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ORIGINAL ARTICLE

# Superficially described and ignored for 92 years, rediscovered and emended: *Apodera angatakere* (Amoebozoa: Arcellinida: Hyalospheniformes) is a new flagship testate amoeba taxon from Aotearoa (New Zealand)

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## Abstract

Eukaryotic microbial diversity is known to be extensive but remains largely undescribed and uncharted. While much of this unknown diversity is composed of inconspicuous flagellates and parasites, larger and morphologically distinct protists are regularly discovered, most notably from poorly studied regions. Here we report a new flagship species of hyalospheniid (Amoebozoa; Arcellinida; Hyalospheniformes) testate amoeba from New Zealand and an unusual story of overlooked description under a preoccupied name and subsequent oversight for nearly one century. Through a process involving The Māori Language Commission, we named the species *Apodera angatakere*, meaning "a shell with a keel." This species resembles *Apodera vas* but differs by the presence of a distinctive hollow keel. Cytochrome Oxidase Subunit 1 (COI) sequence data show that this species forms a distinct clade nested within genus *Apodera*. This conspicuous species is so far known only from New Zealand and is restricted to peatlands. It is one of the few examples of endemic microorganisms from this biodiversity hotspot and biogeographer's paradise. As over 90% of New Zealand's peatlands have been lost since European colonization and much of the remaining surfaces are threatened, *Apodera angatakere* could be a flagship species not only for microbial biogeography but also for island biodiversity conservation.

**KEYWORDS**
*Apodera vas*, biodiversity conservation, biogeography, *Gibbocarina*, Gondwana, Hyalospheniidae, Māori language and culture, microbial diversity, peatlands, *Sphagnum*, taxonomy

ANYONE with a sense for adventure may dream about the age of discovery (15th–17th century period), during which time the New World was (re)discovered and many new inventions made that changed our perception of the world. Traveling back in time to experience such thrill first hand is, unfortunately, not possible. However, when we consider the lack of knowledge of the microbial world, every sample can be an unexplored island for the curious protistologist with an inclination for natural history.

The invention of the microscope in the late 16th century paved a new era of observation and discovery by making the microbial world accessible to scientific researchers. With subsequent improvements in optics, along with the exploration of various habitats and regions of the World a broad range of microbes was gradually described, gaining momentum in the 19th and early 20th century by pioneers such as Christian Gottfried Ehrenberg, Ernst Haeckel, Josef Leidy and Eugène Penard (Ehrenberg, 1838; Haeckel, 1899–1904; Leidy, 1879; Penard, 1902). More recent developments such as high throughput sequencing of environmental DNA (eDNA) are allowing large amounts of genetic data to be generated revealing a huge, mostly unknown, diversity of microorganisms including bacteria (Delgado-Baquerizo et al., 2018), fungi (Nilsson et al., 2019), protists (Mahé et al., 2017) and micro-Metazoa (van den Hoogen et al., 2019). The magnitude of protist diversity is now believed to exceed that of bacteria (Delgado-Baquerizo et al., 2018) and fungi (Tedersoo et al., 2014), at least in the ocean (de Vargas et al., 2015) but recent work also suggests that this may be the case for terrestrial soil (Geisen et al., 2018). This diversity is confirmed by numerous examples of cryptic diversity reported in classical DNA barcoding studies (Fontaneto et al., 2008; Kosakyan et al., 2012; Kumar & Foissner, 2016; Mann, 2010; Pawlowski et al., 2008), as was first documented for insects (Hebert et al., 2004).

These newly available molecular identification tools have stimulated another golden age of protist discovery, comparable to that triggered by the invention of the microscope (Geisen et al., 2015; Heger et al., 2014; Mitchell, 2015). Novel protist diversity can now be found virtually anywhere. DNA barcoding studies are regularly revealing the existence of numerous species within known groups, questioning long-held ideas about their geographical distribution or ecology that were formerly based on only morphological similarities (Singer et al., 2015; de Vargas et al., 1999). Taxa known from ancient morphological descriptions are now being redescribed and placed in the tree of life using the full range of molecular and detailed microscopy techniques (Burki et al., 2019; Dumack et al., 2016, 2018; Lax et al., 2018).

