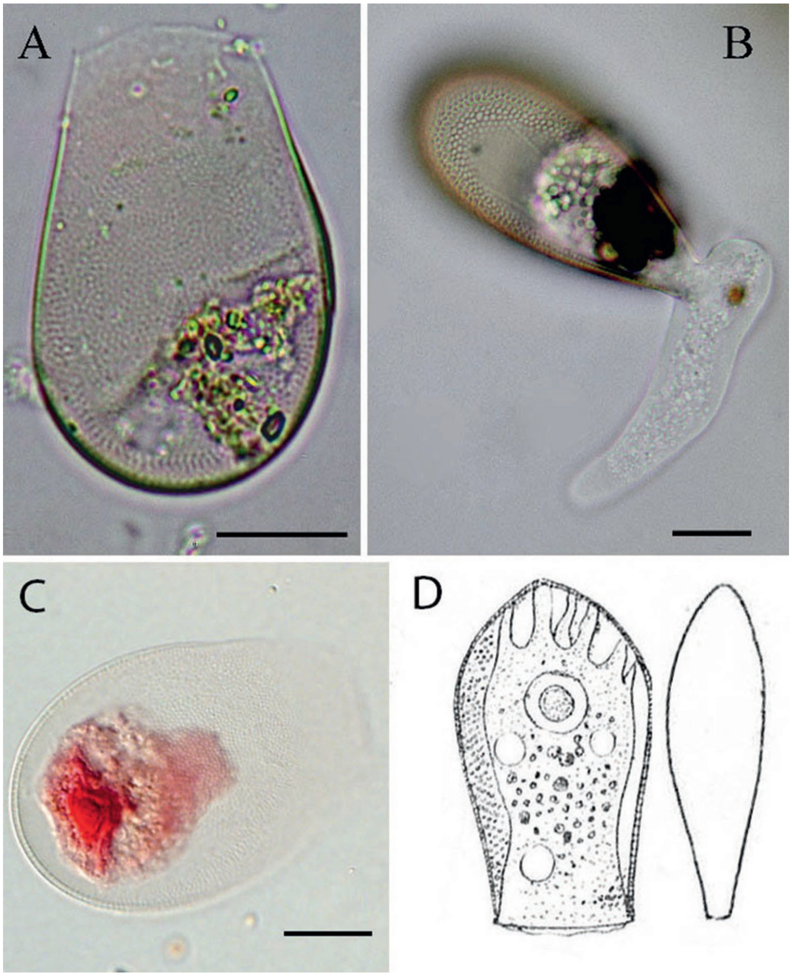

Fig. 42. *Hyalosphenia punctata*: (A) LM broad view image of an empty test from the Netherlands; (B) Profile view of an active individual from the Netherlands; (C) LM broad view image of a specimen from the Eugène Penard slide collection, no. 468-1-1 (Natural History Museum, Geneva, Switzerland); (D) Original drawings from PENARD (1891): broad view of an active individual and profile view of empty test. Scale bars = 20 µm. Images by: (A & B) Siemensma, and (C) Thierry Arnet (Wikimedia, Penard MHNG, specimen 468-1-1).

Museum, Geneva, Switzerland), reproduced here as Fig. 42C, as the type.

Etymology: The species name is derived from the punctuated test structure.

Habitat: Deep alpine lakes (PENARD, 1891, 1902), swamps (PENARD, 1902), running waters (OPRAVILOVA, 1974, 1980; TÖRÖK, 2001), mud (ŠTĚPÁNEK, 1967), sediments in a ditch of a nature preservation area, and forest soil in Ecuador (KRASHEVSKA et al., 2007).

Geographical distribution: South America: Ecuador (KRASHEVSKA et al., 2007); Asia: Kashmir, India (BHATIA, 1930), Russia (SAMSONOV, 1908); Europe: Belgium (BEELI, 1931), Czech Republic (ŠTĚPÁNEK, 1967; OPRAVILOVA, 1974, 1980), France (CHARDEZ, 1979), Hungary (TÖRÖK, 2001), Iceland (DECLOITRE, 1965), Italy (MONTI, 1906), the Netherlands (SIEMENSMA, www.arcella.nl, accessed Aug. 25, 2018), Switzerland (PENARD, 1891,1901; VAUCHER & BÉNIER, 1988).

Remarks: This is a rare and problematic species. TÖRÖK (2001) suggested it may possibly belong to the genus *Nebela* because of its non-hyaline test structure; however, unlike genus *Nebela*, this species does not appear to recycle mineral materials, but rather secretes its test entirely, using proteinaceous single units, as in genus *Arcella*. ŠTĚPÁNEK (1967) found a species below Bitov Castle, Vranov, Czech Republic (approximately 48.939497°, 15.700331°) that bares a strong resemblance to *Hyalosphenia papilio* except for its smaller size (L = 85 µm, B = 45 µm, P = 15 µm) and test structure (made up of small six-sided prisms, as in genus *Cyphoderia*). Accordingly, ŠTĚPÁNEK (1967) created a new genus *Pseudohyalosphenia* and described this new species as *P. prismatica* by stating that is very similar to *Hyalosphenia papilio*, the only difference being the test structure: "The main characteristic of the genus is the test structure similar to *Cyphoderia*: it is composed of small organic units such as six-sided prisms that are connected by a basic cement of unknown origin". However, as the descriptions of *P. prismatica* and *H. punctata* Penard, 1891 overlap, the two species must be synonymized. As *H. punctata* was described first, this name takes priority (ICZN Art. 23, Principle of priority). Molecular data are needed to clarify the phylogenetic position of this species and more generally the phylogenetic relationships within genera *Hyalosphenia*.

The report of this species in neotropical high-altitude forest soils (KRASHEVSKA et al., 2007) stands in contrast to all previous records from aquatic environments but agrees with findings of other aquatic or subaquatic taxa (e.g., *Archerella*, *Paulinella*, and *Pyxidicula*) found within these samples (KRASHEVSKA, pers. comm.). Indeed, the investigated habitat at 2000 m.a.s.l. was very wet (high rainfall), possibly explaining the presence of this species, which occurs in otherwise aquatic habitats of temperate regions in the Northern Hemisphere.

Hyalosphenia rectangularis Decloitre, 1965

1965 *Hyalosphenia rectangularis* Decloitre, Bull. I.F.A.N., ser A1: 170, Fig. 3.

Description (based on the original description): Test in broad view oval-elliptical at the aboral end and rectangular with rounded edges at the pseudostome end, transparent to yellowish. Test bending sharply to almost square angles at the level of the pseudostome, which is thus much narrower than the test (ca. 1/3rd; see Fig. 43). L = 45–55 µm, B = 30–32 µm, depth (in profile): 12–15 µm, P = 10 µm Pseudostome elliptical with a thickened margin.

Differential diagnosis: Differs from other *Hyalosphenia* species by its general contour in broad view, especially the rounded rectangular angles near the pseudostome.

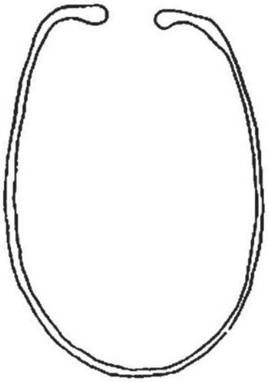

Fig. 43. *Hyalosphenia rectangularis*: Original drawing from DECLOITRE (1965): broad view.

Type locality: Dimonika, Congo, Africa. Likely coordinates: -4.2573°, 12.361541°.

Type specimen: Not provided. We thus declare Fig. 3 by DECLOITRE (1965), reproduced as Fig. 43 here, as the type.

Etymology: The species name derives from the test morphology, namely, the rectangular angles near the pseudostome.

Habitat: Not specified. Likely forest litter (Dimonika is a biosphere forest reserve).

Geographical distribution: Africa: Congo (DECLOITRE, 1965).

Remarks: A rare and problematic species. DECLOITRE (1965) mentioned their uncertainty regarding whether this species belonged to genus *Hyalosphenia* or not owing to the thickening of the test at the edges of the pseudostome. The author drew a parallel with the difference between *Awerintzewia* and *Heleopera*; however, VAN OYE (1926) previously described another species from the Congo, *H. schoutedeni*, with a similar thickening of the test near the pseudostome. He therefore suggested the possible close affinity of *H. rectangularis* and *H. schoutedeni* Van Oye, 1926, predicting that these two taxa may one day be split from genus *Hyalosphenia*.

Hyalosphenia savoiei Chardez, 1978

1978 *Hyalosphenia savoiei* Chardez, Rev. Verv. Hist. Nat. 35th year (no. 7–9): 2, Figs. 1–3.

Description (based on the original description): Test in broad view elongated, round in the aboral end, and circular in frontal view. A partial narrowing of the test delineates a neck and corresponds to a slight flattening which increases near the pseudostome. Pseudostome oval-elliptical in frontal view (Fig. 44). Test entirely chitinoid, smooth, and hyaline. L = 39–42 µm, B = 25 µm, depth (in profile) = 23–25 µm (section approximately circular), P = 15–18 µm x 8 µm. Cytoplasm clear, finely punctuated, with small green inclusions. A single lobose pseudopodium.

Differential diagnosis: Differs from *H. minuta* by the circular cross-section and possibly the habitat as well. *H. minuta* is primarily associated with *Sphagnum* mosses, although CHARDEZ (1978) mentioned that DECLOITRE (1975) found *H. minuta* in green algae growing on seashore rocks in Southern France (Var. department); however, it may well have been confused with *H. savoiei.*

Type locality: Oostende, Belgium. Likely coordinates: -51.203075°, 2.984396°.

Type specimen: Not provided. We declare Fig. 1 by CHARDEZ (1978), reproduced here as Fig. 44A, as the type.

Etymology: The species named after the French protozoologist Albert Savoie.

Habitat: Marine littoral fine sand, just above the high tide limit. The sand surface at the sampling location was green owing to green algal growth.

Geographical distribution: Europe: Belgium (CHARDEZ, 1978).

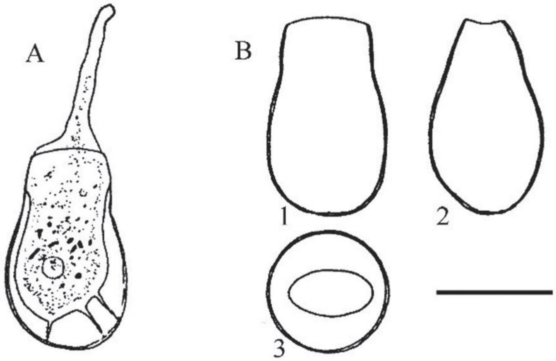

Fig. 44. *Hyalosphenia savoiei*: Original drawings from CHARDEZ (1978): (A) Broad view of a living individual, (B) Empty test: (1) broad view, (2) profile view, and (3) frontal view. Scale bar = 25 µm.

Remarks: To the best of our knowledge, this species has not been reported since its description. Accordingly, this species may represent the only (marginally) marine arcellinid known to date.

Hyalosphenia schoutedeni Van Oye, 1926

1926 *Hyalosphenia schoutedeni* Van Oye, Arch. de Zool. Exp. & Génér. 65: 64–74, Abb. 2, Figs. 1– 5.

Icon.: VAN OYE, 1926, Abb. 2, Figs. 1–5; DECLOITRE, 1948, Fig. 54.

Description (based on the original description): Test ovoid in broad view, narrow elliptical in profile, transparent and hyaline. Pores absent. L = 40–65 µm, B = 23–40 µm. Pseudostome elliptical in frontal view, strongly thickened inwards, and thus clearly visible.

Differential diagnosis: Morphologically similar to *H. subflava*, from which it differs by a more pronounced bulge around the pseudostome (GROSPIETSCH, 1965).

Type locality: Eala, Democratic Republic of Congo, Africa. Likely coordinates: 0.042789°, 18.334803°.

Type specimen: Not provided. We declare Abb. 2, Figs. 1–2 by VAN OYE (1926), reproduced here as Fig. 45A, as the type.

Etymology: The species is named in the honour of the zoologist Henri Schouteden from Belgium.

Habitat: Freshwater, mud, *Sphagnum*, soils, on bat guano in caves (DECLOITRE, 1948).

Geographical distribution: Africa: Congo (VAN OYE, 1926, 1958), West Africa (DECLOITRE, 1948); South America: Chile (ZAPATA & RUDOLPH, 1966); Asia: Vietnam (BALIK, 1995).

Remarks: This species was rarely reported. Given the rather narrow ecological preferences of most hyalospheniids, records of this species across very contrasted habitats (from nutrient-rich guano to nutrient-poor *Sphagnum*, both terrestrial and aquatic) appear highly unlikely. The close relationships between this species

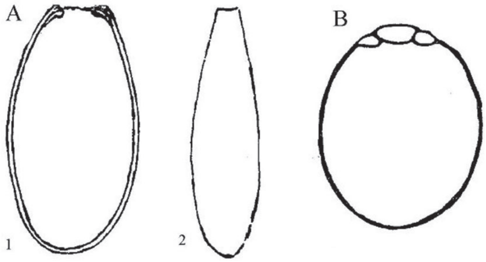

Fig. 45. Original drawings of: (A) *Hyalosphenia schoutedeni* from VAN OYE (1926), in (1) broad and 2) profile views; (B) H. *schoutedeni rotunda* from VAN OYE (1958) in broad view.

and *H. subflava*, and likely existence of several closely related species with different ecological optima and geographical distributions, should be further explored. The apparent broad ecological tolerance (from very oligotrophic *Sphagnum* to extremely eutrophic bat) suggests that there is more than one species.

Hyalosphenia schoutedeni rotunda Van Oye, 1958

Icon.: *Hyalosphenia schoutedeni* var. *rotunda*, in VAN OYE, 1958, Hydrobiologia 10(1): 85-137, Fig. 29.

Description & differential diagnosis: differs from the type by its smaller size, and almost circular shape in broad view: L = 20 µm, B = 17 µm (Fig. 45B).

Type locality: Wetland in the high Ngovi, near Masaruzi, ca. 16 km SW from Uvria, elevation: ca. 3000m a.s.l., likely coordinates: -3.439047°; 29.008764°.

Type specimen: Not provided. We declare Fig. 29 from Van Oye (1958) here reproduced as Fig. 45B as the type.

Etymology: Not specified. The name obviously refers to the almost circular shape in cross view.

Habitat: *Sphagnum* mosses, pH 3.8.

Geographical distribution: Africa: Republic of Congo (VAN OYE, 1958)

Hyalosphenia subflava Cash, 1909

1909 *Hyalosphenia subflava* Cash, in CASH et al., 1909, Brit. Fr. Rhiz. 2: 87–89, Pl. XXXI, Figs. 9–12.

1994 *Hyalosphenia subflava* var. *undulata* Balik (Infrasubspecific [not available] name: var. published after 1960, ICZN Art. 45.6.3).

Icon.: CASH et al., 1909, Pl. XXXI, Figs. 9–12; JUNG, 1936, Fig. 8; BONNET & THOMAS, 1960, T. 9, Figs. 125–126; CHARDEZ, 1963, Fig. 9; OGDEN & HEDLEY, 1980, Pl. 26, a–c; LÜFTENEGGER et al., 1988, Fig. 7; CHARMAN et al., 2000, Fig. 24b.

Description: Test ovoid in broad view, compressed, with convex sides, slightly tapering towards the pseudostome. In profile, test elliptical with a small, notched pseudostome. Test colourless or yellowish, very smooth. L = 45–87 µm, B = 30–53 µm, P = 13–14 µm. Pseudostome curved in broad view and thickened at the edges in profile.

Differential diagnosis: According to GROSPIETSCH (1965), *H. subflava* differs from *H. schoutedeni* by the lack of a bulge around its pseudostome (for additional details, see the Differential diagnosis for *H. schoutedeni*).

Type locality: Irlam Moss, near Manchester, Pentlands, Midlothian, UK. Likely coordinates: 53.394025°, - 1.88852°.

Type specimen: Not provided. We declare Fig. 9 by CASH et al. (1909), reproduced here as Fig. 46C-1, as the type.

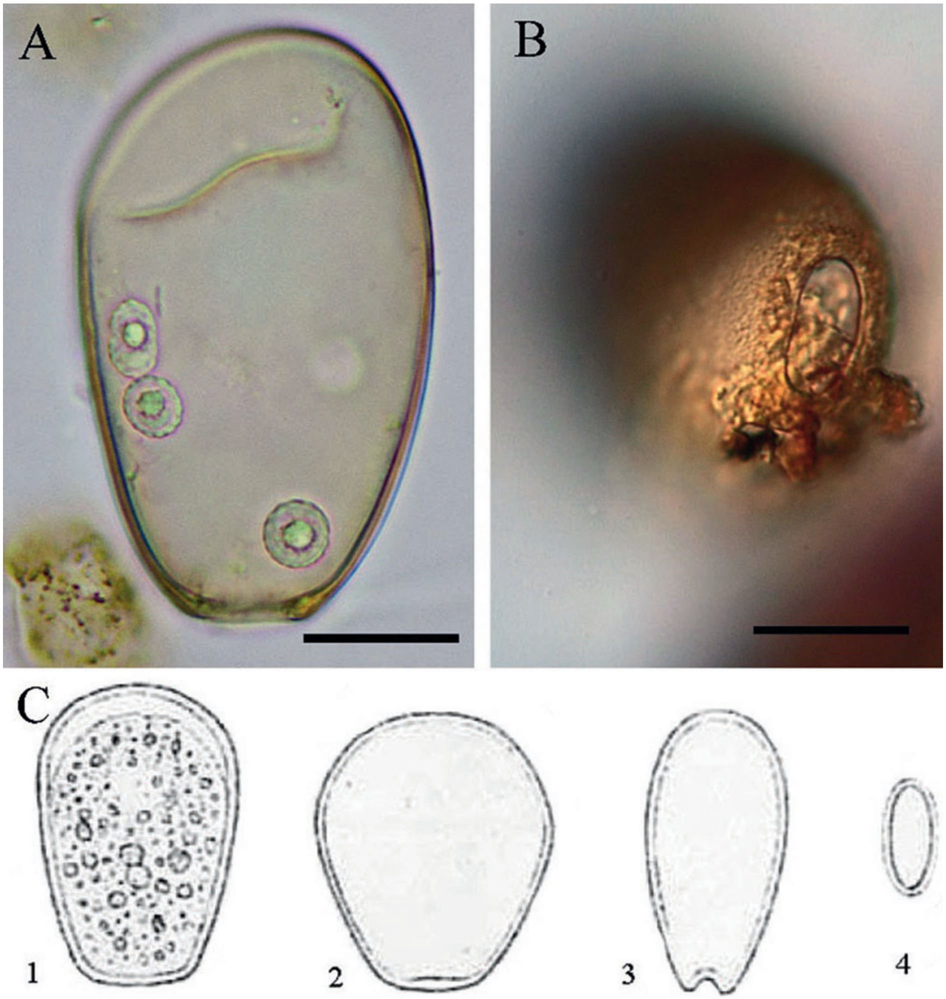

Fig. 46. *Hyalosphenia subflava*: (A) LM image of an empty test from the Netherlands; (B) Higher magnification frontal view of the pseudostome for an individual with a non-typical structure; (C) Original drawings of *H. subflava* from CASH et al., (1909): (1) living individual in broad view, (2) empty test in broad view, (3) empty test in profile view, and (4) frontal view of the pseudostome. Scale bars = 20 µm. Images (A & B) by Ferry Siemensma.

Etymology: The species name refers to the colour of the test, as “flavus” in Latin means “yellow”; the prefix “sub-” suggests “below yellow” or “yellowish”.

Habitat: Acid forest humus and litter, peaty soils, *Sphagnum* mosses.

Geographical distribution: Africa: Angola (BONNET, 1969a), Congo (BONNET, 1969b), Gabon (BONNET, 1966), Ivory Coast (BONNET, 1978; COÛTEAUX & MUNSCH, 1978), Seychelles (WAILES, 1912a); North America: Canada (CHARMAN & WARNER, 1997; WARNER et al., 2007), USA (CHARMAN & WARNER, 1997); South America: Argentina (VUCETICH, 1980), Brazil (HARDOIM & HECKMAN, 1996; LANSAC-TOHA et al., 2001), Bolivia (CERDA, 1986), Chile (JUNG, 1942a), Columbia (HEINIS, 1914), Ecuador (KRASHEVSKA et al., 2007), Guadalupe (COÛTEAUX & MUNSCH, 1978), Malvinas/Falkland Islands (VUCETICH, 1980), French Guyana (COÛTEAUX, 1979), Venezuela (DECLOITRE, 1955); Caribbean: Puerto Rico (BAMFORTH, 2007); Australasia: Australia (PENARD, 1911; MEISTERFELD & TAN, 1998), Maluku Islands (BONNET, 1992), New Guinea (Papua New Guinea, BONNET, 1980a; Irian Jaya, BONNET, 1992), New Zealand (HOOGENRAAD, 1948; CHARMAN, 1997), Samoa (KORGANOVA, 1985); Asia: China (JIAJI, 1977), India (DASH & GARU, 1980), Japan (COÛTEAUX, 1978), Java (Hoogenraad & DE GROOT, 1940a; BONNET, 1992; BONNET, 1985), Nepal (BONNET, 1977), Philippines (BONNET, 1980b), Russia (KORGANOVA & RAKHLEEVA, 1997), Sulawesi (BONNET, 1992), Thailand (BONNET, 1987), Vietnam (BALIK, 1995); Pacific Ocean: Hawaii (MITCHELL & DUCKERT unpublished); Europe: Austria (FOISSNER, 1987; LÜFTENEGGER et al., 1988; AESCHT & FOISSNER, 1989), Belgium (BEYENS, 1984), Bulgaria (TODOROV, 1998, 2001; DAVIDOVA, 2011), Czech Republic (BARTOŠ, 1949), Denmark (STOUT, 1968), Estonia (SILLASOO et al., 2007), Finland (TOLONEN et al., 1992), France (BONNET, 1953, 1989), Germany (JUNG, 1936; HARNISCH, 1951; MEISTERFELD, 1980; WANNER, 1991; FOISSNER, 1994), Greece (BONNET, 1989), Hungary (TÖRÖK, 1993), Ireland (SWINDLES & ROE, 2007), the Netherlands (HOOGENRAAD & DE GROOT, 1940b), Poland (OFFIERSKA-WAWRZYNIAK, 1993), Romania (GODEANU, 1972a), Spain (BONNET, 1989), Switzerland (MITCHELL et al., 1999), UK (CASH et al., 1909; OGDEN & HEDLEY, 1980), Greenland (BEYENS et al., 1992); Antarctica: Ross Island (DECLOITRE, 1964b; SMITH, 1992). Likely cosmopolitan, if indeed a single species.

Remarks: CASH et al. (1909) observed cells with several variations in different samples from Britain, mentioning that these differences could be attributed to the environment (i.e., phenotypic plasticity). BALIK (1994) described a subspecies, *Hyalosphenia subflava* var. *undulata* (in Casopis Slez. Muz. Opava (A) 43, 3, 237–252, Fig. 6). Although this variety differs from the type by its wavy lateral margins, it was described after 1960 and thus treated here as an infra-subspecific taxon in accordance with ICZN Art. 45.6.3. The observed size variability and wide geographical distribution suggest the existence of a species complex rather than a single species.

Hyalosphenia tamdaoensis Balik, 1995

1995 *Hyalosphenia tamdaoensis* Balik, Acta Soc. Zool. Bohem. 59: 1–16, Fig. 6.

Description (based on the original description): Test bilaterally symmetrical, long, narrow ovoid-, egg-, or vase-shaped; in cross section,

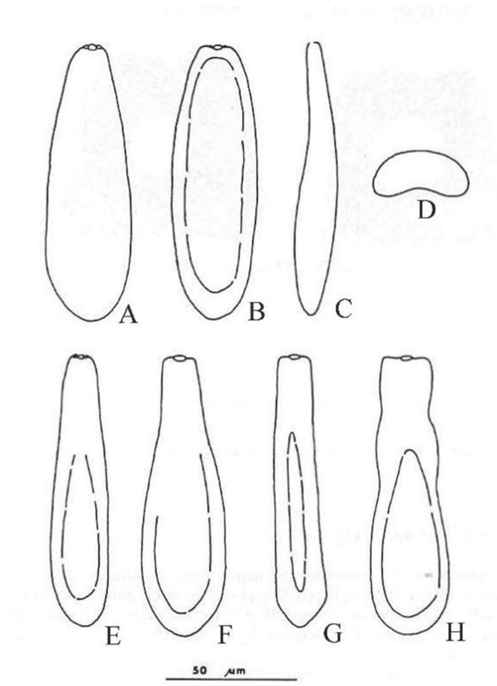

Fig. 47. *Hyalosphenia tamdaoensis*: Original drawings from BALIK (1995): (A) Dorsal broad view; (B, E–H) Ventral broad views; (C) Profile view, and (D) Cross section. Scale bar = 50 μm.

bean- or kidney-shaped. "Dorsal" side vaulted, "ventral" side depressed, depression elliptical. Test organic, with a relatively robust test wall, and smooth surface. Lateral pores absent. Test pellucid, translucent, light yellow or yellowish-orange. L = 107–115 μm, B = 31–36 μm, P = 9–11 μm. Pseudostome small, elliptical in frontal view, with a thick organic rim.

Differential diagnosis: BALIK (1995) mentioned that *Hyalosphenia tamdaoensis* is similar to *H. schoutedeni*, *H. subflava*, and *H. gigantea* in general shape, but differs from these taxa by the test and pseudostome size. In our opinion, *H. tamdaoensis* is notably different from the other aforementioned species in general shape, size, the kidney shaped cross section, as well as the vaulted "ventral" side and depressed "dorsal" side of the test.

Type locality: Tam-Dao region, Vietnam. Likely coordinates: - 21.460792°, 105.64681°; Elevation: ca. 1200 m.a.s.l..

Type specimen: Not provided. We declare Fig. 45 by BALIK (1995), reproduced here as Fig. 47, as the type.

Etymology: The species name derives from that of the locality where it was found.

Habitat: Rainforest leaf litter. The morphology of the test shows characteristic adaptations often found among soil taxa, with a compressed or arched test, and ventral small or hidden pseudostome. According to BALIK (1995), this species is likely characteristic of the humic soil horizon.

Geographical distribution: Vietnam (BALIK, 1995).

Remarks: This is seemingly a very rare species, and to the best of our knowledge, it has not been reported since its description. No living individual has ever been observed, and the description was based on eight empty tests.

7.9. Genus *Longinebela* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell & Lara, 2016

Type species: *Longinebela tubulosa* (Penard, 1890) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

2016 *Longinebela* gen. nov. Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 621.

Description: Test compressed, except for *L. golemanskyi*, which has a circular section. Test elongated-cylindrical to elongated-piriform, with a distinct (sometimes short—e.g., *L. ampulla*) neck; lateral margins straight or wavy, tapering towards the aperture. Test hyaline, colourless, or slightly yellowish, composed of circular to elongated shell plates most likely recycled from euglyphid testate amoeba prey. Pseudostome linear to slightly curved.

Remarks: This genus was established by KOSAKYAN et al. (2016) when the genus *Nebela* was split into six monophyletic genera based on molecular data and the general shape of the test—*Nebela s.str.*, *Cornutheca*, *Gibbocarina*, *Longinebela*, *Mrabella*, and *Planocarina*. All *Nebela* species with an elongated-cylindrical to elongated-piriform shape, and a linear to slightly curved pseudostome, were placed into the genus *Longinebela*. This genus differs from *Planocarina* by the absence of a flat keel, from *Gibbocarina* by the absence of a hollow keel combined with a wavy outline, and from *Alabasta* by the less curved pseudostome; however, no apparent single set of diagnostic morphological characters for the genus exists, and its monophyly is thus poorly supported by phylogenetic analyses. Further molecular work including additional species is therefore needed to assess validity.

Etymology: The genus name refers to the elongated species shape and their otherwise similar morphology to the genus *Nebela*.

Five species are listed here, but see also the *incertae sedis* list, as well as notes on *Nebela penardiana* and its subspecies, which share the morphology of this genus:

Key to the species

1. Test not compressed 2
– Test compressed 3

2. Test piriform or elongated-piriform, composed of globular, hollow siliceous plates: L = 198–219 µm, B = 111–132 µm *L. golemanskyi* (p. 108)
– Test elongated-cylindrical, L = 116–132 µm, B = 43–51µm *L. ampulla* (p. 107)

3. Lateral margins of the test wavy in broad view: L = 147–160 µm, B = 69–85 µm *L. meisterfeldi* (p. 111)
– Lateral margins of test not wavy in broad view 4

4. Two small, lateral triangular bumps present on the sides of the test in broad view, where lateral pores are clearly visible 5
– Lateral bumps absent, and lateral pores not clearly visible: L = 190–264 µm, B = 80–155 µm, pseudostome slightly curved in broad view *L. tubulosa* (p. 114)

5. Very large species. L = 236–270 (310) µm, B = 115–122 µm *L. speciosa* (p. 112)
– Smaller species: L < 200 µm 6

6. Test narrow in broad view: L = 115 µm, B = 42 µm, L/B = 2.7 *Nebela penardiana elongata* (see *incertae sedis* list p. 204)
– Test less narrow in broad view: L/B < 2 7

7. Larger species: L = 115–175 µm, B = 65–80 µm *Nebela penardiana* (see *incertae sedis* list p. 202)
– Smaller species: L = 78–110 µm, B = 41–62 µm *Nebela penardiana minor* (see *incertae sedis* list p. 205)

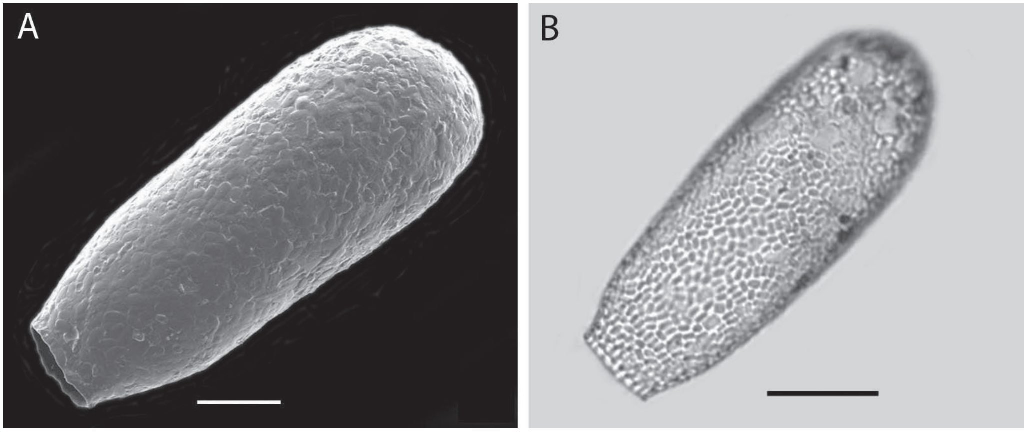

Fig. 48. *Longinebela ampulla*: (A) SEM broad view image of a specimen from Bulgaria, (B) LM broad view image of a specimen from the same locality. Scale bars: A = 20 µm, B = 30 µm. Images modified from TODOROV et al. (2018).

Longinebela ampulla Todorov, Bankov, & Ganeva, 2018

2018 *Longinebela ampula* Todorov, Bankov, & Ganeva, in TODOROV et al., 2018, Acta Zool. Bulg. 70: 285-292 (Figs. 1, 3 original images).

Description (based on the original publication): Test elongated-cylindrical, with a distinct short neck and a rounded posterior region, laterally flattened only in the neck region. All remaining parts of the test relatively uncompressed, with neither lateral margins nor lateral pores. Test colourless, composed mainly of small oval, infrequently circular shell plates, arranged regularly without overlap. Shell plates embedded in a thick layer of organic cement, outer part appears covered with a layer of cement; thus, edges not clearly defined. L = 116–132 µm, B = 43–51 µm, depth of the test = 42–45 µm, P = 21-27 µm. Pseudostome oval, truncate but not convex, and bordered by a thin collar of organic cement.

Differential diagnosis: Morphologically, *L. ampulla* is most similar to *Nebela penardiana* (see notes in incertae sedis list for *N. penardiana*, p. 202), from which it can clearly be discriminated by its size, shape, and structure. The primary morphological differences between the two species are: 1) *L. ampulla* has an almost uncompressed, elongated-cylindrical test, with a distinct short neck, whereas the test of *N. penardiana* is always compressed, piriform, tapering evenly from the swollen and rounded posterior region to the pseudostome; 2) *L. ampulla* has neither lateral margins nor lateral pores, which are characteristic and almost always well visible in N. penardiana. 3) In broad view, the pseudostome of *L. ampulla* is truncate; whereas in *N. penardiana*, it is usually convex in broad view and concave in profile; 4) The test of *L. ampulla* is composed mainly of small ovoid, infrequently circular shell plates, embedded in a thick layer of organic cement, whereas the shell of *N. penardiana* is composed of larger and clearly defined plates, embedded in a thin layer of organic cement. Aside from the morphological differences, these two species differ significantly in several metric characteristics; 5)

N. penardiana is significantly more variable in size, as well as much larger and wider than L. ampulla: 152.9 ± 15.7 μm and 70.7 ± 8.4 μm (n = 100) vs. 125.8 ± 3.53 μm and 45.9 ± 1.92 μm (n = 33) for L. ampulla. They also differ in depth/breadth ratios: 0.62 ± 0.03 μm (n = 84) in *N. penardiana*, and 0.95 ± 0.02 μm (n = 27) in *L. ampulla* (adapted from TODOROV et al., 2018).

Although the general test outline resembles that of *Nebela cylindrica*, the latter is notably smaller L = 48–50 μm, B = 17–22 μm, and cylindrical, and in some individuals, two small symmetrical bulges are visible near the pseudostome.

Type locality: Near Kopilovtsi Village, below the Kopren hut, Western Stara Planina Mountains, Bulgaria. Coordinates: 43.330439°, 22.860931°; Elevation: ca. 881 m.a.s.l..

Type specimen: Holotype and paratypes mounted in Canada balsam on a glass slide are retained in the collection of Prof Milcho Todorov, Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia; preparations Nos. LA-H/2016 (holotype) and LA-P-01/2016, LA-P-02/2016, LA-P-03/2016 (paratypes).

Etymology: The species name refers to its shape, as in Latin "ampulla" means "small vessel containing liquids".

Habitat: Wet *Sphagnum flexuosum*.

Geographical distribution: Bulgaria (TODOROV et al., 2018; TODOROV & BANKOV, 2019).

Remarks: Ecology: *Longinebela ampulla* inhabits the wet moss *Sphagnum flexuosum* growing on a small mire in a mixed deciduous forest of beech (Fagus sylvatica L.) and birch (Betula pendula L.). It was found in associations with *Nebela collaris*, *Argynnia dentistoma*, *Assulina muscorum*, *Corythion dubium*, *Euglypha tuberculata*, *Heleopera rosea*, *Quadrulella symmetrica*, and *Trinema lineare*, as well as in lower abundance with *Longinebela tubulosa*, *Nebela guttata*, *N. pechorensis*, *Quadrulella longicolis*, and *Q. variabilis*. The mosses, where *L. ampulla* was found, were characterized by a low pH (= 4.93), low conductivity (82.3 μS), low water table (36 cm below the surface), and moderate water content (92.3%; TODOROV et al., 2018).

Biometry: Analyses of the coefficients of variation showed that the studied population of the newly described species was homogeneous, and almost all characters measured were weakly to moderately variable (CV ranging from 1.9% to 15.9%). Test length (L), B, and depth, as well as B/L and depth:breadth ratios were the most stable characters (CV 1.9–4.18%), whereas the long and small axes of the aperture were more variable (5.83% and 10.60%, respectively), and neck length was the most variable (15.9%). *Longinebela ampulla* is size-monomorphic, characterized by a well-expressed main size class and small size range: Overall range 116–132 μm, 51.5% from 124–128 μm, 24.2% < 124 μm, and 24.3% > 128 μm. Test breadth, depth, and the large axis of pseudostome of all individuals were within relatively closed ranges (43–51 μm, 42–45 μm, and 21–26 μm, respectively). The main size classes for these characters were well expressed: 70% of individuals had B within 44–47 μm, 96.3% had a test depth within 42–44 μm, and 85% a large axis of aperture within 22–24 μm. Furthermore, the arithmetic means of all observed characters correlated with the established main-size classes, supporting the monomorphism of the species (adapted from TODOROV, 2010).

Longinebela golemanskyi (Todorov, 2010) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

2010 *Nebela golemanskyi* Todorov, Acta Protozool. 49: 38 (Figs. 1-6, original images).

2016 *Longinebela golemanskyi*–Todorov, 2010 - Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell,

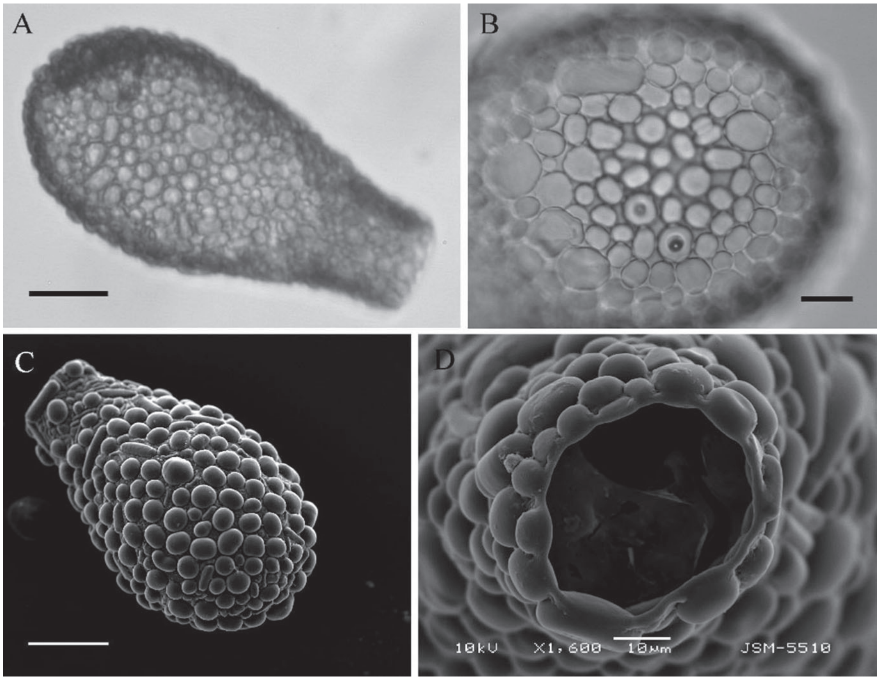

Fig. 49. *Longinebela golemanskyi*: (A & B) LM image of a specimen from Bulgaria in broad view and higher magnification detail of the aboral end showing the test composition, respectively; (C & D) SEM image of a specimen from Bulgaria in broad view and frontal view of the pseudostome, respectively. Scale bars: A = 40 μm, B & D = 10 μm, C = 50 μm. Images by Milcho Todorov.

& Lara, Cladistics 32: 621 (redefinition of genus *Nebela* and establishment of genus *Longinebela*).

Description (based on the original publication): Test piriform to elongated-piriform in broad view, with a distinct short neck aproximately 1/4th of the body length, and a rounded aboral region nearly uncompressed laterally. No lateral pores. Test colourless, composed of characteristic voluminous, globular, or rarely elongated, rounded, and hollow siliceous plates, with an average diameter of ca. 10–15 μm. Occasionally small diatom frustules scattered sparsely over the surface are incorporated among the plates. Large gaps are usually present between plates, interspersed with well visible, small beads of organic cement. L = 198–219 μm, B = 111–132 μm, depth of the test = 89–100 μm. Pseudostome roughly circular to ovoid in frontal view, linear in broad view, (P = 36–40 μm) and bordered by a thin organic rim. Biometry (adapted from TODOROV 2010): Mean sizes: L = 209.1 ± 6.94 μm, n = 24, B = 118.2 ± 5.71 μm, n = 24, test depth = 94.8 ± 3.28 μm, n = 24. The test length, depth, and large axis of aperture were the most stable characters (CV values between 3.28% and 3.46%), whereas test width and neck length were the most variable (4.83% and 5.02%, respectively).

Differential diagnosis: *Longinebela golemanskyi* is most similar to *Gibbocarina galeata* and *L. speciosa*. While *G. galeata* is clearly distinguished by its compression and the presence of a distinct thickened lateral margin, *L. speciosa* is more similar to *L. golemanskyi*, and their differences can only be seen using SEM. TODOROV (2010) noted the following differences between the two species: 1) The test of *L. golemanskyi* is composed of characteristic voluminous, globular (or more rarely elongated), rounded, and hollow plates, usually with large gaps between them interspersed with small beads of organic cement; conversely, the shell plates of *L. speciosa* are smaller, more compressed, and situated closer to each other. 2) *L. golemansky*i has no lateral margins and is nearly uncompressed, whereas *L. speciosa* is always compressed and has small lateral margins. 3) *L. golemanskyi* is comparatively shorter and less elongated than *L. speciosa*. The width/length ratio is higher (0.56 ± 0.02, n = 24 and 0.45 ± 0.03, n = 100, respectively). 4) The pseudostome of *L. golemanskyi* is roughly circular to oval, not convex and bordered by a thin collar of organic cement. In contrast, the pseudostome of *L. speciosa* is regular oval, slightly convex in broad view, and surrounded by a thick collar of organic cement.

Type locality: Near "Aleko" hut, Vitosha Mountains, Bulgaria. Coordinates: 42.6°, 23.283333°; Elevation, ca. 1850 m.a.s.l..

Type specimen: The type specimen and paratypes mounted in Canada balsam on a glass slide are deposited in the collection of Prof Milcho Todorov, Institute of Zoology, BAS, Sofia; preparations No. T-001/2009, P-001/2009, and P-002/2009.

Etymology: The species was named in honour of the Bulgarian protozoologist Vassil Golemansky.

Habitat: *Sphagnum* mosses (high moisture, high organic matter content, pH = 4.9–5.6).

Geographical distribution: Bulgaria (TODOROV, 2010; TODOROV & BANKOV, 2019).

Remarks: This species was found in wet *Sphagnum* peatlands (1800–2000 m.a.s.l.) of the Vitosha Mountains, Bulgaria, and in association with *Hyolosphenia papilio*, *Gibbocarina galeata*, *Longinebela speciosa*, *Nebela penardiana*, *Argynnia dentistoma*, *A. vitraea*, *Quadrulella symmetrica* and *Cyphoderia ampulla*. Despite the presence of thick test plates in *L. golemanskyi*, notably characteristic of genera *Argynnia* and *Physochila*, TODOROV (2010) assigned this taxon to the genus *Nebela* (currently *Longinebela*) owing to the presence of a thin organic rim surrounding the pseudostome (considered as a synapomorphy of family Hyalospheniidae; KOSAKYAN et al., 2016). TODOROV (2010, p. 42) discussed the origins of the test plates of hyalospheniids, noting that *N. (L.) golemanskyi* included voluminous and massive plates, considerably different from those of their possible prey. Todorov continued, "*We suppose that (the) newly described species* N. golemanskyi*, together with some other nebelids (e.g.,* G. galeata, N. speciosa*) are capable of modifying the shell plates of the captured prey. These species may represent an intermediate clone between the nebelids, which use in shell construction almost untreated plates from their preys (e.g.,* N. collaris, N. [Padaungiella] lageniformis, N. [Alabasta] militaris, N. [P.] tubulata, N. [Longinebela tubulosa, *etc.), and the representatives of the family Lesquereusiidae, which build their shells of endogenous plates, produced by the organisms themselves*". Accordingly, the combination of characters (especially the circular cross-section), the unusual thickness of plates, and the roughness of the aperture (despite the presence of a very thin organic rim) suggests that this species may not belong to genus *Longinebela* and possibly not even to the Hyalospheniidae. This, however, should be determined through further molecular analyses.

Longinebela meisterfeldi (Heger & Mitchell, 2012) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

2012 *Nebela meisterfeldi* Heger & Mitchell, in Kosakyan et al. 2012, Protist 163: 429.

2016 *Longinebela meisterfeldi* Heger & Mitchell, 2012, in KOSAKYAN et al., 2012, Cladistics 32: 606–623 (redefinition of genus *Nebela* and establishment of genus *Longinebela*).

Description: Test elongated in broad view, slightly compressed, with characteristic wavy lateral margins (Fig. 50D), and brownish colouration. Pseudostome oval in frontal view, surrounded by a very thin collar of organic cement. Dimensions (based on six individuals): L = 147–160 µm, B = 69–85 µm, P = 37–42 µm.

Differential diagnosis: *Longinebela meisterfeldi* resembles *Gibbocarina gracilis* and *Nebela penardiana* in general shape but is distinguished by the wavy, lateral external margins (similar to that of *Hyalosphenia elegans*). *Hyalosphenia sinuosa* is considerably larger (L = 200-236 µm). Further, mt-COI sequencing (KOSAKYAN et

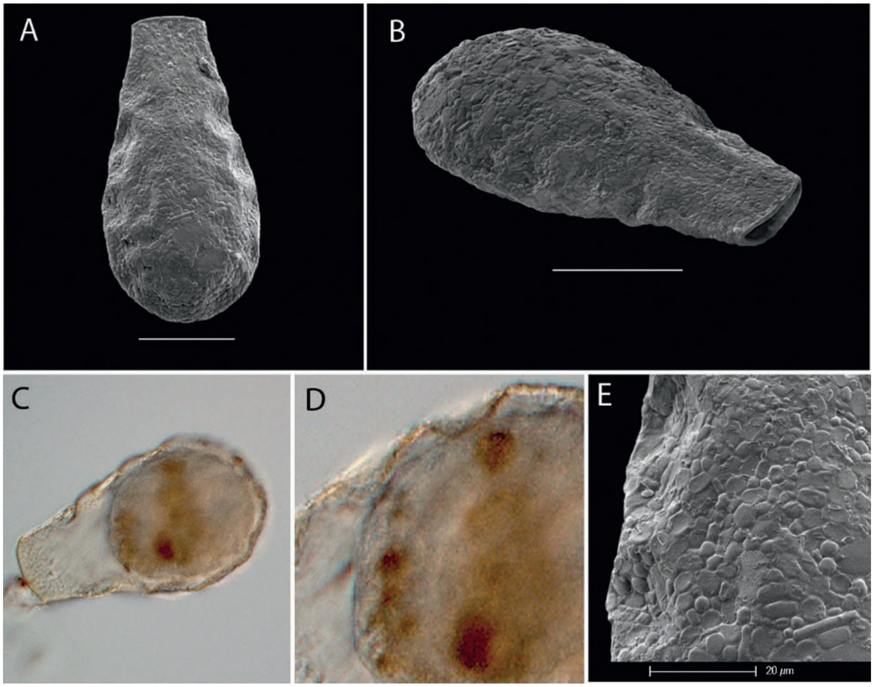

Fig. 50. *Longinebela meisterfeldi*: (A & B) SEM image of a specimen from Canada in broad and oblique side views, respectively; (C & D) LM images of an encysted specimen from Canada in broad view, detail of the test main body showing its wavy margin; (E) SEM image, broad view, detail of the wavy margin and test composition. Scale bars = 50 µm. Images by Thierry Heger.

al., 2012) did not reveal a close affinity between any of these species.

Type locality: Sides of a small stream in Grouse Mountain, British Columbia, Canada. Coordinates: 49.7°, -125.3°.

Type specimen: One SEM stub with several specimens is deposited at the Natural History Museum of Neuchâtel, Switzerland (Ref No. SEM-90, UniNe-EM-1).

Etymology: The species was named in honour of the German protozoologist Ralf Meisterfeld.

Habitat: *Sphagnum* in a peatland and aquatic mosses on the side of a mountain stream.

Geographical distribution: West coast of Canada (KOSAKYAN et al., 2012). Two localities were mentioned: Peatland in Strathcona Park, Vancouver Island, Grouse Mountain, British Columbia, Canada.

Longinebela speciosa (Deflandre, 1936) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

1933 *Nebela americana* sec. Franken, Nat. Ver. Bielefeld: 196, PPl. 6, Fig. 1; not *N. americana* by Tiránek 1882; morphology overlaps with *Longinebela speciosa*).

1936 *Nebela speciosa* Deflandre, Ann. Protistol. 5: 250–251.

1954 *Nebela penardiana* var. *suecica* Grospietsch, Arch. Hydrobiol. 49(4): 573 (Fig. 5; overlapping morphology).

2016 *Longinebela speciosa* (Deflandre, 1936) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 606–623 (redefinition of genus Nebela and establishment of genus *Longinebela*).

Icon.: DEFLANDRE, 1936, Pl. XX, Figs. 3, 6, 8, OGDEN,1984, Figs. 18–22, SEM cement structure; TODOROV & BANKOV, 2019, Fig. 69.

Description: Test very elongated in broad view, compressed, with two readily visible lateral pores, one on each side; elongated-piriform in profile view and almost transparent. Test composed of collected euglyphid and sometimes *Quadrulella* plates, as well as diatom frustules. L = 236–272 µm (extreme reports up to 310 µm), B = 115–123 µm, P = 40–46 µm. Pseudostome ovoid in frontal view, slightly curved in broad view, and surrounded by a very thin organic rim.

Differential diagnosis: Similar to *N. penardiana* in general shape. DEFLANDRE (1936) decided to separate it from the latter based on: 1) the size difference between the two species, which never overlap; and 2) differences in the structure of the pseudostome, often surrounded by a well-developed rim in *N. penardiana*, and very thin or almost absent in *L. speciosa*. DNA barcoding studies confirmed DEFLANDRE's interpretation as the two species have clearly distinct mt-COI sequences (KOSAKYAN et al., 2012).

Type locality: Unspecified in the original description; however, the illustrated specimens (Plate XX, Figs. 3, 6, 8 in DEFLANDRE, 1936) are noted as being from Laonnois (Aisne, France), and we, therefore, declare this as the type locality. Likely coordinates: 49.438888°, 3.59939°.

Type specimen: Not provided. We declare Fig. 3 by DEFLANDRE (1936), reproduced here as Fig. 51C, as the type.

Etymology: The species name refers to its general morphology, especially the large size of the test; i.e., "speciosa" in Latin means "remarkable", "splendid", "eye-catching".

Habitat: *Sphagnum* and other mosses, peaty soils.

Geographical distribution: Europe: Austria (LAMINGER, 1973; AESCHT & FOISSNER, 1989), Belgium (CHARDEZ, 1980), Bulgaria

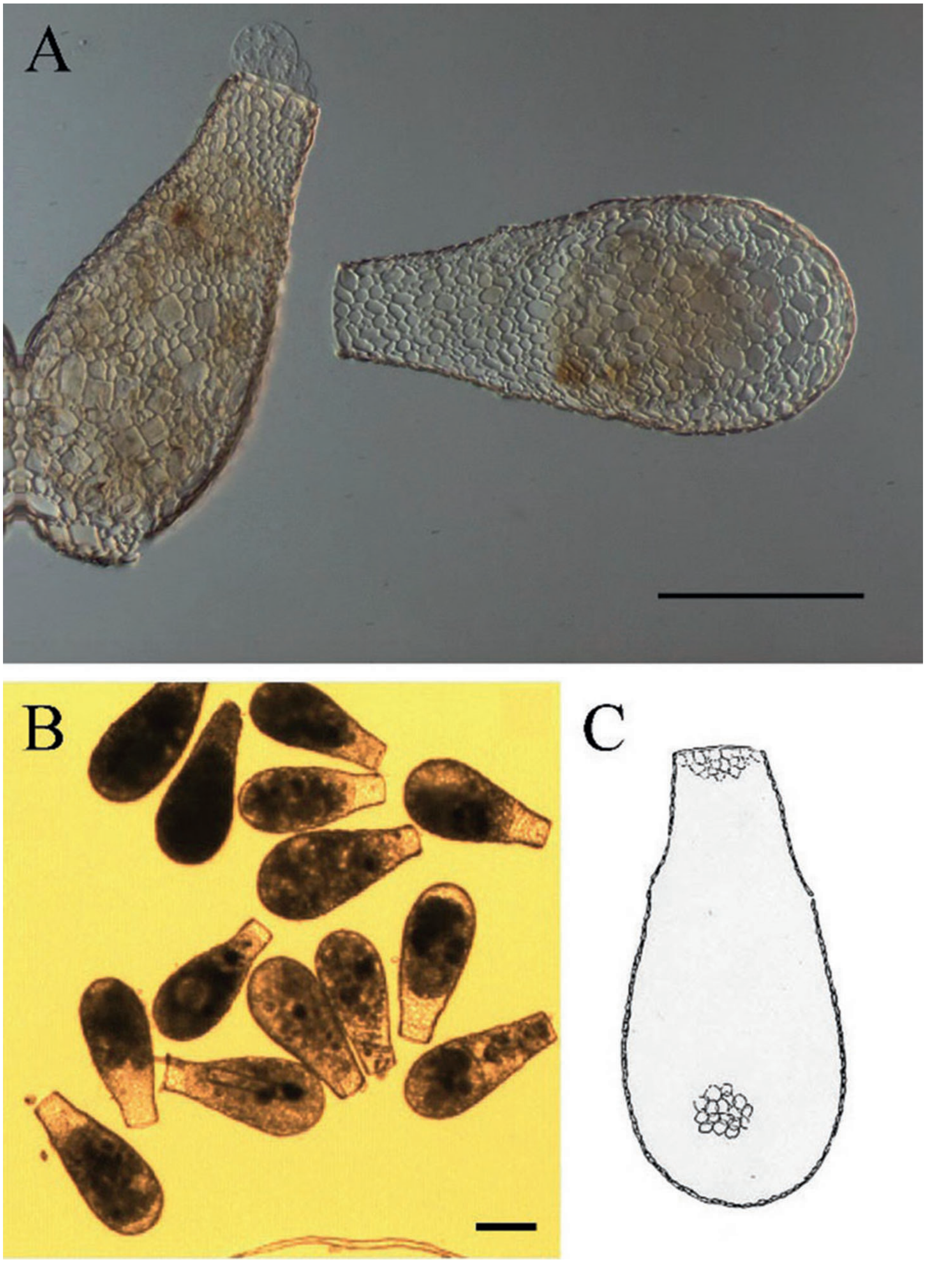

Fig. 51. *Longinebela speciosa*: (A) LM image of two individuals from Germany—the strange outline of the individual on the left is an artefact, (B) LM image of a group of living individuals from Bulgaria, (C) Original drawing from DEFLANDRE (1936). Scale bars = 100 µm. Images by: (A) Meisterfeld and (B) Milcho Todorov.

(GOLEMANSKY, 1967; TODOROV, 1993; GOLEMANSKY et al., 2006; TODOROV & BANKOV, 2019), France (DEFLANDRE, 1936; MORACZEWSKI & BONNET, 1969; BONNET, 1985), Germany (GROSPIETSCH, 1958; LAMINGER, 1973; BADEWITZ, 2002; MEISTERFELD, unpubl.), the Netherlands (HOOGENRAAD & DE GROOT, 1979), Poland (GOLEMANSKY, 1973), Romania (GODEANU, 1972a; GODEANU & PIRVU, 1977; BUNESCU, 1979; BUNESCU et al., 1985), Sweden (SCHÖNBORN, 1975), UK (HEAL, 1961; BEYENS & CHARDEZ, 1984; OGDEN, 1984); Asia: Nepal (BONNET, 1977), North Korea (GOLEMANSKY & TODOROV, 1991); Australia (MEISTERFELD & TAN, 1998).

Remarks: GROSPIETSCH (1954) described *Nebela penardiana* var. *suecica*, which differed from the type by its larger size: L = 200–240 µm, B = 98–114 µm, vs. L = 115–175 µm, B = 65–80 µm for the type species. This variety was documented only once from the Swedish Lapland. As the size and shape of this variety overlap with those of L. speciosa (when considering the broader size ranges documented from studies other than GROSPIETSCH's [1954]), we thus considered it as a synonym of *L. speciosa*.