Finding novel protist diversity can be expected when exploring under-studied regions (Yubuki et al., 2009) or poorly studied groups (Dumack et al., 2018; Siemensma et al., 2020). Although there is a strong sampling bias in favor of Europe and North America where most protistologists work, detailed studies of other regions frequently report many new species, as illustrated in South America, Australia, Africa, and Antarctica (Fernández et al., 2015; Foissner, 1997). Twenty-four years ago, Foissner estimated that at least 70% of the world soil ciliates remained to be described (Foissner, 1997), which is still an underestimation of their true diversity as revealed by eDNA sequencing (Boscaro et al., 2018).

New Zealand is a biogeographer's paradise but has barely been explored for soil protists and especially testate amoebae. Eugène Penard reported 45 testate amoeba species, including three new taxa, *Nebela certesi*, *Hyalosphenia cockayni*, and *Nebela griseola*, from samples collected during the 1907–09 British Antarctic Expedition (Penard, 1911). All three species have since been transferred to new genera, *Certesella certesi*, *Alocodera cockayni*, and *Physochila griseola*. Since then, to our knowledge 19 studies were published on the diversity and ecology of testate amoebae of New Zealand, reviewed in McKeown et al. (2021). A limited number of studies described new species for science, new records for New Zealand or, more recently, focused primarily on the community ecology of testate amoebae and their application in paleoecology (Bamforth, 2015; Charman, 1997; Deevey, 1955; Hoogenraad & de Groot, 1948; McGlone & Wilmshurst, 1999; McKeown et al., 2019; van Oye, 1956; Stout, 1984; Wilmshurst et al., 2002, 2003; Winterbourn & Brown, 1967). However, there has been no modern study on testate amoeba taxonomy that incorporates molecular, morphometrical and ecological data, which are required to accurately describe new species (Lara et al., 2020). As a consequence, it is most likely that many New Zealand species remain overlooked or undescribed.

Here we report *Nebela penardi* from *Sphagnum* peatlands in New Zealand for the first time since its description (Brehm, 1928), a highly conspicuous species that had been superficially described and completely overlooked since then. Based on Cytochrome Oxidase Subunit 1 (COI) data we determine its phylogenetic position within genus *Apodera* and discuss its potential as flagship species for both biogeographical and ecological surveys. Furthermore, as *Nebela penardi* is an invalid name and there is no known available synonym we formally rename it *Apodera angatakere* in collaboration with Te Taura Whiri I te Reo Māori (The Māori Language Commission).

**TABLE 1** Samples collected in New Zealand containing *Apodera angatakere*

| Sample codes | Coord decimal ° Lat (dec °) | Coord decimal ° Long (dec °) | Elevation (m) | Sampling location | Habitat | Sample type |
|---|---|---|---|---|---|---|
| EM-2540 | −39.2550° | 174.0431° | 921 | Egmont National Park, Mt. Taranaki, Pouakai Circuit | Large peatland in saddle between Henry Peak and Taranaki; hollow | *Sphagnum* |
| EM-2616 | −41.6986° | 172.1594° | 1185 | Old Ghost Road trail, shore of "Ghost Lake," km 30, Westland | *Sphagnum* peatland on lake shore | *Sphagnum* |
| EM-2638 | −50.8126° | 166.0653° | 85 | Auckland Island | Low *Metrosideros* forest - moss tuft | Mosses |
| EM-2661 | −45.3892° | 167.5763° | 1214 | Kepler Track, clockwise, day 2 | Alpine terrace with stream, ponds, fens and Sphagnum patches on side (slightly elevated). Collected from lower, more minerotrophic micro-site | Brown mosses |
| EM-2670 | −44.7271° | 168.1728° | 1266 | Routeburn Great Walk trail—pass above Lake Harris, outlet of upper of the two "larger" lakes | *Sphagnum* patch on side of lake outlet | *Sphagnum* |
| EM-2699; X18/109/ SST1 | −43.2173° | 170.2843° | 120 | Okarito Lagoon, Westland | Ombrotrophic bog in dense forest | *Sphagnum* |
| EM-2705; X18/10/ SST1 | −43.5989° | 169.6154° | 5 | Bruce Bay, South Westland | *Sphagnum* lawn | *Sphagnum* |
| EM-2765 | −45.7958° | 170.4829° | 710 | Swampy Summit, NW of Dunedin | Tarn edge: *Sphagnum* growing in water | *Sphagnum* |
| EM-2785 | −44.8618° | 167.8245° | 288 | Milford Track—day 2—Hidden lake, Fiordland | Wetland near lake with bushes, *Sphagnum* and other mosses | *Sphagnum* and other mosses |
| EM-2693 | −42.9071° | 171.5587° | 914 | Arthur's Pass, South Island | Wetland area with ponds, fens and patches of Sphagnum | *Sphagnum* |
| X20/8 | −42.9156° | 171.5524° | 920 | Margaret's Tarn, off the Mt Bealey Track between Arthur's Pass and Mt. Rolleston, South Island | Tarn (small closed-basin lake) | *Sphagnum cristatum* & *S. falcatulum* |

# MATERIAL AND METHODS

## Sampling, single cell isolation, and morphometry

Samples of *Sphagnum*, other mosses (unidentified brown mosses from wetlands) and forest litter were collected from numerous forests, peatlands, and fens across New Zealand's North and South Islands and Campbell and Auckland Islands as well as Macquarie Island as part of a wider project on the diversity of testate amoebae in New Zealand and peri-Antarctic islands. Testate amoebae that could be assigned to *Apodera angatakere* were found in 11 samples (Table 1). Testate amoebae were isolated for further analyses from four samples (Figs S1–S8):

1. EM 2540: *Sphagnum* mosses from a hollow in Ahukawakawa Swamp, along the Pouakai crossing trail, on the saddle between Taranaki Maunga and Pouakai Hut, New Zealand's North Island. Coord: Lat −39.255058°, Long 174.043106°, Elevation: 921 m a.s.l.
2. EM 2543: Forest litter and humus from the Northern foothills of Taranaki Maunga, New Zealand's North Island. Coord. Lat −39.22505°, Long 174.122842°, Elevation: 478 m a.s.l.
3. EM 2935: *Sphagnum cristatum* and *S. falcatulum* from Margaret's Tarn, off the Mt Bealey Track between Arthur's Pass and Mt. Rolleston on the South Island. Coordinates: Lat −42.915655°, Long 171.552487°, Elevation: 920 m a.s.l.
4. EM 2764: *Sphagnum falcatulum* from the north shore of Macquarie Island, collected along Featherbed Track, between Handspike Corner and West Beach. Coordinates: Lat −54.49928200°, Long 158.90512300°, Elevation ~5 m a.s.l.

The samples were placed in closed plastic sampling bags. Once in the laboratory the samples were sub-sampled and material was placed in a container and shaken in tap water for 1–2 min and then filtered over a 200-µm mesh filter. The filtrate was observed under an inverted microscope and testate amoeba specimens that could be assigned to genus *Apodera* were isolated with a narrow diameter pipette and transferred to a new slide with distilled water to remove any unwanted material. Pictures were taken for each individual specimen used for DNA barcoding, which was then transferred to a PCR tube with 50 µl of guanidinium thiocyanate solution (Chomczynski & Sacchi, 1987). Additional living or dead individuals were used for scanning electron microscopy (SEM) imaging. These specimens were further cleaned in ethanol and transferred to a SEM stub on which a carbonate filter had been fixed. The samples were then sputter coated with gold. Images were taken with a Hitachi TM 3030 plus scanning electron microscope operating at 5–15 kV. SEM images were taken at the electron microscopy facility of Manaaki Whenua/Landcare Research, Lincoln, New Zealand.

Measurements were taken on light microscopy and SEM images for each observed specimen: test length, test width, aperture long axis, length of the neck, width at the base of the neck, maximum width of the neck, and length of the main (aboral) part of the test (Figure 1). Depth could only be measured accurately on four individuals resting on their side, but it could be estimated based on the height of the focus plane for individuals resting flat.