Longinebela tubulosa (Penard, 1890) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

1982 *Nebela collaris* var. *pyriformis* Taránek, Sitzungsberichte der Königl. Böhm. Gesellschaft der Wissenschaften in Prag: 32 (overlapping morphology).

1990 *Nebela tubulosa* Penard, Mem. Soc. Hist. Nat. 31: 159.

2016 *Longinebela tubulosa* Penard, 1890 - Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 606–623 (redefinition of the genus *Nebela* and establishment of the genus *Longinebela* based on molecular data).

Icons: PENARD, 1902, Figs. 1–5; DEFLANDRE, 1936, Figs. 90–92; OGDEN & HEDLEY, 1980, Pl. 45; LUKETA, 2020, Fig. 1; TODOROV & BANKOV, 2019, Fig. 70.

Description: Test elongated-piriform in broad view, compressed, with the lateral margins tapering towards the pseudostome, creating a somewhat distinct neck. Small lateral pores usually present, but difficult to observe. In profile, narrow elliptical with a pointed fundus. Test yellowish-brown, composed of scales recycled from prey (euglyphids or *Quadrulella*). L = 190–264 µm, B = 80–155 µm, P = 35–54 µm. Pseudostome ovoid in frontal view, surrounded by a thin organic rim.

Differential diagnosis: Similar to *Nebela penardiana* and *L. speciosa*, from which it differs primarily based on test dimensions and the granular cement structure between plates (DEFLANDRE, 1936; OGDEN & HEDLEY, 1980; A. KOSAKYAN, pers. obs.). In addition, *L. tubulosa* has a pointed (acutely angled) fundus in profile view.

Type locality: Heidelberg, Germany. Likely coordinates: 49.401696°, 8.736859°.

Type specimen: Not provided. We declare a specimen from the E. Penard slide collection, no. 523-1-2 (Natural History Museum, Geneva, Switzerland), reproduced here as Fig. 52F, as the type.

Etymology: "Tubulosa" in Latin means "tubular", likely referring to its shape, although it is compressed.

Habitat: Wet *Sphagnum* mosses, acidic soils.

Geographical distribution: Mentioned as cosmopolitan, but a significant genetic distance has been observed between individuals from

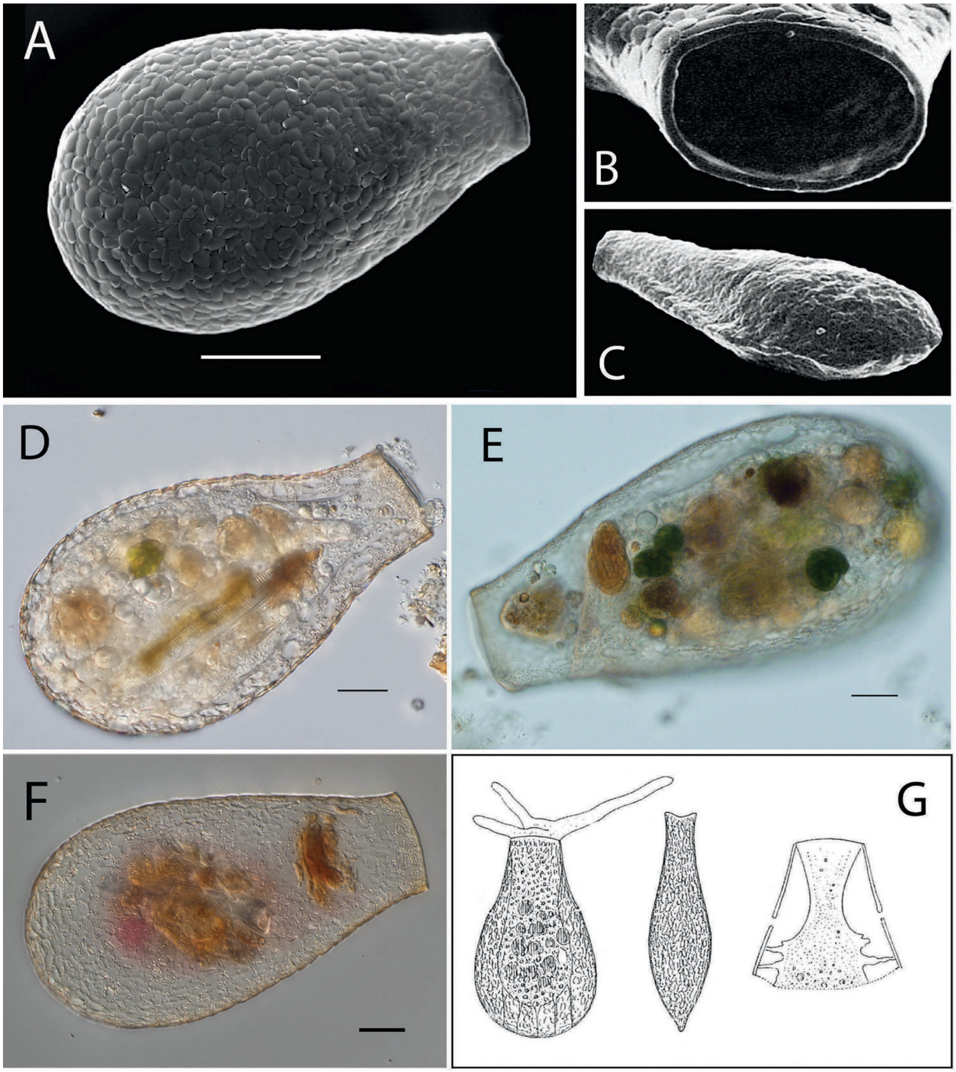

Fig. 52. *Longinebela tubulosa*: (A) SEM broad view image of a specimen from Bulgaria; (B) SEM frontal view of the aperture modified from OGDEN & HEDLEY (1980); (C) SEM oblique posterior profile view modified from OGDEN & HEDLEY (1980); (D) LM broad view image of an active specimen from Fribourg, Switzerland; (E) LM (approximately) broad view image of an active specimen from the Jura Mountains, Switzerland; (F) LM broad view image of a specimen from the Eugène Penard slide collection, no. 523-1-2 (Natural History Museum, Geneva, Switzerland); (G) Original drawings from PENARD (1902); from left to right: active individual in broad view, profile view, and detailed view of the apertural region showing the lateral pores and the cell in transparency. Scale bars: A = 50 µm, D–F= 20 µm. Images by: (A) Milcho Todorov, (D & E) Anush Kosakyan, and (F) Thierry Arnet (Wikipedia).

Bulgaria and Canada, suggesting the existence of several species within this morphospecies (KOSAKYAN et al., 2012).

Remarks: The first short description of the species was provided by PENARD (1890) but without illustration. More than a decade later, PENARD (1902) produced an expanded description with detailed drawings. Subsequently, CASH et al. (1909) observed "fine punctuations" around the neck, which they considered to be an organic cement producing a rough surface. In accordance with these findings, we (A.K.) observed many specimens with a fine, granular structure around the pseudostome and neck. DEFLANDRE (1936) mentioned that this species was a generalist predator, feeding on different amoeboid protists, diatoms, and green algae. The available illustrations (see Iconography and Fig. 52) show a considerable morphological variability within the species, suggesting the existence of several independent taxa. LUKETA (2021) analysed the morphological variability of *L. tubulosa* based on 2,630 individuals from a *Sphagnum*-dwelling population in East Herzegovina. The minimum coefficient of variation (5.49%) was observed for the test L/B ratio, whereas the maximum variability (16.38%) was recorded for the area of the optical section. The size frequency distribution analysis of test length and breadth was interpreted as evidence for continuous polymorphism. LUKETA (2021) suggested that this moderate variability was likely caused by biological and environmental factors. Further detailed observational and experimental studies are needed to determine how environmental factors affect the morphology of this and other similar species.

7.10. Genus *Mrabella* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell & Lara, 2016

Type species: *Mrabella subcarinata* (Gauthier-Lièvre, 1957) Kosakyan et al., 2016

2016: *Mrabella* gen. nov. Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in Kosakyan et al., Cladistics 32: 620.

Description: Test elongated-piriform in broad view, compressed, with the sides gradually tapering towards the pseudostome or neck. The test can be laterally swollen just above the junction between the neck and the main body. Lateral margins distinctly compressed, giving the impression of a thick, wide, hollow keel; accordingly, the test is elongated elliptical with a pointed end in profile. Test colourless, composed of quadrangular shell plates similar to those in *Quadrulella* species. Two species are assigned to the genus.

Remarks: Historically all hyalospheniids presenting square test plates belong to the genus *Quadrulella*. Genus *Mrabella* was established by KOSAKYAN et al. (2016), when mt-COI sequence data showed that *Quadrulella subcarinata* (three specimens collected from South Africa) did not branch with genus *Quadrulella*, but rather belonged to a separate clade, together with *Gibbocarina galeata* (with 99% bootstrap support); thus, hyalospheniids presenting square shell plates are not monophyletic, and the authors suggested two hypotheses to explain the origin of square plates:

"*These two hypotheses depend on whether the square-shaped plates in an organism have autogenous or exogenous origin. This is a relevant aspect because hyalospheniids are known to engage in the behaviour of kleptosquamy,* *or recycling of shell plates produced by other organisms (Lahr et al., 2015). Additionally, we have no knowledge of well-established hyalospheni[i]d cultures, which makes it very difficult to observe certain behaviours.*

Assuming that all amoebae that present square-shaped plates in their shells have produced them autogenously, the phylogenetic hypothesis presented here indicates homoplasy: either the ability to produce square plates is an ancestral character that has been lost in a number of lineages (reversion), or this character has evolved more than once independently (convergence). The phylogenetic hypothesis presented here indicates convergence as the most parsimonious alternative, with only two steps required–one event in the genus Quadrulella *and another independent event in the genus* Mrabella. *Although apparently surprising, other unrelated organisms are in fact capable of producing square plates: the shelled amoeba* Paraquadrula *can produce calcareous square plates (the genus has not been sequenced yet, but while it is almost certainly an Arcellinid, it is most likely unrelated to hyalospheni[i]ds or at best branches in a basal position to the whole group). Additionally, the possibility of convergent morphologies has been put forth in the group for the genus* Hyalosphenia *(Oliverio et al., 2014; Lahr et al., 2014) and is consistent under the framework of "neutral morphologies": briefly, where there is only a limited number of possible morphologies and none of them is affected positively or negatively by selection, then there is a chance that the same morphology may appear multiple times (Bonner, 2013).*

"Alternatively, the very assumption that all amoebae presenting square plates have produced them autogenously might be equivocal. A behaviour exhibited by the majority of members in the hyalospheni[i]ds is kleptosquamy or the ability to scavenge plates from prey and use them to make the shell (Lahr et al., 2015). Under this framework, a possible scenario is that Mrabella *is in fact using scales from preyed upon* Quadrulella *or scavenging these scales from the environment to construct the shell. For instance, the description of* Gibbocarina *(as* Nebela galeata *from Africa by Gauthier-Lièvre (1957) is almost identical to* Q. subcarinata *in the general shape and dimensions of the test (L = 180-200, B = 98-144, P = 31-41 µm). Furthermore, square plates typical for* Quadrulella *can be integrated in the shell of* G. galeata *(Gauthier-Lièvre, 1957, Fig. 10a). Moreover, Gauthier-Lièvre (1957) documented other* Quadrulella *species from the same locality where she found* Nebela galeata *and* Quadrulella subcarinata*; these other* Quadrulella *species could therefore have provided the square plates used by these two species.*

This possibility, however, has a second set of in-built assumptions that make it highly unlikely: (i) Mrabella *would specifically select these plates, a trait that is not known for any other hyalospheni[i]d presenting kleptosquamy, which generally make the shell using a mixture of plates from different origins (for instance: Apodera vas in fig. 69 in Meisterfeld, 2002; or* Padaungiella lageniformis *in Figs. 2, 6 and 7 in Todorov et al. 2010); and (ii) if not specifically selecting, then* Quadrulella *would have to be the most abundant prey organism, or* Quadrulella *plates would have to be the most abundant in the environment, both of which are likely not true as Quadrulella tends to be present in low abundance in comparison to* Euglypha *(although* Euglypha *was not abundant in our sample where we found* Mrabella subcarinata*), a genus of filose testate amoebae which tends to be present in great numbers and produces oval and ornamented siliceous plates"* (KOSAKYAN et al., 2016).

Etymology: The genus name is derived from the Swahili word "mraba", meaning "square".

Two species are known:

Key to the species

1. Test smaller and narrow: L = 111–135 µm, B = 49–62 µm, L/B = 2.2. Neck laterally swollen just above the junction between the neck and the main body of the test *M. plicata* (p. 118)

– Test larger, elongated-piriform: L = 201–218 µm, B = 105–127 µm, L/B = 1.7–1.9 (based on original drawing, ≤2.04). Sides gradually tapering towards the pseudostome *M. subcarinata* (p. 119)

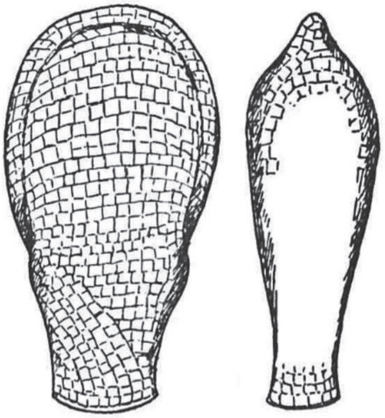

Fig. 53. *Mrabella plicata*: Original drawing from HOOGENRAAD & DE GROOT (1940a): broad and profile views.

Mrabella plicata (Hoogenraad & De Groot, 1940) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

1940a *Quadrulella plicata* Hoogenraad & De Groot, Treubia (Buitenzorg) Bd.17, H. 4: 248 (Figs. 58–59, original drawings).

2016 *Mrabella plicata* Hoogenraad & de Groot, 1940 - Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 620 (evaluation of genus *Quadrulella* and establishment of genus *Mrabella* based on molecular data).

Description (based on the original publication): Test narrow piriform in broad view, compressed, with a rounded fundus. Two lateral pores are situated at the precise point where the neck joins the main body of the test. Swollen sides. Keel starting at the base of the neck, covering entire fundus of the test (as in *Gibbocarina galeata*. This gives the impression of folds on the surface of the test; hence, the name "plicata" (meaning "folded"). In profile, fundus pointed owing to the presence of the keel. Test composed of square plates with smaller circular or irregular, angular plates in between. L = 111–135 µm, B = 49–62 µm. Pseudostome with a narrow organic lip.

Differential diagnosis: Differs from *M. subcarinata* primarily by its smaller size, the swollen sides, and by its narrower outline in broad view.

Type locality: Mount Kerinci (Sumatra, Indonesia). Likely coordinates: -1.696817°, 101.244254°; Elevation, ca. 1400 m asl.

Type specimen: Not provided. We declare Figs. 58–59 (representing the same individual) by HOOGENRAAD & DE GROOT (1940a), reproduced here as Fig. 53, as the type.

Etymology: Not provided. The species name is likely derived from the Latin word "plicatus", meaning "folded in plaits" or "braided", in reference to the test structure.

Habitat: Indicated only as "green mosses". The precise ecosystem type was unspecified but is most likely related to low mountain tropical forest.

Geographical distribution: Asia: Sumatra (HOOGENRAAD & DE GROOT, 1940a).

Remarks: The species is abundant and co-occurs with *Quadrulella tropica*. The two species differ in general shape and the presence of a characteristic keel in *M. plicata*, notably absent in *Q. tropica* (HOOGENRAAD & DE GROOT, 1940a).

Mrabella subcarinata (Gauthier-Lièvre, 1957) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

1957 *Qadrulella subcarinata* Gauthier-Lièvre, 1957, Bull. Soc. Hist. Nat. Afr. Nord. T. 48: 500 (Fig. 4, original drawing).

2016 *Mrabella subcarinata* Gauthier-Lièvre, 1957 - Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 621 (evaluation of genus *Quadrulella* and establishment of genus Mrabella based on molecular data).

Description: Test elongated-piriform, with a rounded fundus in broad view, and sides gradually tapering towards the pseudostome. Hollow keel starting at ca. 1/3rd of the test length from the pseudostome. Two lateral pores visible at the point where the keel starts. Fundus narrowly pointed in profile view (more so than in *M. plicata*). Test colourless, hyaline, composed of square or rectangular plates, regularly or irregularly arranged, and more or less overlapping. Plates on the keel rectangular and arranged regularly side by side. L = (150) 190–220 µm, B = (70) 95–115 µm, P = 33-40 µm. Pseudostome slightly curved with a thin organic lip.

Differential diagnosis: Similar to *Gibbocarina galeata* in general shape and in the presence of a wide, hollow, tuberous keel. *G. galeata* is generally larger, although sizes overlap: L = 180–283 µm, B = 94–190 µm in *G. galeata* vs. L = 201–218 µm, B = 105-127 µm in *M. subcarinata*. To the best of our knowledge, the test of *G. galeata* is never composed entirely of rectangular plates, as is the case in *M. subcarinata*; it can, however, include some square plates, likely taken from prey belonging to genus *Quadrulella*.

Type locality: Thianguel Bore (Guinea); bogs near Brazzaville, Lefini, Ewo, Floumbi, Kinkala, Republic of Congo. Likely coordinates: -3.108997°, 15.276327°.

Type specimen: Fig. 4b (GAUTHIER-LIÈVRE, 1957); paratype Fig. 7a (KOSAKYAN et al., 2016).

Etymology: The name of the species refers to the general morphology of the test; i.e., "carina" in Latin refers to the presence of the "keel" towards the posterior end of the test.

Habitat: Marshes and streams on Kalaharian sands (GAUTHIER-LIÈVRE, 1957) and *Sphagnum* mosses (KOSAKYAN et al., 2016).

Geographical distribution: Africa: Democratic Republic of Congo (GAUTHIER-LIÈVRE, 1957; CHARDEZ, 1964), Republic of Guinea (GAUTHIER-LIÈVRE, 1957), Madagascar (MEISTERFELD, unpubl.), South Africa (KOSAKYAN et al., 2016).

Remarks: GAUTHIER-LIÈVRE (1957) mentioned two morphotypes (wide and narrow) in the original description (Fig. 54F1&2). We (A.K., E.M.) observed both morphotypes in *Sphagnum* samples from Welgevonden Game Park, South Africa, within a minerotrophic valley mire with tall herbaceous vegetation and abundant *Sphagnum* moss cover in the wetter patches (Fig. 54C, E). The narrow morph of *M. subcarinata* resembles *M. plicata* but appears a bit wider proportionally (estimated L/B from Fig. 54F1 = 2.04 vs. 2.2 for *M. plicata*) and larger (smallest reported *M. subcarinata* = 150 µm vs 135 µm for the largest reported *M. plicata*). As these species have not been extensively studied, however, it would not be surprising to locate individuals of intermediate sizes or shapes between the two species and/or to identify additional species within the genus.

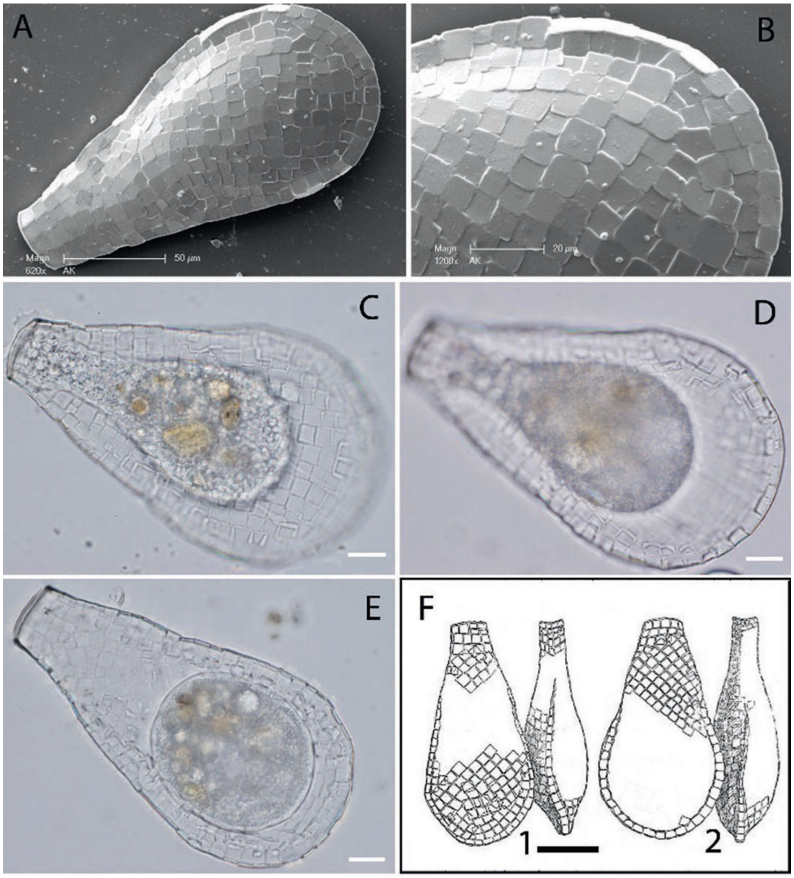

Fig. 54. *Mrabella subcarinata*: (A & B) SEM images of a specimen from South Africa, (B) Detailed view of the keel; (C & D) LM image of the same active individual of the wide morphotype from South Africa, (D) Detail on the quadric plates and the keel; (E) LM image of an encysted individual of the narrow morphotype from South Africa; (F) Original drawings of *M. subcarinata* (as *Q. subcarinata*) modified from GAUTHIER-LIÈVRE (1957), two morphotypes: narrow and wide, found in different localities of the Democratic Republic of Congo. Scale bars: A & F = 50 µm, B-E = 20 µm. Images by Anush Kosakyan.

Furthermore, considering their size and distribution, it appears likely that such isolated populations represent genetically distinct, cryptic, or pseudo-cryptic species.

7.11. Genus *Nebela* (Leidy, 1874) sensu Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Type species: *Nebela collaris* (Ehrenberg, 1848) sensu Kosakyan & Gomaa, 2013

1848b *Difflugia* Ehrenberg, Monatsb. Ak. Wis.: 218.

1876 *Nebela* gen. nov. Leidy, Proc. Ac. Nat. Sc.:157.

Description: Test rounded, ovoid-piriform, or wide-piriform, rarely with a keel (partial or complete) or other lateral expansions. Pseudostome ranging from linear to strongly curved, bordered by an organic rim. Test hyaline or slightly yellowish, usually with embedded circular to elongated shell plates largely recycled from euglyphid testate amoeba prey, sometimes also including fragments of diatom frustules or other small siliceous elements.

Etymology: The genus name is derived from the Hebrew word "nebela" which means "a bottle", referring to the general shape of the test.

Remarks: The genus *Nebela* was established by LEIDY in 1874 for testate amoebae, with a test "composed of discoid plates and minute rods, apparently siliceous and intrinsic to the structure of the animal". *Nebela* species can be found in *Sphagnum* and other mosses, as well as in wet forest litter, although never in exclusively aquatic environments. The prey upon small euglyphids from which they take siliceous scales that are used to construct their test (OGDEN & HEDLEY, 1980; MEISTERFELD, 2002; LAHR et al., 2015) and also on relatively large prey, such as ciliates, nematodes, and rotifers, as well as organic debris (GILBERT et al., 2003).

The genus *Nebela* initially included several other genera, such as: *Apodera*, *Alocodera*, *Argynnia*, *Certesella*, *Cornutheca*, *Difflugia*, *Gibbocarina*, *Longinebela*, *Mrabella*, *Planocarina*, *Padaungiella*, *Porosia*, *Physochila*, and *Quadrulella* (see list of synonymous names on p. 235). Over time, based first on morphological, then combined morphological and molecular taxonomic studies, the definition of the genus was refined, and it is now limited to the former *Nebela collaris* species complex (KOSAKYAN et al., 2013), plus *N. carinatella*, *N. orbicularis*, *N. pulchra*, *N. subsphaerica*, and *N. dydevallei*.

Fifteen taxa are considered valid, but many are problematic, and molecular data are needed to confirm their status (see species descriptions and corresponding notes where molecular data are discussed).

Key to the species

1. Test wider than long in broad view 2
– Test always longer than wide in broad view 3

2. Neck absent: L = 60 µm, B = 70 µm *N. acolla* (p. 122)
– Very short neck present: L = 68–96 µm, B = 72–110 µm *N. flabellulum* (p. 129)

3. Keel present (partial or complete) 4
– Keel absent 6

4. Keel surrounding the lateral margins as well as the fundus of the test 5
– Keel very short, starting near the pseudostome and stopping shortly below, at approximately

1/3rd of the distance between the pseudostome and the fundus. Test wide piriform: L = 69–87 µm, B = 61–69 µm *N. carinatella* (p. 124)

5. Smaller species, test piriform in broad view: L = 104–115 µm, B = 76–93 µm *N. aliciae* (p. 123)
– Larger species, test wide-piriform, almost circular in broad view, except for the short neck and pseudostome: L = 166–208 µm, B = 140–170 µm. Keel less obvious *N. orbicularis* (p. 119)

6. Test piriform in broad view, slightly elongated, with three small conical protuberances 7 µm long and 10 µm wide on the fundus of the test: L = 92 µm, B = 60 µm *N. pulchra* (p. 121)
– Test outline regular in broad view, without conical protuberances 7

7. Test drop-shaped or circular (except for the pseudostome) in broad view 8
– Test ovoid or piriform in broad view 12

8. Test circular in broad view 9
– Test drop-shaped in broad view 10

9. Test very circular in broad view, except for the pseudostome: L = 74–94 µm, B = 67–87 µm, P = 24–26 µm *N. rotunda* (p. 122)
– Larger species with narrower pseudostome, L = 100–121 µm, B = 83–109 µm, P = 23–26 µm and linear *N. subsphaerica* (p. 123)

10. Pseudostome very curved in broad view: L = 80-89 µm, B = 53–65 µm. *N. guttata* (p. 118)
– Pseudostome linear or slightly curved in broad view 11

11. Smaller species: L = 68–78 µm, B = 50–62 µm *N. gimlii* (p. 117)
– Larger species: L = 84–92 µm, B = 67–87 µm *N. pechorensis* (p. 134)

12. Smaller species, L < 100 µm. Test ovoid or circular-piriform, and pseudostome linear in broad view 13
– Test wide-piriform in broad view. Very large (L > 250 µm) or smaller species (L = 90–140 µm), but in this latter instance, with a curved pseudostome in broad view 14

13. Intermediate-sized species: L = 90–95 µm, B = 62–71 µm, P = 24–26 µm *N. tincta* (p. 138)
– Very small species: L = 43–53 µm, B = 37–38 µm, test transparent, yellowish-brown, composed of irregular polygonal plates *N. dydevallei* (p. 138)

14. Medium-sized species: L = 90–140 µm, B = 74–96 µm, P = 28–32 µm. Pseudostome curved in broad view *N. collaris* (p. 125)
– Larger species: L = 270–280 µm, B = 200–210 µm *N. fagni* (p. 129)

Nebela acolla Cash, 1909

1909 *Nebela acolla* Cash, in CASH et al., 1909, The British freshwater Rhizopoda & Heliozoa, 2: 118–119 (Figs. 7–8, original drawings).

Description (based on the original publication): Test broadly elliptic in broad view, wider than long, without neck. Pseudostome invisible in broad view, its presence indicated by a slight thickening of the margin (organic rim). Test transparent and thin, composed of minute circular or polygonal plates, scarcely touching each other at the edges. L = 60, B = 70 µm.

Differential diagnosis: Very similar to *Nebela flabellulum* in general shape but differs by its smaller size and the absence of a neck.

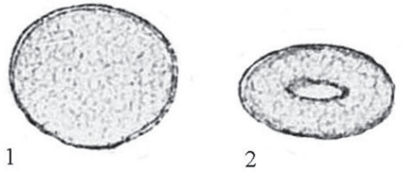

Fig. 55. *Nebela acolla*: Original drawing from CASH & HOPKINSON (1909): (1) broad view of the test (the pseudostome is at the bottom of the image), and (2) frontal view showing the pseudostome.

Type locality: Capel Curig, at the source of a stream above Dolgam, UK. Likely coordinates: 53.099942°, -3.909518°.

Type specimen: Not provided. We declare Figs. 7–8 (representing the same individual) by CASH et al. (1909), reproduced here as Fig. 55, as the type.

Etymology: The species name refers to the general morphology of the test; i.e., “acolla” in Latin means “without a neck”.

Habitat: *Sphagnum* mosses, at the source of a stream.

Geographical distribution: Europe: Romania (GODEANU, 1970; GODEANU & PIRVU, 1977), UK (CASH et al., 1909; HEAL, 1964); Asia: Thailand (BONNET, 1987).

Remarks: This species was rarely reported but may be easily overlooked.

Nebela aliciae Mitchell & Lara, 2013

2013 *Nebela aliciae* Mitchell & Lara, in Kosakyan et al., 2013, Eur. J. Protistol. 49(2): 224 (Figs. 6A, 7B original images).

Icon.: TODOROV & BANKOV, 2019, Fig. 71.

Description: Test wide piriform in broad view, with a lateral, hollow keel ca. 5 µm wide, compressed, with a small lateral pore on each side. Test composed of small oval particles likely obtained from euglyphid testate amoeba prey. Pseudostome ovoid in frontal view, linear in broad view. Dimensions based on seven individuals: L = 104–115 µm, B = 76–93 µm, P = 24–27 µm. The preceding description corresponds to the diagnosis of *Nebela tincta f. galeata* provided by KOSAKYAN et al. (2012). As new isolates were significantly smaller, they were later described as an independent species (KOSAKYAN et al., 2013).

Differential diagnosis: *Nebela aliciae* resembles *Nebela tincta galeata* (as *N. tincta f. galeata*) mentioned by Jung, 1936, from which it differs by its smaller size (L = 104–115 µm vs. 117–143 µm for *Nebela tincta f. galeata*). Molecular and morphological data corroborate *N. aliciae* as an independent species (KOSAKYAN et al., 2013); however, molecular data on *Nebela tincta galeata* are lacking.

Type locality: Near Poás Volcano, Costa Rica. Coordinates: 10.11°, -84.13°.

Type specimen: One SEM stub with several specimens is deposited at the Natural History Museum of Neuchâtel, Switzerland (Ref. No.: UniNe-EM-4).

Etymology: The species name refers to the name Alice for two reasons: The first is a reference to Lewis Carroll’s book “Alice in Wonderland” and the fact that the world of testate amoebae is indeed one of strange and wonderful creatures. The second is a reference to Edward Mitchell’s eldest daughter, Alice, who occasionally enjoyed looking at testate amoebae through his portable microscope.

Habitat: Green mosses.

Geographical distribution: Costa Rica (KOSAKYAN et al., 2013); Bulgaria (TODOROV & BANKOV, 2019).

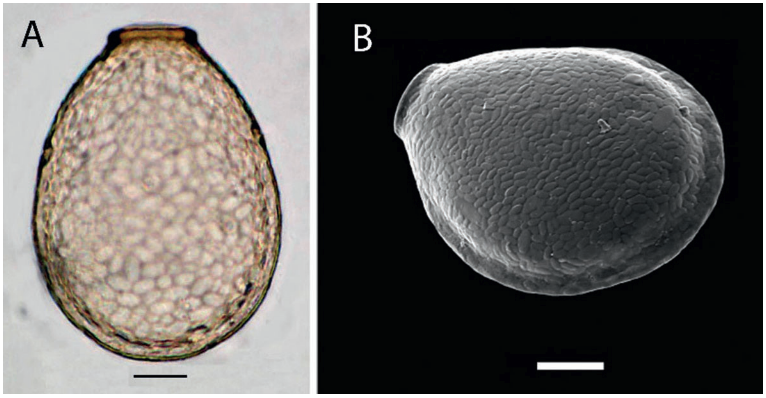

Fig. 56. *Nebela aliciae*: (A) LM image of an empty test from Poás Volcano, Costa Rica; (B) SEM image of a specimen from the same location. Scale bars = 20 µm. Images by Thierry Heger (modified from KOSAKYAN et al., 2013).

Neblela carinatella Beyens & Chardez, 1982

1982 *Nebela carinatella* Beyens & Chardez, Arch. Protistenk. 126: 172 (Fig. 3, original drawing).

Description (based on the original publication): Test regularly rounded in broad view, sides tapering towards a short neck, compressed. A short flat keel present on both sides of the neck region, starting shortly below the neck and ending just before the widest part of the test. Test composed of polymorphic plates from endogenous origin attached together by a chitinoid matrix. L = 69–87 µm, B = 61–69 µm.

Differential diagnosis: *Nebela carinatella* is very similar to *N. carinulata* described by JUNG (1942a), from which it differs by its smaller dimensions and less developed keel. In *N. carinulata*, the keel is continuous, surrounding the entire lateral margins and posterior end of the test; however, *N. carinulata* has been included in the *inquirenda* list, as the description is based on just one individual. Further, the author's interpretation that the test plates are of endogenous origin remains unsubstantiated. Conversely, we believe this material is recycled from the environment or prey. The original drawing suggests these elements are not ovoid, as in most species of the genus.

Type locality: Campine, Belgium. Likely coordinates: 51.4797833°, 4.7794639°; Elevation: ca. 8 m.a.s.l..

Type specimen: Not provided. We declare Fig. 3 by BEYENS & CHARDEZ (1982), reproduced here as Fig. 57, as the type.

Etymology: The species name is derived from the Latin word "carina", meaning "keel", and refers to the presence of the short or small keel.

Habitat: Subatlantic fens (Belgium), Freshwater (China).

Geographical distribution: Belgium (BEYENS & CHARDEZ, 1982; CHARDEZ, 1990a).

Remarks: This species was also reported from China (YANG et al., 2004). We were unable to check this record. However, we consider is

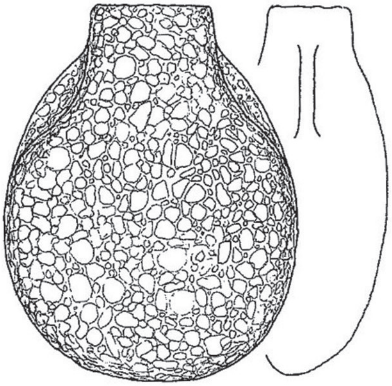

Fig. 57. *Nebela carinatella*: Original drawing from BEYENS & CHARDEZ (1982): broad and profile views.

dubious. Indeed, it is mentioned in freshwater habitat which does not match the type habitat (fen). Given this fact, its characteristic morphology, and the distance between the two regions we therefore consider this record as dubious, possibly rather corresponding to an undescribed species.

Nebela collaris (Ehrenberg, 1848) sensu Kosakyan & Gomaa, 2013

1848b *Difflugia collaris* Ehrenberg, Monatsb. Ak. Wis.: 218.

1848a *Difflugia cancellata* Ehrenberg, Monatsb. Ak. Wis.: 379 (overlapping morphology).

1848 *Difflugia leticulata* Ehrenberg, Monatsb. Ak. Wis.: 218 (overlapping morphology).

1854 *Difflugia carpio* Ehrenberg, Microg.: 119 (overlapping morphology).

1854 *Difflugia laxa* Ehrenberg, Microg.: 331 (overlapping morphology).

1874 *Difflugia cellulifera* Ehrenberg, Microg: 460, 466 (overlapping morphology).

1874 *Difflugia numata* Leidy, Proc. Ac. Nat. Sc.: 157 (overlapping morphology).

1876 *Nebela numata* Leidy, Proc. Ac. Nat. Sc.: 116 (overlapping morphology).

1879 *Nebela collaris* Ehrenberg 1848 – Leidy, Proc. Ac. Nat. Sc.: 145 (evaluation of genus *Difflugia* and transfer to genus *Nebela*).

1882 *Nebela bohemica* Taránek, Sitzungsberichte der Königl. Böhm. Gesellschaft der Wissenschaften in Prag.: 230 (overlapping morphology).

1982 *Nebela collaris* var. *genuina* Taránek, Sitzungsberichte der Königl. Böhm. Gesellschaft der Wissenschaften in Prag: 32 (overlapping morphology).

1933 *Nebela sphagnophila* (Steinecke, 1927) Van Oye, Arch. Naturgesch. 2: 538–573 (overlapping morphology).

1936 *Nebela tincta* var. *major* Deflandre, Annales de Protistologie 5: 256 (overlapping morphology).

1936 *Nebela tincta* f. *stenostoma* Jung, Abhandlungen aus dem Landesmuseum der Provinz Westfalen, Museum für Naturkunde, 7 Jahrgang, Heft 4: 57 (insufficient morphological differences from the type).

2013 *Nebela collaris* (Ehrenberg, 1848) sensu Kosakyan & Gomaa, in KOSAKYAN et al., 2013, Eur. J. Protistol. 49: 233 (improving the taxonomic concept of the species based on molecular data).

Icon.: LEIDY, 1879, Pl. XXV, Figs. 1–8; TARÁNEK, 1881, Fig. 1; OGDEN & HEDLEY, 1980, Pl. 36; KOSAKYAN et al., 2013, Figs. 3, 7E; TODOROV & BANKOV, 2019, Fig. 72.

Description (from KOSAKYAN et al., 2013): Test large, piriform in broad view, slightly yellow or brownish, compressed with small lateral pores (number can vary), which can be difficult to observe. Test composed mainly of ovoid or circular test plates, or solely organic cement. L = (95) 109–112 (140) μm, B = 74–86 (96) μm,

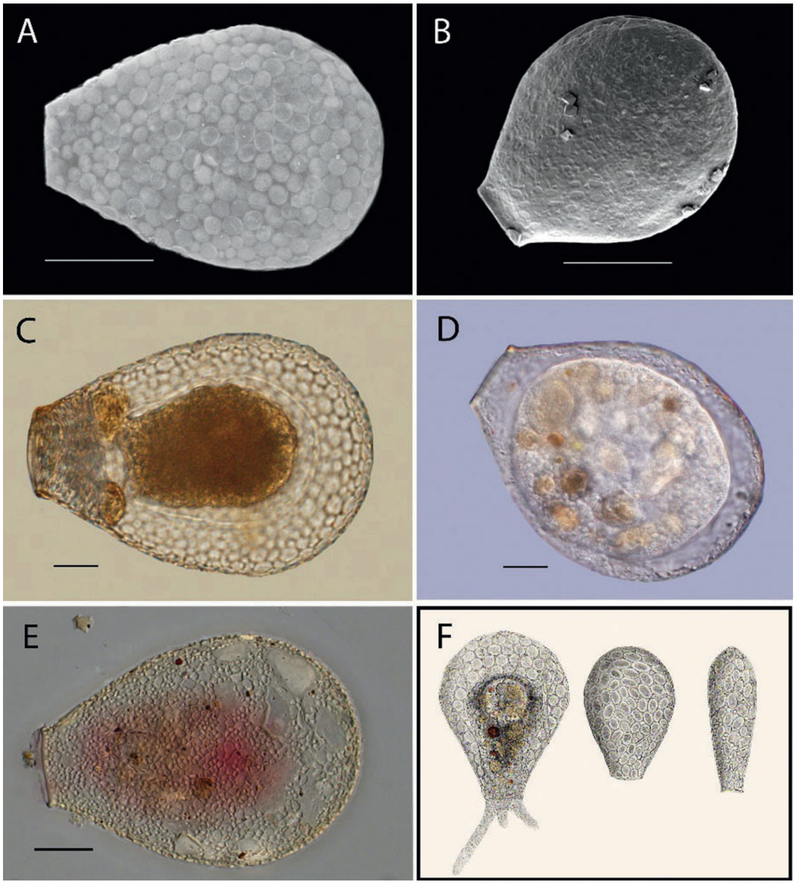

Fig. 58. *Nebela collaris*: (A & B) SEM images of specimens from China and Switzerland, respectively; (C & D) LM images of encysted specimens from China and Switzerland, respectively; (E) LM image of a specimen in broad view from the Eugène Penard slide collection, no. 495-6-3 (Natural History Museum, Geneva, Switzerland); (F) Original line drawings modified from LEIDY (1879), from left to right: broad view of an active living individual, broad and profile views of empty tests. Scale bars: A & B = 50 μm, C–E = 20 μm. Images by: (A–D) Anush Kosakyan, and (E) Thierry Arnet (Wikipedia).

Table 2. *Synoptic key to Nebela collaris and closely related species. All shapes refer to broad view.*

Species	General test	Length (*L*) (µm)	Breadth (*B*) (µm)	*L/B*	Pseudostome shape and width (*P*) (µm)
N. collaris	Wide pear-shaped	95–140	74–96	1.4	Linear or ± curved 28–32
N. dydevallei	Wide pear-shaped	43–53	37–38	1.2–1.4	Linear
N. fagni	Pear-shaped	270–280	200–210	1.3–1.35	Slightly curved
N. gimlii	Drop-shaped	68–78	50–62	1.3–1.4	Slightly curved, 17.5–21
N. guttata	Drop-shaped	80–89	53–65	1.4–1.5	Narrow, protruding, curved, 20–22
N. pechorensis	Drop-shaped	84–92	54–69	1.3–1.5	Narrow, protruding, linear, 19–23
N. rotunda	Round-shaped	74–94	67–85	1.2	Linear, 24–26
N. subsphaerica	Round-shaped	100–121	83–109	1.1–1.2	Slightly protruding, linear, 23–26
N. tincta	Ovoid or round-elliptic	90–95	62–71	1.3–1.4	Linear, 24–26

P = 28–32 µm. Neck very short or nearly absent. Pseudostome linear, more or less curved in broad view, surrounded by an organic rim.

Differential diagnosis: A synoptic key to *N. collaris* and closely related species is provided in Table 2.

Type locality: La Guayara, Venezuela. Likely coordinates: 9.382860°, -69.868294°.

Type specimen: Not specified. We declare Fig. 58E corresponding to specimen nr 6 from permanent slide nr 495 from the Eugène Penard collection at the Natural History Museum of Geneva as the neotype. We preferred using an image from the Penard collection as the type rather than the drawing in Leidy's 1848 monograph due to the fact that these drawings were not made by Leidy himself and that he was not always satisfied with them. It would however be desirable to neotipify this species with material collected from the type locality rather than from Europe as it is likely that the Venezuelan species is different from the European one for a species in this size range.

Etymology: In Latin, the word "collaris" means "necked", referring to the general shape of the test.

Habitat: Wet *Sphagnum* mosses, forest litter.

Geographical distribution (of morphotype *Nebela collaris/bohemica*): Cosmopolitan.

Remarks: The name *N. collaris* has been used to cover a wide variety of forms. Several large taxa (e.g., *N. tincta* f. *stenostoma*, *N. tincta* var. *major*, *N. bohemica*, *N. sphagnophila*), ranging from 95 to 140 µm, are often difficult to distinguish and have thus been lumped into *N. collaris s.l.* The primary discriminating characters between these taxa are: (1) test length, which often overlaps; (2) presence or absence of lateral pores (potentially difficult to see in LM depending on plate density, thus limiting its use as a criterion); and, (3) platelet shape, which depend on the prey consumed (LAHR et al., 2015).

KOSAKYAN et al. (2013) observed that individuals measuring L = 109–112 µm, B = 74–81 µm and with a variable pseudostome morphology (linear, slightly curved, or strongly curved in broad view) formed a separate, robustly supported clade in an mt-COI sequence data-based phylogenetic tree. Accordingly, KOSAKYAN et al. (2013) synonymized the above-mentioned forms with *N. collaris*.

In his monograph on nebelids, TARÁNEK (1882; p. 32) mentioned two varieties of *N. collaris*: var. *genuina*, a slightly more elongated form than the type; and var. pyriformis, approximately twice as large as the type. Considering the broad range of shapes for *N. collaris* (oval, piriform, elongated-piriform), we included *N. collaris* var. *genuina* to the list of synonyms. We suggest treating var. pyriformis as synonymous of *Longinebela (N.) tubulosa*, because its size (227 µm) and general shape (elongated-piriform) falls within the range and corresponds to this morphology. Further studies are thus needed to better define the limits of this species.

Nebela dydevallei Van Oye, 1953

1953 *Nebela dydevallei* Van Oye, 1953, Biologisch Jaarboek Dodonaea (Gent) 20: 198, Fig. 45.

Description (based on the original publication): Test ovoid in broad view, slightly elongated, somewhat resembling Nebela collaris in general shape. Test transparent, yellowish-brown, composed of irregular polygonal plates. Test very small: L = 43–53 µm, B = 37–38 µm. Pseudostome linear in broad view.

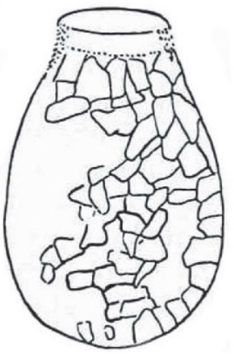

Fig. 59. *Nebela dydevallei*: Original drawing from VAN OYE (1953).

Differential diagnosis: See Table 2 (p. 127) for discriminating characters from closely related species.

Type locality: Beernem, Belgium. Likely coordinates: 51.130477°, 3.328491°.

Type specimen: Not provided. We declare Fig. 45 by Van Oye (1953), reproduced here as Fig. 59, as the type.

Etymology: The author dedicated this species to Knight Hubert Van Outryve D'Ydewalle member of the Belgian resistance who died in deportation in July 1945 and who was the owner of the pond where Van Oye carried out his research.

Habitat: *Sphagnum* mosses (pH = 4.2–6).

Geographical distribution: Belgium (VAN OYE, 1953).

Remarks: The taxonomic position of this species is questionable. This species stands out by its small size as compared to other species in the genus and its unusual test structure with irregular polygonal plates, which is shared only one other species within the genus (*N. carinatella*). The phylogenetic position of both species remains to be established.

Nebela fagni Chardez, 1957

1957 *Nebela fagni* Chardez, Rev. Verviétoise Hist. Nat. 14: 78.

Description (based on the original publication): Test piriform in broad view, with a rounded fundus, compressed; sides gradually tapering towards the pseudostome and finishing in a slight neck. Elliptic in profile. Test yellowish-brown, composed of ovoid, circular, or polygonal plates. Very large species: L = 270–280 µm, B = 200–210 µm. Pseudostome slightly curved in broad–view, P = 80-84 µm wide, surrounded by a thin organic rim.

Differential diagnosis: Chardez (1957) mentioned it resembles *Nebela collaris* in its generalized, giant shape; however, he also believed it may be an intermediate form between *Longinebela (N.) tubulosa* and *Longinebela (N.) speciosa*, two distantly related species in mt-COI phylogenies. It is therefore likely a true species and neither a hybrid nor an intermediate form (see Table 2, p. 127).

Type locality: Hautes Fagnes near Jalhay, Belgium. Likely coordinates: 50.565832°, 6.084382°.

Type specimen: Not provided. We declare Fig. 7 by CHARDEZ (1957), reproduced here as Fig. 60, as the type.

Etymology: The species name is derived from the name of the region (Les Hautes Fagnes) where it was found.

Habitat: Marshy, small pond in meadows, *Sphagnum* mosses.

Geographical distribution: Belgium (CHARDEZ, 1957).

Remarks: A problematic species, as Chardez mentioned its affinity with other species now placed into two different genera: *Nebela* and *Longinebela*. Considering the original drawing and description, we maintained this species in genus *Nebela*, pending confirmation through DNA barcoding.

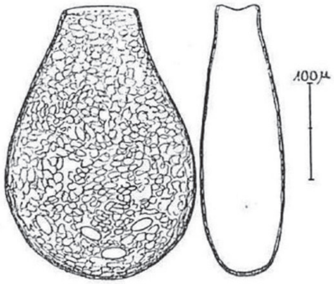

Fig. 60. *Nebela fagni*: Original drawing from CHARDEZ (1957): broad and profile views.

Nebela flabellulum (Leidy, 1874)

1874 *Difflugia flabellulum* Leidy, Proc. Ac. Nat. Sc.: 157.

1876 *Nebela flabellulum* Leidy 1874 – Leidy, Proc. Ac. Nat. Sc.: 118 (re-evaluation of genus *Difflugia*, and transfer to genus *Nebela*).

Icon.: LEIDY, 1876, Figs. 6–7; LEIDY, 1879, Pl. XXIII, Figs. 8–19; DEFLANDRE, 1936, Figs. 84–86; OGDEN & HEDLEY, 1980, Pl. 38; CHARMAN et al., 2000, Fig. 27e; KOSAKYAN et al., 2013, Fig. 6C; TODOROV & BANKOV, 2019, Fig. 73.

Description: Test strongly compressed, wider than long in broad view, as in *Nebela acolla*, but with a short neck. Two lateral pores present, one on each side, often visible. Test colourless or slightly yellowish, composed of circular and ovoid test plates, often covered with a thick organic layer. Sizes vary by author(s): L = 68–99 µm, B = 72–110 µm, P = 17–30 µm. Pseudostome linear or slightly curved in broad view, surrounded by a very thin organic rim.

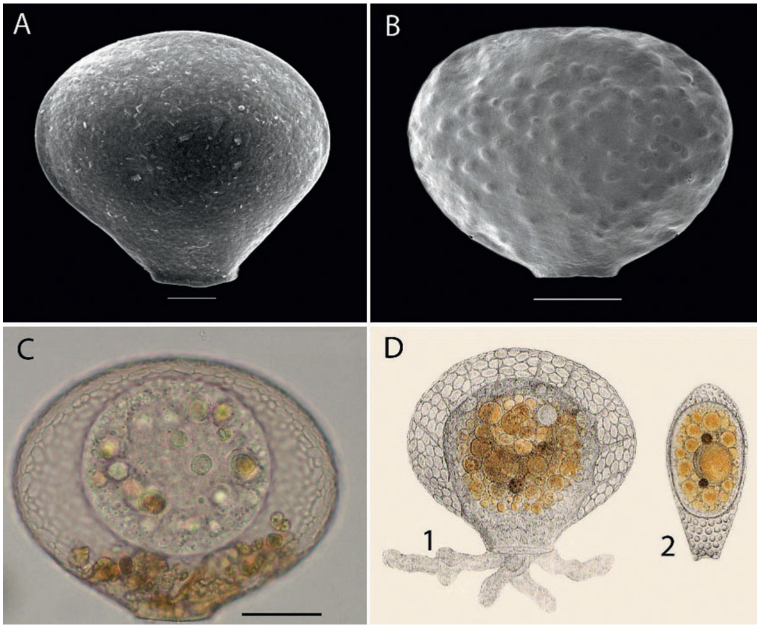

Fig. 61. *Nebela flabellulum*: (A & B) SEM images of specimens from the British Isles and Vancouver, Canada, respectively; (C) LM image of a specimen from Vancouver, Canada; (D) Original drawing from LEIDY (1879): (1) Active individual in broad view, and (2) encysted individual in profile view. Scale bars = 20 µm. Images (A–C) by Thierry Heger.

Differential diagnosis: Owing to its remarkable shape (L/B < 1), it is readily distinguished from other congeneric species. *Nebela acolla* has a comparable shape (L < B) but has no neck and is smaller (L = 68–99 µm in *N. flabellulum* vs. L = 60 µm in *N. acolla*).

Type locality: Absecon, N.J., USA. Likely coordinates: 39.426909°, -74.512855°.

Type specimen: Not provided. We declare Fig. 8 (representing an individual collected in 1874) by LEIDY (1879), reproduced here as Fig. 61D-1, as the type.

Etymology: Not provided. The species name is likely derived from the Latin word "flabella", meaning "fan", referring to the general shape of the test.

Habitat: *Sphagnum* mosses, forest litter. Seems most common under wet temperate (oceanic or hyper-oceanic) climates.

Geographical distribution: North America: Canada (PENARD, 1911; WARNER et al. 2007; KOSAKYAN et al., 2012), USA (LEIDY, 1876); South America: French Guyana (COÛTEAUX, 1979); Europe: Austria (LAMINGER, 1975), Belgium (JUNG, 1936; CHARDEZ, 1987a), British Isles (OGDEN & HEDLEY, 1980; MITCHELL et al., 2000; BLUNDELL & BARBER, 2005; LARA et al., 2008), Bulgaria (GOLEMANSKY et al., 2006; TODOROV & BANKOV, 2019), Czech

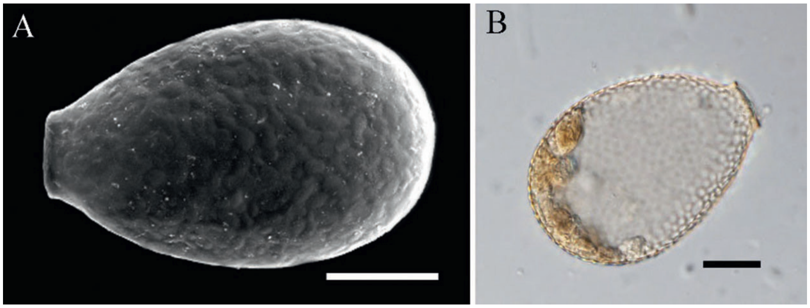

Fig. 62. *Nebela gimlii*: (A) SEM (modified from SINGER et al., 2015), and (B) LM image of a specimen from Switzerland. Scale bars = 20 μm. Images by Anush Kosakyan.

Republic (BALIK, 1994), Finland (LEVANDER, 1900), France (DEFLANDRE, 1936), Germany (JUNG, 1936), Greece (STEPHANIDES, 1948), the Netherlands (HOOGENRAAD & DE GROOT, 1940b), Romania (GODEANU, 1972a), Sweden (GROSPIETSCH, 1954), Switzerland (HEINIS, 1909); Asia: Java (HOOGENRAAD & DE GROOT, 1940a); Australasia: New Zealand (BAMFORTH, 2015; MITCHELL, unpubl.); Pacific Ocean: Hawaii (MITCHELL et al., unpubl.).

Remarks: Leidy (1879) reported occasionally finding specimens bearing quadrate plates (likely recycled from genus *Quadrulella*) intermixed with more conventional structural elements. *Nebela flabellulum* belongs to the *N. tincta* species complex, as shown by molecular phylogenies based on SSU rRNA (LARA et al., 2008) and mt-COI data (KOSAKYAN et al., 2012, 2013); however, as it branches in a basal position with respect to all other taxa of the complex, it is possible that this species, together with the morphologically similar *N. acolla*, and perhaps even other species yet to be described forms a clearly defined clade that would justify the creation of a new genus. Unpublished reports from New Zealand and Hawaii (MITCHELL et al., unpubl.) likely correspond to new species within this species complex.

Nebela gimlii Singer & Lara, 2015

2015 *Nebela gimlii* Singer & Lara, in Singer et al., 2015, Eur. J. Protistol. 51(1): 79–85 (Figs. 1–2, original images).

Description (based on the original publication): Test wide piriform to drop-shaped in broad view, compressed, with a protruding narrow neck, and two lateral pores ca. 1/4 of the distance from the pseudostome to the fundus of the test. A variable number of small pores visible on SEM images in apparently random positions all over the test. Test colourless or slightly brownish, composed of small plates likely obtained from prey (e.g., euglyphid testate amoebae) and covered by a thin layer of organic cement. L = 68–78 μm, B = 50-62 μm, P = 17.5-21 μm. Pseudostome ovoid in frontal view, slightly curved in broad view, surrounded by a thin organic lip.

Differential diagnosis: *Nebela gimlii* can be confused with *N. guttata*, but clearly differs in its wider shape and smaller dimensions of the test. Both species are closely related, differing by only 3.7% on the considered COI fragment, whereas the two COI sequences of *N. gimlii* obtained from two different cells had 99.8% similarity (SINGER et al., 2015).

Type locality: Le Cachot peatland, Jura Mountains, Switzerland. Coordinates: 47.00423°, 6.664675°.