## DNA extraction, PCR amplification, and DNA sequencing

DNA extraction was performed with a guanidinium thiocyanate solution following the protocol of Duckert et al. (2018) adapted from Chomczynski and Sacchi (1987). PCR of partial mitochondrial cytochrome oxidase I (COI) gene were processed using a nested PCR protocol. The first PCR was conducted with the eukaryote-general primers LCO1490 (GGT CAA CAA ATC ATA AAG ATA TTG G) and HCO2198 (TAA ACT TCA GGG TGA CCA AAA AAT CA) (Folmer et al., 1994) under the following conditions: Denaturation step at 95°C for 5 min, then 45 cycles with a denaturation step at 95°C for 15 s, an hybridation step at 43°C for 15 s, an elongation step at 72°C for 1 min, and a final elongation at 72°C for 10 min. *Apodera vas* specimens EM2543-15, EM2543-22 and *A. angatakere* EM2540-14, EM2540-19 were then amplified with LCO1490 and ApocoxR (Kosakyan et al., 2012) under the following conditions: Denaturation step at 95°C for 5 min, then 45 cycles with a denaturation step at 95°C for 30 s, an hybridization step at 50°C for 30 s, an elongation step at 72°C for 1 min, and a final elongation at 72°C for 10 min. On the other hand, *A. angatakere* EM2540-11 and *A. vas* EM2764-2 were amplified using Arcelcox1F (Kosakyan et al., 2012) and Apo2F (a newly designed forward primer: TGG AAT TAG CAT ATC MGG AAT T) respectively, with HCO2198 under the same condition as the first PCR, with the only exception of an hybridization step of 45°C for the former taxa. Positive PCR products were directly purified using Milipore kit and sent for sequencing with an ABI3730XL DNA sequencer (Applied Biosystems) at Macrogen, Amsterdam NL. Sequences were deposited in

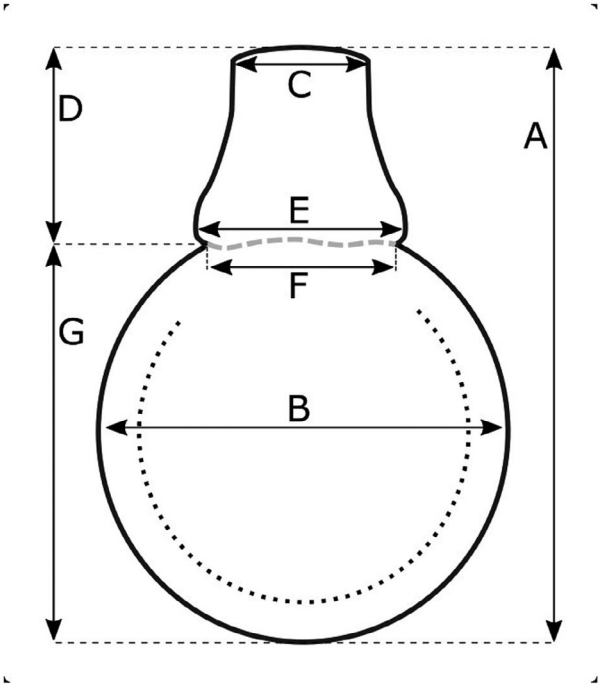


**FIGURE 1** Schematic drawing of *Apodera angatakere* and codes of the measurements taken. (A) Length of the test; (B) width of test; (C) width of the pseudostome; (D) length of the neck; (E) maximal width of the neck; (F) width of the test at the constriction; (G) length of the test without the neck

GenBank with the accession numbers MZ615186–MZ615191. Light microscopy pictures of the corresponding cells are shown in Figure 2.

## Phylogenetic analysis

All sequences obtained were aligned manually using BioEdit (Hall, 1999) together with an exhaustive reference database composed of three previously published sequences of genus *Alocodera* and three of genus *Padaungiella* (Kosakyan et al., 2012) retrieved from the GenBank database (Table S2). The tree was rooted with 10 Hyalospheniformes sequences, corresponding to eight different genera, published in four previous studies (i.e., Duckert et al., 2018; Kosakyan et al., 2012, 2013; Singer et al., 2015). Phylogenetic reconstruction was conducted on the complete LCO-HCO fragment (i.e., 655 nucleotides) using the CIPRES Science Gateway V. 3.3 (Miller et al., 2010). A maximum likelihood phylogenetic tree was built using the RAxML v.8.2.10 algorithm (Stamatakis, 2014) with the GTR + GAMMA model and automatic bootstrapping halt. We further evaluated node robustness using a Bayesian approach with MrBayes (Ronquist & Huelsenbeck, 2003) using the GTR + GAMMA model with default settings on two independent runs sampled every 100 generations. The analysis was automatically stopped when convergence was reached after 260, 100 generations resulting in 5202 trees of which 25% were discarded as the burn-in.