Type specimen: One SEM stub with several specimens is deposited at the Natural History Museum of Neuchâtel, Switzerland; No. UniNe-EM-5.

Etymology: The name of this species refers to the name of Gimli, a dwarf in J.R.R. Tolkien's masterpiece "The Lord of the Rings", because of its small size and stout shape. In addition, it has been found abundantly in forests, and Gimli was unique among his kind to have been travelling in the woods.

Habitat: *Sphagnum* mosses.

Geographical distribution: Switzerland (SINGER et al., 2015).

Nebela guttata Kosakyan & Lara, 2013

2013 *Nebela guttata* Kosakyan & Lara, in KOSAKYAN et al. 2013, Eur. J. Protistol. 49: 234, Figs. 1, 7C.

Description (based on original publication): Test drop-shaped in broad view, with a protruding narrow neck (7.4 ± 0.3 µm long), compressed, with a variable number of small lateral pores. Test colourless or slightly brownish, composed of small particles likely obtained from prey (e.g., euglyphid testate amoebae) and often covered with a thin layer of organic cement. L = 80–89 µm, B = 53–65 µm. Pseudostome oval in frontal view, curved in broad view, P = 20–22 µm wide, surrounded with a thin organic rim.

Differential diagnosis: Resembles *Nebela tincta*, from which it differs by its narrow, protruding, curved pseudostome and slender drop shape of the test (Table 2, p. 127). Molecular data clearly separate these two species as well (COI sequence divergence ≤ 4%; KOSAKYAN et al., 2003). *N. guttata* may also be easily confused with *N. pechorensis*, from which it differs morphologically only by its curved pseudostome (linear in *N. pechorensis*); however, despite sharing a similar morphology, these two species are genetically distinct (COI sequence divergence ≤ 12%) and constitute a clear example of pseudocryptic diversity.

Type locality: Le Cachot bog, Vallée de la Brévine, Switzerland. Coordinates: 47.005829°, 6.664915°.

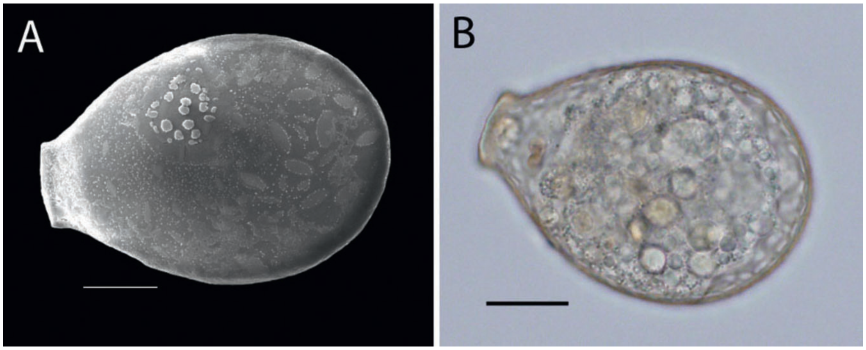

Fig. 63. *Nebela guttata*: (A & B) SEM and LM images of specimens from Switzerland. Scale bars = 20 µm. Images by Anush Kosakyan.

Type specimen: One SEM stub with several specimens is deposited at the Natural History Museum of Neuchâtel, Switzerland; No. SEM-A-2, UniNe-EM-2.

Etymology: The name of this species is derived from the Latin word "gutta", meaning "drop", in reference to the general drop-shape of the test.

Habitat: *Sphagnum* mosses, preferentially on hummocks (i.e., *Sphagnum fuscum*, SINGER et al., 2018).

Geographical distribution: Bulgaria (BANKOV et al., 2018), Switzerland (KOSAKYAN et al., 2013), likely more widespread.

Nebela orbicularis (Deflandre, 1936) comb. nov.

1936 *Nebela galeata* var. *orbicularis* Deflandre, Ann. Protist. 5: 269, Pl. XXIII, Fig. 12; Pl. XXIV, Figs. 5–6, 9–10.

Description (based on original publication): Test wide piriform or almost rounded, with a short neck and a lateral hollow keel (as in *Gibbocarina galeata*), with two lateral pores, difficult to observe. L = 166–208 µm, B = 140–170 µm. Pseudostome surrounded with a thin organic rim.

Differential diagnosis: Differs from *Gibbocarina galeata* (initially described as a variety of this species) by its rounded shape, narrower pseudostome in broad view, and smaller keel. See Remarks of *G. galeata* for further discussion.

Type locality: Haute-Savoie, France. Likely coordinates: 46.210124°, 6.534392°

Type specimen: Not provided. We declare Fig. 5 by DEFLANDRE (1936), reproduced here as Fig. 64, as the type.

Etymology: The species name derives from the Latin word "orbiculus", meaning "small spherical object", in reference to the rounded morphology of the test.

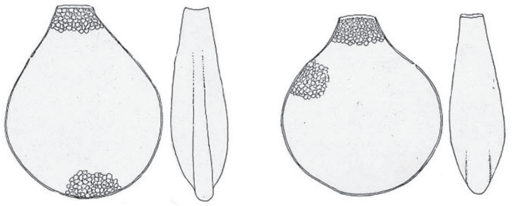

Fig. 64. *Nebela orbicularis*: Original drawing (as *Nebela galeata* var. *orbicularis*) from DEFLANDRE (1936) for two individuals: broad and profile views.

Geographical distribution: Europe: France (DEFLANDRE, 1936), Germany (JUNG, 1938; HARNISCH, 1958), Ireland (BEYENS & CHARDEZ, 1984); Asia: North Korea (GOLEMANSKY & TODOROV, 1991).

Habitat: Very wet green and *Sphagnum* mosses.

Remarks: As this taxon was initially described as *Nebela galeata* var. *orbicularis* before 1961 it should be considered as a subspecies of *Nebela galeata* PENARD in accordance with ICZN's Art. 45.6.4. However, since *N. galeata* is now the type species of the genus *Gibbocarina*, and *Nebela galeata* var. *orbicularis* does not fit the diagnostic criteria of this genus (i.e., elongated-piriform shape), we transfer it back to genus *Nebela as Nebela orbicularis* comb. nov. based on the rounded piriform shape of its shell. Nonetheless this would have to be confirmed by DNA barcoding. In his taxonomic key, HARNISCH (1958) mentioned *N. galeata* var. *orbicularis* as *N. orbicularis*, without any official taxonomic action regarding the elevation of this infraspecific taxon to the species level.

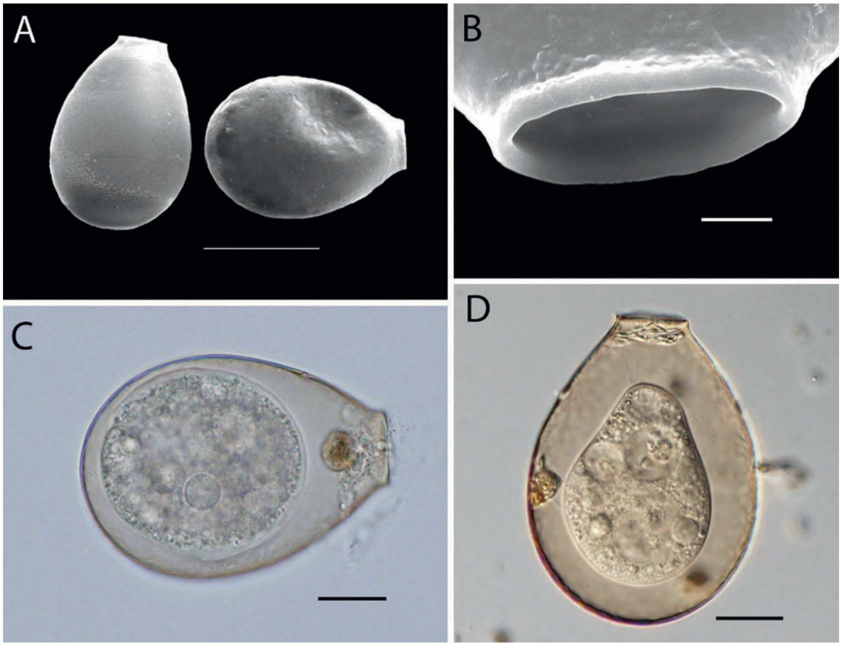

Fig. 65. *Nebela pechorensis*: (A & B) SEM images of specimens from Switzerland: two in broad view and a detailed image of the pseudostome in a slightly oblique broad view, respectively; (C & D) LM images of two specimens from Switzerland in broad view. Scale bars: A = 50 µm, B = 5 µm, C & D = 20 µm. Images by A nush Kosakyan.

Nebela pechorensis Kosakyan & Mitchell, 2013

2013 *Nebela pechorensis* Kosakyan & Mitchell, in KOSAKYAN et al., 2013, Europ. J. Protistol. 49: 234 (Fig. 5, original image).

Description: Test tear or drop shaped in broad view, with a protruding narrow neck (6.2 ± 0.9 µm long), slightly compressed laterally, and a variable number of small lateral pores. Test colourless or slightly brownish, composed of small particles likely obtained from prey (e.g., euglyphid testate amoebae), often covered with a thin layer of organic cement. Dimensions based on 10 individuals: L = 84–92 µm, B = 54–69 µm, P = 19–23 µm. Pseudostome ovoid in frontal view, linear in broad view.

Differential diagnosis: *Nebela pechorensis* strongly resembles *N. guttata* by shape, and it differs from *N. guttata* only by a linear pseudostome in broad view (Table 2, p. 127). Despite their similar morphology, these two species are genetically distinct (sequence divergence ≥ 12% in mt-COI gene; KOSAKYAN et al., 2013).

Type locality: Upper basin of the Pechora River, Russia. Coordinates: 62.090817°, 58.3175°

Type specimen: One SEM stub with several specimens is deposited at the Natural History Museum of Neuchâtel, Switzerland; No. SEM-A-3, UniNe-EM-3.

Etymology: The species name is derived from the Pechora River.

Habitat: Relatively dry *Sphagnum* mosses (i.e., peatland *Pinus* forests; SINGER et al., 2018).

Geographical distribution: Europe: Switzerland (KOSAKYAN et al., 2013), Russia (upper basin of the Pechora River; KOSAKYAN et al., 2013).

Nebela pulchra Bartoš, 1938

1938 *Nebela pulchra* Bartoš, 1938, Arch. Protistenk. 90: 346 (Fig. 1, original drawing).

Description (based on the original publication): Test piriform in broad view, slightly elongated, with three little conical protuberances on the fundus of the test, 7 µm in length and 10 µm in breadth. Test composed of a loose network of large, irregularly arranged hexagonal plates, with numerous narrow rectangular plates filling the free spaces between them. Test intermediate sized, L = 92 µm, B = 60 µm, P = 21 µm. Pseudostome elliptical in frontal view.

Differential diagnosis: Besides the unusual conical structures, the most striking characteristic of this species is clearly the original structure of the test. Indeed, no other member of the family includes hexagonal or narrow rectangular elements such as those seen in Fig. 66.

Type locality: Carpathian Mountains, Slovakia. Likely coordinates: 48.711043°, 19.44049°.

Type specimen: Not provided. We declare Fig. 1 by BARTOŠ (1938), reproduced here as Fig. 66, as the type.

Etymology: The species name is derived from the Latin term "pulchra", meaning "beautiful", in reference to the beautiful test of this species.

Habitat: Green mosses.

Geographical distribution: Slovakia (BARTOŠ, 1938).

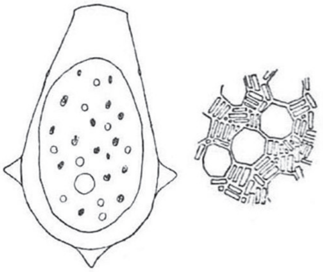

Fig. 66. *Nebela pulchra*: Original drawing from BARTOŠ (1938): (A) test in broad view; (B) detailed view of the test composition.

Remarks: This intriguing species was recorded only once. Bartoš compared this species to *Argynnia caudata* (a species that does not belong to Hyalospheniidae), noting that the two species are similar in their horn-like side projections; however, although these projections are hollow extensions of the test in both cases, they are barely comparable: *A. caudata* has four to five long, tubular extensions ("horns"), while *N. pulchra* has only three much shorter, broadly conical structures. The original description does not mention anything about the shape of the pseudostome, but the original drawing suggests the presence of the characteristic organic lip of Hyalospheniidae. The presence of this trait and the general outline of the test suggest an affiliation to genus *Nebela* rather than to *Argynnia* (that lacks organic cement around the pseudostome).

Nebela rotunda Penard, 1890

1890 *Nebela bursella* var. *rotunda* Penard, Mem. Soc. Phys. Hist. Nat. 31: 164. (Penard had erroneously synonymized *H. tincta* Leidy with *N. bursella* Vejdovsky)

1936 *Nebela tincta* var. *rotunda* Deflandre, Ann. Protistol.: 255 (overlapping morphology).

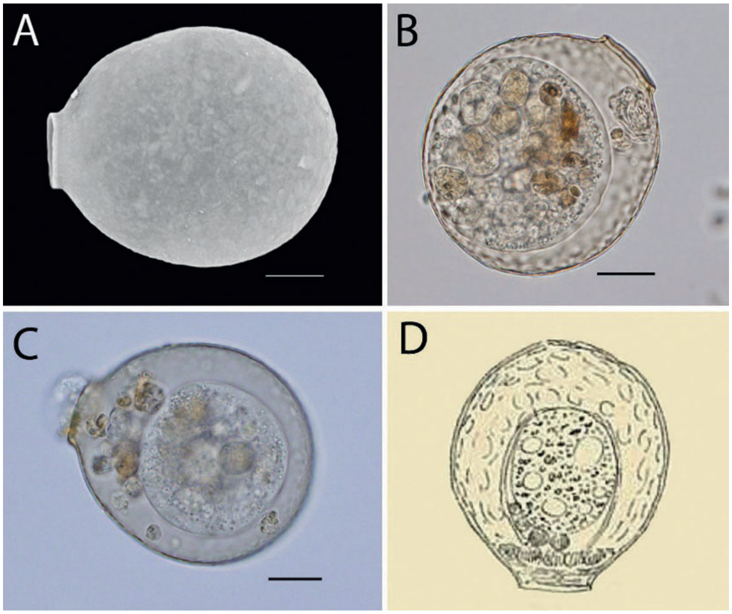

Fig. 67. *Nebela rotunda*: (A) SEM image of a specimen from Switzerland, (B) LM image of a living specimen from Switzerland, (C) LM image of a living (possibly encysted) specimen from France, (D) Original drawing of an apparently encysted specimen modified from PENARD (1890; mentioned as *N. bursella* var. *rotunda*). All images show specimens in broad view. Scale bars = 20 µm. Images (A–C) by Anush Kosakyan.

2013 *Nebela rotunda* Penard, redefined by KOSAKYAN et al., 2013, Eur. J. Protistol. 49: 234.

Icon.: PENARD, 1890, Figs. 12–15; KOSAKYAN et al., 2013, Fig. 4.

Description: Test rounded, almost circular except for the short neck and pseudostome in broad view, compressed with small lateral pores in each side that are sometimes difficult to observe. Test slightly yellow or brownish, composed mainly of ovoid or circular test plates but can also be composed of, or covered by a thick layer of organic cement, giving the impression of a homogenous structure. L = 74–94 µm, B = 67–85 µm, L/B = 1.2, P = 24–26 µm. Neck very short, pseudostome linear in broad view or slightly curved, surrounded by a thin organic rim.

Differential diagnosis: Most similar to *Nebela subsphaerica*, which is larger in size and has narrower pseudostome (Table 2, p. 127).

Type locality: Two localities are mentioned: Göteborg, Sweden (Likely coordinates: 57.726572°, 12.240166°), and Jura, Switzerland.

Type specimen: Not provided. We declare Fig. 12 by PENARD (1890), reproduced here as Fig. 67D, as the type.

Etymology: The species name is derived from the Latin word “rotunda” meaning “rounded”, in reference to the shape of the test.

Habitat: *Sphagnum* mosses in peatland pine forests (SINGER et al., 2018).

Geographical distribution: Only reliably reported from Europe to date.

Remarks: This species was treated as a variety of *Nebela tincta*. A molecular survey of the *N. collaris s.l.* group, combining detailed morphological and molecular (mt-COI) data showed that *N. rotunda* is genetically distinct from *N. tincta* (genetic distance ≥ 10%; KOSAKYAN et al., 2013), suggesting its treatment as an independent taxon. No formal change was made in the authorship (ICZN Art. 45.6.3 and 46.1).

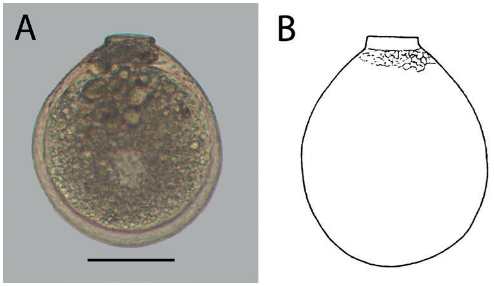

Fig. 68. *Nebela subsphaerica*: (A) LM broad view image of a specimen from New Zealand (by Edward Mitchell), (B) Original drawing from VAN OYE (1956a). Scale bar = 50 µm.

Nebela subsphaerica Van Oye, 1956a

1936a *Nebela subsphaerica* Van Oye, Hydrobiologia: 25 (Fig. 15, original drawing).

Description: Test rounded in broad view, compressed, with small lateral pores on each side that are difficult to observe. Test yellow or brownish, composed of ovoid or circular test plates, and covered by a thick layer of organic cement giving the impression of a homogenous structure. L = 100–121 µm, B = 83-109.4 µm, L/B = 1.12–1.23, P = 22.9–26 µm wide. Neck very short, pseudostome linear in broad view, and surrounded by a thin organic rim.

Differential diagnosis: Can be confused with *Nebela rotunda*, which is smaller in size and has a wider pseudostome (see Table 2, p. 127).

Type locality: Swampy Summit, NW of Dunedin, New Zealand. Likely coordinates: -45.800497°, 170.484162°; Elevation, ca. 700 m.a.s.l..

Type specimen: Not provided. We declare Fig. 15 by VAN OYE (1956a), reproduced here as Fig. 68B, as the type.

Etymology: The species name refers to the "nearly spherical" (rather circular as it is compressed) outline of the test.

Habitat: *Sphagnum* tarn with acidic pH.

Geographical distribution: New Zealand (Van Oye, 1956a).

Remarks: This species was reported only once (VAN OYE, 1956a) and recently observed again by Mitchell (unpubl.) from Swampy Summit, NW of Dunedin, New Zealand. On his new species, Van Oye commented, "Dimensions: L = 100 µm, B = 83 µm, M = 27 µm, N = 5 µm, L/B = 1.2. This new species is at first sight very much like some specimens of *N. collaris*; it differs however in that its neck is translucid and always well developed. The body is on the whole of a Nebelid structure, but the neck is well delimited and without any particularity in its structure. The specimen is slightly Ionger than broad (length/breadth relation 1.2), by which character the species can easily be distinguished from *N. flabellulum*".

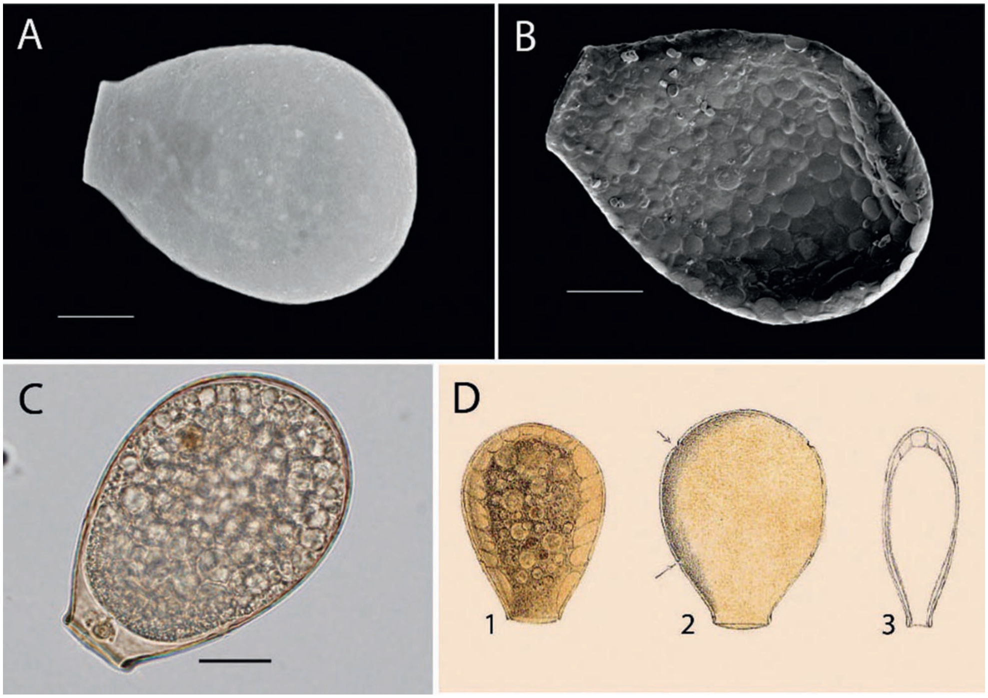

Fig. 69. *Nebela tincta*: (A & B) SEM broad view images of two individuals from Switzerland; (C) LM broad view image of a living specimen from Switzerland; (D) Original drawings of a specimen (labelled as *Hyalosphenia tincta*), modified from LEIDY (1879): (1) living individual in broad view, (2) empty test in broad view with indications of lateral pores, and (3) profile view of an active individual showing the cell in transparency. Scale bars = 20 µm. Images (A–C) by Anush Kosakyan.

Nebela tincta (Leidy, 1879) sensu Kosakyan & Lara, 2013

1879 *Hyalosphenia tincta* Leidy, J. U.S. Geological Survey of the Territories: 138–139 (Pl. XX, Figs. 11–18, original drawings).

1893 *Nebela minor* Penard, Arch. Sci. Phys. Nat. 29: 181 (overlapping morphology).

1906 *Nebela tincta* Leidy, 1879 – Awerinzew, Proc. St. Petersburg Nat. Soc. 36: 249 (observing morphological characters common for the genus *Nebela*).

2013 *Nebela tincta* Leidy, 1879 – sensu Kosakyan & Lara, in KOSAKYAN et al., 2013, Eur. J. Protistol. 49: 233 (improving the taxonomic concept of the species based on molecular data).

Icon.: LEIDY, 1879, Pl. XX, Figs. 11–18; KOSAKYAN et al., 2013, Figs. 2, 7D. Misapplied: VEJDOVSKY, 1881 (Figs. 1–3 as *N. bursella*, two of which are *N. militaris,* and one is a bit broader, but not like *N. tincta*); LUKETA, 2017c, Fig. 1 (as *N. collaris*); LUKETA, 2017d, Fig. 3 (as *N. minor)*.

Description (from KOSAKYAN et al., 2013): Test ovoid or elongated elliptical in broad view, compressed with a variable number of small lateral pores which can be difficult to observe. Test slightly yellow or brownish, composed mainly of ovoid or circular test plates, but can also be composed of, or covered by a thick layer of organic cement, giving the impression of a homogenous structure. L = 90–95 µm, B = 62–71 µm, P = 24–26 µm. Neck very short, pseudostome linear in broad view, surrounded by an organic rim.

Differential diagnosis: Information regarding closely related species can be found in Table 2 (p. 127).

Type locality: Swamps of Tobyhonne, Pocono Mountain, Monroe County, Pennsylvania, USA. Likely coordinates: 41.12444, -75.626111Also near Kirkwood Station, on the Camden and Atlantic Railroad, New Jersey, USA. Likely coordinates: 41.224525°, -75.412658°.

Type specimen: Not provided. We declare Pl. XX, Fig. 16 by LEIDY (1879), reproduced here as Fig. 69D-1, as the type.

Etymology: Although it has not been provided, the term "tincta" in Latin means "dyed", perhaps referring to the slightly yellowish colour of certain individuals.

Habitat: *Sphagnum* lawns in peatbogs often associated with *S. magellanicum* (now either *S. medium* or *S. divinum*) (SINGER et al., 2018).

Geographical distribution: Broad Holarctic distribution but also found (reported as *N. minor*) in Asia: Java (BONNET, 1992), Sulawesi (BONNET, 1992); Austrlasia: Maluku Islands (BONNET, 1992), New Guinea (Irian Jaya (BONNET, 1992).

Remarks: The taxonomic validity of characters used to define *Nebela tincta* has long been a subject of confusion (CASH & HOPKINSON, 1909; HEAL, 1963; LÜFTENEGGER et al., 1988). KOSAKYAN et al. (2013) conducted a study combining detailed morphological and mt-COI sequence data, showing that the presence of lateral pores and composition of the test do not hold any taxonomic value; thus, the authors synonymized several species (see list of synonyms, p. 235) and redefined *N. tincta* via combining molecular and morphological data.

7.12. Genus *Padaungiella* Lara & Todorov, 2012

Type species: *Padaungiella lageniformis* (Penard, 1890)

1942b *Schaudinnia* gen. nov. Jung, Arch. Protistenk. 95: 379 (invalid genus owing to the lack of type designation).

2012 *Padaungiella* gen. nov. Lara & Todorov, in KOSAKYAN et al., 2012, Protist 163: 429.

Description: Test lageniform in broad view, with a distinct elongated neck. Compressed, except for two species (*P. nebeloides* and *P. pulcherrima*) with a circular cross section. In broad view, pseudostome linear to strongly curved. Pseudostome with an organic rim ranging from nearly absent to thick. Test hyaline or slightly yellowish-brown, composed of circular to elongated test plates predated from small euglyphids. One notable exception is *P. nebeloide*s that can use relatively large mineral particles, giving a granulose effect to the test, atypical for Hyalospheniidae (somewhat similar to genus *Difflugia*).

Remarks: This genus was created in 2012 by Lara & Todorov (in KOSAKYAN et al., 2012). Both mt-COI and SSU rRNA (LARA et al., 2008) data have shown that all taxa from genus *Nebela* (with long neck) plus *Apodera vas* form a distinct clade sister to all other Hyalospheniidae in the phylogenetic tree. Accordingly, keeping these species under genus *Nebela* would have rendered it paraphyletic with respect to *Certesella*, *Hyalosphenia*, and *Porosia*. Indeed, JUNG (1942b) noted that this group was distinct from the rest of the genus and thus erected genus *Schaudinnia*, stating that "*it differs from* Nebela *s. str. by a distinct elongated neck that gives the test a bottle shape, and from other nebelid genera by the lack of distinctive features (that characterizes each of them)*". Within the genus, Jung included *N. lageniformis*, *N. tubulata*, and *N. wailesi*. As Jung's classification lacked type designation, the name *Schaudinnia* was deemed unavailable, and these species remained within genus *Nebela*. KOSAKYAN et al. (2012) confirmed the position of hyalospheniid species with a bottle-shaped test and an elongated tubular neck via mt-COI phylogenetic data: *N. lageniformis*, *N. nebeloides*, *N. wailesi*, and *Alocodera cockayni*. Thus, KOSAKYAN et al. (2012) transferred the sub-clade of *N. lageniformis* and closely related species (i.e., those with an elongated, bottle-shaped test and distinct neck) to the newly defined genus *Padaungiella* Lara & Todorov, sister to genera *Alocodera* and *Apodera*. Further, the authors proposed *Padaungiella lageniformis* (Penard) Lara & Todorov as the type species of the new genus.

Etymology: The name of this genus was imagined by Edward Mitchell. It is derived from the name of a Tibetan-Burmese ethnic minority of Myanmar (Burma), known as "Padaung". The women of this tribe traditionally wear very long coiled neck rings, which comprise a single brass coil placed around the neck. The length of the coil is gradually increased with time, and the added weight presses down upon the clavicle and rib cage, giving the appearance of a very long neck.

Ten taxa are considered valid, although many are problematic and require molecular data to confirm their position within the genus. Molecular data are available only for three of these ten species (see species descriptions and corresponding Remarks for further discussion):

Key to the species

1. Pseudostome circular in frontal view 2
– Pseudostome ovoid in frontal view 4

2. Pseudostome with an irregular outline: L = 113–130 (140) µm. Test outline very elongated in broad view, B = 45–55 µm *P. nebeloides* (p. 149)
– Pseudostome with a regular linear outline 3

3. Test consisting of an elongated neck and rounded main body: L = 90–130 µm *P. americana* (p. 141)
– Main part of the test consisting of two identical, flattened hemispherical convexities: L = 180–195 µm, B = 100 µm *P. pulcherrima* (p. 151)

4. Test in profile view with a pointed posterior end or hollow keel 5
– Test in profile view with a rounded posterior end 6

5. Neck sub-cylindrical, slightly swollen on both sides, with a constriction at the base. Hollow keel present, starting from the junction between the neck and the main body of the test, and covering the entire lateral margin of the main body: L = 191–212 µm, B = 136–138.5 µm *P. kenyana* (p. 143)
– Neck cylindrical, not swollen, and without a constriction at its base. Pointed posterior end of the test in profile view *P. cordiformis* (p. 142)

6. Neck elongated but not quite distinct from the main body of the test. Sides gradually tapering towards the pseudostome: L = 120 µm, B = 45 µm *P. longitubulata* (p. 147)

– Neck distinct, clearly separated from the main body of the test 7

7. Smaller species: L < 80 µm 8

– Larger species: L > 80 µm. Neck with parallel sides, sub-parallel, slightly convex sides or getting wider towards the pseudostome in broad view 9

8. Neck wider towards the pseudostome in broad view: L = 65–70 µm, B = 28–32 µm *P. tubulata spatha* (p. 154)

– Neck not wider towards the pseudostome in broad view and with parallel sides in broad view: L = 55–74 µm, B = 28–48 µm *P. tubulata* (p. 152)

9. Intermediate-sized species: L = (83) 100–140 (160) µm *P. lageniformis* (p. 144)

– Larger species: L = 170 µm, B = 103 µm *P. magna* (p. 148)

Padaungiella americana comb. nov.

1882 *Nebela americana* Taránek, Abhandl. Böhm. Ges. Wiss. 11(8), p. 40 (Figs. 15–16, original drawings).

Description: Test lageniform in broad view, with a circular or slightly elliptic main posterior body, a distinct elongated neck, circular in cross-section, with either subparallel or slightly convex margins. Test transparent, composed of elliptical or circular plates. Pseudostome circular in frontal view: L = 90–130 µm.

Differential diagnosis: *Padaungiella americana* can be easily confused with *P. wailesi*, which shares similar outline and dimensions (*N. wailesi*: L = 75–100 µm); however, it differs by its circular cross section. Taránek also mentioned the morphological similarity between *P. americana* and *N. barbata*, although the latter has a much narrower neck, a straight pseudostome (and is covered with spines), whereas Fig. 70 shows the curved pseudostome typical of *P. americana*.

Fig. 70. *Padaungiella americana*: Original drawing from TARÁNEK (1882).

Type locality: Surroundings of Mariannaberg and Falkenberg, near Děčín, Czech Republic. Likely coordinates: 50.807741°, 14.180573°.

Type specimen: Not provided. We declare Fig. 15 by TARÁNEK (1882), reproduced here as Fig. 70, as the type.

Etymology: Not provided. The species name likely refers to the (North) American continent and the speciments found by LEIDY (1879) (see Remarks).

Habitat: Forest litter.

Geographical distribution: Czech Republic (TARÁNEK, 1882).

Remarks: TARÁNEK (1882) mentioned that *Padaungiella* (*Nebela*) *americana* is similar to *N. barbata* found by LEIDY (1879) in general shape but lacks the characteristic fine spines of the latter taxa. Taránek also highlighted two

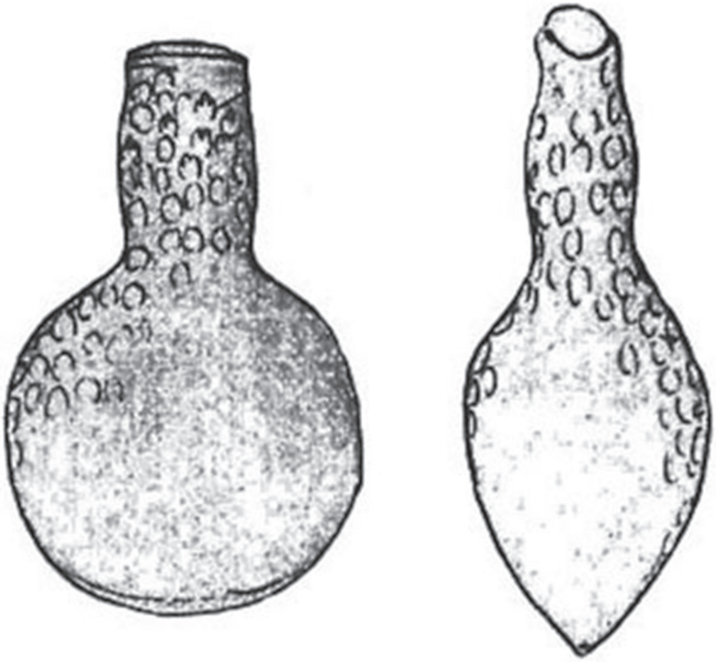

Fig. 71. *Padaungiella cordiformis*: Original drawing from HEINIS (1914): broad and profile views.

specimens found in New Jersey, USA by LEIDY (1879, Pl XXIV, Figs. 18–19), suggesting they represent an intermediate form very similar to *P. (N.) americana*, falling between *N. collaris* and *N. barbata*. WAILES (1912a) described *Nebela americana falcata*, but as this description lacked illustration, we included this infraspecific taxon in the list of *inquirenda* names.

Padaungiella cordiformis (Heinis, 1914) comb. nov.

1914 *Nebela lageniformis* var. *cordiformis* Heinis, 1914, Mem. Soc. Neuchât. Sci. Nat. V: 686 (Figs. 1–2, original drawings).

1942b *Schaudinnia cordiformis* Heinis 1914 - Jung, Arch. Protistenk. 95: 379.

Description: Test bottle-shaped in broad view, compressed, with an elongated distinct neck; very characteristic in profile: elongated neck, main part of the test rounded, gradually tapering to a pointed fundus (originally described as “pointed heart-shaped, like a lance”). Test composed mostly of elliptical plates (including denticulate apertural plates of Euglypha). L = 128–135 μm.

Differential diagnosis: This species was considered a variety of *Padaungiella lageniformis* until JUNG (1942b) suggested to treat it as an independent taxon based on clear morphological differences (rounded fundus in *P. lageniformis* vs. pointed, cordiform fundus in *P. cordiformis*). Indeed, DEFLANDRE (1936) had previously mentioned that these differences could suffice to split *P. lageniformis* into two distinct species; however, LARA et al. (2008) observed a continuum of test shapes between the typical *P. lageniformis* and the much wider *P. cordiformis* in samples from Peru. Accordingly, they considered *P. cordiformis* a product of phenotypic plasticity for *P. lageniformis* but stated that more detailed combined morphological and molecular studies may confirm the existence of two distinct taxa.

Type locality: Paramo Cruz Verde, Colombia. Likely coordinates: 4.530341°, -74.034566°; Elevation, ca. 3600 m.a.s.l..

Type specimen: Not provided. We declare Fig. 1 by HEINIS (1914), reproduced here as Fig. 71 as the type.

Etymology: The name of this species derives from the Latin words “cor” meaning “heart”, and “forma”, meaning “shape”), in reference to the characteristic pointed heart shaped posterior end of the test.

Habitat: *Sphagnum* and other mosses.

Geographical distribution: Asia: Indonesia (HOOGENRAAD & DE GROOT, 1940a), Nepal (BONNET, 1983); South America: Argentina (VUCETICH, 1974, 1975; VUCETICH & LOPRETTO, 1995), Chile (BONNET, 1966), Colombia (HEINIS, 1914); Central America: Costa Rica (LAMINGER, 1973), Guatemala (LAMINGER, 1973); Europe: Bosnia-Herzegovina (LUKETA, 2017), Romania (GODEANU, 1972a).

Padaungiella kenyana (Chardez, 1982) comb. nov.

1982 *Nebela kenyana* Chardez, Rev. Verv. Hist. Nat.: 59 (Figs. 1–8 and 10–12, original image and drawings).

Description (based on the original publication): Test lageniform in broad view, compressed, main body circular, neck elongated sub-cylindrical, slightly swollen at the base (neck 66–73 µm in length, 66.5–72.5 µm in breadth at the junction with the main body). Neck separated from the main body of the test by a slight constriction on both sides, somewhat reminiscent of *Alocodera cockayni*. Main body surrounded by a lateral hollow keel 4.5–5 µm wide, not very visible at times, but always present. Test yellowish, reinforced with regularly arranged circular, ovoid, or polygonal plates. Pseudostome oval in frontal view, curved in broad view, surrounded with an organic rim. L = 191–212 µm, B = 136–138.5 µm, P = 40–48 µm.

Differential diagnosis: The morphology of this species is partly similar to genera *Padaungiella* (distinct elongated neck), *Alocodera* (swollen neck with a constriction at its base on both sides), and *Apodera angatakere* (distinct neck with constriction and presence of a keel); however, the constriction is not strong enough to place it in genus *Alocodera*, and we thus believe this species fits best in genus Padaungiella. Molecular data and detailed morphological investigations are needed to clarify the position of this species within Hyalospheniidae.

Type locality: Mount Kenya: Lake Gallery. Likely coordinates: -0.163594°, 37.324642°; Elevation, 4450 m.a.s.l.. Lake Hausberg (4375 m.a.s.l.) and Lake Nanyuki (nb. spelled Nanyuky by CHARDEZ, 1982; 4485 m.a.s.l.), Kenya.

Type specimen: Type material is deposited in the State Faculty of Agricultural Sciences, Gembloux (currently known as GxABT, University of Liege); No. P66.

Etymology: The name of this species refers Kenya, but it is unknown if referencing the country, mountain, or both.

Habitat: Aquatic, among plankton and benthos.

Geographical distribution: Africa: Kenya. Only known from Mount Kenya (CHARDEZ, 1982).

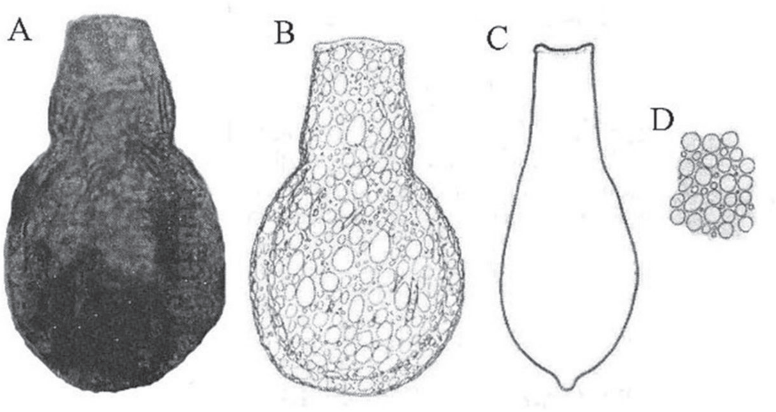

Fig. 72. *Padaungiella kenyana*: (A) original LM images and drawings from CHARDEZ (1982): (B) broad view, (C) profile view, and (D) detail of the test composition.

Padaungiella lageniformis (Penard, 1890)

1890 *Nebela lageniformis* Penard, Mem. Soc. Hist. Nat. 31(2): 158–159 (Pl. VI, Figs. 50–61, original drawings).

1892 *Nebela ambigua* Cash, Trans. Manchester Microsc. Soc. 1891: 47–55 (overlapping morphology).

2012 *Padaungiella lageniformis* Penard, 1890 – Lara & Todorov, in KOSAKYAN et al., 2012, Protist 163: 429–430 (establishment of genus *Padaungiella* based on detailed morphological and molecular data).

Icon.: PENARD, 1890, Pl. VI, Figs. 50–61; DEFLANDRE, 1936, Figs. 98–99; RAUENBUSCH, 1987, T.21; MEISTERFELD, 2002, Fig. 66; LARA et al., 2008, Figs. 1c, 2; KOSAKYAN et al., 2012, Fig. 6A; LUKETA, 2015a, Figs. 1–2; LUKETA, 2017a, Figs. 3–4, 7–8, 11; LUKETA, 2017d, Fig. 1; TODOROV & BANKOV, 2019, Fig. 75.

Description: Test lageniform in broad view, with a circular or slightly elliptical main body. A distinct elongated neck, ovoid in cross-section, with either subparallel or slightly convex margins. In profile, narrow lageniform. Test transparent, composed of elliptical or circular plates. Pseudostome ovoid in frontal view, curved in broad view, somewhat indented in profile, and surrounded with a thin organic rim. L = 100–140 µm, B = 60–90 µm (PENARD, 1890). Extreme size ranges observed by Luketa were considerably broader: 83–160 µm (LUKETA, unpubl.).

Differential diagnosis: Notes on *Padaungiella lageniformis* and closely related species are given in Table 3 (p. 146).

Type locality: Region of Wiesbaden, Germany. Likely coordinates: 50.116135°, 8.234612°.

Type specimen: Not provided. We declare Pl. VI, Fig. 50 by PENARD (1890), reproduced here as Fig. 73D-1, as the type.

Etymology: The species name refers to the lageniform shape of the test.

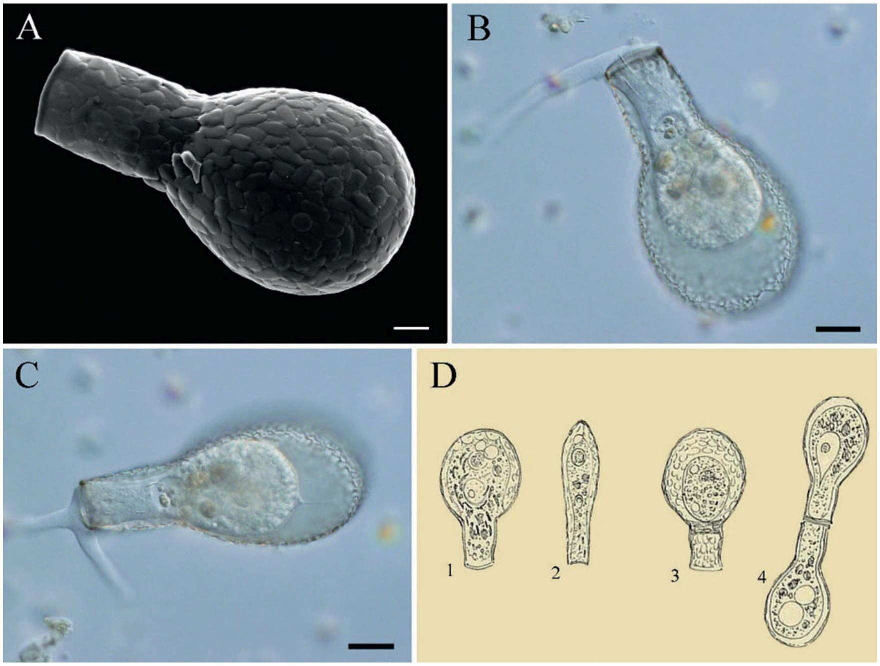

Fig. 73. *Padaungiella lageniformis*: (A) SEM image of a specimen from Bulgaria; (B & C) LM–DIC images of a specimen from Chile, in broad view and in profile view, respectively; (D) Original drawings from PENARD (1890): (1) broad view, (2) profile view, (3) encysted individual, and (4) cell division. Scale bars: A = 10 µm, B & C = 20 µm. Images by: (A) Enrique Lara and (B & C) Edward Mitchell.

Habitat: Wet *Sphagnum* and other mosses, rather minerotrophic (i.e., poor fen).

Geographical distribution: Likely cosmopolitan.

Remarks: This is a very common and problematic species. LARA et al. (2008) recorded morphological variation among individuals of *Padaungiella lageniformis* from the same sample; however, they acknowledged that combined morphological and molecular data may show these variations correspond to distinct species. WAILES (1912) described Nebela lageniformis var. *minor* based on samples from North America, noting that test length varied: L = 85–100 µm. DEFLANDRE (1936) proposed a new taxonomic status and name for this taxon—*N. wailesi*—noting that the test length varied: L = 75–100 µm. CHATTOPADHYAY & DAS (2003) reported similar typical forms based on ten specimens from India, with L = 75–85 µm. More recently, this species was transferred to the genus *Padaungiella* (KOSAKYAN et al., 2012). The test length is the primary character separating *P. wailesi* (L < 100 µm) from P. lageniformis (L > 100 µm); however, some authors have reported intermediate morphotypes between these two species. JUNG (1942a) noted specimens from Chile with variable test lengths: L = 91–105 µm. LUKETA (2015a)

Table 3. *Summary table of* Padaungiella lageniformis *and closely related taxa. All test measurements in µm, and shapes are in broad view. An asterisk indicates that the taxon has been included in the inquirenda list.*

Species	Length	Breadth	Construction of neck & other notes
P. lageniformis	(83) 100–140 (160)	(47) 60–93 (see LUKETA, 2015a, 2017e)	Elongated, with subparallel or slightly convex sides
P. longitubulata	112–120	42–45	Narrow, very elongated (45 µm high)
P. magna *P. nebeloides*	177 113–130 (148)	103 43–59	Neck similar to that of *P. lageniformis* Pseudostome circular, with an irregular outline and undulating rim of organic cement
P. tubulata	55–74	28–48	Elongated, with parallel sides
P. tubulata spatha	65–70	28–32	Neck gets wider towards the pseudostome
*P. wailesi ** *P. wetekampi** *Nebela varia**	75–116 149–159 150–160	50–58 60–70 ---	Neck similar to that of *P. lageniformis* Neck similar to that of *P. lageniformis* Neck similar to that of *P. lageniformis*

*For further details, see these species in the *inquirenda* list (p. 209)

reported a population from the Lake Vlasina region in Serbia where L = 91–127 µm. LUKETA (2017a) noted similar values for test length (L = 93–128 µm) for a moss-dwelling population from the Lake Alagovac region in eastern Bosnia-Herzegovina. He also reported a size-dimorphic population, with small (L = 91–100 µm) and large (101–139 µm) classes from a *Sphagnum* peatland near Lake Alagovac. A population from the Lake Velež region showed an intermediate test length (L = 83–112 µm, mean = 99.07 µm), thus spanning the size ranges of both *P. wailesi* and *P. lageniformis* (LUKETA 2017d) and questioning the validity of these two taxa.

Smaller individuals appear to inhabit drier habitats, while larger individuals are found in wetter locations. The population from the vicinity of Lake Velež was found in extremely dry mosses, growing on dry soils and rocks. The largest individuals in the Balkan Peninsula (L = 101–153 µm, mean = 129.67 µm) were found in extremely moist mosses growing on rocks along the stream edge (LUKETA, 2017a). Accordingly, it is currently impossible to distinguish between *P. wailesi* and *P. lageniformis*. Further morphometric and molecular research is needed to clarify the taxonomy of this group.

JUNG (1942a) described *Schaudinnia wetekampi* as a piriform species with a very long, pronounced neck, noting the following measurements: L = 149–159 µm, B = 60–70 µm, test depth = 30–47 µm, P = 26–33 µm, neck length = 63–68 µm, and neck width = 25 µm. JUNG (1942a) also believed that PLAYFAIR (1917) had observed *S. wetekampi* instead of *N. militaris* var. *tubulata*; however, the specimens described by Playfair had smaller dimensions: L = 60–64 µm, B = 26–30 µm, and P = 9–14 µm. KOSAKYAN et al. (2012) included *S. wetekampi* in the list of *Padaungiella species*, as it is very similar to the type species—*P. lageniformis*. There are three primary arguments supporting *P. wetekampi* as an independent species: 1) individuals are slightly longer than typical specimens of *P. lageniformis*. 2) individuals of *P. lageniformis*, although approximately the same length as *P. wetekampi*, are significantly wider; however, detailed morphometric data for *P. wetekampi* are not available, accordingly, further studies on the morphological variability of *P. wetekampi* are needed to clarify the taxonomic status of this species. 3) individuals of *P. wetekampi* have a longer neck than those of *P. lageniformis*, and although this argument stands out in the original description as a key morphological difference between these two species, it is likely relative considering that the narrower individuals of *P. lageniformis* usually have longer necks. CHATTOPADHYAY & DAS (2003) described specimens of *P. lageniformis* with very long necks (53–59 µm) based on samples from India. LUKETA (2017a) also observed long-neck specimens (≥ 55 µm) in a population inhabiting a peat bog in East Herzegovina; however, intermediate forms between tests with short and long necks were also observed. Based on these facts, we included *P. lageniformis* in the list of valid species here, whereas *P. wailesi* and *P. wetekampi* were placed in the list of *inquirenda* species until detailed molecular analyses can clarify their true taxonomic position. Another closely related species, *N. varia* (DECLOITRE, 1966), described from Iceland, is nearly identical to *N. wetekampi*. Both organisms have been found in only one locality; however, given the extreme distance between the two sites of origin (Iceland and Chile), it is unlikely that they belong to a single species. We therefore also included *Nebela varia* in the list of *inquirenda* species (for further discussion, see p. 222). Additional studies are thus needed to determine the validity of these species.

Padaungiella longitubulata (Gauthier-Lièvre, 1952) comb. nov.

1952 *Nebela longitubulata* Gauthier-Lièvre, Bul. Soc. Hist. Nat. Afriq. Nord: 355 (Fig. 17, original drawing).

1959 *Nebela tubulata* var. *magna* Van Oye, Hydrobiologia 13(3), p. 261, Fig. 32 (overlapping morphology).

Icon.: GAUTHIER-LIÈVR E, 1952, Fig. 17; GAUTHIER-LIÈVRE, 1957, Fig. 13.

Description: Test lageniform in broad view, compressed, with the main body very elongated and a sub-cylindrical narrow neck (45 µm long). Test hyaline greyish, composed of irregular plates widely spaced from one another. L = 120 µm, B = 45 µm. Pseudostome ovoid in frontal view, with a smooth yellowish-brown, organic rim.

Differential diagnosis: This species is very rarely reported and rather problematic. GAUTHIER-LIÈVRE (1952) hypothesized a close relationship to *Padaungiella lageniformis*, from which it differs by a less compressed test in broad view. According to the original descriptions of both species, there is also a difference in test size: L = 120 µm, B = 45 µm in *P. longitubulata* vs. L = 100–140 µm, B = 60–90 µm in *P. lageniformis* (see Table 3 and Remarks under *P. lageniformis*). Another species sharing the same general shape is *N. tubulata* Brown, which differs from the two previous taxa by its smaller size (Table 3, p. 146); however, according to the original drawings of these three species (Figs. 73-74, 78), these species also differ in general shape; whereas the sides of *P. longitubulata* are gradually tapering towards the pseudostome, in *P. tubulata* and *N. lageniformis*, there is a clearer separation between the main body and the neck. L = 55–74 µm, B = 28–48 µm.

Type locality: Danane, Ivory Coast. Likely coordinates: 7.292138°, -8.079651°.

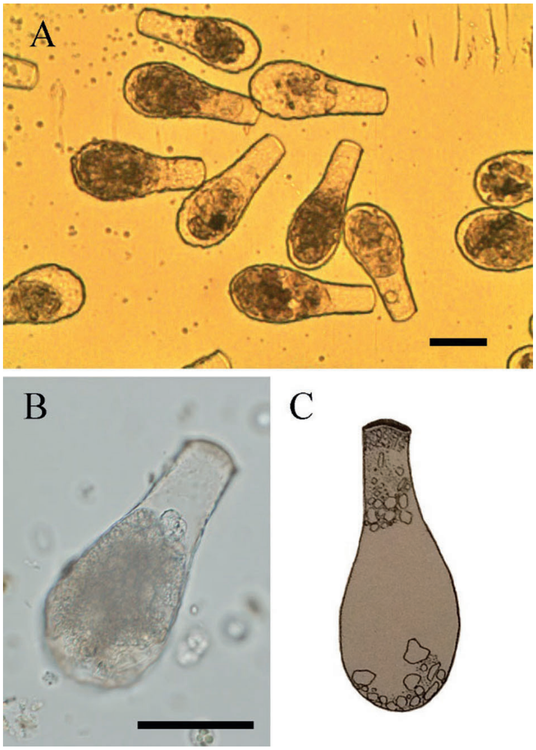

Fig. 74. *Padaungiella longitubulata*: (A) LM image of a population from Bulgaria, (B) LM image of a specimen from Chile, (C) Original drawing from GAUTHIER-LIÈVRE (1952). Scale bars = 50 µm (although that for B is dubious). Images by: (A) Milcho Todorov and (B) Enrique Lara.

Type specimen: Not provided. We declare Fig. 17 by Gauthier-Lièvre (1952), reproduced here as Fig. 74C, as the type.

Etymology: The species name refers to the elongated tubulate morphology of the test.

Habitat: Aquatic sediments and soils.

Geographical distribution (including records for *N. tubulata magna*): Africa: Congo (GAUTHIER-LIÈVRE, 1957; VAN OYE, 1959; ŠTĚPÁNEK, 1963; CHARDEZ, 1964), Guinea (GRACIA, 1963), Ivory Coast (GAUTHIER-LIÈVRE, 1952; BONNET, 1976); Europe: Austria (LAMINGER, 1970; AESCHT & FOISSNER, 1989), Bulgaria (TODOROV, pers. comm.), Romania (GODEANU, 1972a), Spain (GRACIA, 1971, 1972); South America: Chile (KOSAKYAN et al. unpubl.). Notably, LAMINGER (1972) reported *N. tubulata* var. *magna* from Austria, although their specimens were less slender, and necks were slightly shorter, thus casting doubt on whether these findings really represent *P. longitubulata*.

Remarks: VAN OYE (1959) described *N. tubulata* var. *magna* as only slightly smaller than *P. longitubulata*: L = 110 µm, B = 42 µm, P = 17 µm, L/B ~ 2.61. Accordingly, we believe both taxa belong to the same species, although whether this size variation results from natural phenotypic variability of a single species, or if they represent two genetically distinct forms remains unclear.

Padaungiella magna (Van Oye, 1956) comb. nov.

1956a *Nebela wailesi* var. *magna* Van Oye, Hydrobiologia 8: 28 (Fig. 23, original drawing).

2012 *Padaungiella wailesi magna* Van Oye, 1956 - Lara & Todorov, in KOSAKYAN et al., 2012, Protist 163: 429-430 (establishment of genus *Padaungiella* based on detailed morphological and molecular data).

Description: Test lageniform with a thick, distinct apertural rim (“annulus”). Test structure like that of other *Padaungiella*, *Nebela*, and similar taxa.

Differential diagnosis: This subspecific taxon differs from the type by its larger size (Table 3, p. 146). VAN OYE (1956a) also mentioned that “at the end of the mouth there is a distinct

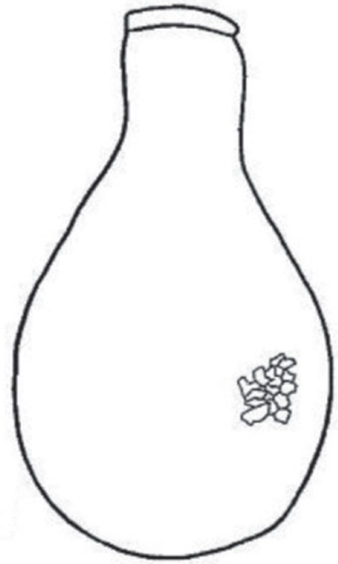

Fig. 75. *Padaungiella magna*: Original drawing from VAN OYE (1956a).

annulus", visible in the original illustration. L = 177 µm, B = 103 µm, P = 35 µm, L/B = 1.72.

Type locality: Described from a swampy and flat range near Dunedin, New Zealand, taken in acidic *Sphagnum* tarn. Likely coordinates: -45.795912°, 170.481805°; Elevation, ca. 700 m.a.s.l..

Type specimen: Not provided. We declare the original illustration, reproduced here as Fig. 75, as the type.

Etymology: The species named after the Latin term "magna", meaning "large".

Habitat: *Sphagnum* peatlands.

Geographical distribution: New Zealand (VAN OYE, 1956a).

Note: The taxon was described based on a single specimen. Because of its large size, however, it is unlikely that it belongs to any previously described species. Further investigations are needed to confirm the validity of this species. Notably, *Nebela subsphaerica* was also described from the same sample. Edward Mitchell successfully found *N. subsphaerica* from the same location in 2018 but was unable to relocate *P. magna*. Thus, the validity of this species requires confirmation.

Padaungiella nebeloides (Gauthier-Lièvre & Thomas, 1958) Lara & Todorov, 2012

1958 *Difflugia nebeloides* Gauthier-Lièvre & Thomas, Arch. Protistenk. 103.

2010 *Nebela nebeloides* Todorov, Golemansky & Meisterfeld, in TODOROV et al., 2010, Acta. Zool. Bulg. 62: 13–20 (detailed observation of the morphology and transfer to genus *Nebela*).

2012 *Padaungiella nebeloides* Gauthier-Lièvre–& Thomas, 1958 - Lara & Todorov, in KOSAKYAN et al., 2012, Protist 163: 429–430 (establishment of genus *Padaungiella* based on detailed morphological and molecular data).

Icon.: GAUTHIER-LIÈVRE & THOMAS, 1958, Fig. 54; TODOROV et al., 2010, Figs. 1–17; KOSAKYAN et al., 2012, Fig. 6G–H; TODOROV & BANKOV, 2019, Fig. 76.

Description (based on TODOROV et al., 2010): Test slim and elongated in broad view, rounded aborally, and tapering evenly from the anterior third part towards the pseudostome, forming a distinct neck. Test circular in cross section (Nb. a rare character in Hyalospheniidae). Test yellowish or light brown, composed of a mixture of predated or collected ovoid, circular (taken from Euglyphida prey), and quadrangular test plates (taken from *Quadrulella* spp.). These "kleptoidiosomes" are usually arranged

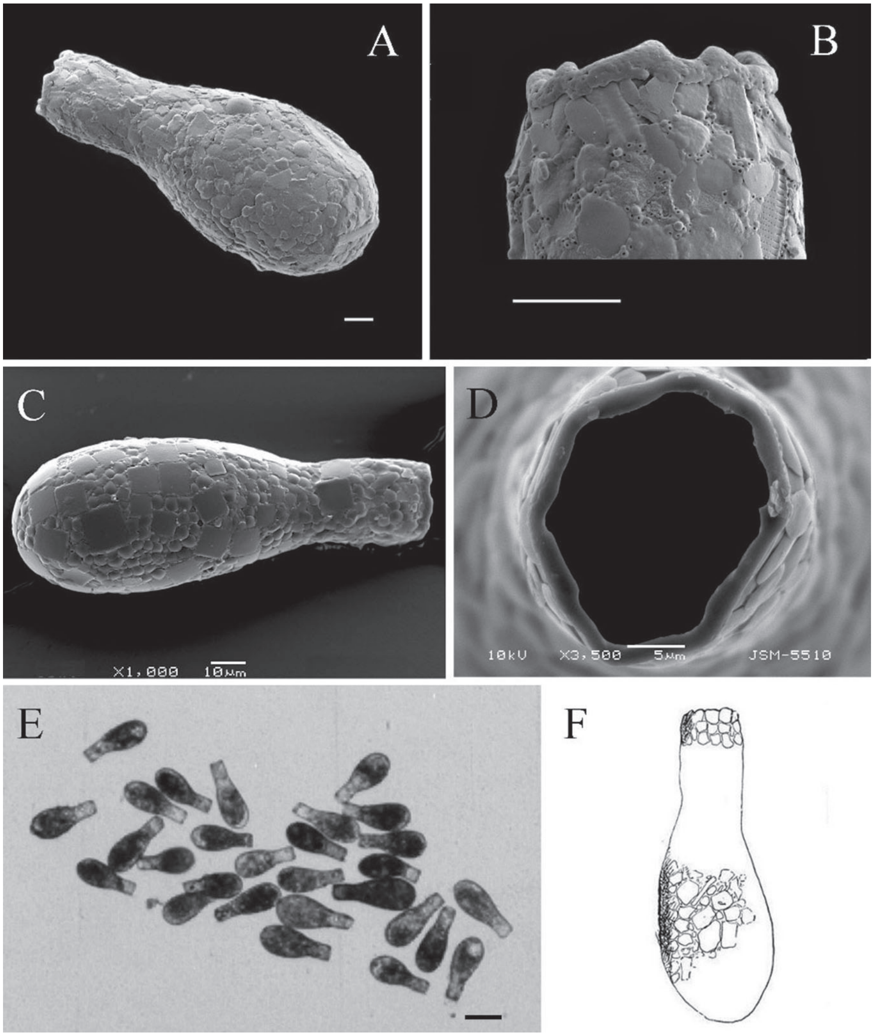

Fig. 76. *Padaungiella nebeloides*: (A & B) SEM broad view images of a specimen from France for the whole test and a detailed view of the pseudostome, respectively (modified from KOSAKYAN et al., 2012); (C & D) SEM images of a specimen from Bulgaria for the whole test in broad view and detailed frontal view of the pseudostome, respectively (modified from TODOROV et al., 2010); (E) LM image of a population from Bulgaria; (F) Original drawing (labelled as *Difflugia nebeloides*) from GAUTHIER-LIÈVRE & THOMAS (1958). Scale bars: A & C = 10 µm, B = 20 µm, D = 5 µm, E = 50 µm. Images by: (A & B) Anush Kosakyan, and (C–E) Milcho Todorov.

haphazardly and overlap. Occasionally, small to medium flattish pieces of quartz are included between siliceous test plates but are arranged in such a way that provides a smooth appearance of the test (Nb. these large particles are atypical for Hyalospheniidae tests, which usually incorporate strictly smaller particles, giving their tests a transparent quality). Organic cement frequently visible between test components, with small pores visible in SEM (diameter ca. 200–250 nm). Pseudostome roughly circular in frontal view, or with an irregular outline, and a characteristic thick, uneven, and undulating rim of organic cement. L = 113–130 (148) µm, B = 43–59 µm, P ~ 17–38 µm.

Differential diagnosis: Differs from all other hyalospheniids by its agglutinated test structure and from most hyalospheniids by its circular cross section. See Remarks below for further details.

Type locality: Location between Dolisie and Kimongo, Congo. Likely coordinates: -4.340322°, 12.849873°.

Type specimen: Not provided. We declare Fig. 54 by GAUTHIER-LIÈVRE & THOMAS (1958), reproduced here as Fig. 76F, as the type.

Etymology: The species name refers to its morphological similarity to members of the genus *Nebela*.

Habitat: Minerotrophic wet *Sphagnum* swards, floating mats of *Sphagnum* in humic, acid-rich lakes.

Geographical distribution: Africa: Congo (GAUTHIER-LIÈVRE & THOMAS, 1958); Europe: Austria (AESCHT & FOISSNER, 1989), Bulgaria (TODOROV et al., 2010; TODOROV & BANKOV, 2019), France (KOSAKYAN et al. 2012), Germany (MEISTERFELD, 1979); South America: Bolivia (CERDA, 1986), Chile (BONNET, 1966). Possibly cosmopolitan.

Remarks: This species was initially described by GAUTHIER-LIÈVRE & THOMAS (1958) from Africa (Congo) as a member of the genus *Difflugia*. In this original description, however, it is mentioned that at first sight, *D. nebeloides* resembles more a *Nebela* than *Difflugia* (as cited in TODOROV et al., 2010). Unfortunately, this description is brief and relies primarily on the drawings, which do not show the detailed test structure.

After an amended description and initial SEM research (MEISTERFELD, 1979), TODOROV et al. (2010) conducted detailed LM and SEM investigations on the test ultrastructure, as well as biometric analyses of this remarkable species. Their results clearly showed that the test is composed of a mixture of ovoid, circular, and quadrangular siliceous test plates, either collected or predated from other Arcellinida or Euglyphida. As their findings also revealed a typical test structure of genus *Nebela*, TODOROV et al. (2010) proposed revising the genus of this species. Molecular data, however, subsequently confirmed its position within hyalospheniids, together with other Padaungiella species in accordance with its lageniform test (KOSAKYAN et al., 2012). This species was renamed *P. nebeloides* following the establishment of genus *Padaungiella*.

Padaungiella pulcherrima (Awerinzew, 1906) comb. nov.

1906 *Nebela pulcherrima* Awerinzew, Proc. St. Petersburg Nat. Soc. 36: 238 (Fig. 4, original drawing).

Icon.: AWERINZEW 1906, Fig. 4.

Description (based on the original publication): Test elongated-piriform in broad view, lateral margins gradually tapering towards the pseudostome. Neck distinct and elongated (ca. 40 µm). Test not compressed laterally, and pseudostome circular in frontal view. The most distinctive characteristic of the species is where

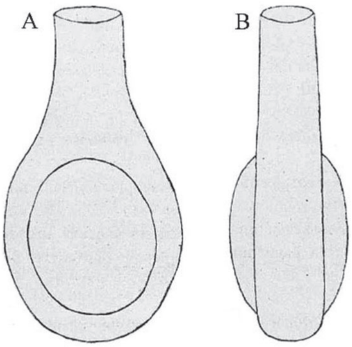

Fig. 77. *Padaungiella pulcherrima*: Original drawing of broad (A) and profile (B) views from AWERINZEW (1906).

the main part of the test body consists of two identical, flattened spherical convexities. Test composed of circular and ovoid plates, slightly overlapping. Pseudostome linear in broad view. L = 180–195 µm, B = 100 µm.

Differential diagnosis: Differs from other Padaungiella species by the typical posterior part of the test (or main body) that consists of two flattened spherical convexities.

Type locality: Arkhangelsk, Russia (AWERINZEW, 1906). Likely coordinates: 64.496109°, 41.171205°.

Type specimen: Not provided. We declare Fig. 4 by AWERINZEW (1906), reproduced here as Fig. 77, as the type.

Etymology: The species name is derived from the Latin word “pulcherrima”, meaning “beautiful”.

Habitat: *Sphagnum* mosses.

Geographical distribution: Asia and Europe: Russia (Arkhangelsk) and Azerbaijan (AWERINZEW, 1906).

Remarks: A very rarely reported species and has only been mentioned twice from Arkhangelsk (Russia) and the Caucasus (Azerbaijan). Both the general shape and elongated neck suggest that this species belongs to genus *Padaungiella*.

Padaungiella tubulata (Brown, 1910) Lara et Todorov, 2012

1910 *Nebela militaris* var. *tubulata* Brown J. Linn. Soc. Zool. 30, p. 361, Pl. 50 (Figs. 9–10, original drawings).

1911 *Nebela tubulata* Brown 1910 - Brown, J. Linn. Soc. Zool. 32, p. 79 (elevation to species level).

2012 *Padaungiella tubulata* Brown, 1911 - Lara & Todorov, in KOSAKYAN et al., 2012, Protist 163: 429–430 (establishment of genus *Padaungiella* based on detailed morphological and molecular data).

Icon.: BROWN, 1911, Figs. 9–10; GAUTHIER-LIÈVRE, 1952, Fig. 16; OGDEN & HEDLEY, 1980, Pl. 44; LÜFTENEGGER & FOISSNER, 1991, Figs. 33–39; TODOROV & BANKOV, 2019, Fig. 77.

Description: Test lageniform in broad view, slightly compressed, with a distinct, elongated, parallel-sided neck. Test colorless, composed of elliptical plates. Pseudostome curved in broad view, surrounded with a thick organic lip. L = 55–74 µm, B = 28–48 µm, P = 13–16 µm.

Differential diagnosis: *Padaungiella tubulata* resembles both *P. lageniformis* and *P. wailesi* in general shape but differs from these species by its smaller size (Table 3, p. 146). GAUTHIER-LIÈVRE (1952) mentioned that it could be challenging to distinguish large individuals of *P. tubulata* from small individuals of *P. wailesi*. For further details, see the notes of *P. longitubulata* (p. 133). A detailed morphological and molecular

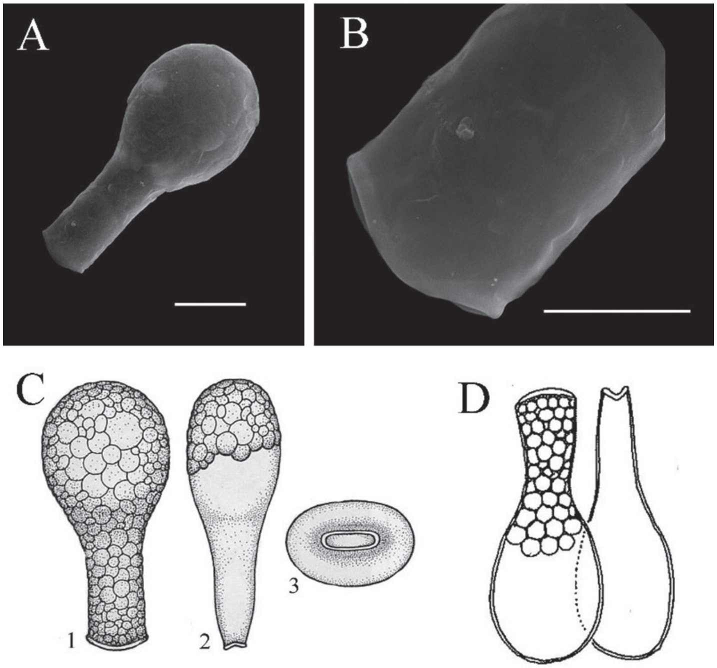

Fig. 78. *Padaungiella tubulata*: (A & B) SEM image of a specimen from Germany, (B) detail of the neck and aperture; (C) Line drawings of *P. tubulata* from LÜFTENEGGER & FOISSNER (1991): (1) broad view, (2) profile view, and (3) frontal view of the pseudostome; (D) *P. tubulata spatha* from THOMAS (1960), broad and profile views. Scale bars: A = 20 µm, B = 10 µm. Images (A & B) by Ralf Meisterfeld.

study of this species complex is thus needed to ascertain its accurate position with respect to these two species.

Type locality: Trossachs Pass, UK. Likely coordinates: 56.223449°, -4.421777°.

Type specimen: Not provided. We declare Fig. 33 by LÜFTENEGGER & FOISSNER (1991), reproduced here as Fig. 78C1, as the type.

Etymology: The species name likely derives from the Latin “tubula”, meaning “tuba” or “small trumpet” in reference to the tubular neck.

Habitat: *Sphagnum* mosses, soils.

Geographical distribution: Likely cosmopolitan (we have > 170 records in our database).

One subspecies is known:

Padaungiella tubulata spatha (Thomas, 1960) comb. nov.

1960 *Padaungiella tubulata spatha* (as *Nebela tubulata* var. *spatha*) Thomas, 1960, Bul. Soc. Pharm. Bordeaux: 15, Fig. 5.

Description (based on the original publication): This subspecific taxon differs from the type by its neck structure, which is progressively wider towards the pseudostome in broad view. L = 65–70 µm, B = 28–32 µm, P = 15-18 µm, neck breadth ~12 µm at the base and ~18 µm at the pseudostome.

Differential diagnosis: *Padaungiella tubulata spatha* resembles *P. lageniformis*, *P. wailesi*, and *P. tubulata* in general shape but differs from these species by its smaller size and by the structure of the neck. See Table 3, p. 146.

Type locality: Pessac Gironde, France. Likely coordinates: 44.751044°, -0.709159°.

Type specimen: Not provided. We declare Fig. 5 by THOMAS (1960), reproduced here as Fig. 78D, as the type.

Etymology: The subspecies name refers to the shape, as spatulate is a common term in botany used to describe a broadly rounded leaf with a narrow, tapering base.

Habitat: Wet forest litter and mosses.

Geographical distribution: Europe: France (Bordeaux, Gironde; THOMAS, 1960); North America: Canada (DE PUYTORAC et al., 1972; BONNET, 1974); South America: Ecuador (KRASHEVSKA et al., 2007); Asia: Indonesia (BONNET, 1985).

7.13. Genus *Planocarina* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Type species: *Planocarina carinata* (Archer, 1866) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

1942 *Pterygia* gen. nov. Jung, Arch. Protistenk. 95: 382 (invalid genus owing to a lack of type designation).

2016 *Planocarina* gen. nov. Kosakyan, Lahr, Mulot, Meisterfeld, & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 621.

Description: Test piriform or elongated-piriform in broad view, compressed or not, margins tapering towards the aperture. A flat keel surrounds either the entire fundus of the test, or only the sides. Outline of the keel either straight or serrated. Test colourless or slightly yellowish, composed of circular to elongated shell plates most likely recycled from euglyphid testate amoeba prey.

Remarks: KOSAKYAN et al. (2016) split genus *Nebela* into six monophyletic genera based on the general morphology of the test and mt-COI sequence data. All piriform and elongated-piriform *Nebela* species with a flat keel but lacking lateral horns (as in genus *Cornutheca*), were transferred to the new genus *Planocarina*. JUNG (1942b) considered the presence of this flat keel as a synapomorphy for his new genus *Pterygia*, which contained *P. carinata* and *P. marginata*. This genus was subsequently invalidated, as it lacked type species designation.

Etymology: The genus name is derived from the Latin terms “planus” and “carina”, meaning “flat” and “keel”, a characteristic trait of congeneric taxa.

Five species are known:

Key to the species

1. Keel complete, surrounding the lateral margins as well as the fundus of the test, 2

– Fundus rounded without keel. Keel starting shortly before the neck, gradually narrowing and finishing immediately before the fundus of the test: L = 176 µm, B = 80 µm *P. semimarginata* (p. 160)

2. Test clearly compressed (B/H > 2) 3

– Very large species. Test less compressed (B/H < 1.5; ca. 1.33 based on original illustration), pseudostome circular in frontal view with a thick organic rim. Outline of the keel wavy or serrated: L = 280–325 µm *P. maxima* (p. 159)

3. Keel wide (5–10 µm) and conspicuous in broad view, clearly starting in the upper half of the test 4

– Keel narrow and inconspicuous in broad view starting near the middle of the test (the keeled part representing ca. 34-55% of the total length of the tests): L = 140–180 µm, B = 110–150 (180) µm, P = 25–40 µm. *P. marginata* (p. 157)

4. Intermediate to large species: L = 140–246 µm, B = 110–175 µm, P = 27–43 µm, keeled part of the test representing ca. 57-74% of the total length of the test *P. carinata* (p. 155)

– Very large species: L = 275—95 µm, B = 205 - 210 µm, P = 50–60 µm *P. spumosa* (p. 161)

Planocarina carinata (Archer, 1867) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

1866 *Difflugia carinata* Archer, J. R. Microsc. Soc. London: 178.

1876 *Nebela carinata* Archer 1866 – Leidy, Proc. Ac. Nat. Sc. 1876: 118 (revision of genus *Difflugia* and transfer to genus *Nebela*).

2016 *Planocarina carinata* Archer 1866 – Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 606–623 (redefinition of genus *Nebela* and establishment of genus *Planocarina* based on detailed morphological and molecular data).

Icon.: ARCHER, 1869, Pl. XX, Fig. 12; LEIDY, 1876, Figs. 10–11; LEIDY, 1879, Pl. 24, Figs. 1–10; OGDEN & HEDLEY, 1980, Pl. 35; MEISTERFELD, 2000, Fig. 67; TODOROV & BANKOV, 2019, Fig. 79.

Description: Test ovoid-piriform in broad view, compressed, with a well-defined and clearly visible flat keel 4 - 16 µm wide, beginning near the pseudostome, colourless or slightly yellowish. Small lateral pores usually visible on each side ca. 1/3rd of the distance between the pseudostome and the fundus of the test. Test almost transparent, composed of ovoid and circular plates often intermixed with pieces of organic cement. Pseudostome slightly curved in broad view, with a thick organic rim. L = 140–246 µm, B = 110–175 µm, P = 27–43 µm.

Differential diagnosis: The flat keel typical for the genus is particularly well developed and can be used to separate it from sister species *P. marginata*. In *P. carinata*, the keel is wider, very conspicuous, and starts nearer the pseudostome (the keeled part of the test representing ca. 57-74% of the total length of the test), whereas it is narrower in *P. marginata* and starts at approximately the middle to two thirds of the test from the pseudostome (MEISTERFELD, unpublished data).

Type locality: Kilbride County, Wicklow, Ireland. Likely coordinates: 53.199532°, -6.46402°.

Type specimen: KOSAKYAN et al. (2016) declared Figs. 10–11 by LEIDY (1876) as the neotype.

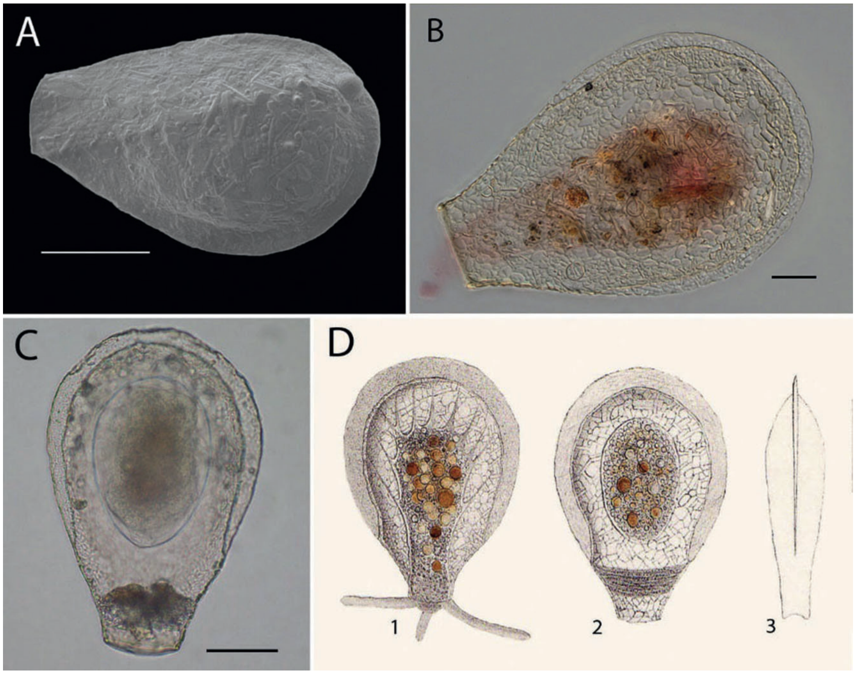

Fig. 79. *Planocarina carinata*: (A) SEM image of a specimen from Vancouver, Canada; (B) LM digitalized image from the Eugène Penard collection, no. 494-4-2 (Natural History Museum, Geneva, Switzerland); (C) LM image of an encysted specimen from Switzerland; (D) Drawings modified from LEIDY (1879): (1) active living individual, (2) encysted individual, and (3) profile view. Scale bars: A & C = 50 µm, B = 20 µm. Images by: (A & C) Thierry Heger, and (B) Thierry Arnet (Wikimedia).

Etymology: The species name is derived from the Latin term “carinata”, meaning “with keel”, referring to morphology—presence of a keel surrounding the posterior end of the test.

Habitat: Wet *Sphagnum* mosses.

Geographical distribution: Africa: Congo (GAUTHIER-LIÈVRE, 1953), Western Africa (SCHAUDINN, 1898); North America: Canada (DE PUYTORAC et al., 1972; KOSAKYAN et al., 2012), USA (LEIDY, 1879); South America: Brazil (LANSAC-TOHA et al., 2001); Asia: Japan (YAMAMOTO, 1981); Europe: Austria (LAMINGER, 1975), Belgium (CHARDEZ, 1987a), British Isles (OGDEN & HEDLEY, 1980; WOODLAND et al., 1998), Bulgaria (TODOROV, 1993; TODOROV & GOLEMANSKY, 1995; TODOROV & BANKOV, 2019), Finland (LEVANDER, 1900; TOLONEN, 1966), France (GRACIA, 1968), Germany (FRANKEN, 1933; HARNISCH, 1937; GROSPIETSCH, 1958), Romania (GODEANU, 1972a), Russia (TARNOGRADSKIJ, 1961), Spain (GRACIA, 1971), Sweden (PENARD, 1890; KOSAKYAN et al., 2012), Switzerland (TARÁNEK, 1882; PENARD, 1899; KOSAKYAN et al., 2012).

Remarks: A detailed morphometric study, coupled with single-cell barcoding, may reveal morphological differences correlated with one of the haplotypes that were previously overlooked. Indeed, *P. carinata* is polymorphic: CASH et al. (1909) reported some variation in the width of the keel among individuals of this species. Further investigations are needed to clarify if there are any discriminating features (e.g., test shape, compression, pseudostome, degree of keel development, or distance between the pseudostome and the origin of the keel) between these two haplotypes, and if they differ in ecology or geographical distribution.

In addition to the difference in the width of their keel, *Planocarina carinata* and *P. marginata* may also differ by their degree of compression (B/H based on original drawing: *P. carinata* = 3, P. *marginata* = 2), but the validity of this criterion should be further tested. Both species are large (L > 120 µm) and restricted to very wet oligotrophic habitats (bog pools or very wet lawns) in *Sphagnum*-dominated peatlands; however, *P. carinata* is more "aquatic" than *P. marginata* (BOOTH, 2008). According to a morphometric analysis (MEISTERFELD, unpubl.), P. marginata can reach a length of 180 µm, overlapping with that of *P. carinata*; however, the two species can be separated by the width of the keel (in *P. marginata*, rarely wider than 4 µm), and the ratio between the length of the keel and the total length of the test: *P. marginata* usually 34–55%, *N. carinata* 57–74%. These two species branch together in an mt-COI-based phylogenetic tree (KOSAKYAN et al., 2012). However, morphological, and molecular data suggest the existence of at least two species within the general *P. carinata* morphotype. Indeed, mt-COI sequence data (KOSAKYAN et al., 2012) separated what we consider *P. carinata* into two haplotypes with a clear 14% divergence in nucleotide sequences, a genetic distance greater than the bar-coding gap usually admitted in Hyalospheniidae (SINGER et al., 2018).

Nomenclature: JUNG (1936) described two forms of *P. carinata* such as *Nebela carinata* f. *acarinata* and *N. carinata* f. *brevicarinata*, which differ from the type by the total absence of a keel (in f. *acarinata*) and a very narrow keel (in f. *brevicarinata*). As the keel in *P. marginata* ranges from narrow to very narrow and may be difficult to observe, we have included these two forms in the list of synonyms for *P. marginata* (p. 235).

Planocarina marginata (Penard, 1902)

1902 *Nebela marginata* Penard, Faune rhizopodique du basin du Léman: 359–360 (Figs. 1–3, original drawings).

1936 *Nebela* f. *acarinata* Jung, Abhandlungen aus dem Landesmuseum Provinz Westfalen. Museum für Naturkunde 4: 55, Fig. 35 (overlapping morphology).

1936 *Nebela carinata* f. *brevicarinata* Jung, Abhandlungen aus dem Landesmuseum Provinz Westfalen. Museum für Naturkunde 4: 55, Fig. 36 (overlapping morphology).

2016 *Planocarina marginata* Penard, 1902 – Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 606–623 (redefinition of genus *Nebela* and establishment of genus *Planocarina* based on detailed morphological and molecular data).

Icon.: PENARD, 1902, Figs. 1–3; DEFLANDRE, 1936, Pl. 25, Figs. 4–11.

Description: Test ovoid-piriform in broad view, compressed, with narrow keel (< 4 µm wide) beginning approximately at the middle of the test, grey, yellowish or brownish. Lateral pores clearly visible, one on each side. Test greyish brown, composed of ovoid and circular test plates often intermixed with pieces of diatom frustules.

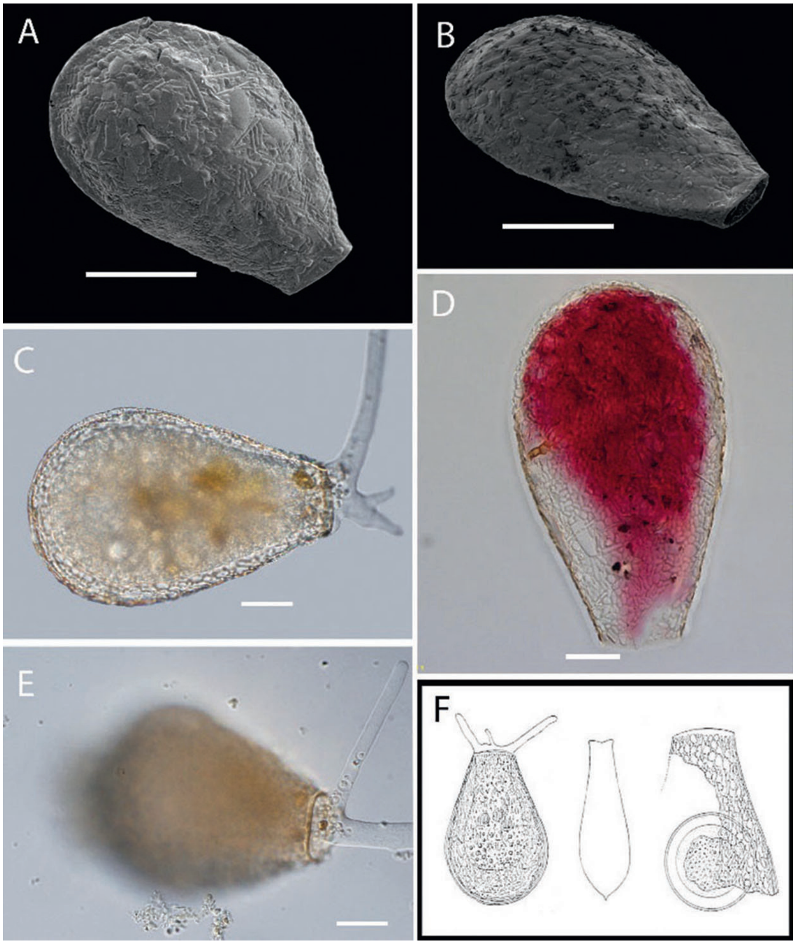

Fig. 80. *Planocarina marginata*: (A & B) SEM broad and oblique view (respectively) images of two specimens from Canada; (C) LM broad view images of an active specimen from Switzerland; (D) LM broad view images of a specimen from the Eugène Penard collection, no. 759-3 (Natural History Museum, Geneva, Switzerland); (E) LM oblique frontal image of an active specimen from Switzerland focusing on the pseudostome; (F) Original drawings modified from Penard (1902) (left to right): living individual in broad view, test outline in profile view, and detailed view of pseudostome and test structure for an encysted specimen. Scale bars: A & B = 50 µm, C–E = 20 µm. Images by: (A & B) Thierry Heger, (C & E) Daniel Lahr, and (D) Thierry Arnet (Wikipedia).

Pseudostome slightly curved in broad view, with an organic rim. L = 140–180 μm, B = 110–150 (180) μm, P = 25–40 μm.

Differential diagnosis: PENARD (1902) found this species associated with *Nebela collaris* and *Planocarina carinata* in floating wet *Sphagnum*. Despite the similarity in shape and size with *P. carinata*, Penard noted that *P. marginata* was readily distinguished by its darker greyish-yellowish-brown (non-transparent) test, much narrower lateral margin which starts at the approximate middle test, whereas in *P. carinata*, the keel is very wide and conspicuous and starts closer to the pseudostome. Penard also noted that although the two species overlap in size (L > 120 μm), *P. marginata* rarely exceeds 170 μm, while *P. carinata* can reach 245 μm (see *P. carinata* for further discussion on these two species, p. 155).

According to a morphometric analysis (MEISTERFELD, unpubl.), *P. marginata* can reach a length of 180 μm, overlapping with that of *P. carinata*; however, the two species can be separated by the width of the keel (in *P. marginata*, rarely wider than 4 μm), and the ratio between the length of the keel and the total length of the test: *P. marginata* usually 34–55%, *P. carinata* 57–74%.

Type locality: Not specified in the description but very likely La Trélasse peatland (formerly referred to as "La Pile"), Canton Vaud, Jura Mountains, Switzerland, coordinates: 46.446279°, 6.094322°, as this site is mentioned as the sampling location for the permanent slide containing this species in the Penard collection at the Natural History Museum of Geneva, Switzerland.

Type specimen: Not provided. We declare the specimen from the E. Penard slide collection, No. 759-3 (Natural History Museum of Geneva, Switzerland), reproduced here as Fig. 80D, as the type.

Etymology: The species name refers to the presence of the narrow margin or keel surrounding the posterior end of the test.

Habitat: Wet *Sphagnum* mosses in *Sphagnum*-dominated peatlands.

Geographical distribution: Holarctic, and possibly even broader, as it has also been recorded from the Galápagos Islands (FOURNIER et al., 2016) and Africa—Annobón Island and Equatorial Guinea (GRACIA, 1963).

Planocarina maxima (Awerinzew, 1906) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

1906 *Nebela maxima* Awerinzew, Proc. St. Petersburg Nat. Soc. 36: 240 (Fig. 3, 76–78, original drawings).

2016 *Planocarina maxima* Awerinzew, 1906 – Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 606–623 (redefinition of genus *Nebela* and establishment of genus *Planocarina* based on detailed morphological and molecular data).

Description (based on the original publication): Test ovoid-piriform in broad view, resembling N. carinata in general shape, but less compressed. As in *P. carinata*, keel present and covering approximately 2/3rd of the test fundus. Keel with wavy (serrated) margin, giving a somewhat undulated impression; totally organic or may include small plates embedded within an organic matrix. Morphology of the neck variable, but more conspicuous than in *P. carinata* and *P. marginata*. Two lateral pores present, one on each side of the test. Test yellowish, composed of circular or elongated plates juxtaposed, but with gaps showing the organic test structure. Pseudostome circular in frontal view, with a thick rim. L = 280–325 μm.

Differential diagnosis: Differs from *P. carinata* and *P. spumosa* by the characteristic wavy keel with a serrated margin and a very large size and from all other species of the genus by

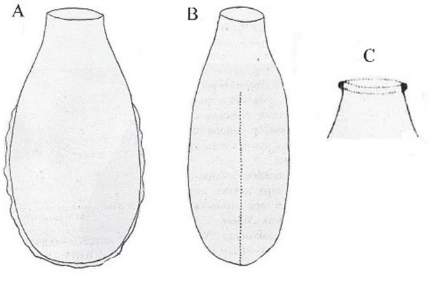

Fig. 81. *Planocarina maxima*: Original drawing from AWERINZEW (1906): (A) test in broad view, (B) profile view, (C) higher magnification view of the pseudostome showing localized thickening.

the lower degree of compression (B/H ca. 1.33 vs 2-3 for other species). Together with *Certesella australis*, *P. maxima* is the largest known hyalospheniid.

Type locality: Arkhangelsk, Russia. Likely coordinates: 64.496109°, 41.171205°.

Type specimen: Not provided. We declare Fig. 3 by AWERINZEW (1906), reproduced here as Fig. 81, as the type.

Etymology: The species name refers to the large size of the test.

Habitat: *Sphagnum* mosses.

Geographical distribution: Europe: England (HEAL, 1961, 1964), Iceland (DECLOITRE, 1965), Russia (AWERINZEW, 1906).

Remarks: This species was very rarely reported. Awerinzew (1906) noted that many individuals were observed without keel from the same *Sphagnum* sample, and only after detailed observation did it appear that the keel had been broken, as remnants could be seen. It may therefore be that the wavy keel margin results from partial damage.

Planocarina semimarginata (Van Oye, 1949) comb. nov.

1949 *Nebela semimarginata* Van Oye, Bijdr. Dierkd. 28: 342 (Fig. 20, original description).

Description (based on the original publication): Test compressed, elongated in broad view, ca. twice longer than wide. Keel starting close to the base of the neck and widest near the pseudostome, becoming gradually narrower towards the fundus. It ends near the fundus (approximately at the lowest 1/16th). Posterior end of the test rounded, without keel. Pseudostome oval surrounded with a thick organic lip. L = 176 μm, B = 80 μm, L/B = 2.2, test thickness = 30 μm, P = 35 μm, P small diameter = 31 μm.

Differential diagnosis: The main distinguishing characteristic of this species is its keel starting shortly after the neck and gradually becoming narrower towards the fundus.

Type locality: Kandang Badak, in 2500 m.a.s.l., Java, Indonesia. Likely coordinates: -6.777007°; 106.974473°.

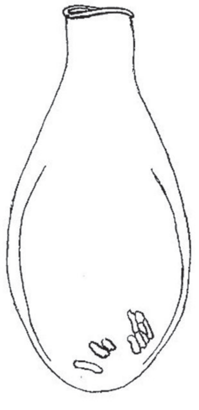

Fig. 82. *Planocarina semimarginata*: Original drawing in broad view from VAN OYE (1949).

Type specimen: Not provided. We declare Fig. 20 by VAN OYE (1949) here reproduced as Fig. 82 as the type.

Etymology: The name of this species refers to the presence of the partial keel.

Habitat: Moist and dry mosses.

Geographical distribution: Indonesia (VAN OYE, 1949).

Remarks: This species has been found only once. However, as Asian rainforests have seldom been prospected for testate amoebae, it may be more widespread.

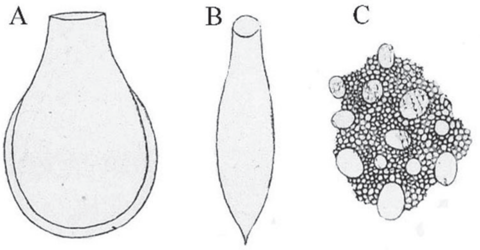

Fig. 83. *Planocarina spumosa*: Original drawings from AWERINZEW (1906): (A) test in broad view, (B) outline in profile view, (C) higher magnification view of test composition.

Planocarina spumosa (Awerinzew, 1906)

1906 *Nebela spumosa* Awerinzew, Proc. St. Petersburg Nat. Soc. 36: 238 (Fig. 2 and Pl. V, Fig. 79, original drawings).

2016 *Planocarina spumosa* Awerinzew, 1906 - Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 606–623 (redefinition of genus *Nebela* and establishment of genus *Planocarina* based on detailed morphological and molecular data).

Description (based on the original publication): Test compressed, with a flat keel, usually starting a little above the middle of the test and covering the entire fundus. In profile, the test has a narrow ovoid shape with a pointed fundus. Test composed of scattered large ovoid to elongated plates likely obtained from euglyphid testate amoeba prey, with test cement composed of smaller granular elements filling the open spaces between larger plates. The scattered larger test plates give it a somewhat frothy appearance (hence the name). Small cavities ca, 1–15 µm in diameter. Pseudostome ovoid in frontal view, surrounded with an organic rim. L = 275–295 µm, B = 205–210 µm, P = 50–60 µm.

Differential diagnosis: HOOGENRAAD & DE GROOT (1940b, in p. 173) suggested that this species could correspond to a larger variety of *P. carinata* (L = 275–295 µm, B = 205–210 µm in *P. spumosa*. vs. L = 140–246 µm, B = 110–175 µm in *P. carinata*). Aside from the size difference, *P. spumosa* has a frothy test structure (see details in Description).

Type locality: Arkhangelsk region, Russia. Likely coordinates: 64.496109°, 41.171205°.

Type specimen: Not provided. We declare Fig. 2 by AWERINZEW (1906), reproduced here as Fig. 83, as the type.

Etymology: The species name refers to the frothy structure of the test, as the Latin term “spumosa” means “frothy or foamy”.

Habitat: *Sphagnum* mosses.

Geographical distribution: Europe: Russia (AWERINZEW, 1906). The specimens of FRANKEN (1933) are most likely misidentified *Planocarina carinata* (L = 200 µm).

Remarks: This very rarely reported species was found only in a single locality to date. The author noted that in many individuals from the same sample, the keel only covered the sides (i.e., not reaching the fundus). This latter observation calls for more detailed studies of this genus in the region and elsewhere.

7.14. Genus *Porosia* Jung, 1942

Type species: *Porosia bigibbosa* (Penard, 1890) Jung, 1942

1942b *Porosia* gen. nov. Jung, Arch. Protistenk. 95: 380.

Description: Test wide piriform in broad view, with or without keel. The main characteristics of the genus are the presence of two lateral depressions with large central pores connected by tubes that cross the entire test, located approximately 2/3rd of the distance between the fundus of the test and the pseudostome. Similar pores also characterize the genus *Certesella*; however, this genus has additional internal teeth in the neck, notably lacking in *Porosia*.

Remarks: The genus was proposed by JUNG (1942b) without type designation, but as it was monospecific, this oversight was of no consequence. The genus resembles *Certesella* owing to its two invaginated pores on the base of the neck; however, it lacks the punctuated neck.

Etymology: The name “Porosia” refers to the presence of the two invaginated pores on the base of the neck.

Two species are known:

Key to the species

1. Keel absent, L mostly < 170 µm
P. bigibbosa (p. 151)

– Keel present, L mostly > 200 µm
P. paracarinata (p. 153)

Porosia bigibbosa (Penard, 1890) Jung 1942

1890 *Nebel bigibbosa* Penard, Mem. Soc. Phys. Hist. Nat. 31: 161–162 (Pl. IV, Figs. 85–97, original drawings).

1942 *Porosia bigibbosa* Penard, 1890 – Jung, Arch. Protistenkd. 95: 380, Fig. 53 (establishment of genus *Porosia* based on morphological characters).

Icon.: PENARD, 1890, Pl. IV, Figs. 85–97; OGDEN & HEDLEY, 1980, Pl. 34; MEISTERFELD, 2002, Fig. 71; TODOROV, 2002a, Figs. 1–7; LUKETA, 2016, Fig. 2; LUKETA, 2017d, Fig. 5.

Misapplied icon.: as *Nebela bohemica* in CHATTOPADHYAY & DAS, 2003, Figs. 152–155.

Description: Test piriform in broad view, compressed, with a rounded fundus. Approximately 1/3rd of test length starting from the pseudostome, two distinct lateral depressions with two large invaginated pores are situated on each side and are connected by internal tubes. In profile, small lateral pores can be observed, just anterior to the large pores. Test yellow, composed of circular or elliptical plates, often covered by a thick layer of organic cement. Pseudostome ovoid in frontal view, curved, surrounded with a thick organic lip. L = 135–171 µm, B = 87–115 µm (to 146 according to Ferry Siemensma on arcella.nl 8.6.2023), P = 52-70 (TODOROV, 2002).

Differential diagnosis: This species is readily recognizable owing to its distinctive characters: presence of lateral depressions with large pores and absence of neck. It differs from *Porosia paracarinata* by the absence of a keel.

Type locality: Wiesbaden, Germany. Likely coordinates: 50.116135°, 8.234612°.

Type specimen: Not provided. We declare Fig. 85 by PENARD (1890) here reproduced as Fig. 84D1 as the type.

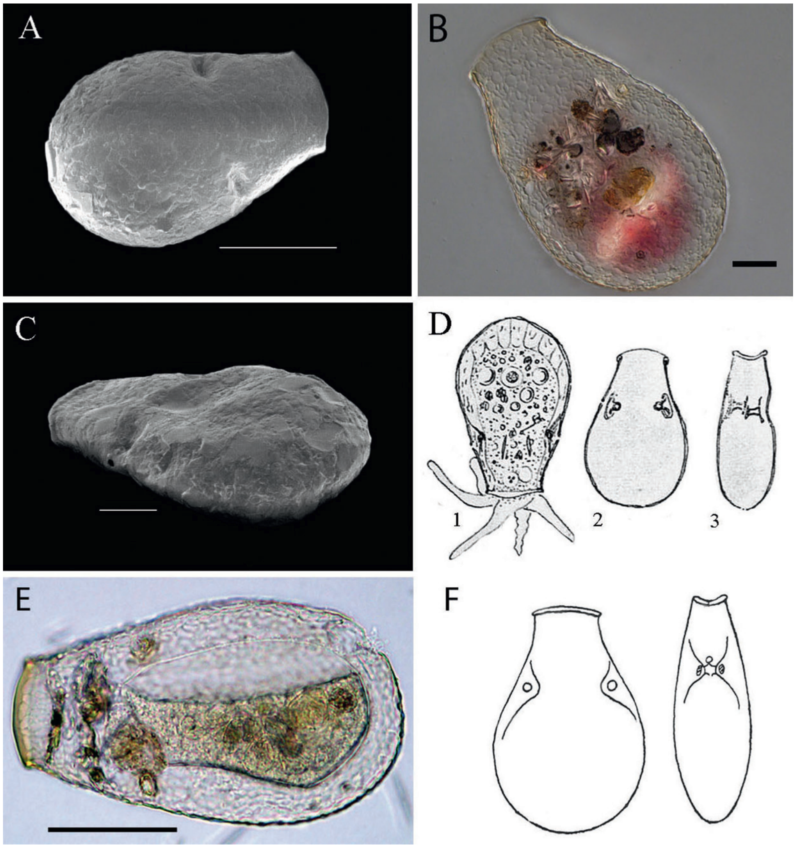

Fig. 84. *Porosia bigibbosa*: (A) SEM broad view image; (B) LM broad view image from the Eugène Penard slide collection, no. 492-1-4 (Natural History Museum, Geneva, Switzerland); (C) SEM image of oblique profile view showing one of the two lateral pores, all for specimen from Canada; (D) Original drawings from PENARD (1890): (1) living individual in broad view, (2) empty test in broad view, (3) empty tests in profile view; (E) LM broad view image of *P.* cf. *bigibbosa* from Italy; (F) Line drawing of P. *bigibbosa* from DEFLANDRE (1936) in broad and profile views showing the position of lateral pores. Scale bars: A & E = 50 µm, B & C = 20 µm. Images by: (A & C) Thierry Heger, (B) Thierry Arnet (Wikimedia), and (E) Edward Mitchell.

Etymology: The species name is derived from the Latin term "bigibbosa", meaning "two humps". This choice is rather surprising, as the most characteristic features of the species are the two tubes connecting both sides of the test (a trait also shared with genus *Certesella*). In his description, Penard wrote, "*Deux pores latéraux, un de chaque côté de la face large à l'endroit où la courbe de la coque devient plus brusque et où la membrane est souvent soulevée en une légère proéminence ou bosse*". Thus, Penard referred not to the two tubes, but rather the lateral pores that are located proximate to the two tubes (slightly further towards the pseudostome, where the shell sticks out slightly), as in *Nebela penardiana*.

Habitat: Terrestrial mosses, as well as deciduous (especially *Fagus* and *Quercus*), and coniferous forest litter (TODOROV, 2002a), rarely in *Sphagnum*. A detailed ecological analysis can be found in BONNET (1990).

Geographical distribution: North America: Canada (PENARD, 1911; DE PUYTORAC et al., 1972), USA (MEISTERFELD, unpubl.); South America: Chile (BONNET, 1966; WILKINSON, 1990), Ecuador (KRASHEVSKA et al., 2007); Asia: Java (HOOGENRAAD & DE GROOT, 1940a), India (misidentified as *Nebela bohemica*, CHATTOPAGHYAY AND DAS 2003), Mongolia (KORGANOVA, 1988), North Korea (GOLEMANSKY & TODOROV, 1991), Philippines (BONNET, 1980b), Thailand (BONNET, 1981; GOLEMANSKY & TODOROV, 2000); Australasia: Australia (SEAMER & CROOME, 2007), New Zealand (MITCHELL, unpubl.); Europe: Belgium (COÛTEAUX, 1969), Bosnia-Herzegovina (LUKETA, 2016), British Isles (CASH et al., 1919; HEAL, 1961; OGDEN & HEDLEY, 1980; FINLAY et al., 2001; ESTEBAN et al., 2006), Bulgaria (TODOROV & GOLEMANSKY, 1995; TODOROV, 2001, 2002a), France (VAUCHER & BÉNIER, 1988), Germany (PENARD, 1890), Greece (BONNET, 1967), Greenland (TRAPPENIERS et al., 1999), Hungary (TÖRÖK, 1998), Italy (RAMPI, 1950; MITCHELL et al., 2004), the Netherlands (DE GRAAF, 1956), Norway (PENARD, 1903), Russia (AWERINZEW, 1906; BOBROV et al., 2003), Switzerland (HEINIS, 1909; VAUCHER & BÉNIER, 1988; LARA et al., 2008).

Remarks: Until the recent description of *Porosia paracarinata* by BOBROV & KOSAKYAN (2015), *P. bigibbosa* was the sole documented species from the genus; however, it appears that the genus is more diverse than previously thought—e.g., the individual illustrated as *P. bigibbosa* in LARA et al. (2008), collected from the Swiss Jura Mountains and corresponding to the DNA sequence (Fig. 1g) is significantly smaller than the type species and has a distinct keel (possibly hollow, similar to genus *Gibbocarina*) (both characters were overlooked at the time). Such a keel is also visible in specimen from Bulgaria (Fig. 3 in TODOROV 2002) and India (Fig. 154 & 155, misidentified as *Nebela bohemica*, in CHATTOPAGHYAY AND DAS 2003). Accordingly, it is probable this sample belongs to another undescribed species. LUKETA (2016) also observed significant morphological variability within a population found in eastern Bosnia-Herzegovina. Thus, the diversity within the genus *Porosia* seem larger than previously thought and should be evaluated further.

Porosia paracarinata Bobrov & Kosakyan, 2015

2015 *Porosia paracarinata* Bobrov & Kosakyan, 2015, Acta Protozool. 54(4): 289–294.

Description (based on the original publication): Test large, piriform in broad view, compressed, with a rounded fundus; narrow elliptical in profile. At ca. 1/3rd of the test length starting from the pseudostome are two distinct lateral

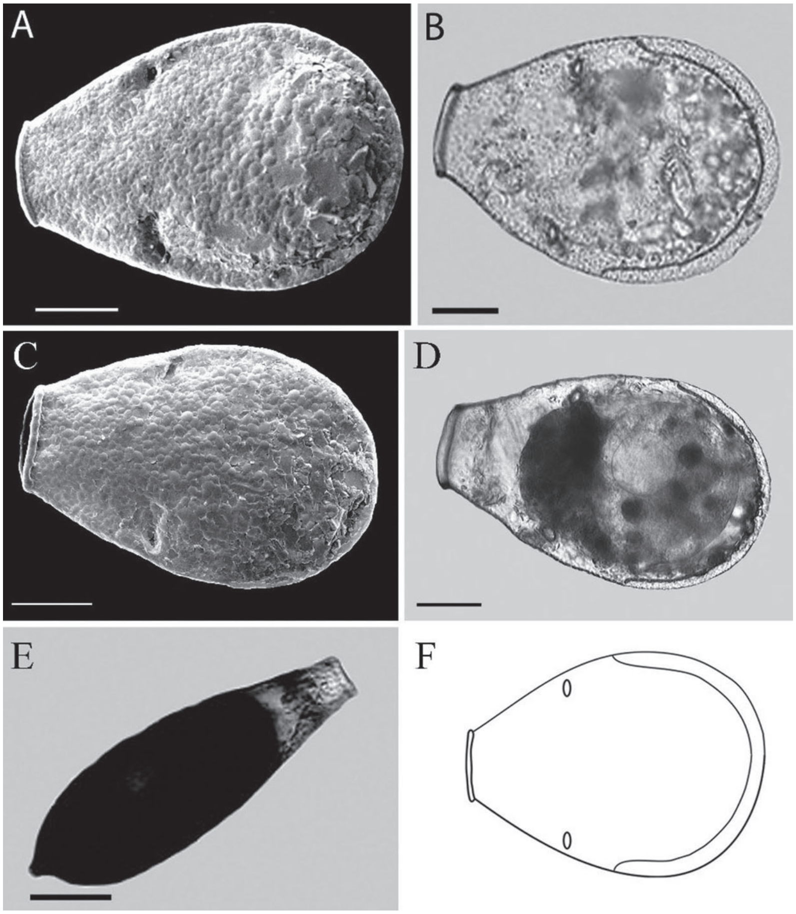

Fig. 85. *Porosia paracarinata* from Japan: (A & B) SEM and LM images of a specimen with a wide keel, respectively; (C & D) SEM and LM images of a specimen with a narrow keel, respectively; (E) LM image of a specimen in profile view; (F) Original drawing modified from BOBROV & KOSAKYAN (2015). *Scale bars = 50 µm.*

depressions (one on each side of the test), with two large invaginated pores connected by internal tubes, as in *Porosia bigibbosa*. In profile view, small lateral pores can be observed just anterior to the larger pores. A flat keel, like that of *Planocarina carinata*, 3.75–13.13 µm wide surrounds the aboral half of the test. Test colourless, composed of circular, elliptical, or irregular plates often covered by a thin layer of organic cement. Pseudostome ovoid, curved in broad view, surrounded by a thick organic rim. L = 202–236 µm, B = 142–157 µm, P = 56–67 µm.

Differential diagnosis: *Porosia paracarinata* shares a flat keel with some other hyalospheniids, such as *Planocarina carinata*, *Pl. marginata*, and *Cornutheca saccifera*. It can readily be distinguished from other keeled species, as none of these have lateral depressions with large invaginated pores. *Certesella australis* has similar pores in addition to a keel like that of *P. paracarinata*, but the keel is hollow, not flat as in *P. paracarinata*. Furthermore, *C. australis* is dark brown, larger, much more elongated, and possesses a distinct neck. Further, the pseudostome of *C. australis* is characterized by a row of punctuations parallel to its collar. Regardless of the presence of a keel, which seems to exist in some specimen of *P. bigibbosa* (see above), *P. paracarinata* is also large than *P. bigibbosa*.

Type locality: Honshu Island, Tatoyama Mountains, Bijyodaria, Japan. Coordinates: 36.5830361°, 137.4609694°; Elevation, ca. 997 m.a.s.l..

Type specimen: The type specimen is deposited in Bobrov's collection (Preparation B-1/2015), Department of Soil Sciences, Moscow State University.

Etymology: The species name refers to the keel (from Latin term "carina"), a distinct morphological character like that of *Planocarina carinata*.

Habitat: Wet leaves (forest litter layer A0 or L-layer) in *Fagus* sp. and *Cryptomeria japonica* forests.

Geographical distribution: Japan (BOBROV & KOSAKYAN, 2015).

Remarks: The width of the keel is quite variable (3.75–13.13 µm). The most stable morphological character is the thickness of the organic lip surrounding the aperture (BOBROV & KOSAKYAN, 2015).

7.15. Genus *Quadrulella* (Cockerell, 1909) sensu Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Type species: *Quadrulella symmetrica* (Wallich, 1863) Cockerell, 1909

1875 *Quadrula* gen. nov. Schulze, Arch. Mik. Anat.: 329 (unavailable name, homonym of already existing genus, see Remarks)

1909 *Quadrulella* Schulze, 1875 - Cockerell, Zool. Anz. 34: 565 (replacement name)

Description: Test piriform, or elongated-piriform, with or without distinct neck. Always compressed. Pseudostome ranging from linear to strongly curved, with an organic rim. Test hyaline, composed of self-secreted square plates.

Differential diagnosis: *Quadrulella* differs from other hyalospheniid genera by its self-secreted square, siliceous plates used in the construction of the test. It may be confused with *Mrabella*, which shares a similar test shape and square plates. The most distinctive characteristic is the presence of a lateral, pronounced hollow keel in genus *Mrabella* (although *Q. alata* also has a keel, it is flat and not hollow, a crucial detail that was overlooked in the original species description), as well as the fact that the square plates of *Quadrulella* are self-secreted, while the origin of square plates in *Mrabella* remains unclear (possibly recycled—i.e., kleptosquamy; see p. 116; KOSAKYAN et al., 2016).

Etymology: The genus name refers to the quadrangular shape of the plates which cover the test surface.