## Collaborating with Māori in the naming process

Naming species that are discovered in regions where indigenous people live should respect the cultural principles. According to the Waitangi tribunal Wai 262 report (Waitangi Tribunal Report Wai 11, 1986), Māori retain "kaitiakitanga" (guardianship) over "taonga" (treasured) species and the cultural relationship between kaitiaki (guardian) and taonga (treasured) species is entitled to reasonable protection. According to Veale et al. (2019), this implies that there is an imperative to conduct processes such as formally naming and describing species of cultural relevance to Māori in partnership with Māori. In agreement with this principle, as a new species name needed to be found, this was done in partnership with Te Taura Whiri I te Reo Māori (The Māori Language Commission). Our aim was to find a name that would be appropriate for the organism and ideally reflect the specific morphology: a flattened gourd with a constriction at the base of the neck and a hollow "keel." The choice of a name was an iterative process involving Ngahiwi Apanui from Te Taura Whiri I te Reo Māori and all authors.

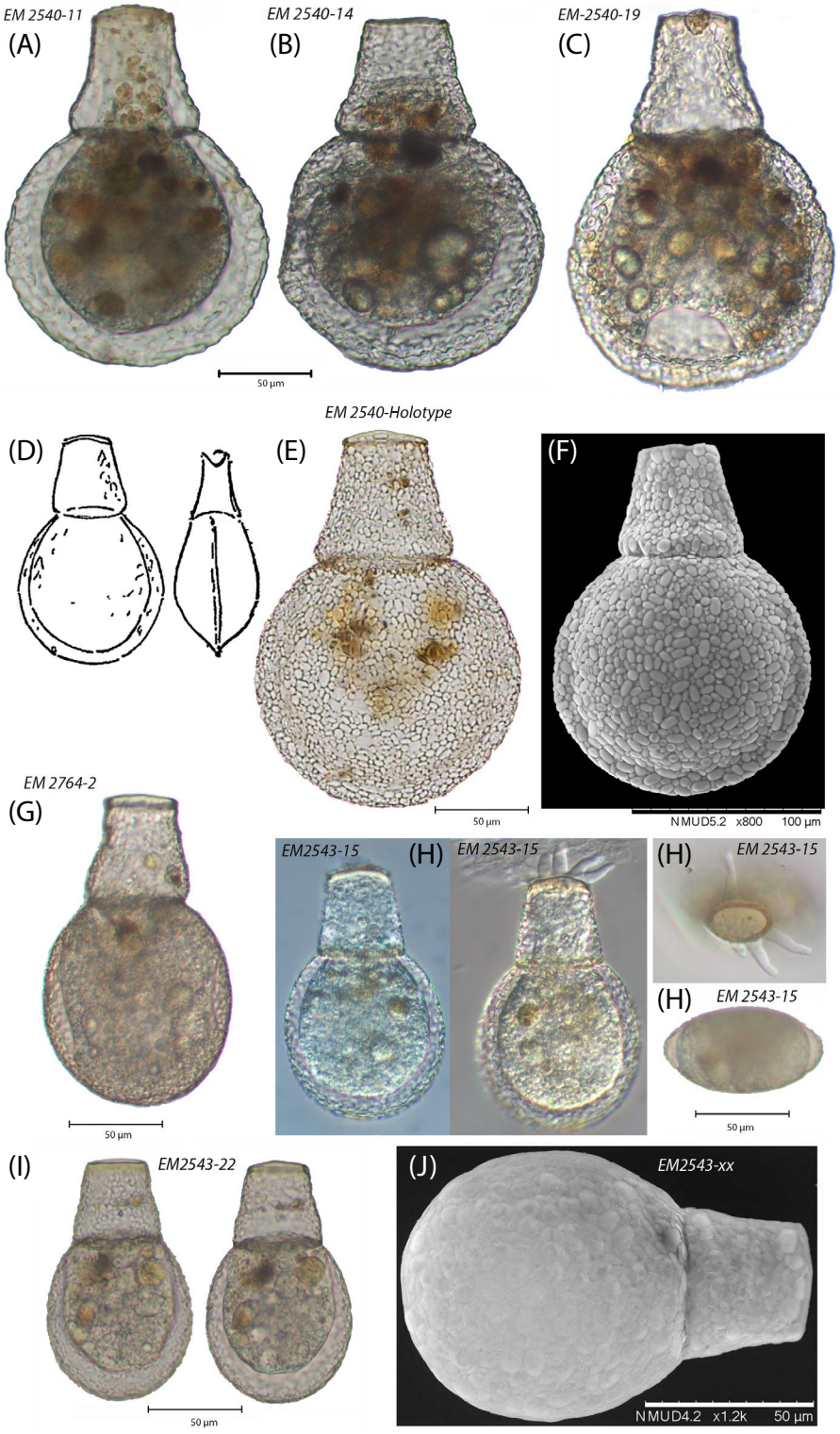


**FIGURE 2** Top half: *Apodera angatakere* n. gen. n. sp. (A–C, E and F), five specimens from Ahukawakawa swamp, Taranaki Maunga, New Zealand's North Island (sample EM-2540): (A–C) three barcoded individuals, (D) Brehm's original drawing of *Apodera angatakere* (described as *Nebela penardi*) from Margaret's Tarn, Arthur's Pass, New Zealand's South Island, (E and F), two individuals from sample EM-2540 (LM