Remarks: The taxonomic position of this genus has changed over time. SCHULZE (1875) first introduced *Quadrula* to designate amoebae found in Dresden, Germany, with tests typically reinforced with square plates; however, similar tests had previously been found in England by WALLICH (1863) and had been described as *Difflugia symmetrica*. SCHULZE considered this structure distinct from *Difflugia*, thus suggesting the name *Quadrula*, but as the name *Quadrula* was a homonym of a Najad mussel (RAFINESQUE, 1820), COCKERELL (1909) proposed the replacement name *Quadrulella*. *Quadrulella* was treated as a distinct genus (TARÁNEK, 1882; CHARDEZ, 1967), or even a separate family, *Quadrulidae* (SCHULZE, 1877).

DEFLANDRE (1932) separated the species with calcareous, rectangular plates into a new genus, *Paraquadrula*, largely consisting of species with a circular to ovoid test, although some species also produced square scales. Here, we have not included genus *Paraquadrula* amongst hyalospheniids, considering its globose test shape, and absence of an organic lip around the pseudostome (with some exceptions, a synapomorphy of Hyalospheniidae). Molecular data remain lacking for this genus.

DEFLANDRE (1936) considered the square scale shapes as insufficient for generic distinction and treated *Quadrulella* as a subgenus of genus *Nebela s.l.*; however, DEFLANDRE, in collaboration with DEFLANDRE-RIGAUD (1958), later decided to re-establish *Quadrulella* as a separate genus.

KOSAKYAN et al. (2016) redefined genus *Quadrulella* (Wallich, 1863) Cockerell, 1909, showing that square-scaled hyalospheniids do not all form a monophyletic assemblage in a phylogenetic tree based on COI sequences (e.g., the former species *Q. subcarinata* does not belong to genus *Quadrulella*, see details in for genus *Mrabella*, p. 116). Additionally, the authors suggested that other *Quadrulella* species may also represent different genera, "[T]here are a number of other described species in genus *Quadrulella* that differ from the tear-shaped morphology of *Quadrulella s.str.* These also present similar shapes to other genera: *Quadrulella vas*, *Q. constricta* - *Apodera vas*, *Q. lageniformis* - *Padaungiella lageniformis*, *Q. tubulata* - *P. tubulata*. These "mirror" species could either be a result of convergent evolution or alternatively represent cases of the "classical" hyalospheniids (*A. vas*, *Padaungiella* ssp.) that live in environments where euglyphids are rare but *Quadrulella* are abundant enough to provide material for building their shells. We have suggested that at this point these *Quadrulella* species must be treated as incertae sedis, and their sequencing will certainly illuminate the conundrum of the evolution of square-shaped plates" (cit. from KOSAKYAN et al., 2016).

Important contributions to the genus include: CHARDEZ (1967), DEFLANDRE (1936), GAUTHIER-LIÈVRE (1953, 1957), and GAUTHIER-LIÈVRE & THOMAS (1961).

We consider 18 taxa as valid here. Of these, molecular data are currently available for only eight species (see Species descriptions and the corresponding remarks for further discussion on molecular data).

Even if KOSAKYAN et al. (2016) suggested the existence of so called "mirror" *Quadrulella* species (e.g., *Q. camerounensis*, *Q. constricta*, *Q. lageniformis*, *P. tubulata*, *Q. vas*) that should be treated as incertae sedis, we included them in the list of valid species with certain position. Further molecular data are needed to clarify their taxonomic position within Hyalospheniidae.

Key to the species

1. Test lageniform, neck distinct, somewhat separated from the main body 2
– Neck not separated from the main body 6

2. Circular constriction present at the base of the neck (at the junction with the main body) 3
– No constriction at the base of the neck 4

3. Larger species: L = 250–360 µm, B = 150–170 µm *Q. vas* (p. 191)
– Somewhat smaller species: L = 168–192 µm, B = 83–104 µm *Q. constricta* (p. 172)

4. Neck very long, cylindrical, plates arranged regularly, non-overlapping: L = 70–95 (100) µm, B = 42–45 (50) µm *Q. tubulata* (p. 188)
– Plates overlapping 5

5. Neck strongly compressed (more than the main body). Overlapping plates rectangular, square, triangular, or circular, most common on the main body and often absent from the neck: L = 80–105 µm, B = 30–32 µm *Q. camerounensis* (p. 171)
– Neck not more compressed than the body. Plates arranged following a helix pattern, and smaller square plates present at the junction of the larger plates, presumably serving as reinforcement: L = 170–192 µm, B = 85–115 µm *Q. lageniformis* (p. 175)

6. Test elongated-piriform; neck gradually tapering towards the pseudostome 7
– Test piriform or ovoid 16

7. Neck laterally curved in broad view (shaped similarly to that of the Euglyphida genus *Cyphoderia*): L = 80–100 µm, B = 33–45 µm *Q. symmetrica curvata* (p. 185)
– Neck not laterally curved in broad view 8

8. Keel (5–10 µm wide) present (most visible in profile): L = 140–150 µm, B = 70–90 µm *Q. alata* (p. 170)
– Keel absent 9

9. Pseudostome elliptical and irregular without organic rim 10
– Pseudostome regular with a linear margin or rim 11

10. Test more or less piriform, with irregular lateral margins: L = 85–100 µm, B = 51–65 µm *Q. cordobensis* (see *incertae sedis* list, p. 206)
– Test elongated-piriform, with regular lateral margins: L = 108–114 µm, B = 42–48 µm *Q. nunciae* (see *incertae sedis* list, p. 207)

11. Two lateral pores present at ca. 1/4th of the distance from the pseudostome to the fundus. Test elongated claviform: L = 90–110 µm, B = 45–50 µm, P = 18–20 µm *Q. elegans* (p. 174)
– Lateral pores absent (if present, not clearly visible in LM) 12

12. Test small, elongated, and very narrow: L = 65 µm, B = 22 µm, L/B ~ 3 *Q. elongata* (see incertae sedis list, p. 207)
– Test larger (L > 65 µm) and wider (L/B < ca. 2.5) 13

13. Species with larger scales (≤ 9–11 µm). Test elongated-piriform: L = 87–91 µm, B = 37–39 µm, L/B = 2.2–2.3 *Q. madibai* (p. 178)
– Species with smaller scales (≤ 7–9 µm) 14

14. Test shape variable, ranging from piriform to elongated-piriform: L = 66–69 (96) µm, B = 35–40.5 (45) µm *Q. variabilis* (p. 190)
– Test similar in shape, but larger: L = 97–126 µm, B = 53–68 µm. 15

15. Test with a distinct elongated narrowed neck; found in *Sphagnum* and other mosses in wetlands *Q. longicollis* (p. 176)
– Neck less well marked; resides in biological soil crusts (arid mountain landscapes in Mexico) *Q. texcalense* (p. 185)

16. Test piriform, posterior end pointed in broad view: L = 102 µm, B = 60 µm, P = 13 µm *Q. acuminata* (p. 169)

– Posterior end of the test rounded in broad view 17

17. Scales overlapping. Test piriform, scales arranged in irregular rows, smaller rectangular plates sometimes superimposed at the junctions of the larger plates: L = 120–135 µm, B = 74–90µm *Q. scutellata* (p. 181)

– Scales not overlapping 18

18. Scales regularly arranged, also near the pseudostome 19

– Scales partly or entirely irregularly arranged 21

19. Smaller species: L < 90 µm 20

– Larger species, test ovoid, larger and wider: L = 100–150 (174) µm, B = 60–100 (120) µm *Q. quadrigera* (p. 180)

20. Larger-scaled (≤ 11 µm) species *Q. symmetrica* (p. 183)

– Small-scaled (≤ 7–9 µm) species. Test shape variable, ranging from piriform to elongated-piriform: L = 66–69 (96) µm, B = 35–40.5 (45) µm *Q. variabilis* (p. 190)

21. Scales irregularly arranged near the pseudostome but more regularly arranged (diagonally) near the fundus: L = 74–93 µm, B = 45–60 µm *Q. tropica* (p. 187)

– Scales mixed and arranged in irregular rows: L = 136–167 µm, B = 85–102 µm *Q. deflandrei* (p. 173)

Quadrulella acuminata Van Oye, 1958

1958 *Quadrulella acuminata* Van Oye, Hydrobiologia 10: 107 (Pl. II, Fig. 15, original drawing).

Description (based on the original publication): Test piriform, laterally tapering towards the pseudostome. Base of the test rounded and ending with a chitinoid point in broad view. Test composed of rectangular plates, never overlapping, but juxtaposed without any gap. Platelets of the posterior point elongated and triangular (not square). Pseudostome curved according to the original drawing. L = 102 µm, B = 60 µm, P = 13 µm.

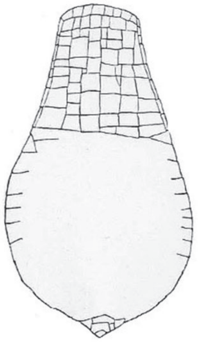

Fig. 86. *Quadrulella acuminata*: Original drawing from VAN OYE (1958).

Differential diagnosis: Similar to *Quadrulella symmetrica* in general shape, the main difference being that *Q. symmetrica* has a totally rounded fundus in broad view, while the fundus is pointed in *Q. acuminata*. Also, the shape of the plates is generally square in *Q. symmetrica*.

Type locality: Southwest Uvira, Congo. Likely coordinates: -3.365936°, 29.115387°.

Type specimen: Not provided. We declare Pl. II, Fig. 15 by VAN OYE (1958), reproduced here as Fig. 86, as the type.

Etymology: The species name is derived from the Latin word “acuminatus”, meaning “pointed”, in reference to the pointed fundus of the test.

Habitat: *Sphagnum* mosses.

Geographical distribution: Southwest Uvira, Democratic Republic of Congo (VAN OYE, 1958).

Remarks: This species was recorded only once.

Quadrulella alata Gauthier-Lièvre, 1957

1957 *Quadrulella alata* Gauthier-Lièvre, Bull. Soc. Hist. Nat. Afr. Nord 48: 502 (Fig. 5, original drawing).

Description (based on the original publication): Test lageniform, with a distinct neck and a rounded main body in broad view. Lateral, hollow keel (5–10 µm wide) present on the margin of the main body in broad view and starting near the base of the neck. In profile, test claviform with a hollow keel ("nipple-shaped" fundus). Junction between the keel and the main part of the test often marked with a bead of chitinoid cement. Test colorless or slightly yellowish, covered with regularly arranged rectangular plates, generally juxtaposed, rarely overlapping. Pseudostome curved, surrounded by a tiny organic rim. L = 140–150 µm, B = 70–90 µm, P = 30 µm.

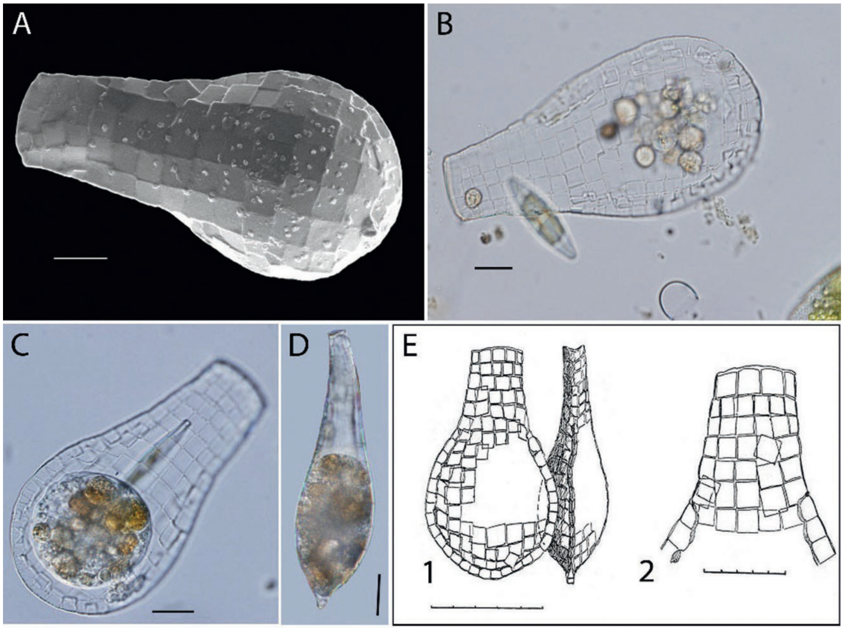

Fig. 87. *Quadrulella alata*: (A) SEM image of a specimen from South Africa; (B) LM image of an empty test from South Africa; (C & D) LM images of two living individuals from South Africa in broad and profile views, respectively; (E) Original drawings from GAUTHIER-LIÈVRE (1957): (1) broad and profile views of the test, and (2) higher magnification view of the neck showing the position of the regularly-arranged plates on the keel. Scale bars: A–D = 20 µm, E = 50 µm. Images (A–D) by Anush Kosakyan.

Differential diagnosis: Differs from other Quadrulella species by the presence of a hollow keel.

Type locality: Unnamed creek between Ewo and Etoumbi, Republic of Congo. Likely coordinates: -0.390934°, 14.891024°.

Type specimen: Not provided. We declare Fig. 5 by GAUTHIER-LIÈVRE (1957), reproduced here as Fig. 87E, as the type.

Etymology: The species name refers to the presence of a keel, as the word "alata" in Latin means "having wings".

Habitat: Aquatic, in a marshy creek on Kalaharian sands, in moss growing on the creekbank (rainforest).

Geographical distribution: Africa: Congo (GAUTHIER-LIÈVRE, 1957), Republic of South Africa (KOSAKYAN et al., 2016); Central America: Costa Rica (MEISTERFELD, unpubl.).

Remarks: The species has rarely been reported, although it remains unclear if it is truly rare, or limited by the relatively few studies having focused on African and other tropical testate amoebae. Molecular data have confirmed its position within genus *Quadrulella* (KOSAKYAN et al., 2016).

Quadrulella camerounensis Gauthier-Lièvre, 1957

1957 *Quadrulella camerounensis* Gauthier-Lièvre, 1957, Bull. Soc. Hist. Nat. Afr. Nord 48: 502 (Fig. 3, original drawing).

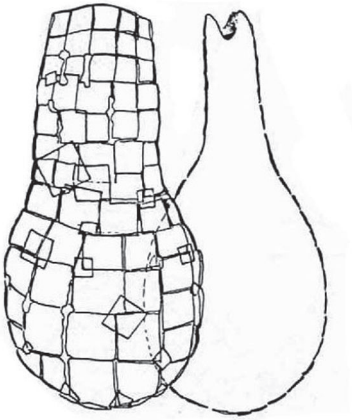

Fig. 88. *Quadrulella camerounensis*: Original drawing from GAUTHIER-LIÈVRE (1957): broad and profile views.

Description (based on the original publication): Test lageniform in broad view, with a distinct neck and rounded main body. In profile view, test lageniform, slightly compressed in the main body portion, and more strongly in the neck, with an indented pseudostome. Test colorless, covered mainly with rectangular or square plates, generally smaller in the neck part, closely juxtaposed or overlapping. Overlapping plates (most common along the main body, and often absent from the neck) are rectangular, square, triangular, or circular. Thick lines of chitinoid cement present at the junction between scales, mostly on the neck. Pseudostome broadly curved, with a thin organic rim. L = 80–105 µm, B = 30–32 µm, P = 24–28 µm.

Differential diagnosis: *Quadrulella camerounensis* is very similar to *Q. lageniformis*; however, the latter species is larger. The neck of *Q. camerounensis* is strongly compressed, and the main body part has a near-circular cross-section. The arrangements of plates in both species are similar.

Type locality: Santa-Bamenda, British Cameroon, Africa (now in NW Cameroon). Likely coordinates: 5.932181°, 10.241275°; Elevation, ca. 1100 m.a.s.l..

Type specimen: Not provided. We declare Fig. 3 by GAUTHIER-LIÈVRE (1957), reproduced here as Fig. 88, as the type.

Etymology: This species was named after British Cameroon, where it was found.

Habitat: Wet liverworts (*Marchantia* sp.).

Geographical distribution: Africa: Santa-Bamenda, British Cameroon, now in NW Cameroon (GAUTHIER-LIÈVRE, 1957).

Remarks: KOSAKYAN et al. (2016) conducted a phylogenetic study of genus *Quadrulella* based on mt-COI sequence data and suggested that *Q. camerounensis* may not belong to the genus (see p. 167 for further detail).

Quadrulella constricta Lopretto & Vucetich, 1997

1997 *Quadrulella constricta* Lopretto & Vucetich, Neotrópica 43(109–110): 3–5 (Figs. 1–4, original images).

Description (based on the original publication): Test yellowish, elongated, compressed, with a rounded fundus. Neck separated from the main body by a clear constriction, giving the test a bicameral impression. Neck length corresponding to ca. 1/3rd of the entire test length. Pseudostome curved, with a well-developed organic lip followed by ≥ 1 line of rectangular plates arranged parallel to the lip edge. From this point, plates (size 1.8–2 µm) arranged in a helix, reaching the fundus of the test. Plates generally juxtaposed with little overlap, except for the constriction at the base of the neck. L = 168–192 µm, B = 83–104 µm, P = 33–48 µm.

Differential diagnosis: *Quadrulella constricta* can be confused with *Q. vas* described by CERDA (1986) and *Q. scutellata vas*; however, *Q. vas* is larger (L = 168–192 µm, B = 83–104 µm in *Q. constricta* vs. L = 250–360 µm, B = 150–170 µm in *Q. vas*), whereas *Q. scutellata* vas has a thin organic rim, and the plates are arranged vertically rather than in a helix, as in *Q. constricta* (see Remarks for further discussion).

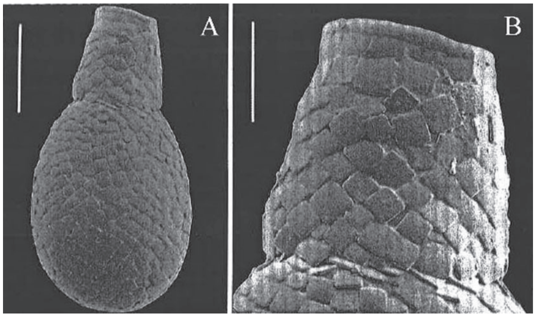

Fig. 89. *Quadrulella constricta*: Original SEM image from LOPRETTO & VUCETICH (1997). Scale bars: A = 50 µm, B = 20 µm.

Type locality: Sierra de la Ventana, Buenos Aires Province, Argentina. Likely coordinates: -38.010325°, -62.058117°.

Type specimen: Not provided. We declare Fig. 1 by LOPRETTO & VUCETICH (1997), reproduced here as Fig. 89A, as the type.

Etymology: The species name refers to the presence of a constriction at the neck-body junction of the test.

Habitat: Among aquatic mosses, in stream water starting from Hill Destierro Primero, Sierra de la Ventana, Province of Buenos Aires.

Geographical distribution: Argentina (LOPRETTO & VUCETICH, 1997).

Remarks: HOOGENRAAD & DE GROOT (1940a) reported specimens of *Quadrulella* with a constricted neck from moss samples collected in Indonesia (Java and Sumatra). Based on this morphological difference from the type species, the authors described it as *Q. scutellata* var. *vas*. Subsequently, LOPRETTO & VUCETICH (1997) claimed that *Q. constricta* is distinct from *Q. scutellata* var. *vas*, arguing that the latter has a thin organic rim, and plates arranged vertically, rather than in a helix, as in *Q. constricta*. Although HOOGENRAAD & DE GROOT

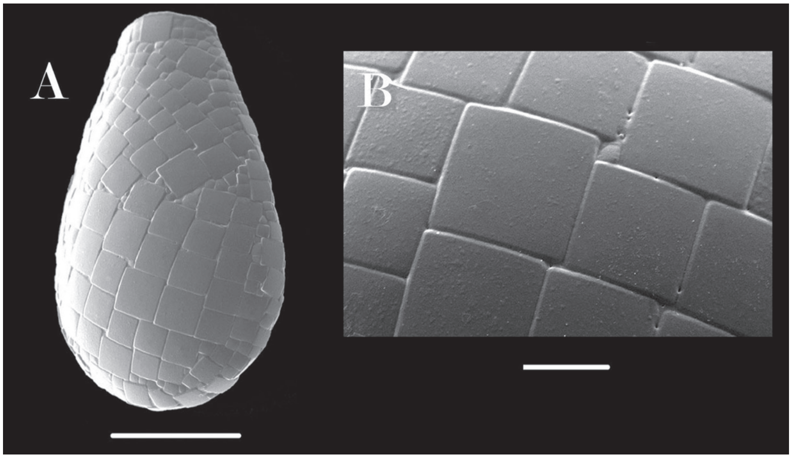

Fig. 90. *Quadrulella deflandrei*: (A) SEM image of a specimen from Bulgaria, (B) Detailed image of the test surface and plates (modified from BANKOV et al., 2021, Figs. 2 and 3). Scale bars: A = 50 µm, B = 10 µm.

(1940b) indicated the dimensions of their test in their description, they did not clearly indicate if these dimensions refered to *Q. scutellata* var. *vas* or to its type (as cited in LOPRETTO & VUCETICH, 1997). KOSAKYAN et al. (2016) conducted a phylogenetic study of genus *Quadrulella* based on mt-COI sequence data and mentioned that *Q. constricta* may not belong to genus *Quadrulella* (see Remarks on p. 167).

Quadrulella deflandrei Bankov, Todorov, & Ganeva, 2021

2021 *Quadrulella deflandrei* Bankov, Todorov, & Ganeva Protistology 15(2) (53–68) (Fig 2 & 3A original images)

Icon.: BANKOV et al., 2021, Figs. 2 & 3A.

Description (based on the original publication): Test large, colorless, ovoid or piriform in broad view, with sides tapering evenly and gradually from the rounded aboral region towards the aperture. Test laterally compressed, with ovoid transverse section, and composed of quadrangular siliceous plates of very different sizes, primarily mixed, and most frequently arranged in irregular rows. Pseudostome ovoid, slightly convex frontally, and concave laterally, bordered by a thin collar of organic cement. Dimensions (based on 22 individuals): L = 136–167 µm, B = 85–102 µm, P = 33–47 µm.

Differential diagnosis: *Quadrulella deflandrei* resembles *Q. symmetrica* in its general shape, but is approximately twice as large. Furthermore, *Q. deflandrei* has significantly more and larger plates (size ≤ 15–19 µm) vs. a maximum plate size of 11 µm in *Q. symmetrica*. By test size, *Q. deflandrei* is comparable with *Q. quadrigera* and *Q. scutellata* but can be easily distinguished by plate size and arrangement: in *Q. quadrigera*, the plates are relatively small and similar in size (8–10 µm), arranged in numerous rows, and often mixed with singular round or elliptical plates, whereas in *Q.*

scutellata, small quadrangular plates are usually superimposed at the junctions of larger plates. Both *Q. quadrigera* and *Q. scutellata* are primarily distributed in the Americas, Asia, Africa, while the lone account of *Q. scutellata* from Europe (Hungary) by GROSPIETSCH (1982) appears dubious, as no illustration was provided (adapted from BANKOV et al., 2021).

Type locality: Nearby the Village Kopilovtsi, below the "Kopren" hut, Western Stara Planina Mountain, Bulgaria. Coordinates: 43.33044°, 22.86055°; Elevation, 881 m.a.s.l..

Type specimen: Holotype and paratypes mounted in Canada balsam on a glass slide are retained in the collection of M. Todorov, Institute of Biodiversity and Ecosystem Research, BAS, Sofia, Bulgaria; No. QD-H/2021 (holotype) and QD-P01/2021, QD-P-02/2021 (paratypes).

Etymology: The species is named after Dr Georges Deflandre, a prominent French scientist in the field of micropaleontology and protistology, who first illustrated the unusually large form of *Quadrulella symmetrica*.

Habitat: *Sphagnum* mosses in Stara Planina and Pirin Mountains.

Geographical distribution: Europe: Bulgaria, France (BANKOV et al., 2021).

Remarks: *Quadrulella deflandrei* was found in a small mire within a mixed deciduous forest of beech (*Fagus sylvatica* L.) and birch (*Betula pendula* L.), in association with other dominant species: *Assulina muscorum*, *Corythion dubium*, *Heleopera rosea*, *Nebela collaris*, and *Q. symmetrica*, in addition to other more sparsely represented hyalospheniids, such as *Longinebela tubulosa*, *N. guttata*, *N. pechorensis*, *Padaungiella lageniformis*, *P. tubulata*, *Q. longicollis*, and *Q. variabilis*. The habitat, where almost all *Q. deflandrei* specimens were found is characterized by its acidity (pH = 5.05), low hydrological conductivity (86.4 µS), moderate water content of mosses (93.5%), and low water table depth (0 cm). No living specimens were observed, and the description is based on 22 empty tests (adapted from BANKOV et al., 2021).

Quadrulella elegans Gauthier-Lièvre, 1954

1954 *Quadrulella elegans* Gauthier-Lièvre, Bull. Soc. Hist. Nat. Afrique du Nord 44: 333 (Fig. 3, original drawing).

Icon.: GAUTHIER-LIÈVRE, 1954, Fig. 3; GAUTHIER-LIÈVRE, 1957, Fig. 2C.

Description: Test elongated-claviform, almost lageniform, with a rounded fundus. Sides gradually tapering towards the pseudostome. Two lateral pores clearly visible in LM at ca. 1/4th of the distance from the pseudostome to the fundus. Test colourless, covered with little juxtaposed square or rectangular plates (ca. 4–6 µm, although biometric data are lacking), sometimes overlapping. On the neck, plates smaller and arranged much more regularly than the rest of the body. Pseudostome linear or curved. L = 90–110 µm, B = 45–50 µm, P = 18–20 µm.

Differential diagnosis: *Quadrulella elegans* can be easily confused with *Q. longicollis*; however, the former has more conspicuous pores, and the organic rim is much thinner.

Type locality: Man Region, Ivory Coast, Africa (GAUTHIER-LIÈVRE, 1953). Likely coordinates: 7.444782°, -7.647104°.

Type specimen: Not provided. We declare Fig. 3 by GAUTHIER-LIÈVRE (1954), reproduced here as Fig. 91B, as the type.

Etymology: The species name likely refers to the slender outline of the test.

Habitat: *Sphagnum* mosses, among aquatic mosses in a river with high humic acid content.

Geographical distribution: Africa: Guinea (DECLOITRE, 1955), Republic of Congo (GAUTHIER-LIÈVRE, 1957), Ivory Coast (GAUTHIER-LIÈVRE, 1953), Republic of

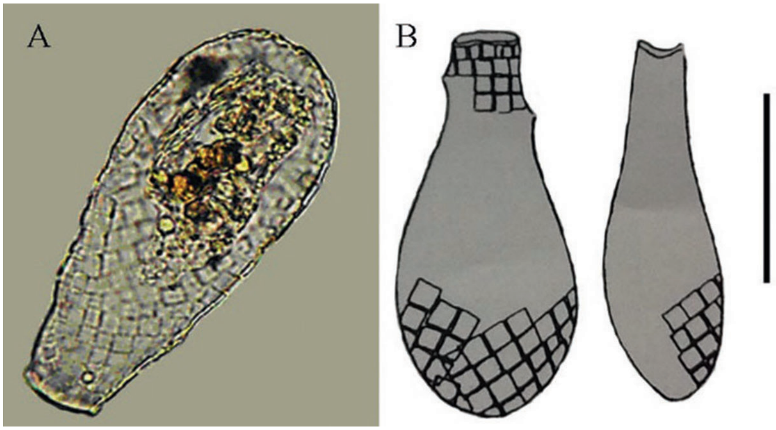

Fig. 91. *Quadrulella elegans*: (A) LM image of a specimen from Brazil (from Maria Beatriz Gomes & Souza, www.tecamebas.com.br), (B) Original drawing from GAUTHIER-LIÈVRE (1953): broad and profile views. Scale bar = 50 μm.

South Africa (Perez-Juarez et al., 2017), Rhodesia—now Zimbabwe (CHARDEZ, 1964), Seychelles (KORGANOVA, 1990); South America: Argentina (VUCETICH, 1983; VUCETICH & LOPRETTO, 1995), Brazil (www.tecamebas.com.br), Paraguay (BONNET, 1979); Australasia: New Guinea (BONNET, 1980a).

Remarks: This species has been found several times, first in Africa (Man, Ivory Coast; GAUTHIER-LIÈVRE, 1953), then in cave stream water near Segea, Guinea (DECLOITRE, 1955), and in different localities within the Republic of Congo: swamps among *Cyperus papyrus* in a locality between Dolisie and Kimongo, swamps among *Sphagnum* and Xyridaceae in the Batéké uplands, and in a marshy creek between Ewo and Etombi (GAUTHIER-LIÈVRE, 1957). It was later found in South America and New Guinea.

Quadrulella lageniformis Van Oye, 1949

1949 *Quadrulella lageniformis* Van Oye, Bijdragen Dierkunde 28: 345, Fig. 23.

Icon.: VAN OYE, 1949, Fig. 23.

Description (based on the original publication): Test lageniform in broad view, with an elongated neck (exactly as in *Padaungiella lageniformis*) but composed of square plates arranged in a helix and little square plates reinforcing the corners of the larger plates (as in *Q. scutellata*). Pseudostome with a very thin organic lip. L = 170–192 μm, B = 85–115 μm, P = 30–41 μm.

Differential diagnosis: *Quadrulella lageniformis* and *Padaungiella lageniformis* share identical test outlines; however, the two species differ in size: *P. lageniformis* is smaller (L = 100–140 μm) that *Q. lageniformis* (L = 170–192 μm), and the test of *Q. lageniformis* is composed of square plates reinforced with little platelets (as in *Q. scutellata*); whereas the test in *P. lageniformis* is constructed from round or oval plates and not square plates.

Type locality: Pangerango, Java, Indonesia. Likely coordinates: -6.769395°, 106.962157°.

Type specimen: Not provided. We declare Fig. 23 by VAN OYE (1949), reproduced here as Fig. 92, as the type.

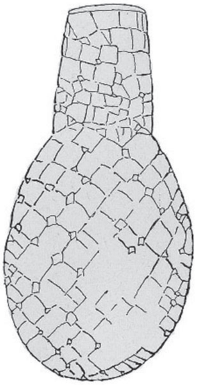

Fig. 92. *Quadrulella lageniformis*: Original drawing from VAN OYE (1949).

Etymology: The species name refers to the lageniform shape of the test.

Habitat: Mosses, forest soil, volcanic soil, forest soil on black basalt (BONNET, 1992).

Geographical distribution: Asia: Java, Indonesia (VAN OYE, 1949; BONNET, 1992), Southern Sulawesi (Southern Sulawesi, Celebes) (BONNET, 1992); Australasia: New Guinea (Irian Jaya, BONNET, 1992).

Remarks: There is some confusion in the literature related to the original drawing and the name of *Quadrulella lageniformis*. HOOGENRAAD & DE GROOT (1940a) published the original drawing of *Q. lagenifomis* under the name *Q. scutellata* var. *vas*. In this publication (Figs. 64–66), the authors illustrated three distinct tests resembling *Q. scutellata*, *Q. scutellata* var. *vas* with a constricted neck, and *Q. lageniformis* with an elongated but non-constricted neck. All three individuals were labelled as *Q. scutellata*. Later, VAN OYE (1949) observed tests without constriction at the base of the neck, associated these organisms with the illustrations of HOOGENRAAD & DE GROOT, and described *Q. lageniformis* as a new species.

As indicated in the Differential diagnosis section, *Q. lageniformis* closely resembles *Padaungiella lageniformis* (see p. 163) and is another "mirror *Quadrulella* species" which could possibly be placed in as separate genus (as suggested by KOSAKYAN et al. (2016; see p. 167 for further detail).

LUKETA (2017) found several specimens completely covered by square plates in a population of *Padungiella lageniformis* from Šargan Mountain, Serbia, stating that this population lives in the environment where euglyphids are rare, but *Q. symmetrica s.l.* and *Q. longicollis* are abundant He discussed the origin of their square plates as follows: "*I think that* Q. lageniformis *and* P. lageniformis *are different species with square plates originated by different ways –* Q. lageniformis *possess self-secreted plates, while* P. lageniformis *possess predated or collected plates. Van Oye (1949) reported clearly different morphometric data and shape of shell plates for these two species from the same locality. Namely, he noted smaller dimensions for* P. lageniformis *(shell length 107–156 µm, shell width 62–80 µm) than for* Q. lageniformis *(shell length 170–192 µm, shell width 85–115 µm). If* Q. lageniformis *possesses predated or collected square shell plates, why then the typical P. lageniformis from the same environment do not have square plates? However, without the detailed observations of* Q. lageniformis *based on material from the type population (or another population from Indonesia) all explanations are speculative*.".

Quadrulella longicollis (Taránek, 1882)

1882 *Quadrula symmetrica* var. *longicollis* Taránek,1882, Abh. König. Böhm. Ges. D. Wiss. 6: 48

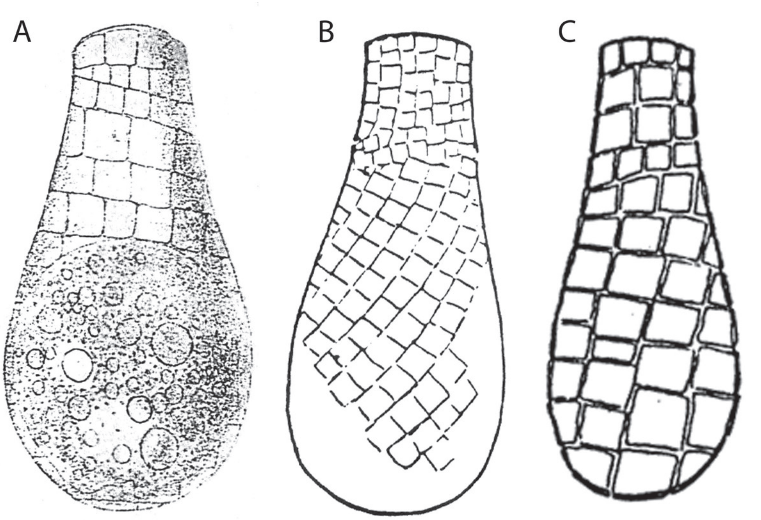

Fig. 93. *Quadrulella longicollis*: Original drawings of *Quadrulella symmetrica* var. *longicollis* from: (A) TARÁNEK (1882), (B) HOOGENRAAD & DE GROOT (1951), and (C) CHARDEZ (1956). Note the differences in the plate arrangement patterns and sizes among the three illustrations.

2012 *Quadrulella symmetrica longicollis* Taránek, 1882 – Taránek, 1882, in KOSAKYAN et al., 2012, Protist 163: 429.

Icon.: TARÁNEK, 1882, T. IV, Fig. 19; GAUTHIER-LIÈVRE, 1957, Fig. 1C, F; LUKETA, 2015b, Fig. 1; LUKETA, 2017e, Fig. 1; TODOROV & BANKOV, 2019, Fig. 80.

Description: Test elongated-piriform in broad view, compressed, with a distinct elongated narrow neck. Test colourless, composed of square or rectangular plates, regularly or slightly irregularly arranged in a horizontal or helical manner. Aperture slightly curved with a tiny organic lip. L = 100–150 µm, B = 40–90 µm (see Remarks below), P = 18–29 µm.

Differential diagnosis: The general elongated-piriform outline of *Quadrulella longicollis* may resemble *Q. madibai* and larger forms of *Q. variabilis*. It differs from these two species primarily by its larger size (LMAX in *Q. madibai* = 91 µm and in *Q. variabilis* = 96 µm, but see detailed discussion under *Q. variabilis* for additional information). Another species with similar morphology is *Q. elegans* (see corresponding Differential diagnosis). *Q. longicollis* may also be confused with *Q. texcalense*, from which it differs mainly in its ecology (*Sphagnum* and green mosses vs. organic-poor soils developed on sedimentary rocks—limestones and conglomerates, respectively). *Q. longicollis* may also have a slightly longer neck than *Q. texcalense*; however, comparative morphometric data are lacking.

Type locality: Not provided, most likely South Bohemia, Czech Republic (other specimens illustrated on Pl. IV by TARÁNEK (1882) were collected from Soběslav). Likely coordinates: 49.234599°, 14.627361°.

Type specimen: Not provided. We declare Fig. 19, Pl. IV by TARÁNEK (1882), reproduced here as Fig. 93A, as the type.

Etymology: The species name refers to its morphology, as in Latin, "longicollis" means "elongated neck".

Habitat: *Sphagnum* and green mosses.

Geographical distribution: Likely cosmopolitan, as we have > 100 records in our database, but see remarks.

Remarks: The taxonomic story behind this species is rather complicated. *Quadrulella longicollis* was initially described as a variety of *Quadrula symmetrica* by TARÁNEK (1882), differing from the type by its elongated neck, and including specimens 80–150 µm in length. KOSAKYAN et al. (2012) observed elongated specimens (L = 96 µm), and mt-COI sequence data placed them as a distinct species from *Q. symmetrica*, thus elevating this variety to the species level. As this variety was described prior to 1961, the original authorship remained (ICZN Arts. 45.6.3 and 46.1).

Quadrulella symmetrica longicollis can be quite variable. For instance, *Q. symmetrica* var. *longicollis* forma *lanceolata* Gauthier-Lièvre, 1952 was included, and separate size ranges were used by different authors to describe the true *Q. longicollis*. DEFLANDRE (1936) noted that specimens of this taxon usually have L > 100 µm; whereas a half century later, CERDÁ (1986) observed specimens with L = 130–150 µm, B = 60–70 µm, and P = 20–30 µm. LUKETA (2015b) reported the following measurements for eight individuals collected from the Vlasina Lake region of Serbia: L = 111–131 µm, B = 50–57 µm, P = 27–28 µm. Later, LUKETA (2017e) conducted a detailed morphometric study based on 130 individuals from Šargan Mountain, Serbia, reporting measurements of: L = 103–137 µm, B = 45–64 µm, P = 21–29 µm. LUKETA (2017e) also mentioned the existence of two test types (narrow and broad) within the studied *Q. longicollis* populations.

Illustrations published by various authors also suggest the existence of more than one species within this taxon. Two of these individuals (illustrated in Fig. 93B & C) do not correspond to the species outline, but rather the plate drawings, if accurate, suggest that several species may exist. HOOGENRAAD & DE GROOT (1951) reported and illustrated specimens somewhat smaller than the type: L = 90µm, B = 40µm, some of which had lateral pores in the neck.

KOSAKYAN et al. (2016) conducted a detailed morphological and molecular study based on mt-COI genes of *Q. symmetrica* and closely related species. The molecular data showed that the sequence of *Q.* cf. *longicollis* (individual with an elongated neck, L = 96 µm) was identical to the sequence of the small-scaled *Q. variabilis*; however, considering the wide size range provided for *Q. longicollis*, the authors did not exclude that the sequenced individual may not correspond to the typical *Q. longicollis*. Thus, the identity of the true *Q. longicollis* remains to be determined.

Here, we refer to *Q. longicollis* for specimens with tests with L > 100 µm until molecular data assessing specimens with different lengths can clarify the true taxonomic position of this species.

Quadrulella madibai Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

2016 *Quadrulella madibai* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., 2016 Cladistics 32: 606–623.

Icon.: KOSAKYAN, LAHR, MULOT, MEISTERFELD, MITCHELL, & LARA, 2016, Fig. 4.

Description: Test elongated-piriform in broad view, with a rounded posterior end, compressed towards the pseudostome. Test colorless,

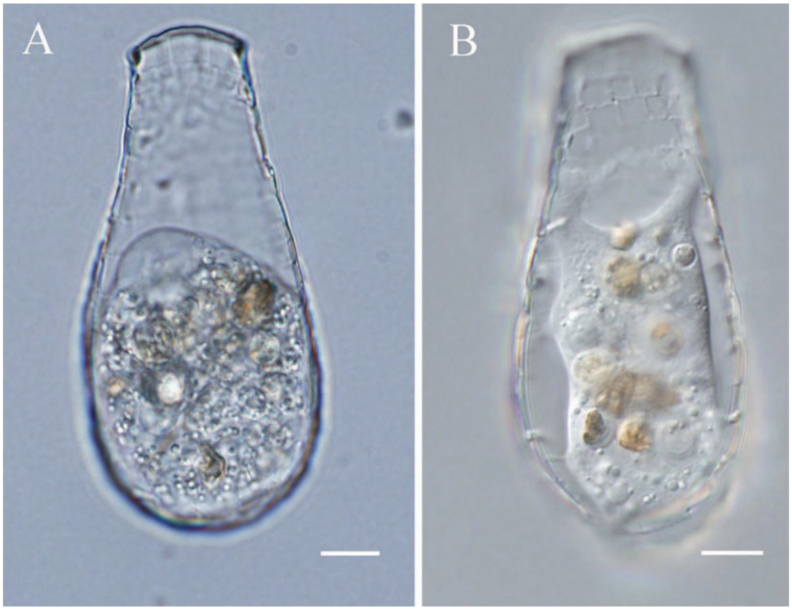

Fig. 94. *Quadrulella madibai*: Original LM images of two individuals from South Africa from KOSAKYAN et al. (2016). Scale bars = 10 µm.

composed of square plates, regularly arranged in rows. Plates smaller near the pseudostome (5–6 µm), gradually becoming larger (9–11 µm) towards the posterior end of the test. Pseudostome curved and bordered by a tiny organic rim. L = 87–91 µm, B = 37–42 µm, P = 21–23 µm.

Differential diagnosis: *Quadrulella madibai* resembles *Q. symmetrica*, differing by its slender and more elongated test (L/B= 2.0–2.3 in *Q. madibai* vs. 1.7–1.9 in *Q. symmetrica*), and its more pronounced neck. Molecular data based on mt-COI sequences (KOSAKYAN et al., 2016) also clearly separate these two species (sequence divergence ≤ 10%; see further notes under Q. symmetrica and *Q. longicollis*).

Type locality: Pitse mire, a valley peatland in a landscape of upland grassland in the Welgevonden Game Park adjacent to Marakele National Park, Republic of South Africa. Coordinates: -24.403772°, 27.807597°; Elevation, ca. 1500 m.a.s.l..

Type specimen: Fig. 4b in KOSAKYAN et al., 2016.

Etymology: The species named in honor of Nelson Mandela, the South African revolutionary and president, who was known as "Madiba" by his friends, in reference to the name of his clan.

Habitat: *Sphagnum* mosses.

Geographical distribution: Africa: Republic of South Africa (KOSAKYAN et al., 2016).

Remarks: WAILES (1912a) observed *Quadrula symmetric*a from the Seychelles, noting that all individuals have elongated-type tests (L = 84–90 µm), with larger scales (8–10 µm in breadth). Later, KOSAKYAN et al. (2016)

described *Quadrulella madibai* as morphologically similar to *Q. symmetrica s.s.* because of its large shell plates (LMAX = 9–11 μm in *Q. madibai* versus 10–12 μm in *Q. symmetrica s.s.*); however, *Q. symmetrica s.s.* can be distinguished from *Q. madibai* based on its less slender and elongated test (L/B = 1.7–1.9 in *Q. symmetrica* s.s. vs. 2.0–2.3 in *Q. madibai*). In addition, the general test outline in *Q. madibai* is globally more tubular and does not present a distinct neck. Based on the detailed morphological and morphometric analyses of two populations from the central part of the Balkan Peninsula, LUKETA (2017e) concluded that it is not possible to distinguish *Q. symmetrica s.s.* from *Q. madibai*, as a large number of transitional individuals according to the L/B ratio were present between these two "species". This conclusion supports the findings of a detailed morphometric analysis of a population from Serbia (LUKETA, 2015b). This analysis suggests that *Q. madibai* could represent one extreme of a continuum of morphotype. The clear molecular distance reported by KOSAKYAN et al. (2016) however do not support this view. Further molecular and morphological studies based on a larger number of populations are clearly needed to resolve the taxonomic status of these two taxa and, more generally, to determine the diversity within this genus.

Quadrulella quadrigera Deflandre, 1936

1936 *Quadrulella quadrigera* Deflandre, Ann. Protistol. 5: 233.

1961 *Quadrulella quadrigera* var. *africana* Gauthier-Lièvre and Thomas, Bul. Soc. Hist. Nat. Afrique Nord 52: 43 [Infrasubspecific (not available) name: var. published after 1960, ICZN A rt. 45.6.3].

Icon.: DEFLANDRE, 1936, Pl. XI, Figs. 3–10; Pl. XXVII, Fig. 3.

Description: Test ovoid in broad view, with a rounded fundus, sides regularly tapering towards the pseudostome, which can be straight or slightly curved. We also noted lateral pores in the Australian materials. Test composed of square or rectangular plates, often interspersed with round, circular, or elliptical elements. These elements are juxtaposed and rarely overlapping. Pseudostome often with a thin organic rim (the size of the pseudostome is unspecified in the description). L = 100–150 (174) μm, B = 60–100 (120) μm.

Differential diagnosis: *Quadrulella quadrigera* may be confused with *Q. scutellata*, from which it differs by: 1) its more ovoid test (as opposed to piriform in *Q. scutellata*), 2) the shape of the pseudostome (pseudostome rim formed by scales, and sometimes indented depending on their shape and orientation in *Q. scutellata* vs. pseudostome often with a thin organic lip in *Q. quadrigera*), and 3) the arrangement of plates (internal platelets reinforce the test at the corners of the large plates in *Q. scutellata*, with often overlapping external plates, while such plates are missing in *Q. quadrigera*).

Type locality: Determined as Mahé Island, Seychelles by WAILES (1912a), stating "In the Seychelles it is found without the small covering-plates, but having an admixture, usually 5 to 10 per cent., of circular discs in the composition of the tests". The type specimen (Fig. 5 in DEFLANDRE (1936)) is from Mahé Island, Seychelles. Likely coordinates: -4.684031°, 55.502018°.

Type specimen: Not provided. We declare Pl. XI, Fig. 5 by DEFLANDRE (1936), reproduced here as Fig. 95C, as the type.

Etymology: Unspecified, but in Latin "quādrī" is the genitive of "quādrum", meaning "square", likely referring to the quadrangular shape of the

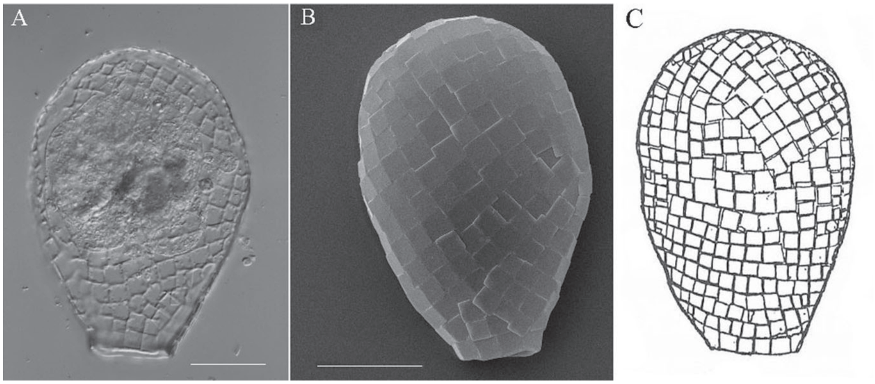

Fig. 95. *Quadrulella quadrigera*: (A) LM and (B) SEM images of specimens from Australia, (C) Original drawing of *Q. quadrigera* from DEFLANDRE (1936). (A) represents a stack of combined individual images (extended depth focus imaging). Scale bars = 40 µm. Images modified from KOSAKYAN et al. (2016).

plates, whereas the verb "gerō" means "to carry, bear, wear (as clothing), or possess (as traits)". Thus, "quadrigera" can roughly translate to "that wears or bears squares".

Habitat: Mosses.

Geographical distribution: North America: Canada (DE PUYTORAC et al., 1972), USA (DEFLANDRE, 1936); South America: Bolivia (CERDA, 1986), Ecuador (KRASHEVSKA et al., 2007), Guadeloupe (BONNET, 1977); Africa: Congo (GAUTHIER-LIÈVRE & THOMAS, 1961), Guinea (GOLEMANSKY, 1962), Seychelles (DEFLANDRE, 1936); Asia: Java (BONNET, 1992), (Sulawesi, BONNET, 1992), Malaysia (CHARDEZ, 1978), Russia (Siberia; RAKHLEEVA, 2002), Thailand (BONNET, 1987; GOLEMANSKY & TODOROV, 2000), Vietnam (BALIK, 1995); Australasia: Australia (KOSAKYAN et al., 2016), New Guinea (Papua New Guinea, BONNET, 1980a; Irian Jaya, BONNET, 1992).

Remarks: GAUTHIER-LIÈVRE & THOMAS (1961), found this species in *Cyperus papyrus* swamps between Dolise and Kimongo, as well as in the *Sphagnum* bogs with Xiridaceae between Brazzaville and Kinkala, Republic of Congo. As all observed tests were notably narrower than the typical form with a comparatively narrower pseudostome, the authors described a new variety, *Q. africana*. L = 110–115 µm, B = 55–65 µm, P = 20–25 µm. As it is an infra-subspecific name published after 1960, and thus unavailable according to ICZN Art. 45.6.3, we have listed it here together with the synonymous names. Further work on genus *Quadrulella* in Africa and elsewhere will almost certainly reveal more diversity, including *Q. quadrigera* var. *africana*, that could well represent a distinct species.

Quadrulella scutellata Wailes, 1912

1879 *Quadrulella symmetrica* pars Leidy, Rep. US Geol. Surv. Terr. 12, Pl. 24, Fig. 25 (Note: Smaller plates overlapping at the corners of the larger plates are missing in the figure, but

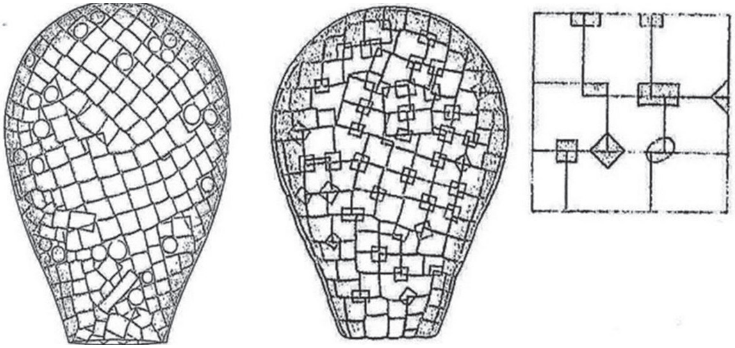

Fig. 96. *Quadrulella scutellata*: Original drawing from WAILES (1912): two individuals with different test compositions, and a higher magnification view of the scale plate placements from Seychelles (left) and New Jersey (right).

otherwise it corresponds to the description of *Q. scutellata*).

1912 *Quadrulella scutellata* Wailes, 1912, J. Linn. Soc. Zool. 32: 139 (Pl. 12, Figs. 11–12, 43, original drawings).

Description (based on the original publication): Test moderately large, piriform in broad view, compressed. Test hyaline, composed of small rectangular plates arranged in irregular rows, yet smaller rectangular plates may be superimposed at the junctions of the larger. Pseudostome margin often irregular. L = 120–135 µm (HOOGENRAAD & DE GROOT, 1940: up to 153), B = 74–90 µm, P = 24–30 µm (HOOGENRAAD & DE GROOT, 1940: up to 33).

Differential diagnosis: See Differential diagnosis under *Quadrulella quadrigera*.

Type locality: Lakehurst, New Jersey, USA. WAILES (1912a) mentioned both the Seychelles and New Jersey; however, he wrote, “In the Seychelles it is found without the small covering-plates, but having an admixture, usually 5 to 10 per cent., of circular discs in the composition of the tests”. This morphotype was established as a separate species by DEFLANDRE (1936) under the name *Q. quadrigera*. Therefore, the New Jersey location remains the type locality for *Q. scutellata*. Likely coordinates: 40.009867°, -74.33505°.

Type specimen: Not provided. We declare Fig. 25 Pl. 24 of LEIDY (1879), reproduced here as Fig. 97, as the type. We give priority to this record despite the lack of smaller plates in the illustration, as these plates may have been overlooked, or simply omitted from the final illustration. We prefer to give precedence to the older of the two possible records, considering the distance between the two localities. It is also possible that the Seychelles taxon (Fig. 43 in WAILES, 1912a), reproduced here as Fig. 96, represents a separate species.

Etymology: Not provided, although “scutellate” in Latin means “saucer-shaped” or “small shield”, possibly referring to the plates (even though they are quadrangular, not circular or ovoid).

Habitat: *Sphagnum* and wet mosses.

Geographical distribution: North America: Canada (BEYENS & CHARDEZ, 1995), USA

(Leidy, 1879, but see Remarks; WAILES, 1912a); South America: Bolivia (CERDA, 1986); Asia: Java (HOOGENRAAD & DE GROOT, 1940a), Sumatra (HOOGENRAAD & DE GROOT, 1940a), Philippines (BONNET, 1990); Australasia: New Guinea (Irian Jaya (BONNET, 1992); Europe: Hungary (problematic record from Heviz by GROSPIETSCH, 1982, lacking illustration; TÖRÖK, 1998); Pacific Islands: Galápagos (FOURNIER et al., 2016).

Remarks: WAILES (1912a) noted that the test of the individuals collected from Lakehurst, New Jersey, possessed small platelets, thus resembling *Argynnia vitrea*. In the Seychelles, WAILES found individuals without small covering plates but having an admixture (usually 5–10%) of circular discs in the composition of the tests (see Fig. 96).

This species also resembles the illustrations of *Quadrulella symmetrica* by LEIDY (1879, Fig. 25, Pl. 24, see Fig. 97 here), which differs from the other illustrations of *Q. symmetrica* in shape and test structure. L = 140 µm, B = 100 µm, P = 30 µm.

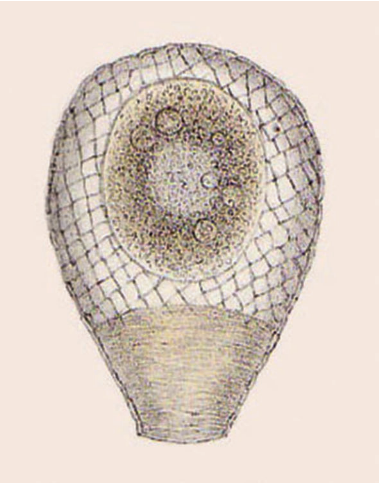

Fig. 97. *Quadrulella symmetrica*: Illustration from LEIDY (1879, Pl. 24, Fig. 25). This illustration resembles *Q. scutellata*, but lacks the characteristic small plates.

Quadrulella symmetrica (Wallich, 1863) Cockerell, 1909

1863 *Difflugia proteiformis* var. *symmetrica* Wallich, An. Mag. Nat. Hist. xii: 458«

1863 *Difflugia pyriformis* var. *symmetrica* Wallich, An. Mag. Nat. Hist. xiii: 232 (synonymous name, overlapping morphology).

1864 *Difflugia symmetrica* Wallich, An. Mag. Nat. Hist. xiii: 245 (new synonym).

1871 *Difflugia assulata* Ehrenberg, Abh. Ak. Wis. Berlin: 249 (new synonym).

1871 *Assulina assulata* Ehrenberg, Abh. Ak. Wis. Berlin: 246 (new synonym).

1871 *Difflugia carolensis* Ehrenberg, Abh. Ak. Wis. Berlin: 250 (new synonym).

1871 *Assulina leptolepis* Ehrenberg, Abh. Ak. Wis. Berlin: 246, 274 (new synonym).

1875 *Quadrula symmetrica* Schulze, Arch. Mik. Anat.: 329. (homonym)

1909 *Quadrulella symmetrica* Wallich, 1864 - Cockerell, Zool. Anzig. 34: 565 (establishment of genus *Quadrulella* and assignment of *Q. symmetrica* Wallich, 1864, as the type species).