and SEM, respectively). E is the holotype. Note the presence of a ca. 10 µm wide keel. All specimens illustrated here as well as in Figures S2–S8 were used for morphometrical analyses (Figure 1). Scale bars (20, 50, or 100 µm) are shown for all specimen but were not provided in the original description. Bottom half: *Apodera vas*. (G) barcoded specimen from Macquarie Island (sample EM-2764), (H–J) three specimens from forest litter collected on the lower slopes of Taranaki Maunga, New Zealand's North Island (sample EM-2543). (H and I) Two barcoded specimen, (J) SEM of a third individual; note the absence of a keel. The codes of the barcoded specimens are the same as in the phylogenetic tree (Figure 3)

**TABLE 2** Summary morphometricstatistics of Apodera angatakere. A: Length of the test; B: Width of test; C: Width of the pseudostome; D: Length of the neck; E: Maximal width of the neck; F: Width of the test at the constriction; G: Length of the testwithout the neck. Full details are given in Table S1

| | a | b | c | d | e | f | g | a/b ratio | g/b ratio |
|---|---|---|---|---|---|---|---|---|---|
| *n* | 62 | 60 | 59 | 62 | 61 | 61 | 63 | 60 | 60 |
| Average | 208.2 | 147.0 | 44.0 | 70.5 | 75.6 | 71.0 | 137.7 | 1.42 | 0.94 |
| Median | 209.0 | 148.0 | 44.0 | 70.7 | 75.9 | 72.0 | 137.7 | 1.42 | 0.94 |
| Min | 186.0 | 120.0 | 39.1 | 61.0 | 60.4 | 58.4 | 125.0 | 1.19 | 0.77 |
| Max | 225.9 | 167.0 | 50.2 | 79.3 | 87.6 | 79.1 | 148.9 | 1.67 | 1.10 |
| SD | 8.59 | 8.55 | 2.04 | 4.40 | 4.29 | 4.49 | 5.87 | 0.07 | 0.06 |
| CV | 4.12 | 5.82 | 4.64 | 6.23 | 5.68 | 6.32 | 4.26 | 5.19 | 5.95 |