1966 *Quadrulella symmetrica* var. islandica Decloitre, Vidensk. Medd. Dansk. Naturh. Foren. 129: 70 [Infrasubspecific (not available) name: var. published after 1960, ICZN 45.6.3].

2016 *Quadrulella symmetrica* Wallich, 1864 - sensu Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell & Lara 2016, in KOSAKYAN et al., 2016, Cladistics 32: 606–623 (revision of genus *Quadrulella* based on molecular data, and improvement of the taxonomic concept for *Q. symmetrica*).

Icon.: WALLICH, 1863, Pl. X, Fig. 16; EHRENBERG, 1871, taf. Ii, Figs. 4–5; SCHULZE, 1875, taf. xviii, Figs. 1–6; OGDEN & HEDLEY, 1980, Pl. 47, Figs. A–D; MEISTERFELD, 2002, Fig. 57; LUKETA, 2015b, Figs. 2-4; LUKETA, 2017e, Figs. 4–5, 8; TODOROV & BANKOV, 2019, Fig. 81.

Description: Test ovoid or piriform in broad view, with a rounded posterior end, compressed towards the pseudostome. Test colorless, composed of square plates, regularly arranged in rows. Plates smaller near the pseudostome (4–5 µm), gradually getting larger towards posterior end of the test (≥ 10–12 µm). Pseudostome often curved and surrounded with a tiny organic lip. L = 72–85 µm, B = 40–46 µm, P = 20–23 µm.

Differential diagnosis: *Quadrulella symmetrica* can be confused with *Q. variabilis*, from which it differs by its larger square plates and larger dimensions. It is also similar to *Q. madibai*, which is more elongated, and has a slimmer outline. For more detail, see the morphological notes in Remarks below.

Type locality: Hampstead pools, England. Likely coordinates: 51.563836°, -0.170028°.

Type specimen: WALLICH (1863) did not provide a type specimen. KOSAKYAN et al. (2016) declared Fig. 16 from WALLICH (1863) as the type; however, the illustration is of low quality, nor does it fully represent the typical *Q. symmetrica* outline; thus, we suggest Fig. 98A here, as a neotype.

Etymology: Unspecified. Most likely in reference to the symmetry and arrangement of the square plates. The illustration given by WALLICH (1863; Fig. 16), reproduced here as Fig. 98B, shows plates arranged in parallel lines to the long axis of the shell, but this drawing is most likely inaccurate.

Habitat: *Sphagnum* and other wet mosses in fens, water streams in rainforests, also in humus.

Geographical distribution: Found on all continents, except Antarctica.

Remarks: The most common species of the genus; indeed, almost all *Quadrulella* findings in Europe were assigned to this species or its infraspecific taxa (but see *Q. tropica*, Fig. 187).

KOSAKYAN et al. (2016) conducted a phylogenetic study (using mt-COI gene sequences) on Q. symmetrica individuals collected in Europe, Canada, and Africa. Detailed morphological and molecular observations showed that *Q. symmetrica* is indeed a species complex, and based on the available molecular and morphological data, *Q. symmetrica* was split into three distinct species:

1) *Q. symmetrica sensu str.* – larger test and scales: L = 72–85 µm, B = 40–46 µm, scales = 10–12 µm;
2) *Q. variabilis* – smaller test and scales: L = 66–69 (96) µm, B = 35–40.5 (45) µm, scales ≤ 7–9 µm; and
3) *Q. madibai* – large-scaled species with a slimmer outline; L/B = 2.2–2.3 vs. 1.7–1.9 in *Q. symmetrica sensu str.*; a sister group of *Q. symmetrica sensu str.*

Several additional specimens from the Holarctic realm, differing strongly in plate shape, were barcoded (KOSAKYAN et al., 2012, 2016). Molecular data clearly indicate these represent a new species, which should be formally described based on detailed morphometric and molecular characterization.

Several subspecies of *Q. symmetrica* have been described. We are listing only one here—see *Q. symmetrica* curvata below. The rest are included in the list of *inquirenda* species. Whether these infraspecific taxa result from phenotypic plasticity or represent distinct taxonomic units (likely given our results mentioned above) must be determined by further combined morphological and molecular analyses.

Quadrulella symmetrica var. *islandica* was described by DECLOITRE (1966, Fig. 6). It differs from the type by the presence of a line of small plates running parallel to the pseudostome; however, DECLOITRE did not provide any information on how many individuals of this type he had observed. Regardless, since this variety was described after 1960, this name was not available in accordance with ICZN Art. 45.6.3, and it is listed together with synonymous names.

Quadrulella symmetrica var. *genuina* is the type variety and therefore corresponds to *Q. symmetrica symmetrica.*

Quadrulella symmetrica curvata Wailes, 1912

1912 *Quadrulella symmetrica curvata* (as *Q. symmetrica* var. *curvata*) Wailes, J. Linn. Soc. Zool. 32: 142, Pl. 12, Fig. 21.

Description: Pseudostome polygonal, formed by 6–7 plates. L = 80–100 µm, B = 33–45 µm, P = 11–16 µm.

Differential diagnosis: This subspecies differs from the type by its curved neck (as in *Cyphoderia*).

Type locality: Penney's Pond, Good Ground, Long Island, USA. Likely coordinates: 40.897154°, -72.555449°.

Type specimen: None. We declare Plate 12, Fig. 1 from WAILES (1912), reproduced here as Fig. 97C as the type.

Etymology: The name of this subspecies refers to its shape.

Habitat: Not specified, likely water or mosses from the side of the pond.

Geographical distribution: North America: USA; South America: Brazil

Remarks: The original description mentioned that the degree of test curvature is subject to variability.

Quadrulella texcalense Pérez-Juárez, Serrano-Vázquez, & Lara, 2017

2017 *Quadrulella texcalense* Pérez-Juárez, Serrano-Vázquez & Lara, in Pérez-Juárez et al., Eur. J. Protistol. 61: 253–264, Fig. 2.

Description (based on the original publication): Test piriform in broad view, with a rounded posterior end (posterior 1/3rd of the test); sides converging towards the pseudostome, either straight, slightly convex, or slightly concave, compressed, and transparent. Test composed of square endogenous plates (size 3.3–6.5 µm in a single cell), typically regularly arranged. Pseudostome convex in broad view, ovoid in frontal view, with an organic rim. Test dimensions based on 21 individuals: L = 97–126 µm, B = 53–68 µm, P = 24–32 µm.

Differential diagnosis: The size of *Quadrulella texcalense* exceeds that of all other congeneric taxa, save for *Q. scutellata*, *Q. quadrigera*, and *Q. longicollis*. It differs from *Q. scutellata* and *Q. quadrigera* by its more regular plates. The size of its plates and its general piriform shape reminds of the much smaller *Q. variabilis*. Differs from *Q. longicollis* by its general test outline (*Q. longicollis* has a more elongated neck), and its ecology (see remarks on Ecology below).

Type locality: *Quadrulella texcalense* was found on the Northeast side of Cerro Marrubio, San Antonio Texcala, Puebla State, Mexico. Likely coordinates: 18.189791°, -97.247362°; Elevation, ca. 2030–2360 m.a.s.l..

Type specimen: One permanent preparation containing *Q. texcalense* cells embedded in Euparal was deposited at the Museo de Historia Natural, Secretaría del Medio Ambiente, Mexico City, Mexico (no. MHN-2757). Dried mosses containing *Q. texcalense* are conserved in the Laboratorio de Ecología Microbiana, in the Unidad de Biotecnología y Prototipos, Facultad de Estudios Superiores, Iztacala of the Universidad Nacional Autónoma de México at

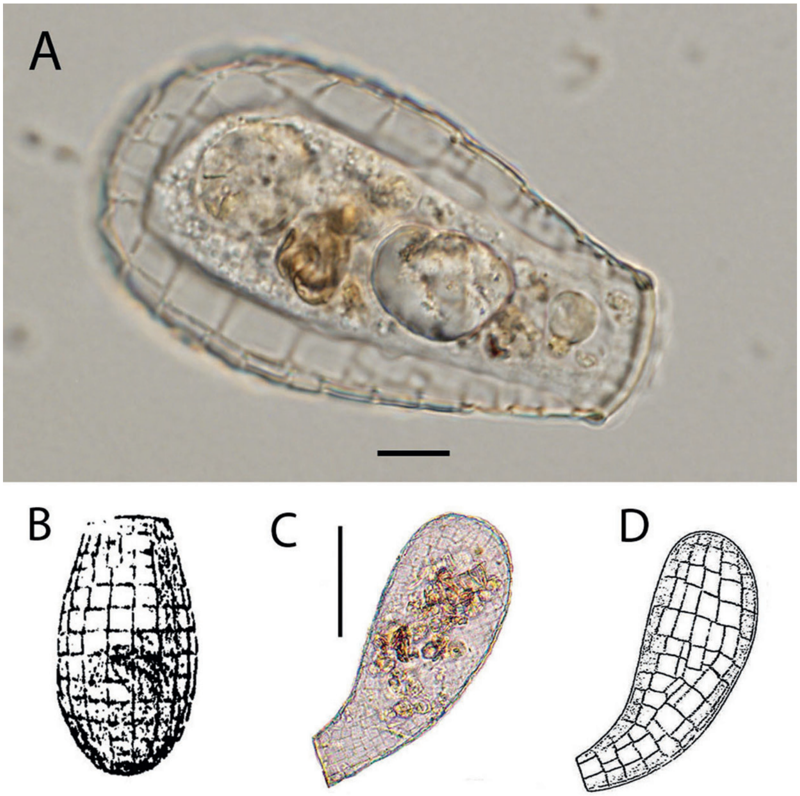

Fig. 98. *Quadrulella symmetrica*: (A) LM image of *Q. symmetrica sensu str.* from Switzerland, (B) Original drawing of *Q. symmetrica* from WALLICH (1863), (C) LM image of *Q. symmetrica curvata* from Brazil, (D) Original drawing of *Q. symmetrica curvata* from WAILES (1912). Scale bars: A = 10 µm, B = 50 µm. Images by: (A) Anush Kosakyan, and (C) Maria Beatriz Gomes & Souza.

Iztacala, Mexico City (nos. vmra-cbs 115–119). Sequences of the COI gene for *Q. texcalense* (560 bp) were deposited in GenBank (no. MF581577). The new scientific name (*Quadrulella texcalense*) was registered in ZooBank lsid: zoobank.org:pub:22CBF523-07AD-44EB-9876-64ABC258C85D.

Etymology: The species name was assigned as a tribute to the inhabitants of San Antonio Texcala. "Texcala" means "place where water springs from rock" in Nahuatl (the ancient indigenous language of this region). According to the oral history of this locality, this word refers to the "Onyx Waterfall" located on the cliff, a main site of onyx extraction. Here, there is a natural spring of salt water that feeds the local salt evaporation ponds.

Habitat: Sedimentary rocks (limestones and conglomerates) that present evidence of water erosion.

Fig. 99. *Quadrulella texcalense*: LM from Mexico, LM image by Horacio Pérez-Juárez. Scale bar = 30 µm.

Geographical distribution: Mexico (PÉREZ-JUÁREZ et al., 2017).

Remarks: PÉREZ-JUÁREZ et al. (2017) discussed in detail the molecular phylogeny and unusual ecology of this species. Although *Q. texcalense* branches with *Q. variabilis*, with relatively low support its placement in genus *Quadrulella* is considered correct. The sequencing of additional markers would clarify the phylogenetic relationships among congeneric taxa.

The presence of *Q. texcalense* in an arid habitat is at odds with the known ecology of all other species in genus *Quadrulella* which are associated with aquatic and wetland habitats. Even stranger is the fact that *Q. texcalense* is comparatively large, while the general trend in testate amoebae is for test size to decrease in drier conditions (FOURNIER et al., 2012). This apparent contradiction may, however, be explained by the association of *Q. texcalense* with mosses of the family Pottiaceae, which are well adapted to arid environments, accumulating water from the air and dew. Accordingly, these mosses create wet micro-habitats perfectly suited for the development of aquatic micro-organisms, such as *Q. texcalense*. This finding should stimulate protistologists to search for new species in such unusual habitats that are typically under-sampled.

Quadrulella tropica Wailes, 1912

1912 *Quadrulella tropica* Wailes, 1912, J. Linn. Soc. London Zool.: 140, Figs. 13–14, 44.

1959 *Quadrulella debonti* Van Oye, Hydrobiologia 13 (3): 256–257 (overlapping morphology).

Icon.: WAILES, 1912a, Pl. 12, Figs. 13–14, 44; GAUTHIER-LIÈVRE, 1957, Fig. 2A–B.

Description (based on the original publication): Test piriform in broad view, compressed, hyaline, composed of rectangular plates. Arrangement of plates more regular (diagonally) near the fundus than near the pseudostome. In profile, pseudostome dilated with a clear notch (Fig. 100). According to the original description, pseudostome almost circular in frontal view. L = 74–93 µm, B = 45–60 µm, P = 20–30 µm.

Differential diagnosis: Test outline in broad view somewhat similar to that of *Alabasta militaris*, with a less curved and wider pseudostome. The structure and general appearance are very similar to those of *Quadrulella scutellata*, except that the reinforcement plates are missing.

Type locality: Sarawak Borneo, Indonesia. Likely coordinates: 3.216868°, 113.847674°.

Type specimen: Not provided. We declare Figs. 13–14, representing the same individual by WAILES (1912a), and reproduced here as Fig. 100B, as the type.

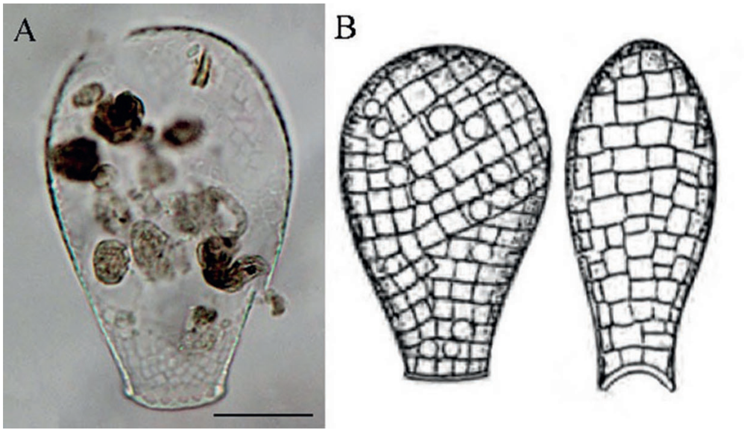

Fig. 100. *Quadrulella tropica*: (A) LM image of an individual from the Netherlands (by Siemensma), (B) Original drawings from WAILES (1912): broad and profile views. Scale bar = 20 µm.

Etymology: Not provided, but the name of the species almost certainly refers to the tropical region where it was found.

Habitat: Mosses, humus.

Geographical distribution: South America: Argentina (VUCETICH, 1983); Brazil (VELHO et al., 2001), Martinique (BONNET, 1977), Peru (WAILES, 1912a); Africa: Republic of Congo (GAUTHIER-LIÈVRE, 1957; MAES et al., 1972), Guinea (GOLEMANSKY, 1962; GRACIA, 1963), Ivory Coast (BONNET, 1976, 1978), Senegal (GAUTHIER-LIÈVRE, 1953); Asia: Borneo (Sarawak, Malaysia) (WAILES, 1912a), Java (HOOGENRAAD & DE GROOT, 1940a), Philippines (BONNET, 1980b), Sumatra (HOOGENRAAD & DE GROOT, 1940a); Australasia: New Guinea (Irian Jaya (BONNET, 1992); Indian Ocean: Seychelles (WAILES, 1912a; KORGANOVA, 1990); Europe: the Netherlands (SIEMENSMA, Microworld), Spain (GRACIA, 1971).

Remarks: GAUTHIER-LIÈVRE (1957) reported this species from mosses mixed with Trentepohlia lichens growing on an Eleis trunk in Ewo, Republic of Congo. The observed specimens were slightly smaller in size (L = 68–80 µm, B = 45–50 µm) and with circular plates in the neck region.

Quadrulella tubulata (Gauthier-Lièvre, 1953) Gauthier-Lièvre & Thomas, 1961

1953 *Quadrulella symmetrica* var. *tubulata* Gauthier-Lièvre, Soc. Hist. Nat. Afr. Nord: 330 (Fig. 20).

1961 *Quadrulella tubulata* Gauthier-Lièvre, 1953 – Gauthier-Lièvre & Thomas Bul. Soc. Hist. Nat. Afrique Nord 52: 44 (elevation to the species level).

1967 *Quadrulella tubulata* var. *cylindrica* Chardez, 1967, Bull. Rech. Agron. Gembloux: 240 (Pl. 2, Fig. 8–11) – [Infrasubspecific (not available) name: var. published after 1960, ICZN Art. 45.6.3].

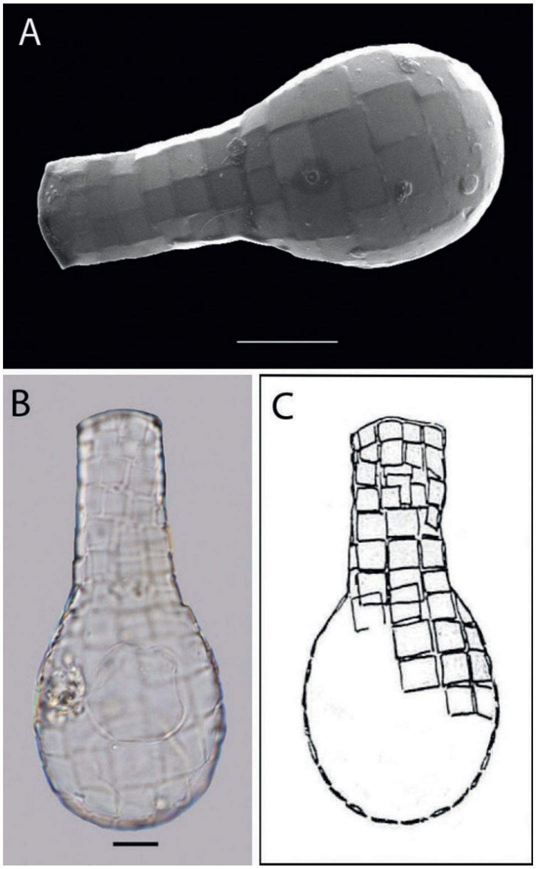

Fig. 101. *Quadrulella tubulata*: (A & B) SEM and LM images of a specimen from South Africa, (C) Original drawing from GAUTHIER-LIÈVRE (1953). Scale bars: A = 20 µm, and B = 10 µm. Images (A & B) by Anush Kosakyan.

Description: Test lageniform or bottle-shaped in broad view, with a distinct elongated neck, parallel sides (ca. 40 µm long), and a rounded fundus. Test composed of square or rectangular plates arranged either regularly or slightly irregularly. Pseudostome curved with a thin organic rim. L = 70–95 (100) µm, B = 42–45 (50) µm, P = 20 µm (our observations A. Kosakyan & E. Mitchell).

Differential diagnosis: Can be confused with *Q. longicollis*, which is > 100 µm, an elongated form of *Q. varabilis*. See Remarks for detailed discussion on similarity between these two species.

Type locality: Ivory Coast, approximately half way between Man and Kouibly. Likely coordinates: 7.292962°, -7.405318°.

Type specimen: Not provided. We declare Fig. 20 by GAUTHIER-LIÈVRE (1953), reproduced here as Fig. 101C, as the type.

Etymology: The species name refers to the tubular shape of the neck of the test.

Habitat: Aquatic (freshwater).

Geographical distribution: South America: Argentina (VUCETICH & LOPRETTO, 1995), Brazil (WALKER, 1982; GOMES E SOUZA, 2008); Africa: Congo (GAUTHIER-LIÈVRE, 1954), Guinea (GOLEMANSKY, 1962), Ivory Coast (GAUTHIER-LIÈVRE, 1953), Madagascar (MEISTERFELD, unpubl.), South Africa (KOSAKYAN et al., unpubl.); Europe: Bulgaria (GOLEMANSKY, 1974), Romania (GODEANU, 1981), Spain (GRACIA, 1972); Australasia: New Guinea (Papua New Guinea, GRACIA, 1968).

Remarks: This species was first considered as a variety of *Q. symmetrica* until GAUTHIER-LIÈVRE & THOMAS (1961) elevated it to the species level. Even if *Q. tubulata* differs from *Q. variabilis* by its dimensions, it is still possible to find intermediate forms. *Quadrulella tubulata* has a very distinct neck with parallel sides, whereas in *Q. variabilis*, the sides gradually taper towards the pseudostome. GAUTHIER-LIÈVRE (1953) reported *Q. tubulat*a with small scales from Ivory Coast and with large scales from Congo, whereas *Q. variabilis* always has small scales. As plate size is considered as an important taxonomic criterion, it is probable that these two forms represent distinct species. Accordingly, it may be correct to consider the morphotype with very small plates as *Q. tubulata*, as it morphologically differs the most from the other species. KOSAKYAN et al. (2016) suggested that *Q. tubulata* may even belong to a different genus (see p. 167 for more details).

CHARDEZ (1967) described var. *cylindrica* from Belgium (Wallones bogs near a locality known as Marie-Thérèse), which differs from the type by its circular cross section and linear pseudostome; however, CHARDEZ also mentioned that sometimes only the neck is slightly compressed. We believe this to be an insufficient differential character to warrant consideration as an independent taxon. Further, it is a var. described after 1960; thus, we are considering it an infrasubspecific taxa and listing it within the synonymous names (ICZN 45“6.3).

Quadrulella variabilis Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

2016 *Quadrulella variabilis* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, in KOSAKYAN et al., 2016, Cladistics 32: 606–623.

? 1882 *Quadrulella symmetrica* var. *longicollis* Taránek, Abh. König. Böhm. Ges. d. Wiss. IV: 48 (Figs. 2, 7D) pars! (but see Remarks below).

? 1882 *Quadrulella longicollis* Taránek, in KOSAKYAN et al., 2012, Protist 163: 15 (Fig. 5D; see Remarks below).

Description: Test variable in general shape, from ovoid or piriform to elongated-piriform in broad view, with a rounded posterior end, compressed towards the pseudostome (similar to that of *Q. symmetrica*) and sometimes with an elongated neck. Test colourless, composed of square plates, regularly arranged in rows. Plates smaller near the pseudostome region (3–4 µm), gradually becoming larger towards the posterior end of the test (≤ 7–9 µm). Pseudostome often curved with a very thin organic rim. L = 66–69 (96) µm, B = 35–40.5 (45) µm, P = 17–18.5 µm.

Differential diagnosis: See Differential diagnosis under *Q. symmetrica*, *Q. tubulata*, and *Q. longicollis*.

Type locality: Le Cachot bog, Vallee de la Brévine, Canton of Neuchatel, Switzerland (47.00556°, 6.665°).

Type specimen: Figs. 2 and 8D as paratypes from KOSAKYAN et al. (2016).

Etymology: The species refers to the variability in neck length.

Habitat: *Sphagnum* mosses, other mosses, and aquatic environments.

Geographical distribution: Europe: Switzerland (KOSAKYAN et al., 2016); Bulgaria (TODOROV & BANKOV, 2019).

Remarks: *Quadrulella symmetrica* was believed to be a single species until KOSAKYAN et al. (2016) revealed unexpected morphological and genetic variability. The authors demonstrated that this taxon includes at least three genetically distinct species, all of which were well supported by morphological characters: *Q. symmetrica sensu str.* with large scales, *Q. madibai* is an elongated species with large scales, and *Q. variabilis* with small scales (for further details, see notes on *Q. symmetrica*, p. 183). Molecular data (mtCOI) showed that the sequence of *Q. longicollis* Taránek 1882 was identical to that of the small scaled *Q. variabilis*. *Quadrulella longicollis* was initially described as a variety of *Q. symmetrica*, differing by its elongated neck; however, *Q. symmetrica longicollis* can be quite variable, as ≥ 3 forms have been described: *Q. symmetrica* var. *longicollis* f. *lanceolata* Gauthier-Lièvre, 1952, f. *major* Hoogenraad & de Groot, and f. *minor* Hoogenraad & de Groot (mentioned in GAUTHIER-LIÈVRE & THOMAS, 1961). Thus, *Q. variabilis* includes small-scaled species with variable neck lengths. Further, the authors (KOSAKYAN et al., 2016) did not rule out the possibility that the specimen they studied in 2012 may not correspond to the typical *Q. longicollis*. They considered the

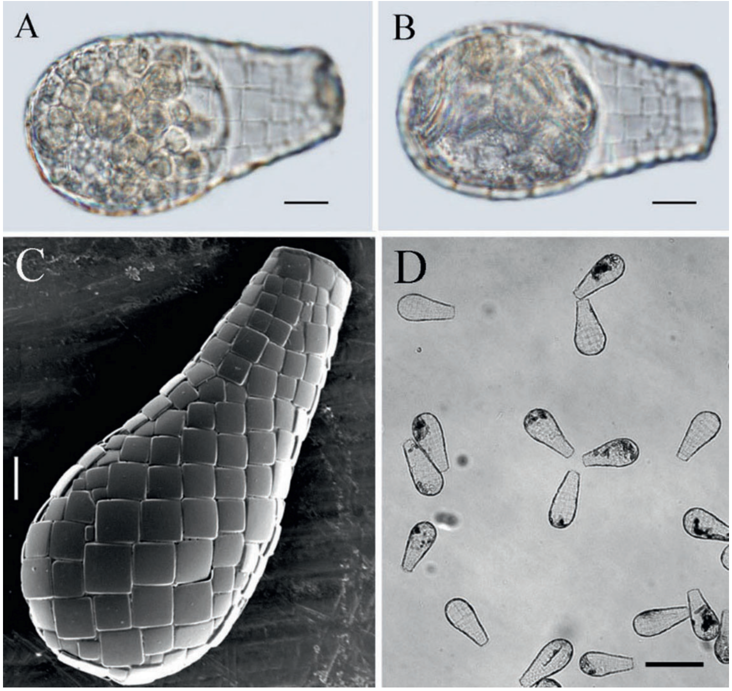

Fig. 102. *Quadrulella variabilis*: (A & B) LM image of pyriform cells from Switzerland, (C) SEM image of elongated-pyriform cells from Bulgaria, (D) LM image of elongated-pyriform shapes of specimens from Bulgaria. Scale bars: A–C = 10 µm, D = 100 µm. Images by: (A & B) Anush Kosakyan, and (C & D) Milcho Todorov.

typical *Q. longicollis* to being larger L > 100 µm, thereby excluding the sequenced specimen (thus named *Q. variabilis*). See also Remarks under *Q. longicollis* (p. 178).

Quadrulella vas Cerda, 1986

1986 *Quadrulella vas* Cerda, Cordillera Real Andina: 300 (p. 301–303).

1986 *Quadrulella vas* var. *longicollis* Cerda, La Cordillera Real Andina: 304 (Infrasubspecific (not available) name: var. published after 1960, ICZN Art. 45.6.3).

1986 *Quadrulella vas* var. *oblicua* Cerda, La Cordillera Real Andina: 305 (Infrasubspecific (not available) name: var. published after 1960, ICZN Art. 45.6.3).

Description (based on the original publication with some questionable passages removed – see Remarks): Test yellowish, compressed, elongated, with a rounded fundus, and a well-separated neck in broad view. Neck length ca. 1/3rd of whole test, with a clear constriction at its base (as in *Apodera vas*), giving the impression of a

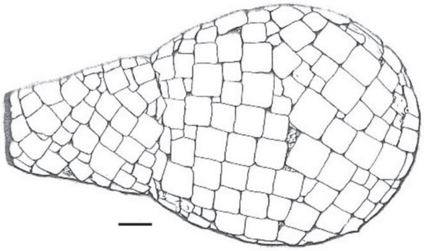

Fig. 103. *Quadrulella vas*: Original drawing from CERDA (1986). Scale bar = 10 µm.

bicameral test. Plates generally not overlapping, except along the constriction at the base of the neck. Pseudostome with an organic lip. L = 250–360 µm, B = 150–170 µm.

Differential diagnosis: Very similar to *Q. constricta*, from which it differs by its larger dimensions (L = 250–360 µm, B = 150–170 µm in *Q. vas* vs. L = 168–192 µm, B = 83–104 µm in *Q. constricta*).

Type locality: Huayna Potosi (and Chacaltaya), Peru. Coordinates: -16.297481°, -68.156323°; Elevation, ca. 4820 m.a.s.l..

Type specimen: Not provided. We declare the figure on the book cover from CERDA (1986), reproduced here as Fig. 103, as the type.

Etymology: The species name derives from the name of the species “*Apodera vas*”, which shares a similar test shape.

Habitat: Mosses.

Geographical distribution: Peru (CERDA, 1986).

Remarks: KOSAKYAN et al. (2016) conducted a phylogenetic study of genus Quadrulella based on mt-COI sequence data, suggesting the inclusion of *Q. vas* into the list of *incertae sedis* species, as it may represent a separate genus (see p. 167).

Two infraspecific taxa were described from the same location by the same author, both considerably smaller than the type: *Q. vas* var. *longicollis*, which differs from the type by it elongated neck (L = 150–170 µm, B = 80–90 µm), and *Q. vas*. var. *oblicua*, which differs from the type by its bent neck, and is very similar to *Apodera (Nebela) vas* var. *oblicua* described by GROSPIETSCH (1971), from which it differs by the presence of characteristic quadric plates. L = 130 µm, B = 80 µm. Both varieties were described after 1960 and are thus treated as infrasubspecific names (ICZN Art. 45.6.3).

8. LIST AND NOTES TO *INCERTAE SEDIS* NAMES

This list includes those species with detailed, clear descriptions and illustrations, thus representing true species; however, these species are characterized by a set of taxonomic characters corresponding to more than one genus and thus cannot be placed unambiguously into any given genus. Further detailed studies, including molecular data analyses, are therefore necessary to accurately determine to which genus they belong. Many of these species were included in the taxonomic keys above to facilitate with the identification process. Here, we list 13 *incertae sedis* names (the total would be 17 if the four species of the *Nebela bipes* - *bicornis* - *triangulata* - *cornuta* complex are considered separately).

8.1. *Incertae sedis* taxa from genus *Hyalosphenia*

Hyalosphenia nobilis Cash, 1909

1909 *Hyalosphenia nobilis* Cash, in CASH & HOPKINSON, 1909, Brit. Freshw. Rhiz. (Printed for the Ray. Soc.), ": 92.

? 1909 *Nebela nobilis* Cash, in DEFLANDRE (1936) Annales de Protistologie 5: p. 282 (see Remarks below).

Icon.: CASH et al., 1909, Pl. XXV, Figs. 1–3; Deflandre, 1936, Figs. 156–158; BEYENS et al., 1986, Pl. III, Fig.7; CHARDEZ, 1990a, Fig. 2.

Description: Test lageniform in broad view, with an elliptical body and long cylindrical neck (as in genus *Padaungiella*). In transverse view, test uniformly rounded and its entire surface pitted with irregularly-formed depressions. Test transparent. L = 200–216 µm, B = 90–112 µm, P = 30–43 µm, Lneck = 60–70 µm (BEYENS et al., 1986; CHARDEZ 1990a). Pseudostome slightly undulated.

Differential diagnosis: Differs from other *Hyalosphenia* species by its rough surface owing to the presence of the pits.

Type locality: Knutsford Moor, Cheshire, UK. Likely coordinates: 53.321364°, -2.35122°.

Type specimen: Not provided. We declare Pl. XXV, Fig. 1 by CASH et al. (1909), reproduced here as Fig. 104A, as the type.

Etymology: Not provided. The species name is likely derived from the Latin term "nobilis", meaning "remarkable", in reference to the extraordinary shape and composition of the test.

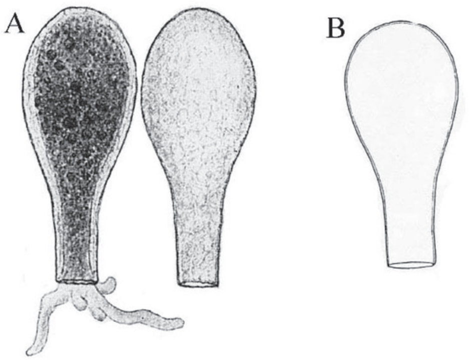

Fig. 104. *Hyalosphenia nobilis*: Original drawings, (A) Living and dead individuals from CASH (1909) and (B) *H. nobilis compressa* from PLAYFAIR (1918).

Habitat: Aquatic mosses (mainly *Aulacomnium palustre* (CASH & HOPKINSON, 1909)).

Geographical distribution: Asia: China (YANG et al., 2004), Japan (YAMAMOTO, 1981), Korea (CHUNG et al., 1992); Europe: Norway (BEYENS et al., 1986), Sweden (CHARDEZ, 1990a), UK (CASH et al., 1909; HARRIS, 1935, 1936).

Remarks: CASH et al. (1909) noted that the test was totally colourless and transparent, but the surface was rough and devoid of incrustation owing to the presence of the pits. Because the test differs strongly from those of other congeneric species, Cash first thought to place it within genus *Difflugia*, opting instead to assign it to genus *Hyalosphenia* based on its homogenous test; however, there is currently no general consensus among authors on the appropriate position of this species. The shape of the test and rough surface (as mentioned in the original description) call for the taxonomic reconsideration of this species using molecular tools.

One subspecific taxon is known for this species:

Hyalosphenia nobilis compressa Playfair, 1918

1918 *Hyalosphenia nobilis compressa* Playfair, Proc. Linn. Soc. New South Wales 42: 658 (Pl. 39, Fig. 1, original drawing).

Description: Body of the test somewhat compressed. L = 154–175 µm, B = 70 µm; Pseudostome circular, P = 27–30 µm.

Differential diagnosis: Differs from the type by its smaller size and the compression of the test.

Type locality: Coogee, Australia. Likely coordinates: -33.963079°, 151.262053°.

Type specimen: Not provided. We declare Fig. 1 by PAYFAIR (1918), reproduced here as Fig. 104B, as the type.

Etymology: The name refers to the compressed shape of the test.

Habitat: *Sphagnum* mosses.

Geographical distribution: Australasia: Australia (PLAYFAIR (1918).

Remarks: PLAYFAIR (1918) did not provide any information on test composition, but mentioned that the neck and pseudostome are circular.

Hyalosphenia sinuosa Cash, 1909

1909 *Hyalosphenia sinuosa* Cash, in CASH & HO PKINSON, Brit. Fr. Rhiz. 2: 91–92, Pl. XXIV, Figs. 15–16, 3–84.

? 1936 *Nebela sinuosa* Deflandre, Annales de Protistologie 5: p. 282 (see Remarks below).

Description (from the original description): Test in broad view elongated-piriform, compressed. Aboral end of the test semi-circular, with the sides tapering towards the truncated mouth. Test surface pitted with circular depressions giving the impression of a crenulated outline. Pits

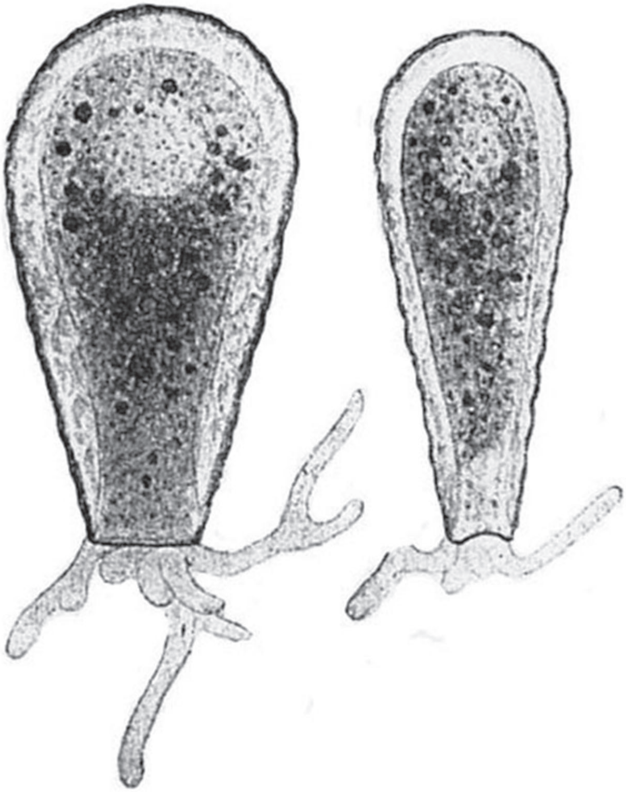

Fig. 105. *Hyalosphenia sinuosa*: Original drawing from CASH (1909): broad and profile views.

normally circular, but sometimes from very close appear crowded and sub-hexagonal. Test hyaline, colourless. Pseudostome forming a shallow notch in profile. The plasma, seen through the transparent membranous envelope, does not fill the cavity, but almost reaches the fundus, where the nucleus (visible as a circular pale space) is situated. Pseudopodia numerous, bifurcated, or simple. L = 200–236 µm, average B in profile = 65 µm.

Differential diagnosis: Differs from other *Hyalosphenia* species by its unusual test structure — i.e., rounded pitted test, giving an impression of roughness. *Longinebela meisterfeldi*, also has a waving edge, but is much smaller (L = 147–160 µm) and has a shell composed of recycled siliceous plates.

Type locality: Dunham, UK. Likely coordinates: 53.379917°, -2.397036°.

Type specimen: Not provided. We declare Fig. 15 by CASH et al. (1909), reproduced here as Fig. 105, as the type.

Etymology: Not provided. The species name likely refers to the rough structure of the test, since in Latin "sinuosa" means "having folds".

Habitat: Found in tufts of Philonotris fontana.

Geographical distribution: UK (CASH et al.,1909).

Remarks: This is a very rarely reported and problematic species. DEFLANDRE (1936) mentioned that it is difficult to include in genus *Hyalosphenia*, and it is more likely an insufficiently studied *Nebela*. Considering its test structure, one of the primary discriminating characteristics of genus *Hyalosphenia*, we are including this species into the list of *incertae sedis* species until further molecular and ultrastructural data can help clarify its true position within the family Hyalospheniidae.

8.2. *Incertae sedis* taxa from genus *Nebela*

Nebela barbata (Leidy, 1874) Leidy, 1876

1874 *Difflugia barbata* Leidy, Proc. Ac. Nat. Sc. 1874: 157 (Fig. 18, original drawing).

1876 *Nebela barbata* Leidy, Proc. Ac. Nat. Sc. 1876: 119 (evaluation of genus *Difflugia* and transfer to genus *Nebela*).

Icon.: LEIDY, 1879, Pl. XXIV, Figs. 14–17; OGDEN & HEDLEY, 1980, Pl. 33.

Description: Test elongated claviform in broad view, with a distinct elongated neck; laterally almost not compressed. Test transparent, composed of ovoid, circular, and elongated plates, with numerous short, fine spines projecting from the junctions of the plates. L = 80–148 μm, B = 38–62 μm, P = 10–23 μm. Pseudostome ovoid or almost circular, surrounded by a thick organic rim. Approximately, eight tooth-like structures protrude from the inner margin of the pseudostome towards the centre of the opening, more or less arranged equidistantly.

Differential diagnosis: Differs from all other hyalospheniids by the presence of fine spines projecting from the junctions of the plates.

Type locality: Absecon, NJ, USA. Likely coordinates: 39.426909°, -74.512855°.

Type specimen: Not provided. We declare Pl. XXIV, Fig. 14 by LEIDY (1879), reproduced here as Fig. 105F, as the type.

Etymology: The species name refers to the presence of the spines.

Habitat: *Sphagnum* mosses.

Geographical distribution: Africa: Congo (GAUTHIER-LIÈVRE, 1957), Republic of South Africa (KOSAKYAN et al., unpubl.), Sierra Leone (WAILES, 1912b); North America: Canada (WARNER, 2007), USA (LEIDY, 1876, 1879; WAILES, 1913; BOOTH, 2001), Puerto Rico (BAMFORTH, 2007); South America: Argentina (VUCETICH, 1974; VUCETICH & LOPRETTO, 1995), Chile (WILKINSON, 1990), Ecuador (KRASHEVSKA et al., 2007); Asia: China (YANG, 2004), Indonesia (HOOGENRAAD & DE GROOT, 1942), Japan (YAMAMOTO, 1981); Europe: British Isles (WEST, 1901; OGDEN & HEDLEY, 1980; WOODLAND et al., 1998), Czech Republic (BARTOŠ, 1954), France (DEFLANDRE, 1936; LUKETA, unpubl.), Iceland (DECLOITRE, 1965), the Netherlands (DE GRAAF, 1956), Norway (SCOURFIELD, 1897), Poland (MIECZAN, 2007), Russia (KASSIMOV, 1972), Spain (GRACIA, 1971, 1972); Pacific Ocean: Galápagos (FOURNIER et al., 2016); Antarctica (WILKINSON, 1994). Possibly cosmopolitan.

Remarks: This remarkable species is rather problematic, as its distinct morphological characters (presence of spines, structure of the

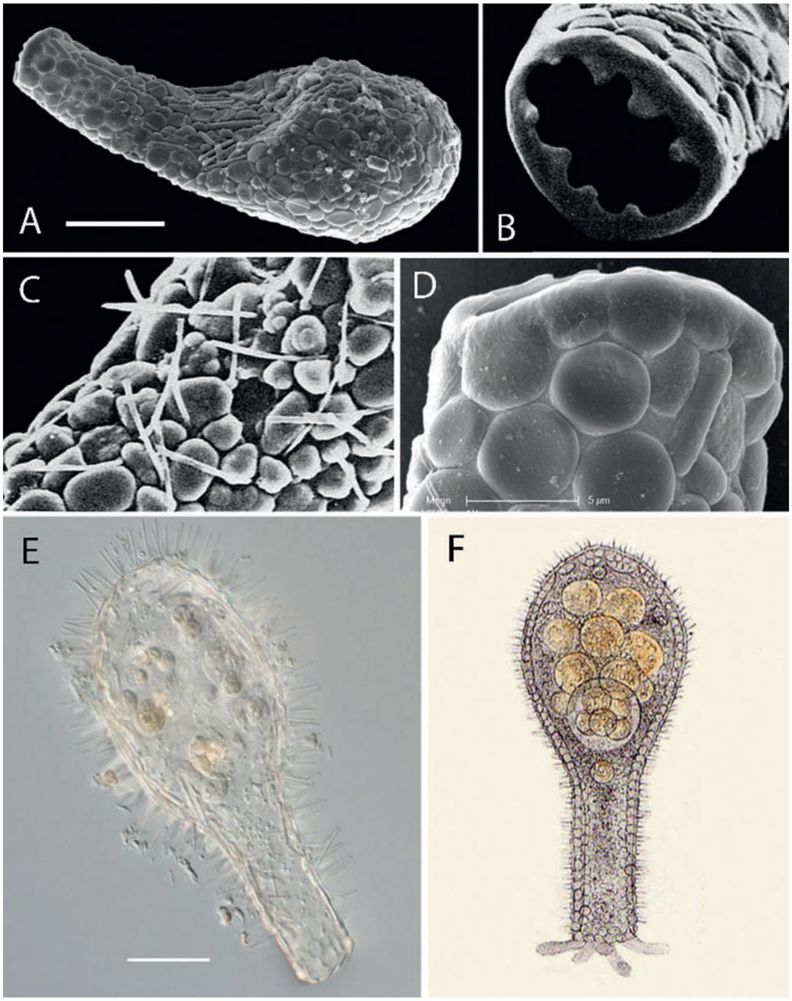

Fig. 106. *Nebela barbata*: (A) SEM image of a specimen from South Africa with a partly collapsed test; (B) Pseudostome of a specimen from the British Isles showing its tooth-like protrusions x 2000 (modified from OGDEN & HEDLEY, 1980); (C) Portion of the test for a specimen from the British Isles showing its spines x 2300 (modified from OGDEN & HEDLEY, 1980); (D) Higher magnification view of the pseudostome and test composition of a specimen from South Africa (same individual as in A); (E) LM image of a specimen from South Africa; (F) Original drawing of *N. barbata* from LEIDY (1879). Scale bars: A & E = 20 µm, D = 5 µm. Images (A, D, & E) by Anush Kosakyan.

pseudostome, very elongated and distinct neck) are atypical for the genus. It is very fragile, and the spines are easily lost during handling, especially during preparation for SEM observations (personal experience, KOSAKYAN; see SEM images in OGDEN & HEDLEY, 1980). CASH et al. (1909) also noted that the tooth-like protrusions on the pseudostome were absent in one of their specimens, suggesting that it can instead be a variable character. Molecular data are thus needed to assess if this species and its infraspecific taxa (*Nebela barbata psilonota*) do in fact belong to genus *Nebela* or even to the family Hyalospheniidae.

One subspecies has been described:

Nebela barbata psilonota Jung, 1942

1942a *Nebela barbata psilonota* Jung, Arch. Protistenk. 95: 308 (Fig. 44a–c, original drawings).

Description (from the original description): Test elongated claviform in broad view, with a distinct elongated neck; laterally slightly compressed, lacking spines. L = 118-139 µm, B = 50-57 µm, depth: 38-50, P = 15-24 µm. Pseudostome composed of larger platelets forming a kind of necklace, either partially overlapping or lined up next to each other like teeth.

Differential diagnosis: Differs from the type by the absence of spines.

Etymology: the subspecies name "psilonota" refers to the lack of hair (spines), "psilonota" in Greek meaning scarcity of short hair.

Type locality: Southern Chile, likely coordinates: -53.458153°, -71.195878°.

Type specimen: Not specified. We declare Fig. 44a of the original description by JUNG (1942), reproduced here as 107 as the type.

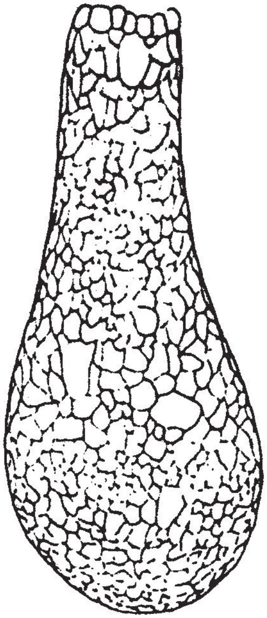

Fig. 107. *Nebela barbata psilonata*: Original drawing from JUNG (1942).

Habitat: Swamps and forest creeks.

Geographical distribution: Southern Chile JUNG (1942).

Remarks: Differs from the type by the complete absence of spines; however, as these spines are extremely fragile and can be lost easily during testing, the validity of this criterion is unclear. Molecular data are therefore needed to establish the affinity between spinose and spineless forms (as well as the phylogenetic position of both taxa). JUNG (1942) commented on the biogeography of this taxon and *N. barbata* as follows (translated and adapted): "Nebela barbata *is one of the protists that have long attracted the attention of biogeographers. It has only been known from the northern hemisphere, where the hairless variant Just described has also been seen several* *times. It was thought to be a circumatlantic thecamoeba (DEFLANDRE 1936), which inhabited exclusively the* Sphagnum *of Atlantic bogs. If this view was already insufficiently substantiated before, this proves to be wrong by the finds from southern Chilean sites reported here*".

Nebela bipes, bicornis, triangulata, cornuta complex

(The listed species can represent independent taxa or are synonyms, see Remarks below)

1865 *Difflugia triangulata* Lang, Q. J. Micr. Sci. 5: 285.

1870 *Difflugia bipes* Carter, Ann. Nat. Hist. 4: 323.

1905 *Nebela biconis* West, Ann. Scott. Nat. Hist.: 91-93.

1905 *Nebela bipes* (Carter,1870) Murray, Proc. Roy. Soc. Edinburgh, 25: 609–615.

1909 *Nebela triangulata* (Lang,1865) Cash & Hopkinson, Brit. Freshw. Rhizopoda & Heliozoa II: 125–127.

1909 *Nebela triangulat* var. *bicornis* (West, 1905) Cash & Hopkinson, Brit. Freshw. Rhizopoda & Heliozoa II: "27, 128.

1910 *Nebela cornuta* Voronkoff, Trudy Otdela Ikhtiologii Obshchestva Akklimatizatsii Moskva 7: 217–218 (Fig. 1).

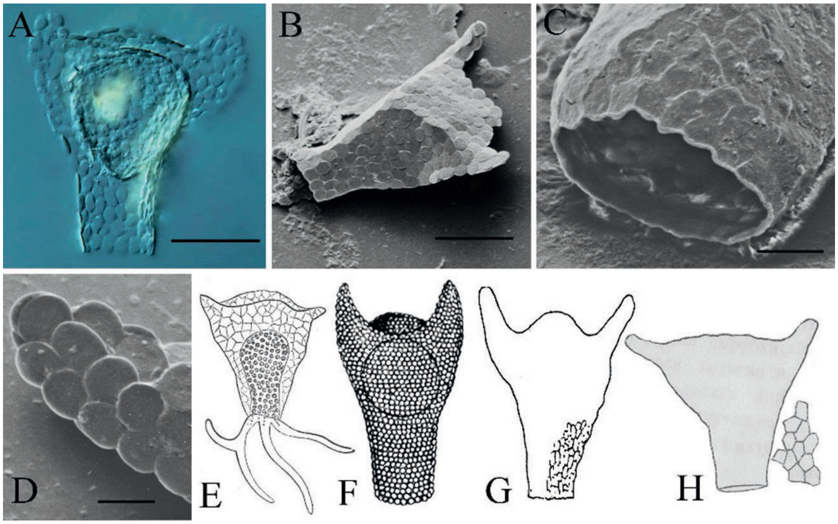

Fig. 108. *Nebela bipes* (A–D & F) and similar species: (A & B) Specimens from Gschöd, Germany; (A) Encysted individual (permanent mount. col. Meisterfeld), and (B) SEM of the same population; (C & D) SEM image of the aperture with a thin organic rim and higher magnification view of the test structure; (E) Original drawing of *Difflugia triangulata* from LANG (1865); (F) Original drawing of *N. bipes* from CARTER (1870); (G) Original drawing of *N. bicornis* from WEST (1905); (H) Original drawing of *N. cornuta* from VORONCOFF (1910). Scale bars: A & B = 50 µm, C = 10 µm, D = 8 µm. Images (A–D) by Ralf Meisterfeld.

1974 *Mixoglypha trapezoides* Baumeister, Mitt. Zool. Ges. Braunau 2: 39–48.

Description: The test shapes of these very rarely reported species are almost identical: Test oblong, often forming an irregular triangle in broad view, with two posterior horn-like projections. Test somewhat compressed, narrowed towards the ovoid aperture. Test very transparent. L = 100–155 µm. The (often vague) original descriptions mention different test compositions: *Nebela triangulata* Lang 1865 with surface markings of mathematical regularity, *Nebela bipes* (Carter) Murray, 1870 with circular scales, and *Nebela bicornis* West, 1905 with minute, irregular plates.

Differential diagnosis: Differs from other hyalospheniid species primarily by its irregular, nearly triangular shape, as well as the presence of two posterior horns.

Type locality: Budleigh Salterton, England (possible coordinates: 50.650848°; -3.364986°) for *N. bipes* (CARTER, 1870); Reading, England (possible coordinates: 51.46longatete70278°) for *N. triangulata* (LANG, 1865); Moscow, Russia (possible coordinates: 55.856269°; 37.796951°) for *N. cornuta* (VORONCOFF, 1910).

Type specimen: Not provided.

Etymology: All names refer to either the triangular shape of the test (*N. triangulata*), or the presence of two posterior horns (*N. bipes, N. cornuta*).

Habitat: Plankton, lake sediments, and *Sphagnum*. *Nebela bipes* was recorded living on filamentous diatoms (*Oscillaria*).

Geographical distribution:

(*N. bipes*) Europe: Bulgaria (PATEFF, 1928; GOLEMANSKY et al., 2006), Germany (BAUMEISTER, 1974), UK (CARTER 1870; CASH et al., 1909; WAILES & PENARD, 1911; HEAL, 1961); North America: Canada (WAILES, 1928); Africa: Democratic Republic of Congo (ŠTĚPÁNEK, 1963), Niger (GAUTHIER-LIÈVRE, 1953).

(*N. triangulata*) Europe: Austria (HIMMER, 1914), Bulgaria (GOLEMANSKY & TODOROV, 2003), Czech Republic (BARTOŠ, 1954), Finland (ŠTĚPÁNEK, 1963), Hungary (SCHERFFEL, 1933), Iceland (CHARDEZ, 1973), the Netherlands (HOOGENRAAD & DE GROOT, 1940b), UK (CASH et al., 1909); North America: Canada (FANTHAM & PORTER, 1948), Mexico (LAMINGER, 1973); South America: Colombia (PENARD, 1914); Africa: Senegal (DECLOITRE, 1953; GAUTHIER-LIÈVRE, 1953); Asia: China (FIELD“, 1887, as *Difflugia triangulata*), Japan (EDMONDSON & KINGMAN, 1913).

(*N. cornuta*) Europe: Russia (VORONCOFF, 1910).

Remarks: The taxonomy of these species is rather complicated, as it is not clear from the test composition or aperture structure whether they belong to *Nebela*, *Argynnia* (as in MAZEI & TSYGANOV, 2006), a new genus, or perhaps even several genera. These species were often considered synonymous (DEFLANDRE, 1936). *N. cornuta* differs from *N. bipes* by its smaller size (*N. cornuta*: L = 108 µm vs. *N. bipes*: L = 132–155 µm), but these ranges sometimes overlap. A thin organic lip surrounds the pseudostome, suggesting that these species belong to Hyalospheniidae. Molecular data are needed to clarify the relationship between these morphospecies and to identify their position in Arcellinida.

Nebela cylindrica Bonnet, 1979

1979 *Nebela cylindrica* Bonnet, Bull. Soc. Hist. Nat. de Toulouse: 108 (Figs. 19–20, Pl. I, Figs. 15–16, original images and drawings).

Description (based on the original publication): Test small, transparent, cylindrical, sub-circular in cross section at all levels. L = 48–50 µm, B = 17–22 µm. Neck indistinct

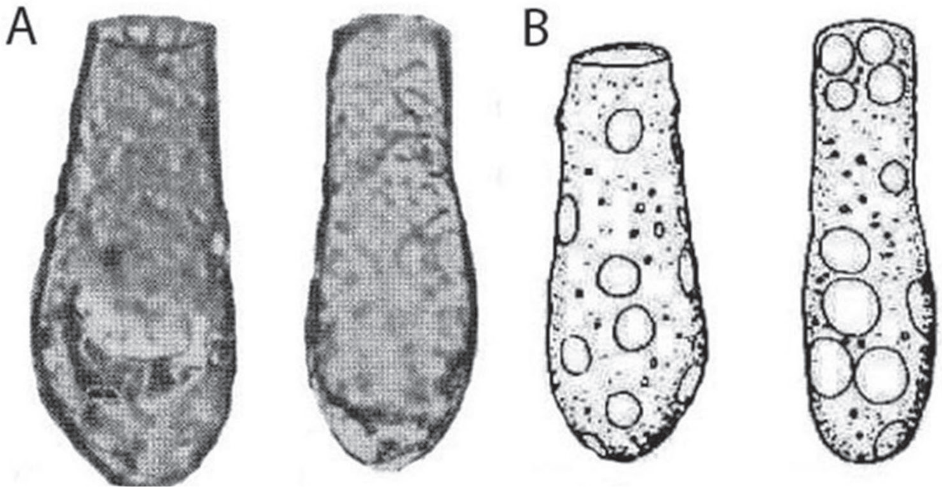

Fig. 109. *Nebela cylindrica*: (A) Original LM images in broad lateral and profile views, and (B) corresponding line drawings from BONNET (1979) in broad lateral and profile views.

from the main body. Pseudostome slightly curved in broad view, with an organic rim and two barely visible lateral notches. In some individuals, two small symmetrical bulges are visible near the pseudostome (Fig. 109).

Differential diagnosis: Differs from other hyalospheniids by the cylindrical cross section of the test.

Type locality: Nepal (no further detail provided).

Type specimen: Not provided. We declare Fig. 19 by BONNET (1979), reproduced here as Fig. 109B, as the type.

Etymology: The species name refers to cylindrical shape of the test.

Habitat: Forest litter (under *Pinus excelsa*, Nb. invalid name for *Pinus wallichiana*), soils (under Hypnaceae mosses and *Hymenophyllum* ferns), and in *Quercus semicarpifolia* forests.

Geographical distribution: Asia: Java (BONNET, 1985, 1992), Nepal (BONNET, 1979; DECLOITRE, 1982), Philippines (BONNET, 1980b), Sulawesi (BONNET, 1992), Thailand (BONNET, 1987); Australasia: Maluku Islands (BONNET, 1992), New Guinea (Papua New Guinea, BONNET, 1980a; Irian Jaya BONNET, 1992).

Remarks: This species has rarely been found, possibly because its natural habitat (tropical forest litter) has not been thoroughly sampled. The general shape of the species does not meet the criteria of hyalospheniids (circular, ovoid, piriform, elongated-piriform, lageniform); however, BONNET (1980) described its morphology as an intermediate between *Nebela* (now *Alabasta*) *militaris* and *Nebela* (now *Padaungiella*) *tubulata*. It therefore remains unclear if this species indeed belongs to genus *Nebela*.

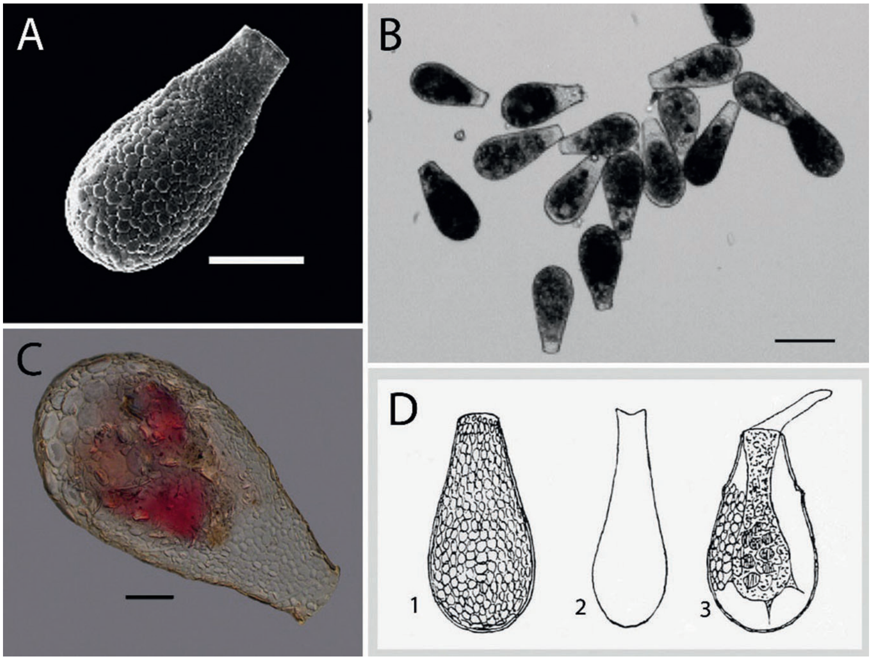

Fig. 110. *Nebela penardiana*: (C) SEM broad view image of a specimen from Bulgaria; (B) LM image of group of specimens from Bulgaria; (C) LM broad view image of a fixed specimen from the Eugène Penard slide collection, no. 505-1 (Geneva Natural History Museum, Switzerland); (D) Original drawings from DEFLANDRE (1936): (1) broad view of an empty test, (2) outline profile view, and (3) active individual in broad view showing the cell in transparency and part of the test structure. Scale bars: A = 50 µm, B = 100 µm, C = 20 µm. Images by: (A & B) Milcho Todorov, and (C) Thierry Arnet (Wikimedia).

Nebela penardiana Deflandre, 1936

1879 *Nebela collaris* Leidy, Pl. XXIII, Fig. 7 (Nb. The specimen illustrated in Fig. 7 is a misidentification).

190 *Nebela americana* sec. Penard el aucl.: 363, Figs. 1–6, non *Nebela americana* Taránek (misidentification as *N. americana* described by TARÁNEK 1882, overlaps in morphology with *N. penardiana* Deflandre 1936).

1936 *Nebela penardiana* Deflandre, Ann. Protistol. 5: 257 (Figs. 87–89, original drawings).

1977 *Nebela penardiana* var. *retorta* Decloitre, Arch. Protistenk. 119 (Infrasubspecific (not available) name: var. published after 1960, IC ZN Art. 45.6.3).

Icon.: DEFLANDRE, 1936, Figs. 87–89, Pl. XIX, Figs. 1–9, Pl. XX, Fig. 1–2, 4–5, 7; OGDEN & HEDLEY, 1980, Pl. 42 (note: not a typical *N. penardiana*); LARA et al., 2008, Fig. 1k; KOSAKYAN et al., 2012, Fig. 3F; LUKETA, 2017b, Fig. 4 (as *Gibbocarina penardiana*); TODOROV & BANKOV, 2019, Fig. 4 (as *Longinebela penardiana*).

Description: Test elongated-piriform in broad view, compressed. Two small lateral pores are usually present where two small lateral "notches" are located, at a distance of 1/3rd of the body length from the pseudostome. Test brownish, composed of circular, ovoid plates, sometimes mixed with a few rectangular test plates. The size of the test varies by authors: L = 115–175 µm, B = 65–80 µm, pseudostome ovoid in frontal view, slightly curved in broad view, surrounded with a thin organic collar rim, P = 23–35 µm wide.

Differential diagnosis: Similar to *Longinebela tubulosa* and *L. speciosa*, from which it can be easily distinguished by its smaller size. In addition, *L. tubulosa* has a very characteristic and easily recognizable granular cement structure near the pseudostome (DEFLANDRE, 1936; OGDEN & HEDLEY, 1980), as well as an acute angle-shaped fundus.

Type locality: Lac de Conches, Collombey-Muraz, Valais, Switzerland. Likely coordinates: 46.264776°, 6.863362°.

Type specimen: Not provided. We declare Fig. 88 by DEFLANDRE (1936), reproduced here as Fig. 110D-3, as the type.

Etymology: The species was named in honour of the Swiss protozoologist, Eugène Penard (1855-1954).

Habitat: Wet *Sphagnum* and other mosses, in relatively minerotrophic habitats (hygrophilous species from wet, poor, to intermediately rich fen), and also reported from litter and soil.

Geographical distribution: Africa: Algeria, Benin (GAUTHIER-LIÈVRE, 1953; DECLOITRE, 1954), Cameroon (GAUTHIER-LIÈVRE, 1957), Guinea (DECLOITRE, 1955; GOLEMANSKY, 1963), Congo (VAN OYE, 1959); North America: Canada (DE PUYTORAC et al., 1972; BONNET, 1974), USA (BEYENS & CHARDEZ, 1995; BOOTH, 2001); South America: Argentina (VUCETICH, 1973), Bolivia (CERDA, 1986), Brazil (LANSAC-TOHA et al., 2001), Chile (JUNG, 1942a; WILKINSON, 1990), Ecuador (KRASHEVSKA et al., 2007); Central America: Costa Rica, Guadeloupe (BONNET, 1977a), Guatemala (LAMINGER, 1973), Martinique (BONNET, 1977a); Antarctica (WILKINSON, 1994); Asia: China (YANG et al., 2004), Java (HOOGENRAAD & DE GROOT, 1940a; BONNET, 1985), Japan (SUDZUKI, 1979), Korea (CHUNG et al., 1992), Nepal (BONNET, 1977b), Malaysia (GREEN, 1996), Philippines (BONNET, 1980b), Sulawesi (BONNET, 1992), Sumatra (HOOGENRAAD & DE GROOT, 1940a; 1942), Thailand (BONNET, 1981), Vietnam (BALIK, 1995); Australasia: Australia (MEISTERFELD & TAN, 1998), Maluku Islands (BONNET, 1992), New Guinea (Papua New Guinea, GRACIA, 1968; Irian Jaya (BONNET, 1992), New Zealand (HOOGENRAAD, 1948; WILKINSON, 1990); Europe: Austria (LAMINGER, 1970; FOISSNER, 1987), Belgium (CHARDEZ, 1987a), Bosnia–Herzegovina (LUKETA, 2017b), British Isles (OGDEN & HEDLEY, 1980; WOODLAND et al., 1998), Bulgaria (GOLEMANSKY, 1967; TODOROV, 1993), Czech Republic (BARTOŠ, 1950), France (DEFLANDRE, 1936; BONNET, 1953), Germany (JUNG & SPATZ, 1938; GROSPIETSCH, 1982), Greece (PAYNE & MITCHELL, 2007), Greenland (DECLOITRE, 1956), Iceland (CHARDEZ, 1973), the Netherlands (HOOGENRAAD & DE GROOT, 1940b) Norway (CHARDEZ & BEYENS, 1987), Romania (GODEANU, 1970; BUNESCU, 1979), Russia (TARNOGRADSKIJ, 1959; KASIMOV, 1972), Serbia (OGDEN, 1984; LUKETA, unpubl.), Spain (GRACIA, 1964), Sweden (GROSPIETSCH, 1954), Switzerland (HEINIS, 1959; KISHABA & MITCHELL, 2005).

Remarks. *Nebela penardiana* is morphologically well characterized, fitting well within genus *Longinebela* based on its elongated-piriform shape. Its phylogenetic position, however, remains unclear. It branches together with *Gibbocarina galeata* in an mt-COI sequence data-based phylogenetic tree

(KOSAKYAN et al., 2016), standing in contradiction with the absence of a hollow keel (a synapomorphy for genus *Gibbocarina*); however, it should be noted that only a single sequence of *N. penardiana* was obtained from the DNA extraction of several cells. It is therefore possible that *G. galeata*, or a species closely related to *G. galeata*, was isolated together with *N. penardiana* and that the analysed sequence corresponds to the former. Considering this possible source of error and the morphological characteristics of *N. penardiana*, we have included it in the *incertae sedis* list. Another possible explanation could be that *N. penardiana* has a very faint keel that has escaped our attention until present (see Fig. 110A, D-1). Further detailed morphological and molecular data are clearly needed to clarify this question.

Taxonomic position: Morphological and morphometric data for sympatric populations from eastern Bosnia-Herzegovina show that *N. penardiana* is closely related to *Gibbocarina galeata*. Therefore, LUKETA (2017b) proposed a novel taxonomic combination: *Gibbocarina penardiana*. According to LUKETA, the key morphological difference between these two species lies in the visibility of the hollow keel, which is clearly visible in *G. galeata*, but less so in *G. penardiana*. Conversely, BANKOV et al. (2018) and TODOROV et al. (2018) used the name *Longinebela penardiana*, as they believed this action had been taken by KOSAKYAN et al. (2016). However, this action was not carried out by KOSAKYAN et al. (2016). Ultimately, the taxonomic position of this species remains uncertain, and resolving this issue is crucial for understanding the taxonomic status of the genera *Gibbocarina* and *Longinebela*, as the species in question shows characteristics of both genera. These two genera share a similar shape and test dimensions but differ in the presence (*Gibbocarina*) or absence (*Longinebela*) of a hollow keel. Significantly, *N. penardiana* has a weakly expressed keel, a transitional feature between the two genera. Further morphological and molecular analyses of these two genera are needed.

Nomenclature: In his monograph, DEFLANDRE (1936) mentioned var. *falcata* Wailes, 1912a, J. Linn. Soc. Zool. XXXII: 135, under the species of *Nebela penardiana*. This created confusion, as WAILES (1912a) described this subspecific taxon under *N. americana* based on its curved test as a differentiating character from the type. DECLOITRE (1977, Arch. Protistenk. 119) described a variety of *N. penardiana* (var. *retorta*) that is slightly bent. According to the ICZN, this is an infra-subspecific name and therefore unavailable. Aside from the nomenclatural aspect, this taxon is rather problematic, as it has been found only in one site, and there is no indication of how many cells were observed.

We are listing two subspecies for *Nebela penardiana* (Fig. 111):

Nebela penardiana elongata Gauthier-Lièvre, 1957

1957 *Nebela penardiana* f. *elongata* Gauthier-Lièvre, Bull. Soc. Hist. Nat. Afrique de Nord: 516.

Description (based on the original publication): This subspecific taxon differs from the type by its elongated form in broad view and its small size. It is slenderer than *Nebela penardiana minor*. The main body is more or less ovoid, with an elongated neck; however, the neck is formed by the sides gradually tapering towards the pseudostome, notably not distinctly separated from the main body of the test (as in *Padaungiella lageniformis*). L = 115 µm, B = 42 µm, P = 22 µm wide.

Differential diagnosis: *N. penardiana elongata* (L/B = 2.7) is much slenderer than *N. penardiana* minor (L/B = 1.8–1.9) and *Padaungiella lageniformis* (L/B = 1.5–1.6; PENARD, 1890), but see also Remarks under *P. lageniformis*, p. 145).

Type locality: Republic of Congo, about 25 km from Brazzaville, on the road to Kinkala. Likely coordinates: -4.318629°; 15.077065°.

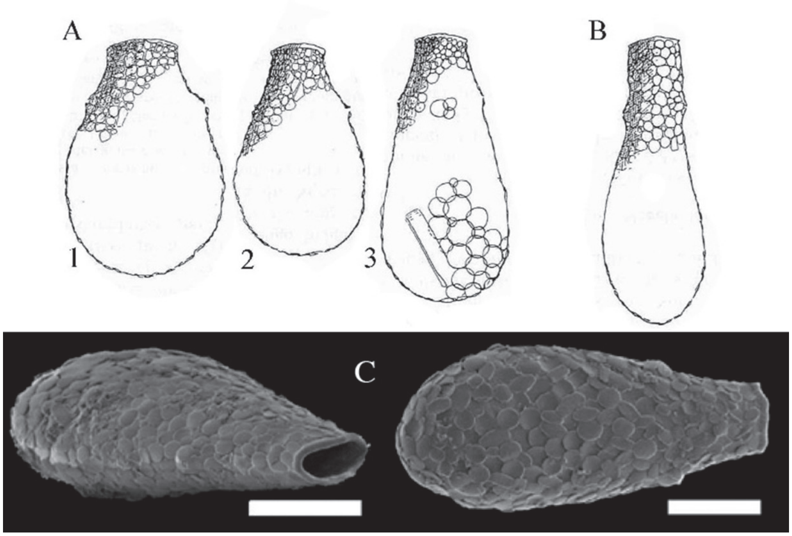

Fig. 111. (A) *Nebela penardiana minor*: Original drawings from GAUTHIER-LIÈVRE (1957). (B) *Nebela penardiana elongata*: Original drawings from GAUTHIER-LIÈVRE (1957) (C) *Nebela penardiana minor*: SEM of DNA barcoded specimen from Costa Rica (modified from LARA et al., 2008).

Type specimen: Not provided. We declare Fig. 11E by GAUTHIER-LIÈVRE (1957) here reproduced as Fig. 111 B as the type.

Etymology: This subspecies name refers to the elongated shape of the test.

Habitat: Wet *Sphagnum* and other mosses, in relatively minerotrophic habitats (hygrophilous species from wet, poor to intermediately rich fen), but also reported from litter and soil.

Geographical distribution: Africa: Republic of Congo (GAUTHIER-LIÈVRE, 1957).

Nebela penardiana minor Gauthier-Lièvre, 1957

1957 *Nebela penardiana* f. *minor* Gauthier-Lièvre, Bull. Soc. Hist. Nat. Afrique du Nord: 515.

Description: Smaller than the nominal subspecies. L = 78–110 µm, B = 41–62 µm, P = 21–40 µm wide (GAUTHIER-LIÈVRE, 1957).

Differential diagnosis: This subspecific taxon is very similar to the type and differs from it only by its smaller size (≤110 µm) and more transparent test. GAUTHIER-LIÈVRE (1957) mentioned that test shapes were "variable".

Type locality: Between Mamfe and Mbam-et-Inoubou, Cameroon. Likely coordinates: 5.285334°, 10.104533°.

Type specimen: Not provided. We declare the original drawing, reproduced here as Fig. 111A3, as the type. As three different morphotypes were included in the description, the third was selected, as it best resembled most *N. penardiana*, as the other two were clearly broader, possibly representing another species.

Etymology: The species name refers to its small size.

Habitat: Seeps on rocks, temporary marshes, rainforests, forest mosses.

Geographical distribution: Africa: Cameroon (GAUTHIER-LIÈVRE, 1957), Congo (GAUTHIER-LIÈVRE, 1957), Guinea (GOLEMANSKY, 1963), Seychelles (KORGANOVA, 1990); Central America: Costa Rica (LARA et al., 2008).

Remarks: GAUTHIER-LIÈVRE (1957) acknowledged that small-sized *N. penardiana* had already been found by DECLOITRE in Dahomey (present day Republic of Benin) and Guinea (Ségéa caves, Kolenté region). This subspecies was found later in forest mosses from Costa Rica. SSU rRNA sequences revealed that it indeed branched robustly with the nominal form, but genetically strongly divergent, thus suggesting a specific status (LARA et al., 2008). It is most likely a circumtropical form.

8.3. *Incertae sedis* taxa from genus *Quadrulella*:

Quadrulella cordobensis Vucetich, 1983

1983 *Quadrulella cordobensis* Vucetich, Limnobios 2, Fasc. 7: 529 (Figs. 7–8, original images).

Description (based on the original publication): Test more or less piriform, with irregular margins and rounded fundus and weakly compressed laterally. Test colourless, composed of square and rectangular plates arranged side by side, sometimes overlapping. L = 85–100 µm, B = 51–65 µm, P = 22–35 µm. Pseudostome elliptical and irregular, consisting of eight to nine plates, without an organic margin or rim.

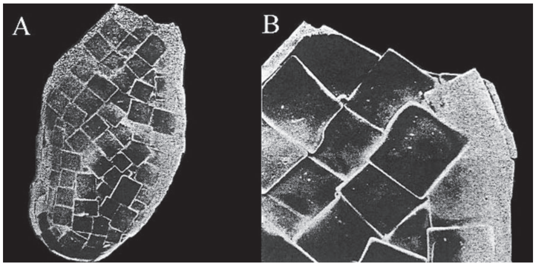

Fig. 112. SEM original image of *Quadrulella cordobensis* from VUCETICH (1983): (A) broad view and (B) close views of the pseudostome.

Differential diagnosis: Differs from other hyalospheniids by its irregular pseudostome, with the exception of *Q. nunciae*, another *incertae sedis* species. See details under *Q. nunciae* (p. 207).

Type locality: Near the dam along the Embalse de Rio Tercero, on the river Arroyo Las Vacas, and in Villa Giardino, Province of Córdoba, Argentina. Likely coordinates: -31.033723°, -64.461372°.

Type specimen: Testate amoebae collection of Institute of Limnologia “after R.A. Ringuelet”, no. 309.

Etymology: The species was named after the Province of Córdoba, Argentina, where it was found.

Habitat: Among wet mosses, on rocks along a stream bank.

Geographical distribution: Argentina (VUCETICH, 1983).

Remarks: We have included *Quadrulella cordobensis* in the list of incertae sedis species, as the irregular pseudostome does not fit the criteria of family Hyalospheniidae (lacking an aperture with an organic rim, a usual synapomorphy for the family). Molecular data are therefore needed to determine the true position of this species within the Arcellinida.

Quadrulella elongata Van Oye, 1956

1956b *Quadrulella elongata* Van Oye, Ergebnisse der Deutschen Limnologischen Venezuela-Expedition 1952, 1: 352 (Fig. 41, original drawing).

Description: Test elongated-piriform, with an elongated neck and a rounded body. Test transparent, colourless, composed of square plates. Lateral pores absent. L = 65 µm, B = 22 µm, P = 11 µm. Pseudostome slightly curved and undulated.

Differential diagnosis: Differs from *Q. longicoliis* by its smaller size and its absence of an organic rim around the pseudostome.

Type locality: Canoa peatland, Venezuela. Likely coordinates: 10.191884°, -66.142441°; Elevation, ca. 3800 m.a.s.l..

Type specimen: Not provided. We declare Fig. 41 by VAN OYE (1956b), reproduced here as Fig. 113, as the type.

Etymology: The species name refers to the elongated shape of the test.

Habitat: Mosses.

Geographical distribution: South America: Ecuador (KRASHEVSKA et al., 2007), Venezuela (VAN OYE, 1956b).

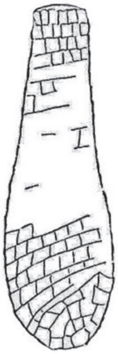

Fig. 113. *Quadrulella elongata*: Original drawing from VAN OYE (1956b).

Remarks: *Quadrulella elongata* is very similar to *Q. longicollis*, or the elongated type of *Q. variabilis* (see discussion on these taxa, p. 178). Initially, VAN OYE (1956b) wanted to name it *Q. longicollis*, but as TARÁNEK (1882) had already given this name to a variety of *Q. symmetrica*, Van Oye decided to name it "*Quadrulella elongata*", differing from *Q. symmetrica* var. *longicollis* by its smaller size and the absence of an organic rim around the pseudostome. We included this species into the list of *incertae sedis* names because the characters mentioned in the description (undulated pseudostome and pseudostome without an organic rim) do not meet the criteria of the family Hyalospheniidae. However, as several species that clearly belong to the Hyalospheniidae do not share this morphological feature its validity as a synapomorphy of the group is questionable.

Quadrulella nunciae Vucetich, 1983

1983 *Quadrulella nunciae* Vucetich, 1983, Limnobios 2, Fasc. 7: 529 (Figs. 1–6, original images).

Description (based on the original publication): Test piriform, compressed, very elongated, with a rounded fundus. Test colourless, very transparent, and thus can be very difficult to notice. Test composed of juxtaposed, relatively large square and rectangular plates, among which little plates are spread. No lateral pore. L = 108–114 µm, B = 42–48 µm, P = 17–21 µm. Pseudostome irregular, made up of a few plates (approximately six) without any organic rim or margin.

Differential diagnosis: Readily identifiable by the irregular construction of the pseudostome (made up of plates without any margin or lip). *Quadrulella nunciae* is very similar to *Q.*

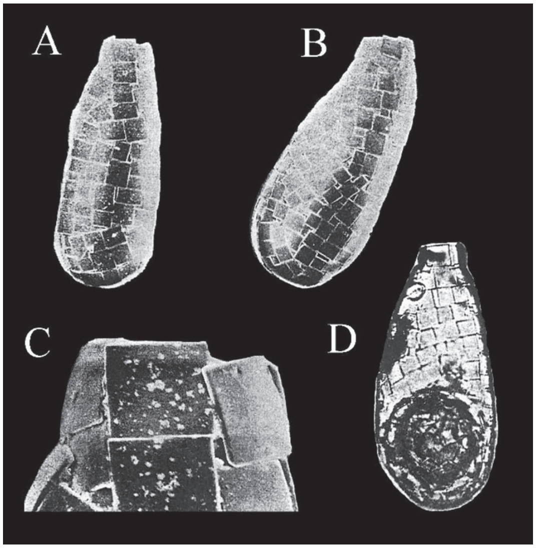

Fig. 114. *Quadrulella nunciae*: Original images modified from VUCETICH (1983). SEM images of: (A) an individual with a straight outline (x700), (B) an individual with a curved outline (x800), (C) a pseudostome (x3000), and (D) LM image of an individual with a straight outline (x700).

cordobensis, from which it differs by a much more regular, elongated, and slimmer shape (L/B = 2–3 in *Q. nunciae* vs. L/B = 1.5–1.6 in *Q. cordobensis*).

Type locality: Alto de la Totora, San Pedro de Colalao, Provence of Tucman, Argentina among humid mosses. Likely coordinates: -26.235055°, -65.536926°; Elevation, ca. 1300 m.a.s.l.. Other localities are mentioned: Province of Córdoba, La Cumbrecita, among humid mosses at 1700 m.a.s.l.; Villa Giardino, in liverworts at 700 m.a.s.l.; Pampa de Achala, humid mosses and liverworts at 1200 m.a.s.l..

Type specimen: Testate amoebae collection of Institute of Limnologia "R.A. Ringuelet", no. 308.

Etymology: Not provided. "Nuncia" in Latin means "female messenger; she who brings tidings". In Spanish "nuncio" means "messenger".

Habitat: Humid mosses at 1300–1700 m.a.s.l..

Geographical distribution: Argentina (VUCETICH, 1983).

Remarks: The author mentioned that she observed individuals with a curved outline representing ca. 5% of the specimens. We have included *Quadrulella nunciae* in the list of incertae sedis species, as the irregular pseudostome does not fit the criteria of family Hyalospheniidae (an aperture with an organic rim is a synapomorphy for the family). However, as several species that clearly belong to the Hyalospheniidae do not share this morphological feature is validity as a synapomorphy of the group is questionable. Molecular data are thus needed to understand the position of this species within the Arcellinida.

9. LIST AND NOTES TO *INQUIRENDA* (*NOMEN DUBIUM*) NAMES

This list includes species with doubtful identity, including those for which the original descriptions are poor, the original illustrations are of low quality, and those that cannot be reliably classified without further information. In many cases the type locality, type specimen, habitat or distribution are unknown. We are listing here 26 *inquirenda* names (including one complex of three species) for family Hyalospheniidae. Further detailed morphological and molecular taxonomic studies are needed to determine the validity of these taxa.

9.1. *Inquirenda* taxa from genus *Apodera*

Apodera vas var. *recticollis* Jung, 1942

1942a *Apodera vas* var. *recticollis* Jung, Arch. Protistenk. Bd. 95. H.3: 314 (Fig. 54 h–k, original drawings).

Description: Test dimensions similar to those of the type: L = 118–158 µm, B = 75 µm, P = 28–38 µm, but neck with approximately parallel sides of the, near absence of widening at the base of the neck, and darker brown colour.

Differential diagnosis: Differs from the type by its approximately parallel sides of the neck, near absence of widening at the base of the neck, and darker brown colour.

Type locality: Southern Chile; Likely coordinates: -53.458153°, -71.195878°.

Etymology: The name of this subspecies refers to its morphology.

Geographical distribution: South America: CHILE Jung (1942)

Remarks: This is a problematic taxon, as the identification criterion (less swollen neck) is not convincing based on the illustrations. *Apodera vas* is most likely a species complex (PENARD, 1911; ZAPATA & FERNANDEZ, 2009). When the diversity within this complex will be better documented the validity of this taxon may be re-evaluated.

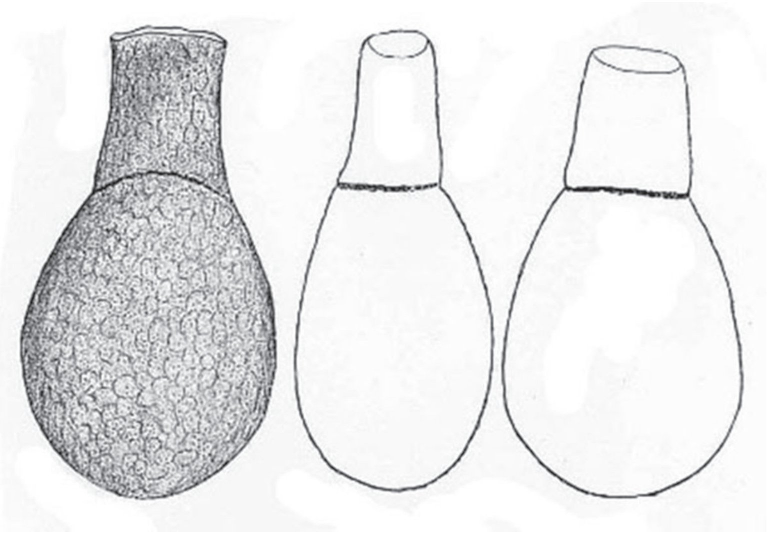

Fig. 115. *Apodera vas recticollis*: Original drawing from JUNG (1942).

9.2. *Inquirenda* taxa from genus *Hyalosphenia*

Hyalosphenia angulata Schouteden, 1905

1905 *Hyalosphenia angulata* Schouteden, Ann. Soc. Roy. Soc. Zool. & Malacol. de Belgique 40: 3 (Figs. 1–2, original drawings).

Description: Test in broad view ovoid, slowly narrowing towards the anterior end, compressed; in profile, slim ovoid, with a slightly pointed aboral end. Test transparent, very smooth, without any visible structure (in LM). Test relatively small (L = 45–60 μm). Pseudostome narrow, lacking a conspicuous rim.

Etymology: The name of this species refers to its characteristic angular shape.

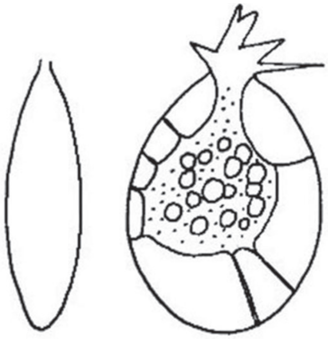

Fig. 116. *Hyalosphenia angulata*: Original drawing from SCHOUTEDEN (1905): profile and broad views.

Remarks: This species was found only once in an algal culture from the Botanical Garden of Brussels. A very rarely reported and problematic species. GROSPIETSCH (1965) questioned if it even belonged to genus *Hyalosphenia*, as the morphology of its pseudopodia are different from those of other congeneric members; however, the author did not go into any further detail. Accordingly, we have included this species in the *inquirenda* list. This species is similar to *Cryptodifflugia compressa* Penard, which is notably smaller (L = 13–35 µm). GROSPIETSCH (1965) noted the difficulty in making a clear decision, as the species was found only once. New observations are thus needed to determine if this species indeed belongs to genus *Hyalosphenia*. Documenting living cells would be also beneficial, as species from genera *Cryptodifflugia* and *Phryganella* can be differentiated from those of genus *Hyalosphenia* based on their pointed (vs. lobose) pseudopods.

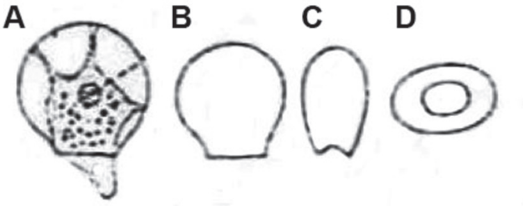

Fig. 117. *Hyalosphenia inconspicua*: Original drawing from WEST (1903). (A) broad view of living individual, (B) broad view of empty test, (C) profile view, and (D) view of the pseudostome.

Hyalosphenia inconspicua West, 1903

1903 *Hyalosphenia inconspicua* West, J. Linn. Soc. 29: 108–117 (T.13, Figs. 7–11, original drawings).

Icon.: WEST, 1903, T. 13, Figs. 7–11; CASH et al., 1909, T. 31, Figs. 5–6; DECLOITRE, 1948, Fig. 56.

Description: Test small, almost circular, laterally tapering towards the pseudostome; in profile wide ellipsoid. L = 14–17 µm, B = 12–16 µm, P = 6.5–7.7 µm wide. Pseudostome ellipsoid, notched in profile view.

Etymology: The name of this species refers to its very small shape making it easy to overlook.

Habitat: *Sphagnum* mosses.

Geographical distribution: Africa: West Africa (WEST, 1903); Europe: France (DECLOITRE, 1948), UK (CASH et al., 1909).

Remarks: The species was found in *Sphagnum* mosses in Africa (West Africa) and Europe (France, UK). The species description is very similar to that of *Cryptodifflugia compressa* Penard, 1902. Young tests of *C. compressa* are transparent and hyaline, while older tests are yellowish-brown. Additional morphological and molecular data are needed to assess the true phylogenetic position of this species. We have included this species in the *inquirenda* list, as the author did not specify its distinguishing characteristics from *C. compressa*. A clear image of the pseudopodia could easily resolve the question.

Hyalosphenia insuetua Štěpánek, 1967

1967 *Hyalosphenia insuetua* Štěpánek, Hydrobiologia 22: 41, Fig. 19 (16).

Description: Test elliptical, narrowing towards the pseudostome, transparent, colourless with all the features of Hyalosphenia. Test small: L = 42 µm, B = 22 µm, P = 10 µm wide.

Etymology: Not specified.

Type locality: Thaya River, Czech Republic

Remarks: This species was found only once in the Thaya River, Czech Republic. The description is very brief, "*Länge 42 u, Breite 22 u, Öffnung 10 u. Kleine, elliptische an der öffnung eingeengte Hülle ist farblos durchsichtig. Sie besitzt alle Merkmale von Individum der Art Hyalosphenia. Die Öffnung ist eng, spaltenförmig*", the drawing is very poor (see Fig. 118B), and no information is provided regarding on how many individuals the description is based.

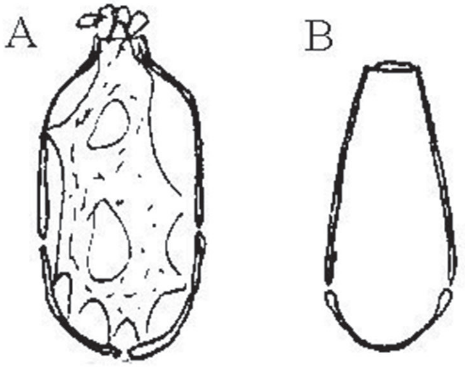

Fig. 118. Original drawing of (A) *Hyalosphenia lucerna*, and (B) *H. insuetua* from ŠTĚPÁNEK (1967).

Hyalosphenia lucerna Štěpánek, 1967

1967 *Hyalosphenia lucerna* Štěpánek, Hydrobiologia 29: 41, Fig. 19(20).

Description: Test shape resembles the "piston of a small car bulb". In profile, it is flattened, as with all representatives of genus *Hyalosphenia*. Test light brown, transparent. L = 42 µm, B = 22 µm, P = 5 µm. Pseudostome narrow.

Etymology: Not specified.

Remarks: The species was reported only once from a reservoir of the Thaya River (Czech Republic). The original description is quite short, and it is not specified on how many individuals it is based: "*In der Gestalt erinnert die Hülle an den Kolben einer kleinen Automobilglühbirne. Bei Seitenansicht ist sie jedoch wie bei allen Repräsentanten der Gattung* Hyalosphenia *abgeflacht. Die Hülle ist an der Öffnung verengt. Die Öffnung selbst ist spaltenförmig. Farbe der Hülle ist hellbraun, des Plasma vacuolisiert mit einem Stich gelber Farbe*». Translation**:** «*The shape of the shell is reminiscent of a small automobile bulb. When viewed from the side, however, it is flattened, as in all representatives of the genus* Hyalosphenia*. The shell is narrowed at the opening. The opening itself is cleft-shaped. Colour of the envelope is light brown, of the plasma vacuolated with a tinge of yellow colour.*».

The original drawing is poor (see Fig. 118A).

Hyalosphenia mraconiae Godeanu, 1972

1972 *Hyalosphenia mraconiae* Godeanu, Rev. Roum. Biol. Zoologie 17(4): 227–236 (Fig. 7, original drawing).

Description: Test piriform, with a rounded body, and sides tapering towards the pseudostome (as in *Nebela collaris*). Rim of the pseudostome finely crenulated. Two conspicuous pores are located ca. 40 µm from the pseudostome (ca. 2/3rd of the distance from the pseudostome to the fundus), similar to those of *Certesella martiali*, except for their position. Test transparent, hyaline, without any structure, very small. L = 60–65 µm, B = 42–45 µm. P = 11–13 µm, with a serrated margin. Cross section of the pseudostome circular.

Etymology: The name of this species refers to the Mraconia River, a left tributary of the Danube in Romania, close to Serbia.

Remarks: This species was found only twice in samples from the Mraconia and the Danube (Romania) Rivers among the microphytobenthos (pH = 8.8, T = 18°C; GODEANU, 1972b). The author also noted that although the test has characters similar to those of different species of genus *Nebela*, its entirely organic structure supported assignment to genus *Hyalosphenia*. If confirmed, this would be the first *Hyalosphenia* species with a serrated pseudostome, and there is no mention of an organic collar near the aperture. For these reasons we listed the species as a hyalospheniid *inquirenda*.

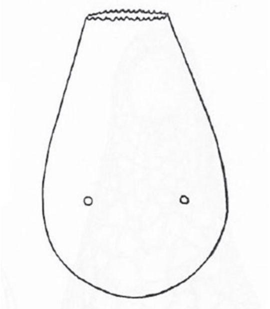

Fig. 119. *Hyalosphenia mraconiae*: Original drawing from GODEANU (1972).

Fig. 120. *Hyalosphenia obliqua*: Original drawing from DECLOITRE (1979).

Hyalosphenia obliqua Decloitre, 1979

1979 *Hyalosphenia obliqua* Decloitre, Annales de la Société des Sciences Naturelles & d'Archéologie de Toulon & du Var, 31: 152, Fig. 7.

Description: The original species description is very short. Differs from other *Hyalosphenia* by its curved neck. L = 30–40 µm, B = 10–12 µm, P = 4–6 µm.

Etymology: The name of this species refers to its morphology.

Habitat: Litter of vine plants

Remarks: This species was found only twice in the litter of vine plants. Furthermore, information regarding the type locality is missing. The original illustration (represented here as Fig. 120) does not reveal any useful criterion for taxonomic assessment.

Hyalosphenia planctonica (Minkiewicz, 1900) Chardez, 1987

1900 *Difflugia planctonica* Minkiewicz, Zool. Anzeiger. 23: 618–620. (Fig. I).

1987b *Hyalosphenia planctonica* Minkiewitz, 1900 – Chardez, Trav. Lab. Zool. Gen. Faun. Gembloux. 12: 1–2 (transfer to a new genus based on test morphology).

Icon.: MINKIEWICZ, 1900, Fig. I; CHARDEZ, 1987b, Figs. 1–8.

Description: According to MINKIEWICZ (1900): Test ovoid, sometimes slightly globular, chitinous, yellowish-brown, with more or less (or sometimes no) mineral particles of different sizes and small diatoms, save for the very edge of the aperture. Aperture usually with three lobes, sometimes ≥ 4 (and then very small). Chitinous collar ranging from absent to 7 µm in length, always bordered by relatively large mineral grains. Pseudopods finger-shaped, large nucleus is bean-shaped. L = 61–96 µm, B = 48–84 µm. According to CHARDEZ (1987b): Test ovoid, slightly compressed and ovoid in cross-section. Pseudostome irregularly lobed with a chitinous rim. Test composed of thick, light brown organic material, with very fine punctuations sometimes visible (also in the pseudostome region). No extraneous material (xenosomes) attached. Pseudopods lobed. Cytoplasm always containing green organic matter, giving it a dark colour. Nucleus spherical, diam. 9–10 µm. L = 75–85 µm, B = 56–60 µm, thickness = 50–59 µm, P = 20–23 µm.

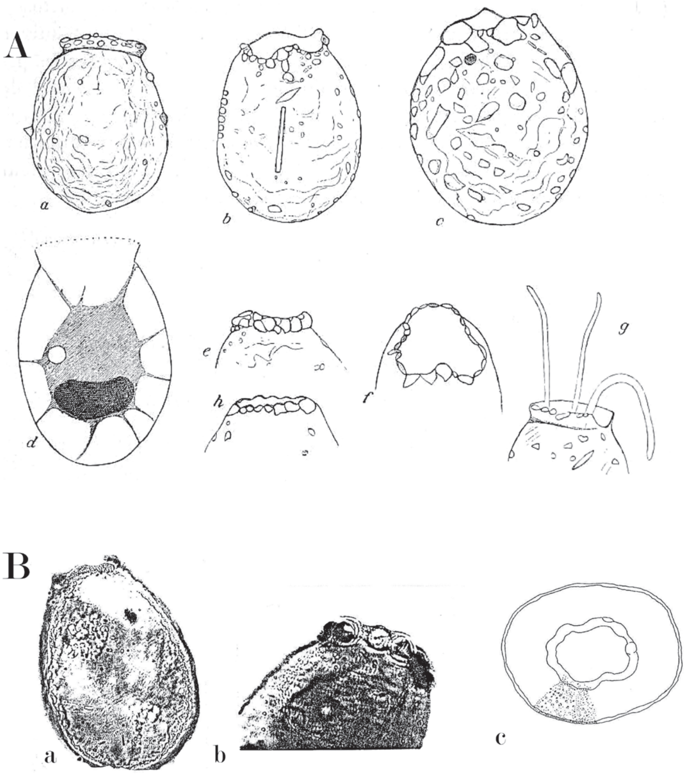

Fig. 121. *Hyalosphenia planctonica*: (A) Original drawings from MINKIEWICZ (1900) (a–c) different forms of *Difflugia planctonica*, (d) longitudinal cut of the test showing the plasma with epipodes and nucleus, (e–h) variations of the aperture, (g) pseudopods; (B) LM images of *H. planctonica* (a) broad lateral view, (b) close view of the aperture, and line drawing of apertural cross section from CHARDEZ (1987b).

Type localities: MINKIEWICZ (1900): Glubokoye Lake, Antarctica: 60.552955°, 29.326256°; Elevation, ca. 18 m.a.s.l.; CHARDEZ (1987b): Faroe Islands. Likely coordinates: 61.891111°, -6.871667°, Elevation, ca. 120 m.a.s.l..

Habitat: MINKIEWICZ (1900): Planktonic, CHARDEZ (1987b): Submerged parts of Potamogeton sp., collected in a small bog pond with 10 cm water depth; pH = 5.4 Conductivity = 145 µS·cm-1.

Etymology: The name of this species refers to it being planctonic.

Geographical distribution: Europe: Russia (MINKIEWICZ, 1900), Faroe Islands (CHARDEZ, 1987b).

Remarks: MINKIEWICZ (1990) described a planktonic species he named *Difflugia planctonica*, which usually has xenosomes, including around the aperture. GROSPIETSCH (1972) did not find this species and considered its taxonomic position uncertain. CHARDEZ (1987b) transferred this species to genus *Hyalosphenia*; however, the species Chardez illustrates clearly does not bear any xenosomes. Indeed, he specifically wrote that the few mineral grains and small diatoms are always simply loosely attached to the surface of the test, unable to withstand a simple transfer into distilled water. It is unclear if these two descriptions correspond to the same or two distinct species. Although their sizes and general morphology overlap, the species described by Minkiewicz clearly bears xenosomes, thus fitting into genus *Difflugia (s.l.)*. The morphology, however, is also very similar to that of *Netzelia oviformis* (Cash, 1909) Ogden, 1979, with which both could equally be synonymized (the name *Difflugia planctonica* would take precedence, implying that *Netzelia* oviformis (Cash, 1909) Ogden, 1979 would be emended as *Netzelia planctonica*). We therefore placed this species in the *inquirenda* list.

Hyalosphenia schönborni Štěpánek, 1967

1967 *Hyalosphenia schönborni* Štěpánek, Hydrobiologia 29: 42, Fig. 19 (14).

Description: Test lenticular in shape, transparent, and colourless. L = 55 µm, B = 50 µm, P = 28 x 8 µm. Pseudostome slit-shaped, small in comparison with the whole test.

Etymology: This species is named after the German protistologist Wilfried Schönborn (1934-2016).

Type locality: Thaya River in Vranov, Czech Republic. Likely coordinates: 48.935767°, 15.776749°

Habitat: River benthos.

Habitat: *Sphagnum* mosses

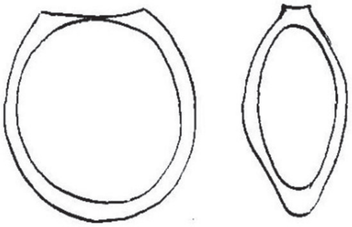

Fig. 122. *Hyalosphenia schönborni*: Original drawing from ŠTĚPÁNEK (1967): broad and profile views.

Geographical distribution: Europe: Czech Republic ŠTĚPÁNEK (1967)

Remarks: Found only once. The original description is insufficiently detailed, without any differentiating characters listed from similar species. The illustration (Fig. 122) is also very poor.

9.3. *Inquirenda* taxa from genus *Nebela*

Nebela bartosi Haager & Haagerova, 1970

1970 *Nebela bartosi* Haager & Haagerova, Acta Univ. Carol. Biol. 1–10, (Pl. 13. Fig. 17, original drawing).

Description (based on the original publication): Test bottle- to pear-shaped in broad view, with a small neck. Two pores are situated on the sides of the neck near the pseudostome. L = 213–215 µm, B = 135–137 µm, P = 56–59 µm. Test surface covered with three types of plates: large disc-shaped platelets, diameter ca. 11–12 µm; small disc-shaped platelets, diameter = 4 µm; and elliptical plates, ca. 8 x 4 µm. Furthermore, a few individuals were found with some quadratic

Fig. 123. *Nebela bartosi*: Original drawing from HAAGER & HAAGEROVA (1970).

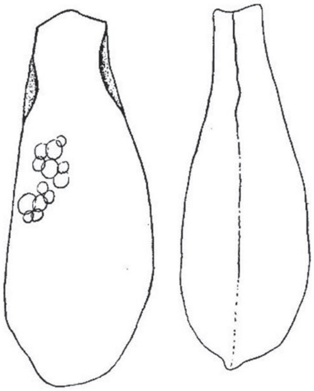

Fig. 124. *Nebela carinulata*: Original drawing from JUNG (1942).

plates attached on the test (as in genus *Quadrulella*). Test bright yellow, with a slightly rose tint. Pseudostome curved.

Etymology: This species is named after the Czech zoologist Emanuel Bartoš (1902-1966).

Habitat: *Sphagnum* mosses

Geographical distribution: Europe: Czech Republic HAAGER & HAAGEROVA (1970).

Remarks: The species was found in *Sphagnum* mosses of the Czech Republic. According to HAAGER & HAAGEROVA (1970), this species is very similar to *Longinebela tubulosa*, but differs by its size, the form and nature of test composition (plates), and the placement of the pores; however, hyalospheniids that incorporate plates from prey organisms may use plates from several different species or even recycle plates from empty shells; therefore, the exact composition of a shell may in some cases depend on plate availability, implying that it is neither a consistent nor valid differential diagnosis criterion (KOSAKYAN et al., 2012). Furthermore, the presence of pores may vary depending on environmental conditions (KOSAKYAN et al., 2012). Sizes can also overlap: L = 213–215 µm, B = 135–137 µm in *N. bartosi* vs. L = 190–264 µm, B = 80–155 µm in *Longinebela tubulosa*. We therefore included this species in the list of *inquirenda* taxa.

Nebela carinulata Jung, 1942

1942a *Nebela carinulata* Jung, Arch. Protistenk.: 313 (abb. 52 a, b, original drawings).

Description: Test elongated-piriform (resembling that of *Gibbocarina galeata*), compressed, with the sides gradually tapering towards the pseudostome; however, the outline is somewhat asymmetrical. Keel starting near the pseudostome, surrounding the entire test, but differing in width across the outline (see Fig. 124). Keel widest (ca. 5 µm) in the neck region where the test narrows. Test composed of loosely abutting circular plates. L = 152 µm, B = 61 µm, P = 28 µm. Pseudostome strongly curved.

Type locality: A swamp near the side of Lake Risopatron, Patagonia, Chile (JUNG 1942a). Likely coordinates: -44.286221°, -72.533152°

Etymology: The name of this species refers to the presence of a keel. "Carinula -ae" in Latin means "a little carina or keel-like ridge".

Habitat: JUNG (1942a) could not say much regarding the ecology of this species, as only one individual was found; however, he did speculate that based on the shape of the test, this species could live in half submerged plants and mosses.

Geographical distribution: South America: Patagonia, Chile (JUNG 1942a).

Remarks: The species was reported only once.

Nebela deflandrei Decloitre, 1955

1955 *Nebela deflandrei* Decloitre, Hydrobiologia 7: 335-336, Fig. 7a–b.

Description: In general shape, test resembling that of *Physochila tenella*. The author mentions the following discriminating characters compared to *P. tenella*: covered with scales, either circular or rectangular with rounded corners, some of which can overlap; scales reaching the pseudostome border, are readily visible at low magnification (unlike those of *P. tenella*); the edges of the test are clearly bent back outwards in a funnel shape; lateral pores are present in the middle of the test, and very difficult to see; test colourless.

Etymology: This species is named after the French protistologist and micro-paleonotologist Georges Deflandre (1897-1973).

Remarks: The species was found only once in green mosses of Venezuela. Considering that the discriminating characters are not convincing (e.g., scale composition, which depends on the prey consumed), and as the original drawing was deemed insufficiently informative (Fig. 125), we have included it in the list of *inquirenda* taxa, pending further observations.

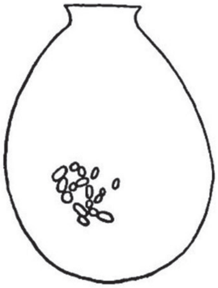

Fig. 125. *Nebela deflandrei*: Original drawing from DECLOITRE (1955).

Nebela fabrei Certes, 1889

1889 *Nebela fabrei* Certes Protozoaires [Mission scientifique du Cap Horn 1882–1883]: 1–53 (Pl. II, Fig. 6).

Description: Test has almost no neck and a curved shape. This peculiar shape, notably different from that of other *Nebela* species, persuaded CERTES (1889) to describe a new species. Test is composed of almost uniform plates. L = 140 µm, B = 40 µm. Because the original description is not overly informative, in addition to the limited number of individuals, we believe that new data are necessary to confirm that this species does indeed belong to family Hyalospheniidae.

Etymology: Not specified. The name of this species may have been chosen to honour Jean-Henri Fabre (1823-1915), the great French entomologist and author of "Souvenirs Entomologiques". The first three of the ten volumes of his masterpiece having been published before 1889, the timing would be logical.

Type locality: Cape Horn (CERTES, 1889; Likely coordinates: -55.521438°, -68.100129°; Elevation, ca. 10 m.a.s.l.),

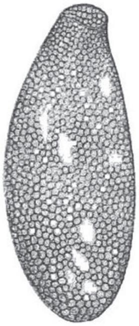

Fig. 126. *Nebela fabrei*: Original drawing from CERTES (1889).

Geographical distribution: South America: Argentina (Cape Horn CERTES, 1889), Africa: Madagascar (DECLOITRE, 1956), Australasia: New Guinea (Papua New Guinea, BONNET, 1980a).

Remarks: A very rarely reported species found only three times

Nebela himalayana Chattopadhyay & Das, 2003

2003 *Nebela himalayana* Chattopadhyay & Das, Zool. Surv. India 19: 67 (Table 65, Figs. 182–184, original drawings).

Description: Test lageniform in broad view, highly compressed, widest at the fundus, asymmetrically converging towards the pseudostome, forming a broad parallel-sided neck. Pseudostome ovoid in frontal view, bordered by comparatively small rectangular platelets. Test transparent, composed of polygonal platelets; neck and fundus equipped with groups of divergent, fine needle-like spines grouped together, and distributed unequally. L = 115–117 µm, B = 68–72 µm.

Type locality: Himalayas, India. Likely coordinates: 28.967597°, 95.956212°; Elevation, ca. 2655 m.a.s.l.. CHATTOPADHYAY & DAS (2003)

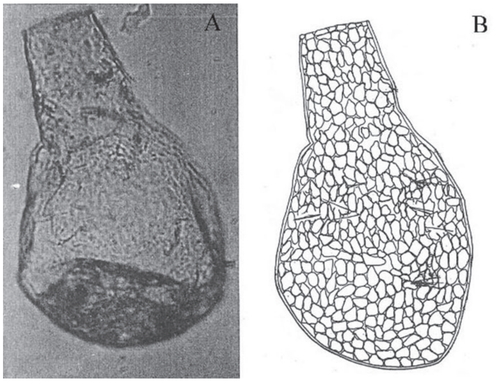

Fig. 127. *Nebela himalayana*: (A) Original LM image and (B) drawing from CHATTOPADHYAY & DAS (2003).

Etymology: The name of this species refers to the Himalayas where it was found.

Habitat: Tree moss

Remarks: Comparative analyses with the relative species as follows, "This species distinctly differs from all the described species of *Nebela* except *N. barbata* in having very fine needle-like spines diverging from its test. However, it can conveniently be separated from *N. barbata* by its flask-shaped test with asymmetrically broad-ovoid fundus and distinctly demarcated broad parallel-sided neck (vs. lageniform test with rounded posterior extremity and slender collar, not distinctly demarcated as neck in *N. barbata*) and lesser number of spines (vs. numerous spines in *N. barbata*)".

We include this species in the *inquirenda* list because we believe that the characteristic "needles" for this species are likely epibiontic bacteria. They are not visible in the LM image, although appear on the drawing as spines (or other debris) attached to the test (notably, not

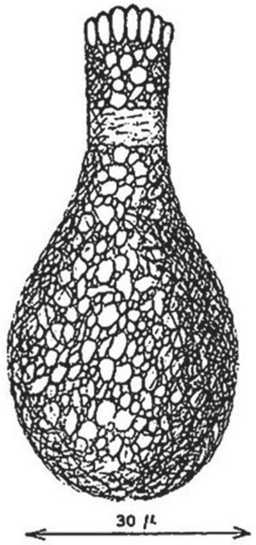

Fig. 128. *Nebela lageniformis elegans*: Original drawing from ŠTĚPÁNEK (1963).

spines projecting from the test). New findings and molecular data are thus needed to assess the validity of this species, as well as its possible affinity with *N. barbata* or genus *Padaungiella*.

Nebela lageniformis elegans Štěpánek, 1963

1963 *Nebela lageniformis elegans* Štěpánek, Ter. Belg. Ann. 117: 78 (Fig. 44, original drawing).

Description: ŠTĚPÁNEK (1963) described *Nebela lageniformis* var. *elegans* from Tshishilu, Democratic Republic of the Congo. Likely coordinates: -9.796524°, 22.571629°. This species, with a test and pseudostome structure provided, differs greatly from other hyalospheniids (see Fig. 128). It appears clearly unrelated to *Padaungiella* (*Nebela*) *lageniformis* and more likely represents a new species with unclear affinities.

Fig. 129. *Nebela parvula*: Original drawing from CASH et al. (1909).

Nebela parvula Cash,1909

1909 *Nebela parvula* Cash, in Cash & Hopkinson, Brit. Freshw. Rhiz. II: 123–124 (Pl. 28, Figs. 20–21).

Description: The taxonomic story behind this species is rather confusing. *Nebela parvula* was found in *Sphagnum* mosses across several localities: Sychnant Pass, N. Wales (Likely coordinates: 53.276945°, -3.864450°); above Dolgam, Capel Curig, N. Wales; Pendland Hills, Modlothian; and Ben Ledi, Scotland. CASH et al. (1909) also mentioned that the species was abundant.

Remarks: The description of this species is very similar to those of *Nebela tincta*. Cash describes it as follows: "*Test ovoid, small, membranous and transparent, with a surfacing (sometimes almost or quite imperceptible) of minute discs, colourless or yellowish; perfectly smooth. The outline ovoid (narrower in some examples than in others) complete down to the neck, which is short and abrupt; the mouth truncated. Test strongly compressed; in dorsal, or transverse view, narrowly elliptic. Length 80 µm, breadth 55 µm*".

We have included *Nebela parvula* in the list of *inquirenda* species because: 1) It is not clear on how many individuals the species measurements were based, as only one value is provided for length and breadth. 2) It is not clearly stated how this species differs from other *Nebela* species, e.g., *Nebela tincta* Leidy (sharing the size range L = 76–92 µm, B = 56 –64 µm). CASH et al. (1909) discuss the similarity of *N. parvula* with other species as follows:

"*This pretty species was taken at first for a diminutive form of* N. collaris *Leidy, or one of its allies, but its occurrence in Sphagnum from localities mentioned was so frequent, and the characters of the individuals were so constant, that careful study led us to the conclusion that it could not be referred to any previously described species. The test is remarkably transparent. A form closely resembling it, but rather longer in proportion, occurred at Dunham in the previous year. It may not improbably have been the same, the difference being due to environment, but without more examples for comparison (only one or two were found in Cheshire) it is impossible to say definitely*".

Indeed, LÜFTENEGER et al. (1988) discussed in detail the difference between *N. tincta* and *N. parvula*, concluding that the main difference could be the absence of the lateral pores in the latter. KOSAKYAN et al. (2013) conducted a detailed morphological and molecular study of the *N. collaris s.l.* group, ultimately listing *N. parvula* as synonymous to *N. tincta* based on the fact that the presence or absence of lateral pores is not a taxonomic character. KOSAKYAN et al. (2013) defined *N. tincta* with a size range: L = 90–95 µm, B = 62–71 µm, notably larger than *N. parvula* (L = 80 µm, B = 55 µm); however, CASH et al. (1909) mentioned that they found larger *N. parvula* "*A form closely resembling it, but rather longer in proportion, occurred at Dunham the previous year*", without giving its exact size. Another possible close species to *N. parvula* could be *N. pechorensis* (L = 84–92 µm, B = 67–87 µm), but as the true size range of *N. parvula* remains unclear, it is difficult to say whether it is an independent taxon, a synonym of *N. tincta* or *N. pechorensis*, or an intermediate form between these two species. Sampling of the original locality and combined detailed morphological and molecular observations may clarify its true position.

Nebela strangularia Decloitre, 1965

1965 *Nebela strangularia* Decloitre, The Zoology of Iceland, 2: 1–58.

Icon.: DECLOITRE, 1977, Arch. Protistenk. 119: 344, Fig. 49.

Description: DECLOITRE (1965) described this species as follows: "The theca resembles habitually that of *Nebela cockayni* (i.e., *Alocodera cockayni*), but it differs from it in the shape of the much stronger constriction at the base of the neck, the truncate pseudostome, the straight (rectilinear) sides of the neck, the dimensions, and the aspect of the membrane. The membrane seems to be smooth except for some occasional thicker plates. The neck is attached to the rest of the theca as were it a tube fixed by pressing it a little to strengthen it and slightly deform the part of the theca supporting it." L = 170–180 µm, B = 100–105 µm, P = 40 µm.

Type locality: Grímsey, a small island 40 km off the northern coast of Iceland. Likely coordinates: 66.542225°, -17.990585°.

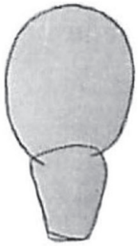

Fig. 130. *Nebela strangularia*: Original drawing from DECLOITRE (1965).

Etymology: The name of this species refers to the constriction at the base of the neck, as if the shell had been subject to strangulation.

Habitat: Shallow, small pond.

Geographical distribution: Europe: Iceland (DECLOITRE, 1965).

Remarks: Only a very simple illustration is given (line drawing of the outline, see Fig. 130). Other illustrations in the original publication remain dubious; for example, that of *Cylindrifflugia* (*Difflugia) bacillifera* does not correspond to this species at all. Although the description and illustration clearly suggest that this species belongs to genus *Apodera* (rather than *Alocodera*, as stated in the description, as the constriction indeed seems to be present around the entirety of the neck base, as the species name also suggests), this would be a rather surprising finding considering the geographical location, as neither *Alocodera* nor *Apodera* have been found North of the Tropic of Cancer desert belt (SMITH et al., 2008). One possible explanation could be that the observed individual (or individuals, as it remains unclear how many specimens were observed) corresponded to another similar species, such as *Lagenodifflugia vas* (MITCHELL & MEISTERFELD, 2005), but this seems unlikely, as L. vas typically has numerous mineral xenosomes attached to the test. We have thus included this species in the list of *inquirenda* taxa until new data are available to reassess its validity.

Nebela tincta galeata complex

Each of the three following species can represent an independent taxon, or perhaps some or all may be synonymous. See remarks below.

1936 *Nebela tincta* f. *galeata* Jung, Ann. Protistol. 5: 89.

1952 *Nebela collaris* var. *galeata* Hoogenraad & de Groot, Arch. Hydrobiologie 47:

231 (Fig. 3).

1959 *Nebela galeata* var. *orbicularis* f. *minor* Tarnogradskij, Raboty severo kavkazskoj Gidrobiologiceskoj Sta. Trudy Severo-osetinskogo Sel'skokhozyaistv. Inst. 6: 46 (Fig. 55)

Description: JUNG (1936) mentioned a form of *Nebela tincta* f. *galeata* without providing an illustration. According to the description, it resembles *Nebela aliciae*, from which it differs by its larger size (117–143 µm in *N. tincta* f. *galeata* vs. L = 104–115 µm in *N. aliciae*).

HOOGENRAAD & DE GROOT (1952) observed tests that differed from those of *Nebela collaris* by their dimensions, especially its wider shape (i.e., lower L/B), and the presence of a "*more or less distinct but always present flattening of the marginal zone of the fundus*" (i.e., a hollow keel). In addition, the brownish coloured, clearly thickened pseudostome was a feature not found in *N. collaris*. Several specimens also had visible lateral pores, typically missing from *N. collaris* (but the validity of this criterion is now questioned, see discussion under *Nebela parvula* and KOSAKYAN et al. (2013)). TARNOGRADSKIJ (1959) described a smaller form of *N. galeata* var. *orbicularis* (currently *N. orbicularis*) as f. *minor*, which differs from the

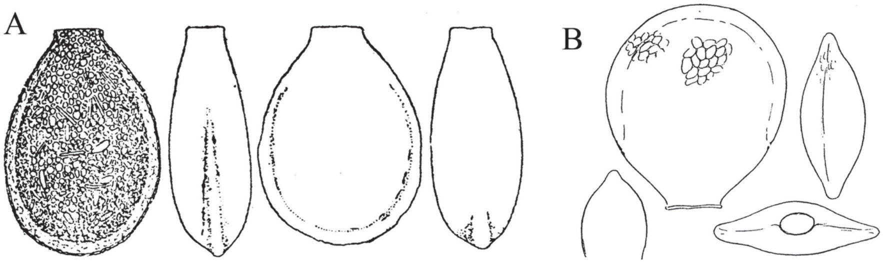

Fig. 131. *Nebela tincta galeata* complex: (A) Original drawings of *N. galeata* var. *orbicularis* f. *minor* from TARNOGRADSKIJ (1959), and (B) N. *collaris* var. *galeata* from HOOGENRAAD & DE GROOT (1952).

type by its less rounded outline and smaller size: L= 135–150 µm, B = 100–108 µm.

Ferry Siemensma (www.arcella.nl) observed *Nebela tincta* f. *galeata* with L = 130–146 µm.

Apparently, a continuum exists between each of these described forms. A careful morphological and molecular analysis is thus needed to clarify the status of these described forms, as well as their relationship with *N. aliciae*.

Nebela varia Decloitre, 1966

1966 *Nebela varia* Decloitre, Vidensk. Medd. Dansk. Naturh. Foren. 129: 69 (Fig. 5, original drawing).

Description: Test lageniform, with a distinct neck. Test composed of large circular plates situated far from one another, with small circular plates in between (the primary distinguishing character according to DECLOITRE, 1966). L = 150–160 µm.

Type locality: Iceland, likely coordinates: 65.547859°, -17.058249°.

Habitat: Pond

Remarks: The species was found in Iceland. A rather problematic species, as the description is somewhat scarce and confusing. For example, it is mentioned that by its general shape, the test resembles *Longinebela tubulosa* except that the neck is more distinct; but the original drawing shows a very similar shape to *Padaungiella lageniformis*. It may be that the confusion was simply between *Longinebela* L. (*Nebela*) *tubulosa* and *Padaungiella* (*Nebela*) *tubulata*, a somewhat common confusion based on their names, but the size would not match. The main distinguishing

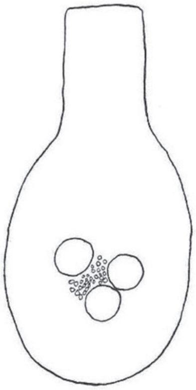

Fig. 132. *Nebela varia*: Original drawing from DECLOITRE (1966).

taxonomic criterion from other species (as stated) is the test composition, but, as this can depend upon prey availability, it has been deemed an invalid taxonomic criterion here. *N. varia* is larger (L = 150–160 µm) than other *Padaungiella* species, except for: *P. wetekampi* (L = 149 µm), supposedly endemic to Chile; *P. magna* (L = 177 µm) from New Zealand; and *P. pulcherrima* (L = 180–195 µm) from Russia (Arkhangelsk) as well as the Caucasus (Azerbaijan).

9.4. *Inquirenda* taxa from genus *Padaungiella*

Padaungiella wailesi (Wailes, 1912) Lara & Todorov, 2012

1912 *Nebela lageniformis* var. *minor* Wailes, J. Linn. Soc. London. Zool. 32: 157.

1936 *Nebela wailesi* Deflandre, Ann. Protistol. 5: 265 (nom. nov. replacement name).

2012 *Padaungiella wailesi* Wailes, 1912 - Lara & Todorov, in KOSAKYAN et al., 2012, Protist 163: 429–430 (establishment of genus *Padaungiella* based on detailed morphological and molecular data).

Icon.: DEFLANDRE, 1936, Fig. 100, 103, Pl. XXII, Figs. 6–9; GAUTHIER-LIÈVRE, 1952, Fig. 15; KOSAKYAN et al., 2012, Fig. 6 E–F; TODOROV & BANKOV, 2019, Fig. 78.

Missappl. figures: *Nebela lageniformis* p.p.; PENARD, 1902, p. 356, Fig. 3; WAILES & PENARD, 1911, Pl. V, Fig. 28.

Description: Test lageniform in broad view, with an ellipsoid main posterior body part, and distinct elongated neck. Neck ovoid in cross-section, with either subparallel or slightly convex margins in broad view. Test transparent, composed of elliptical or circular juxtaposed plates recycled from its euglyphid prey. Pseudostome ovoid in frontal view, curved in broad view, surrounded with a thin organic rim. L = 75–100 µm, B = 52–58 µm.

Differential diagnosis: The general shapes of *Padaungiella wailesi* and *P. lageniformis* are similar. *P. wailesi* is generally identified by its smaller size. Indeed, WAILES (1912) cited this as the only distinguishing characteristic. However, subsequent studies have gradually increased the size range of

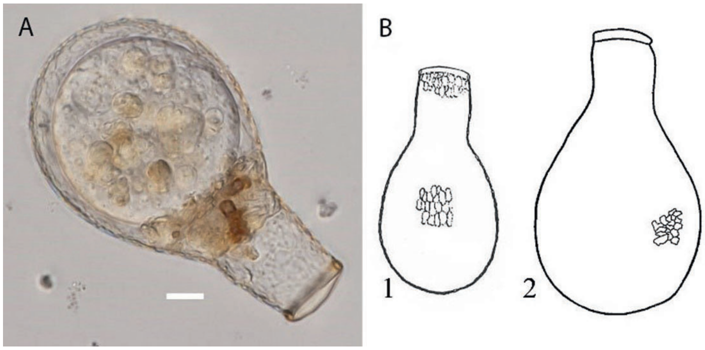

Fig. 133. *Padaungiella wailesi*: (A) LM image of a specimen from Chile (by Edward Mitchell), and (B) Original drawing of *P. wailesi* from DEFLANDRE (1936). Scale bar = 10 µm.

the two species: LUKETA (2015) extended the size range of *P. lageniformis* to 91 µm, which would imply that the two species overlap in shell length. These species also differ in their ecology: *P. wailesi* is frequent in forest litter and tolerates drought conditions, whereas P. lageniformis is a wetland species. A molecular study of mt-COI sequence data confirmed that *P. wailesi* and *P. lageniformis* are two distinct species (KOSAKYAN et al., 2012). But this study was but notably based solely on one individual for each species.

Type locality: Mahé (Seychelles). Likely coordinates: -4.684031°, 55.502018°.

Etymology: The species named in honour of the English protistologist George Herbert Wailes (1862-1945).

Habitat: Forest litter, mosses including *Sphagnum*.

Geographical distribution: Likely cosmopolitan (we have > 140 records in our database).

Remarks: *Padaungiella wailesi* and *P. lageniformis* show a continuum of neck shapes ranging from the side generally tapering towards the aperture to the presence of a bulge in the middle of the neck. It remains unclear if this corresponds to intraspecific variability or points to the existence of some hitherto undescribed species (see detailed discussion under *P. lageniformis*). We maintain *P. wailesi* as an *inquirenda* species until *P. lageniformis* and its closely related species can be studied using more detailed morphological and molecular analyses.

Padaungiella wetekampi (Jung, 1942) Lara & Todorov, 2012

1942 *Schaudinnia* wetekampi Jung, Arch. Protistenk. 95: 312 (Fig. 51a–c, original drawings).

2012 *Padaungiella wetekampi* Jung, 1942 - Lara & Todorov, in Kosakyan et al., 2012, Protist 163: 429–430 (establishment of genus *Padaungiella* based on detailed morphological and molecular data).

Fig. 134. Original drawing of *Padaungiella wetekampi* from JUNG (1942): broad, lateral, and profile views.

Description and differential diagnosis: Like other lageniform species in general shape, (e.g., *P. lageniformis*, *P. tubulata*), differs only by its (slightly) larger size. L = 149 µm, B = 60–70 µm, P = 26–33 µm, Lneck = 63–68 µm (JUNG, 1942; see also discussion under *P. lageniformis*).

Type locality: Calbuco, Chile. Likely coordinates: -41.780682°, -73.136297°; Elevation, ca. 20 m.a.s.l..

Etymology: This species was named in honour of Wilhelm Jung's biology high school professor (Oberrealschule zu Hamm (Westf.) Dr F. Wetekamp.

Geographical distribution: Chile (JUNG, 1942; WILKINSON, 1990).

Habitat: Sediment in a forest creek.

Remarks: A problematic species, as it is identical to another subsequently described from Iceland, *Nebela varia* (DECLOITRE, 1966). Both species have been found in only one locality, and considering the distance between the two locations of origin (Iceland and Chile), it is unlikely that they belong to a single species. The only discriminating factor to separate *P. wetekampi* from *P. lageniformis* and *P. wailesi* is size, and as the size ranges of these species overlap, it is similarly impossible to distinguish among these three taxa as well (see detailed discussion under *P. lageniformis*). We thus consider *P. wetekampi* as an *inquirenda* species until *P. lageniformis* and its closely related species can be studied using detailed morphological and molecular analyses.

9.5 *Inquirenda* taxa from genus *Quadrulella*

Quadrulella scutellata vas Hoogenraad & De Groot, 1940

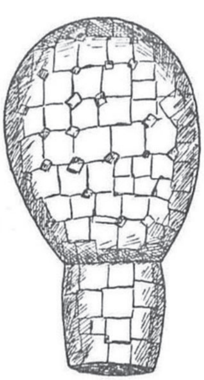

Fig. 135. *Quadrulella scutellata vas*: Original drawing from HOOGENRAAD & DE GROOT (1940a).

1940a *Quadrulella scutellata vas* Hoogenraad & De Groot, 1940a, Treubia (Buitenzorg) Bd.17, H. 4: 214, 224, 233, 247.

Description: HOOGENRAAD & DE GROOT (1940) found tests in Java and Sumatra with the same composition as that of *Q. scutellata* but a notably different test shape from the type. Their samples revealed a test with an elongated distinct neck with a deep constriction (as in *Apodera vas*), thus motivating their description of a new variety, which they named *Quadrulella scutellata* var. *vas*.

Remarks: There is some confusion in the literature surrounding this variety, as the illustrations indicated in HOOGENRAAD & DE GROOT (1940a; Figs. 64–66) are not clearly labelled (all the three very distinct drawings are identified as *Q. scutellata*). The dimensions are unclear as well, as different dimensions were acquired from distinct samples: L = 83–110 µm, B = 53–93 µm, Lneck = 40–50 µm, P = 30–37 µm from sample II (*Minodendron divaricatum*, Tjibeureum, Gedch, W. Java; Elevation, ca. 1700 m.a.s.l.); L = 123–153 µm, B = 67–80 µm from sample IX (Bryales, Kerintji Peek, Sumatra, 1400 m); L = 123–150 µm, B = 67–93 µm from sample XIII (Bryales, Tjibodas, W. Java, 1400 m). Further, it is unclear whether these dimensions referred to *Q. scutellata* var. *vas* or the type. *Quadrulella scutellata* var. *vas* can be confused with *Q. constricta* described by LOPRETTO & VUCETICH (1997) from Argentina (see p. 172 for further discussion on these taxa).

Type locality: Tjibeureum, Gedch, W. Java; Likely coordinates: -6.753934°, 106.985868°; Elevation, ca. 1700 m.a.s.l.

Geographical distribution: Asia: Indonesia (HOOGENRAAD & DE GROOT, 1940)

Quadrulella symmetrica irregularis Penard, 1911

1911 *Quadrulella symmetrica* var. *irregularis* Penard, in WAILES & PENARD, 1911, P. Roy. Irish. Acad. B 31: 6651, Pl. VI, Fig. 31 (original drawing), also Deflandre, 1936, Pl. XI, Figs. 1–2.

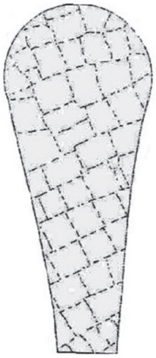

Fig. 136. *Quadrulella symmetrica irregularis*: Original drawing from WAILES & PENARD (1911).

Non. *Quadrula irregularis* Archer, 1877.

Description: PENARD (1891) described this variety with a short description, but neither name nor illustration. He cited it again in 1905 (PENARD 1905), but still did not include any illustration. In their original description, WAILES & PENARD (1911) wrote:

"Quadrulella symmetrica *is generally distributed over Great Britain and occurs in two forms: (a) with a pseudostome devoid of lips and to which the sides descend in nearly straight lines and (b) the pseudostome is furnished with a lip and the sides descend to it in concave lines, a form which, except for the structure of the test, is hard to distinguish from a large* Nebela militaris. *The sizes of these two forms vary from 60 to 110 µm long. There is, however, a variety of form (a) from 130 - 150 µm long has been found by Dr. Penard in North America and named by him var. irregularis; this he recorded from Loch Nessin 1905, but it has not been recorded from elsewhere in Europe. The Inishbofin individuals were 130 µm long, 55 µm wide, 23 µm pseudostome. Similar ones from Goathland moor, N. York, measured: Length 133 µm, width 55 µm, pseudostome 25 µm."*

The original illustration is hard to distinguish from *Quadrulella longicollis* (as mentioned by DEFLANDRE, 1936). PENARD provided two plates for comparison: Pl. X, Figs. 13–14 for *Q. longicollis* and Pl. XI, Figs. 1-2 for *Q. symmetrica* var. *irregularis* with more irregularly arranged plates. The situation is not clarified, however, since in the original description, it is clearly stated that var. *irregularis* belongs to form (a) of *Q. symmetrica*, which is lacking an organic lip, whereas in DEFLANDRE's (1936) illustration (Pl. XI, Fig. 1), the individual clearly has an organic lip. Notably, KOSAKYAN et al. (2012, Fig. 5) also observed *Q. longicollis* with a tiny organic rim.

Quadrulella symmetrica kivuensis Van Oye, 1958

1958 *Quadrulella symmetrica* var. *kivuensis* Van Oye, Hydrobiologia 10: 107 (Fig. 16, original drawing).

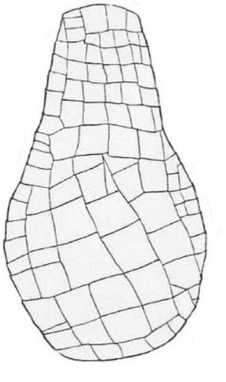

Fig. 137. *Quadrulella symmetrica kivuensis*: Original drawing from VAN OYE (1958).

Description: VAN OYE (1958) described this variety noting that it may represent an intermediate form between *Quadrulella symmetrica longicollis* and *Q. tubulata*. The main characters are: irregular plates of different sizes and a pseudostome lacking an organic lip. Test size variable, indicated as L = 130 µm, B = 77 µm. Detailed morphometric data are lacking.

Type locality: Southwest Uvira, Democratic Republic of Congo. Likely coordinates: -3.482696°, 29.034265°; Elevation, ca. 3030 m.a.s.l.,

Etymology: Kivu was the name for a region that bordered Lake Kivu in the Democratic Republic of the Congo.

10. LIST AND NOTES TO NON-VALID, *NOMEN NUDUM*, OR EXCLUDED NAMES

In this list, we have included the names of 13 species with inadequate descriptions or clear erroneous identification or known only as fossils.

Hyalosphenia baueri † Schönborn, Dorfelt, Foissner, Krienitz, & Schafer 1999

Description (based on the original publication): Test indistinctly vase-shaped, compressed, with two opposite lateral pores and a small collar around the terminal aperture, membranous, structureless, brown. L =95.5 µm, B = 60 µm.

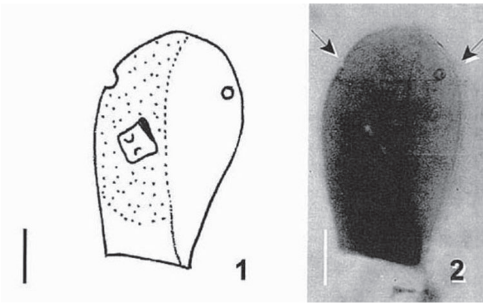

Fig. 138. Reconstruction (1) of the fossilized *Hyalosphenia baueri* (2) found in Triassic amber from Mount Leitnernase, Bavaria, Germany. Arrows indicate two lateral pores. Scale bars = 15 µm. Image is taken from SCHÖNBORN et al. (1999).

Remarks: This species was described as a fossil from amber. The authors describe the aperture as probably oval. Only one complete specimen and some fragments (showing a pore) were found. The authors consider it as similar to *H. humicola*, but lacking xenosomes, with pores, and a different shape. We do not find enough morphological evidence to unambiguously accept this species as a valid *Hyalosphenia* species or even a member of the hyalospheniidae. We nevertheless encourage further studies of fossils from amber, ideally based on more specimens.

Fig. 139. *Hyalosphenia coogeeana*: Original drawing from PLAYFAIR (1917).

Hyalosphenia coogeana Playfair, 1918

Remarks: Erroneous identification. This description corresponds most likely to a rotifer (e.g., genus *Habrotrocha* Bryce, 1910, some of which, such as *H. angusticollis* (Murray, 1905), build organic tests called lorica.

Hyalosphenia jiroveci Štěpánek, 1953

1953 *Hyalosphenia jiroveci* Štěpánek, Přírodověd. sb. ostrav. kraje 14: 470–505, Fig. 8.

Description (based on the original publication): Test transparent, hyaline, vase-shaped in broad view, with a long-developed neck and rounded body. Test slightly compressed laterally, transparent. L = 84 µm, B = 49 µm. Neck widens near the pseudostome. According to the illustration of the description, the pseudostome is curved in broad view. Pseudostome size unspecified.

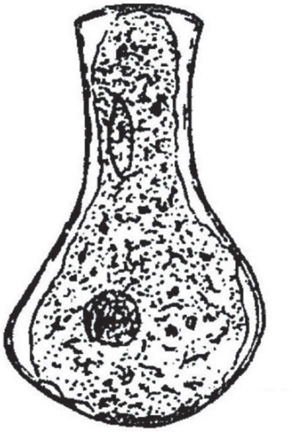

Fig. 140. *Hyalosphenia jiroveci*: Original drawing from ŠTĚPÁNEK (1953).

Remarks: The species was reported from River Moravice, and tributaries between Bruntal and Kruzberk, Czech Republic. Likely coordinates: 49.908547°, 17.502566°. It was found in aquatic benthos, among decaying plants. In our opinion, this is misidentified, and most probably, corresponds to a ciliate (*Vaginicola* cf. *terricola*).

Hyalosphenia triquetra Imhof, 1895 - *nomen nudum*

1895 *Hyalosphenia triquetra* Imhof, Faunistische Studien in achtzehn kleineren und grösseren österreichischen Süsswasserbecken. Sber. Akad. Wiss. Wien, v. 91, p. 203-226.

Remarks: This species is considered as a nomen nudum according to the Austrian Catalogue (Erna Aescht pers. comm to Ralf Meisterfeld).

Hyalosphenia turfacea Taránek, 1881 - *nomen nudum*

1881 *Hyalosphenia turfacea* Taránek, R. Böhm. Ges. Wiss. Prag. 229–230.

Original description: "*Die Schale ist der* H. elegans *sehr ähnlich, also flaschenförmig gegen die Pseudopodienöung durch einen breiten Hals verengt. Der hals ist aber in dem ersten Drittheil knieförmig geobogen und das hintere Ende der hyalinen Schale trägt eine kurze membranöse Carina, welche der bei* Nebela carinata *ähnlich ist. In den Torfmooren auf dem* Sphagnum *von Wittingau, Wittmanov ect*". Translation: "*The shell is very similar to that of* H. elegans*, i.e., bottle-shaped, with a broad neck narrowing towards the pseudostome. However, the first third of the neck is bent knee-shaped and the rear end of the hyaline shell bears a short membranous carina, which is similar to that of* Nebela (i.e., Planocarina) carinata*. In* Sphagnum *from the peat bogs of Wittingau, Wittmanov etc.*"

Differential diagnosis: The test by shape is very similar to that of *Hyalosphenia elegans* but has a curved neck and a short membranous keel at the aboral end of the test, as in *Planocarina carinata*. It was found in peat bog *Sphagnum* mosses.

Remarks: We placed this species in the list of *nomen nudum* taxa owing to its insufficient description—no indication of size and no drawing.

Hyalosphenia undans Coûteaux & Munsch, 1978

Remarks: Misidentification, as the description most likely corresponds to a rotifer (e.g., genus *Habrotrocha* Bryce, 1910, some of which, such as *H. angusticollis* (Murray, 1905), build organic tests called lorica).

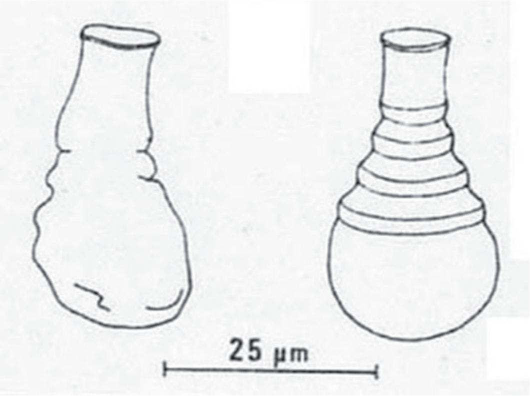

Fig. 141. *Hyalosphenia undans*: Original drawing from COUTEAUX & MUNSCH (1978).

Nebela americana var. *falcata* Wailes, 1912a

1936 *Nebela penardiana* var. *falcata* – Deflandre 1936, p. 259 (new combination).

Remarks: We have included this subspecies in the list of *nomen nudum* owing to the lack of original drawings.

Nebela labiata Tarnogradskij 1945 - *nomen nudum*

(in: Trav. Stat. Biol. Caucase Nord 4: 27–31)

Remarks: The species name was mentioned by TARNOGRADSKIJ 1945 (twice in the same volume) but without any description or figure.

Nebela ciliata – nomen nudum

Remarks: The species name was mentioned in FANTHAM & PORTER (1945), with neither the name of the author(s) nor the test dimensions.

Nebela complanata Levander, 1900 – *nomen nudum*

Remarks: No official description was provided.

Nebela militaris var. *penardina* – *nomen nudum*

Remarks: The species name was mentioned by GRACIA (1968) without any authority.

Quadrulella symmetrica f. *major* Hoogenraad and de Groot – *nomen nudum*

Remarks: No official description was provided.

Quadrulella symmetrica f. *minor* Hoogenraad & de Groot – *nomen nudum*

Remarks: No official description was provided.

The story behind the last two *Quadrulella* taxa is complicated. These forms are mentioned by CHARDEZ (1967), who named HOOGENRAAD & DE GROOT, 1940 as the original authors; however, there is no record of these taxa from any publication of HOOGENRAAD & DE GROOT, 1940. CONRAD (1942a, b) also mentioned these taxa by clearly citing the work of HOOGENRAAD & DE GROOT as the source, although no year was stated.

The situation is quite confusing, as the information in the works of HOOGENRAAD & DE GROOT (1940a, b), CONRAD (1942a, b), and CHARDEZ (1967) is contradictory.

CHARDEZ (1967) presented illustrations for both forms of *Q. symmetrica* f. *major* and f. *minor*, although these illustrations were not cited in CONRAD'S (1942) publications. Another issue is that Chardez cited data different from those of Conrad, namely, stating that the tests of the f. *minor* have L < 60 µm. Conrad showed *Q. symmetrica* and *Q. symmetrica* f. *minor* together, and reported finding many individuals of smaller shape. Conrad further noted aggregate morphometric data for these two taxa: L = 67–93 µm, B = 40–53 µm.

From this comparison, we concluded that f. *minor* sensu Chardez is smaller (L < 60 µm) than f. minor sensu Conrad (L > 67 µm). By contrast, f. *major* sensu Conrad is smaller (L = 117–137 µm; B = 50–63 µm, nb. mentioned as "maior") than f. *major* sensu Chardez (L > 125 µm). This suggests that Chardez did not use information (neither illustrations nor morphometric data) from Conrad. Conrad most likely had direct correspondence with Hoogenraad & de Groot through letters. Since Conrad was not a specialist, it is possible that he cited Hoogenraad & de Groot as the authors of these forms, not knowing if or where they published the descriptions of these taxa, and perhaps that is why, he did not state the year of the publication. If this assumption is correct, the question arises, from where did CHARDEZ (1967) get the data on these forms? It could be that he did not directly copy the illustrations from another publication, rather publishing his own drawings. Most likely, the drawings for f. *minor* and f. *major* were based on descriptions, as these forms differ only in their dimensions from typical specimens of *Q. symmetrica*. CHARDEZ (1967) presented different morphometric data in relation to CONRAD because his definition of *Q. symmetrica* fully (f. *minor*) or partially (f. *major*) encompassed the morphometric range of forms. Namely, he stated that *Q. symmetrica* has L = 68–120 µm and B = 45–74 µm. Because Conrad did not separate the data for *Q. symmetrica* and *Q. symmetrica* f.

minor, Chardez probably thought that Conrad had made a mistake by only providing data for typical individuals but not f. *minor*. Chardez may have concluded that f. minor referred to the individuals with L < 60 µm. Because f. *major* sensu Conrad partially overlaps with *Q. symmetrica* sensu Chardez, CHARDEZ (1967) considered that typical individuals of forma major were L > 125 µm. CHARDEZ (1967) probably cited 1940 as the publication year of the description of these two forms because CONRAD (1942) cited only the paper published in 1940 from Hoogenraad and de Groot.

Support for the claim that CHARDEZ (1967) did not see the original descriptions of f. *minor* and f. *major* may derive from the fact that he stated f. *major* was present only in Belgium, an information he attributed to CONRAD, who notably did not state the location where this taxon was found by Hoogenraad and de Groot. The reason why CHARDEZ (1967) renamed f. *maior* into f. *major* likely lies in the fact that this convention is common in the taxonomy of testate amoebae, so he was free to correct this omission by an author who not a specialist in the taxonomy of protists.

Based on this puzzled information, we questioned the taxonomic identity of *Q. symmetrica* f. *minor* and f. *major*. Notably, the test length in individuals of *f. minor* best corresponds to that of *Q. variabilis* and f. *major* to *Q. longicollis* (LUKETA, 2016, 2017).

11. SYNONYMOUS NAMES

We list here 65 synonymous names for hyalospheniid testate amoebae. Of these, 8 are new combinations (comb. nov., indicated with an asterisk), based on the general morphology and morphometry of the species.

In this list of synonymous names, we follow the International Code of Zoological Nomenclature. In the case of taxa with revised names, in addition to the original author(s) in brackets, as is the rule in the ICZN, the current authorities are included to give readers easier access to the authors of taxonomic actions. To follow the ICZN code, simply remove the names and dates listed after the closing bracket.

Hyalosphenia lata Schulze, 1875 - current name: *Hyalosphenia cuneata* Stein, 1857

Hyalosphenia ligata Tatem, 1870 - current name: *Hyalosphenia cuneata* Stein, 1857

Hyalosphenia papilio f. *multiporifera* Jung, 1936 - current name: *Hyalosphenia papilio* Leidy, 1879

Hyalosphenia tincta Leidy, 1879 - current name: *Nebela tincta* (Leidy, 1879) sensu Kosakyan & Lara, 2013

Nebela ambigua Cash, 1892 - current name: *Padaungiella lageniformis* (Penard, 1890) Lara & Todorov, 2012

Nebela ansata Leidy, 1879 - current name: *Cornutheca ansata* (Leidy, 1879) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela bohemica (Ehrenberg, 1848) Taránek, 1882 - current name: *Nebela collaris* (Ehrenberg, 1848) sensu Kosakyan & Gomaa, 2013

Nebela bursella Vejdovsky, 1881 - current name: *Alabasta militaris* (Penard, 1890) Duckert, Blandenier, Kosakyan, & Singer, 2018

Nebela bursella var. *rotunda* Penard, 1890 - current name: *Nebela rotunda* Penard, 1980

Nebela carinata (Archer, 1866) Leidy, 1876 - current name: *Planocarina carinata* Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela carinata var. *acarinata* Jung, 1942 - current name: *Planocarina marginata* (Penard, 1902) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela carinata var. *brevicarinata* Jung, 1942 - current name: *Planocarina marginata* (Penard, 1902) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela collaris var. *genuina* Taránek, 1882 - current name: *Nebela collaris* (Ehrenberg, 1848) sensu Kosakyan & Gomaa, 2013

Nebela collaris var. *pyriformis* Tаránek, 1882 - current name: *Longinebela tubulosa* (Penard, 1890) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela cordiformis * (Heinis, 1914) Jung, 1942 - current name: *Padaungiella cordiformis* comb. nov.

Nebela digitiformis Vucetich, 1973 - current name: *Nebela barbata* var. *psilonata* Jung, 1942

Nebela duttoni Gericke, 1932 - current name: *Nebela tincta* (Leidy, 1879) sensu Kosakyan & Lara, 2013

Remarks: This specimen was found in South Africa and proposed as a new species. In the original description, GERICKE (1932) mentioned that this species is extremely similar to *N. collaris*, differing where its mouth is surrounded by a thickened organic rim "not provided with scales". KOSAKYAN et al. (2013) later conducted detailed morphological and molecular analyses of the *N. collaris s.l.* group, revealing that the original description of *N. duttoni* completely corresponded to that of *N. tincta* (Leidy, 1879) sensu Kosakyan & Lara, 2013 (see also Fig. 2C, E in KOSAKYAN et al., 2013). Thus, we suggest synonymizing *N. duttoni* Gericke, 1932 with N. tincta (Leidy, 1879) sensu Kosakyan & Lara, 2013.

Nebela equicalceus Leidy, 1874 - current name: *Cornutheca equicalceus* (Leidy, 1874) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela galeata Penard, 1890 - current name: *Gibbocarina galeata* (Penard, 1890) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell & Lara, 2016

Nebela galeata f. *minor* Hoogenraad, 1937 - current name: *Gibbocarina gracilis* (Penard, 1910) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Note: The general shape and size of *N. galeata* f. *minor* completely corresponds to the description of *G. gracilis*; thus, we suggest synonymizing both species.

Nebela galeata var. *orbicularis* * Deflandre, 1936 - current name: *Nebela orbicularis* comb. nov.

Nebela golemanskyi Todorov, 2010 - current name: *Longinebela golemanskyi* (Todorov, 2010) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela goudinii Gericke, 1932 - current name: *Apodera vas* (Certes, 1889) Loeblich & Tappan, 1961

Note: The species description corresponds to *Apodera vas*, the only difference is the size of the test (L = 120–138 µm, B = 62–67 µm in *N. goudinii* vs. L = 130–170, B = 55–103 µm in *A. vas*), although the two overlap. We therefore suggest to synonymize *N. goudinii* with *A. vas*.

Nebela gracilis Penard, 1910 - current name: *Gibbocarina gracilis* (Penard, 1910) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela hippocrepis Leidy 1874 - current name: *Cornutheca equicalceus* (Leidy, 1874) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela jiuhuensis Qin, Mitchell, & Lara, 2016 – current name: *Cornutheca jiuhuensis* (Qin, Mitchell, & Lara, 2016) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela kenyana * Chardez, 1982 - current name: *Padaungiella kenyana* comb. nov.

Nebela kivuense Gauthier-Lièvre & Thomas, 1961 - current name: *Alabasta kivuense* (Gauthier-Lièvre & Thomas, 1961) Duckert, Blandenier, Kosakyan, & Singer, 2018

Nebela lageniformis Penard, 1890 - current name *Padaungiella lageniformis* (Penard, 1890) Lara & Todorov, 2012

Nebela lageniformis var. *cordiformis** Heinis, 1914 - current name: *Padaungiella cordiformis* comb. nov.

Nebela lageniformis var. *minor* Wailes, 1912 – current name: *Padaungiella wailesi* (Deflandre, 1936) Lara & Todorov, 2012

Nebela longicollis Penard, 1890 - current name: *Alabasta longicollis* (Penard, 1890) Duckert, Blandenier, Kosakyan, & Singer, 2018

*Nebela longitubulata** Gauthier-Lièvre, 1953 - current name: *Padaungiella longitubulata* comb. nov.

Nebela marginata Penard, 1902 - current name: *Planocarina marginata* (Penard, 1902) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela maxima Awerinzew, 1906 - current name: *Planocarina maxima* (Awerinzew, 1906) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela meisterfeldi Heger & Mitchell, 2012 - current name: *Longinebela meisterfeldi* (Heger & Mitchell, 2012) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchel, & Lara, 2016

Nebela minor Penard, 1902 - current name: *Nebela tincta* (Leidy, 1879) sensu Kosakyan & Lara, 2013

Nebela militaris Penard, 1890 - current name: *Alabasta militaris* (Penard, 1890) Duckert, Blandenier, Kosakyan, & Singer, 2018

Nebela militaris var. *tubulata* Brown, 1911 - current name: *Padaungiella tubulata* (Brown, 1911) Lara & Todorov, 2012

Nebela nebeloides (Gauthier-Lièvre & Thomas, 1958) Todorov, Golemansky, & Meisterfeld, 2010 (note: only TODOROV et al. (2010) have used this name) - current name: *Padaungiella nebeloides* (Gauthier-Lièvre & Thomas, 1958) Lara & Todorov, 2012

Nebela numata Leidy, 1874 - current name: *Nebela collaris* (Ehrenberg, 1848) sensu Kosakyan & Gomaa, 2013

Nebela penardi Brehm, 1928 - current name: *Apodera angatakere* (Brehm, 1928) Mitchell, Blandenier, & Duckert, 2021

Nebela penardi Heinis, 1914 - current name: *Certesella martiali* (Certes, 1889) Loeblich & Tappan, 1961 (junior synonym)

*Nebela pulcherrima** Awerinzew, 1907 - current name: *Padaungiella pulcherrima* comb. nov.

Nebela saccifera Wailes, 1913 - current name: *Cornutheca saccifera* (Wailes, 1913) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela semimarginata Van Oye, 1949 - current name: *Planocarina semimarginata* (Van Oye, 1949) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela speciosa Deflandre, 1936 - current name: *Longinebela speciosa* (Deflandre, 1936) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela spumosa Awerinzew, 1906 - current name: *Planocarina spumosa* (Awerinzew, 1906) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela sphagnophila (Steinecke, 1914) Van Oye, 1933 - current name: *Nebela collaris* (Ehrenberg, 1848) sensu Kosakyan & Gomaa, 2013

Nebela suecica Grospietsch, 1954 - current name: *Planocarina speciosa* (Deflandre, 1936) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela tincta var. *grandis* Bunescu & Matic, 1982 - current name: *Nebela collaris* (Ehrenberg, 1848) sensu Kosakyan & Gomaa, 2013

Nebela tincta var. *major* Deflandre, 1936 - current name: *Nebela collaris* (Ehrenberg, 1848) sensu Kosakyan & Gomaa, 2013

Nebela tincta var. *rotunda* Penard, 1890 - current name: *Nebela rotunda* Penard, 1890

Nebela tincta f. *stenostoma* Jung, 1936 - current name: *Nebela collaris* (Ehrenberg, 1848) sensu Kosakyan & Gomaa, 2013

Nebela tubulata Brown, 1911 - current name: *Padaungiella tubulata* (Brown, 1911) Lara & Todorov, 2012

Nebela tubulata var. *spatha** Thomas, 1960 - current name: *Padaungiella tubulata spatha* (Thomas, 1960) comb. nov.

Nebela tubulosa Penard, 1890 – current name: *Longinebela tubulosa* (Penard, 1890) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Nebela wailesi Deflandre, 1936 – current name: *Padaungiella wailesi* (Deflandre, 1936) Lara & Todorov, 2012

Nebela wailesi var. *magna** Van Oye, 1956 - current name: *Padaungiella wailesi magna* (Van Oye, 1956) comb. nov.

Nebela wellingtonia Decloitre, 1964 - current name: *Apodera wellingtonia* (Decloitre, 1964) Chardez, 1994

Pseudohyalosphenia prismatica Štěpánek, 1967 - current name: *Hyalosphenia punctata* Penard, 1891

Quadrula symmetrica var. *longicollis* Taránek, 1882 - current name: *Quadrulella longicollis* Taránek, 1882

Quadrulella plicata Hoogenraad & De Groot, 1940 - current name: *Mrabella plicata* (Hoogenraad & De Groot, 1940) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Quadrulella subcarinata Gauthier-Lièvre, 1957 - current name: *Mrabella subcarinata* (Gauthier-Lièvre, 1957) Kosakyan, Lahr, Mulot, Meisterfeld, Mitchell, & Lara, 2016

Quadrulella tubulata var. *cylindrica* Chardez, 1967 - current name: *Quadrulella tubulata* Gauthier-Lièvre, 1953

12. SPECIES NAMES NOW CLASSIFIED IN GENERA OUTSIDE OF HYALOSPHENIIDAE

We list here 52 names of testate amoebae that, based on morphological characteristics, are believed to not belong to the family Hyalospheniidae (infraorder Hyalospheniformes). Of these, 28 are new combinations (comb. nov. with an asterisk), as they exhibit clear morphological characters typical for genera *Argynnia* (i.e., pseudostome surrounded with siliceous plates), *Physochila* (i.e., pseudostome with outward recurved collar) or *Heleopera* (i.e., slit-like pseudostome).

Nebela acuminata Van Oye, 1959 - current name: *Cylindrifflugia acuminata* (Ehrenberg, 1838) González-Miguéns, Todorov, Porfirio-Sousa, Ribeiro, Ramos, Lahr, Buckley & Lara 2022

Nebela antarctica Grospietsch, 1971 - current name: *Argynnia dentistoma* (Penard, 1890) Vucetich, 1974

Note: Heger et al., 2009 suggested that *N. antarctica* cannot be confidently distinguished from *A. dentistoma*.

*Nebela batekensis** Gauthier-Lièvre, 1957 - current name: *Physochila batekensis* (Gauthier-Lièvre, 1961) comb. nov.

*Nebela circulata** Bartoš, 1963 - current name: *Argynnia circulata* (Bartoš, 1963) comb. nov.

Nebela caudata Deflandre, 1936 (misspelled also as *Nebela cavdata*) - current name: *Argynnia caudata*, Vucetich, 1974

Nebela collaris var. *retorta* Leidy, 1879 - current name: *Argynnia retorta* (Leidy, 1879) Štěpánek, 1953

*Nebela columbiana** Wailes, 1925 - current name: *Argynnia columbiana* (Wailes, 1925) comb. nov.

Nebela columbiana var. *ivorensis** Gauthier-Lièvre, 1953 - current name: *Argynnia columbiana ivorensis* (Gauthier-Lièvre, 1953) comb. nov.

*Nebela corniculata** Jung, 1942 - current name: *Physochila corniculata* (Jung, 1942) comb. nov.

*Nebela cratera** Wailes, 1912 - current name: *Physochila cratera* (Wailes, 1912) comb. nov.

Nebela crenulata Cash, 1891 - current name: *Argynnia dentistoma* (Penard, 1890) Vucetich, 1974

*Nebela dentata** (Lepsi, 1957) Godeanu (1972) - current name: *Argynnia retorta* (Leidy) Štěpánek.

Notes:

Schönborn (1967) used the name *Nebela dentata* in a publication on testate amoebae from lakes.

The name only appears in a figure indicating that this species occurs in oligotrophic and dystrophic lakes (Fig. 10, p. 183). The name does not appear elsewhere in the paper. We believe that the mention in Schönbon's 1967 paper is a typographical error, and that the species name should have been *Nebela dentistoma* = *Argynnia dentistoma* (Penard, 1890) Vucetich, 1974, which is indeed found in oligotrophic lakes and mentioned by the same author in another study on lake testate amoebae (Schönborn 1965).

GODEANU (1972a) listed *N. dentata* from Romania without giving a diagnosis but mentioned that *N. dentata* = *Cyphoderia dentata* Lepsi. LEPSI (1957) had described *Cyphoderia dentata*, but his illustration shows that this species is not a *Cyphoderia* as its test is not built from self-secreted regular plates but of a mixture of obviously recycled elements, as is common in genera *Nebela* and *Argynnia*. *Cypoderia dentata* Lepsi is very similar to *Argynnia retort*a (Leidy) Štěpánek. The illustration given by Lepsi (1957) does not correspond to a *Nebela* as its aperture is serrated and bordered by plates rather than by an organic rim. Given the morphological similarity between *Cyphoderia dentata* Lepsi and *Argynnia retorta* (Leidy) we consider the two as belonging to the same species *Argynnia retorta* (Leidy 1879) Štěpánek 1953.

*Nebela denticulata** Chattopadhyay & Das, 2003 - current name: *Argynnia denticulata* (Chattopadhyay & Das, 2003) comb. nov.

Nebela dentistoma Penard, 1890 - current name: *Argynnia dentistoma* (Penard, 1890) Vucetich, 1974

Nebela dentistoma var. *lacustris** Wailes, 1912 - current name: *Argynnia dentistoma lacustris* (Wailes, 1912) comb. nov.

Nebela dentistoma var. *lageniformis** Playfair, 1918 – current name: *Argynnia dentistoma lageniformis* (Playfair, 1918) comb. nov.

Nebela dentistoma var. *major** Grospietsch, 1954 – current name: *Argynnia dentistoma major* (Grospietsch, 1954) comb. nov.

Nebela dentistoma var. *oblonga** Gauthier-Lièvre, 1953 – current name: *Argynnia dentistoma oblonga* (Gauthier-Lièvre, 1953) comb. nov.

*Nebela ertli** Laminger, 1973 - current name: *Argynnia ertli* (Laminger, 1973) comb. nov.

*Nebela gauthier-lievrei** Štěpánek, 1963 - current name: *Physochila gauthier-lievri* (Štěpánek, 1963) comb. nov.

Nebela gertrudiana Jung, 1942 - current name: *Argynnia gertrudiana* (Jung, 1942) Vucetich, 1974

Nebela globulosa Štěpánek, 1963 - current name: *Netzelia* sp.

Nebela griseola Penard, 1911- current name: *Physochila griseola* (mentioned in Jung, 1942)

Nebela guninensis Golemansky, 1962 - current name (suggestion): *Heleopera* sp.

*Nebela hesperia** Wailes, 1913 - current name: *Argynnia hesperia* (Wailes, 1913) comb. nov.

*Nebela intermedia** Bartoš, 1963 – current name: *Argynnia intermedia* (Bartoš, 1963) comb. nov.

*Nebela kundulungui** Van Oye, 1959 - current name: *Argynnia kundulungui* (Van Oye, 1959) comb. nov.

Nebela lobostoma (Štěpánek, 1963) Decloitre, 1977 - current name (suggestion): *Netzelia* sp.

Nebela patagonica Vucetich, 1975 - current name (suggestion): *Argynnia* sp.

Nebela petricola Gracia, 1960 - current name: *Heleopera petricola* (typographical error)

*Nebela playfairi** Jung, 1942 - current name: *Argynnia playfairi* (Jung, 1942) comb. nov.

Nebela playfairi var. *elongata** Grospietsch, 1971 - current name: *Argynnia playfairi elongata* (Jung, 1942) comb. nov.

Nebela playfairi var. *lata** Grospietsch, 1971 - current name: *Argynnia playfairi lata* (Jung, 1942) comb. nov.

Nebela podzolica Korganova, 1981 - current name: *Schoenbornia humicola* Schönborn, 1987

*Nebela pusilla** Vucetich, 1973 - current name: *Argynnia pusilla* (Vucetich, 1973) comb. nov.

*Nebela rampii** Štěpánek, 1963 - current name: *Argynnia rampii* (Štěpánek, 1963) comb. nov.

*Nebela repanda** Jung, 1942 - current name: *Argynnia repanda* (Jung, 1942) comb. nov.

Nebela retorta Leidy, 1879 - *Argynnia retorta* (Leidy, 1879) Štěpánek, 1953

Nebela schwabei Jung, 1942 - current name: *Argynnia schwabei* (Jung, 1942) Vucetich, 1974

*Nebela scotica** Brown, 1911 - current name: *Argynnia scotica* (Brown, 1911) comb. nov.

*Nebela silesiaca** Kotulla, 1936 - current name: *Physochila silesiaca* (Kotulla, 1936) comb. nov.

*Nebela similis** Vucetich, 1973 - current name: *Argynnia similis* (Vucetich, 1973) comb. nov.

*Nebela spicata** Wailes, 1913 - current name: *Argynnia spicata* (Wailes, 1913) comb. nov.

Nebela tenella Penard, 1893 - current name: *Physochila tenella* (Penard, 1893) Jung, 1942

Nebela teres Jung, 1942 - current name: *Argynnia teres* (mentioned by Jung, 1942)

*Nebela tuberculata** (Wallich, 1864) Owen & Jones, 1976 - current name: *Netzelia tuberculata* (Wallich, 1864) comb. nov.

Nebela tylophora Jung, 1942 - current name: *Argynnia tylophora* Jung, 1942

Nebela vitraea Penard, 1899 - current name: *Argynnia vitraea* (Penard, 1899) Jung, 1942

Nebela vitraea var. *elongata* Gauthier-Lièvre 1953 - current name: *Argynnia vitraea elongata* (validated by Vucetich, 1974)

Nebela vitraea var. *minor* Wailes, 1912 - current name: *Argynnia vitraea minor* (validated by Vucetich, 1974)

Nebela vitraea var. *sphagni* Penard, 1911 - current name: *Argynnia vitraea sphagni* (validated by VUCETICH, 1974)

Quadrula globosa (Penard, 1891) (note: typographical error for *Q. globulosa*) - current name: *Paraquadrula globulosa* (Penard, 1891) Deflandre, 1932

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Authors

Clément Duckert was introduced to the wonders of the microbial world by his supervisors Edward Mitchell and Enrique Lara at the University of Neuchâtel where he earned his PhD in Biology in 2022. He studied the taxonomy, diversity and phylogeny of testate amoebae using DNA sequencing and high-resolution microscopy. While he is personally interested in protistology, in general, his research focused primarily on the taxonomy, evolution and diversification of Hyalospheniid and Euglyphid testate amoebae. He currently works has an independent biologist in Switzerland but is still active within the community of testate amoebae researchers.

Anush Kosakyan earned her first PhD in Mycology from the University of Haifa, Israel, and her second PhD in Protistology, with a focus on testate amoebae taxonomy and evolution, from the University of Neuchatel, Switzerland. She then continued postdoctoral studies at the University of Sao Paulo, Brazil, focusing on the transcriptomics of testate amoebae, and later at the Biology Centre of the Czech Academy of Sciences, focusing on the transcriptomics and genomics of myxozoan parasites. Currently, she is a researcher at the University of Modena and Reggio Emilia, Italy, working on the diversity and genomics of meiofaunal taxa. Additionally, she collaborates on various projects related to the diversity, transcriptomics and genomics of protists and other microbial eukaryotes.

Enrique Lara obtained his PhD from the Federal Polytechnical School of Lausanne in Environmental Microbiology in 2005. After postdoctoral stays at the Universities of Copenhagen and Paris XI, he worked as a lecturer for nine years at the University of Neuchâtel (Switzerland). He has presently a researcher position at the Spanish Council for Scientific Research (CSIC). Enrique Lara has been working on protist diversity, evolution and ecology. In the last 20 years, he focused mostly on testate amoebae and their diversity patterns across geographical distances and ecosystems. He has mentored several PhD students working primarily on testate amoeba taxonomy, phylogeny and evolution.

Ralf Meisterfeld was Senior Staff Scientist at RWTH University (Rheinisch-Westfälische Technische Hochschule), Aachen, Germany from 1975 until his retirement. He started his scientific work on testate amoebae in the 1970s on the ecology of testate amoebae first in *Sphagnum*, and later in soils and their role in forest carbon cycling. As species identification is key to the use of testate amoebae in ecology, he then also contributed to testate amoeba taxonomy, first using scanning electron microscopy and then DNA sequencing, which led him to being recognised as one of the World's best experts of testate amoeba taxonomy. Ralf Meisterfeld is one of very few people to have successfully grown in culture testate amoebae, and has established cultures for over 100 different species with the help of his wife Susanne. This expertise led him to contribute also to the interpretation of some of the oldest fossils of Eukaryotes (>700 million years old) and to write the two chapters on euglyphid and arcellinid testate amoebae in the illustrated guide to the protozoa edited by the Society of Protozoologists.

Edward Mitchell obtained his PhD from the University of Neuchâtel, Switzerland in 2001 on peatland ecology, palaeoecology and microbial ecology. He started studying testate amoebae as palaeoecological indicators during his MSc thesis. From a simple bioindicator tools, testate amoebae quickly became a passion and he soon realized how many open questions remained including taxonomy, phylogeny and their role in microbial food webs as well as the very wide range of possible applications in ecotoxicology, forensic science and model organisms in biogeography. From community ecology of peatland testate amoebae and their use as indicators of past hydrological changes, his research expanded to microbial ecology, ecosystem ecology, molecular phylogeny and taxonomy of testate amoebae, in collaboration with Enrique Lara and several PhD students. The lab's research also expanded to forensic science and ecotoxicology. His research group makes use of the full range of approaches from observational to field experimental ecology, applying microscopy and molecular methods to a broad range of research questions.

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Since Georges Deflandre published his monograph on the genus *Nebela* in 1936 no systematic revision of this beautiful group of testate amoebae had been done. In the meantime, the genus was split, and many new species were described. A taxonomic revision was clearly overdue. In this monograph, we present a taxonomic revision of the infraorder Hyalospheniformes (Amoebozoa, Arcellinida), which includes a single family, the Hyalospheniidae. A total of 14 genera, and 97 species and infraspecific taxa are presented in detail.

The monograph includes taxonomic keys; taxon descriptions; ecological, geographical, and taxonomical notes; annotated lists of dubious and *incertae sedis* species; a list of synonymous names; notes on molecular data; and light and scanning electron microscopic pictures; and/or original line drawings for each species.

This book is designed to benefit protistologists in general, and particularly ecologists and palaeoecologists, by assisting with the ease and accuracy of identification of hyalospheniid testate amoeba species, many of which are useful bioindicators. We also hope that this book will serve as a useful basis for future work regarding the taxonomy, biogeography, and ecology of these beautiful organisms.

Joseph Leidy famously once wrote "*How can life be tiresome sol long as there is still a new rhizopod undescribed?*" There is no shortage of new Hyalospheniformes awaiting to being described. We hope this book will make the life of passionate taxonomists easier!

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