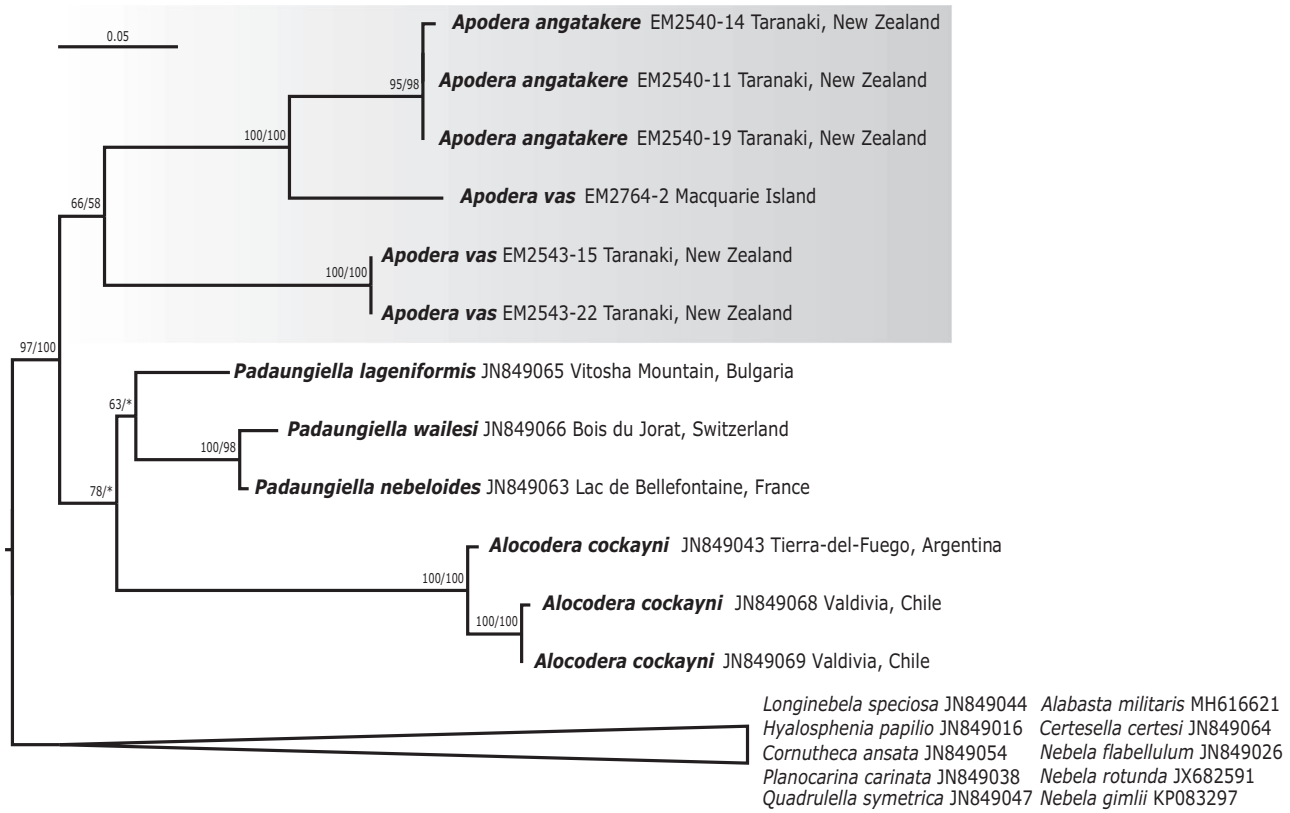


**FIGURE 3** Maximum likelihood phylogenetic tree of the Hyalospheniformes with a focus on *Apodera*, *Alocodera*, and *Padaungiella* based on COI gene sequences. Bootstrap values (bs) and Bayesian posterior probabilities (p.p.) are indicated respectively between branches. COI sequences from genera other than *Apodera* were retrieved from GenBank

# RESULTS AND DISCUSSION

## Morphological characterization of the tests

We found two distinct morphotypes that could be assigned to genus *Apodera* based on their lageniform shell composed of recycled xenosomes, with a clear constriction that separates the neck from the body. These two morphotypes could easily be distinguished based on their size and the presence of a hollow keel on the larger morphotype (Figure 2). The smaller morphotype (mean length: 147 µm, data not shown) corresponds well to the description of *Apodera vas* (Certes) and our measurements fall in the middle of the range recorded for this taxon (Zapata & Fernandez, 2008). It must be noted that the high degree of variability in dimensions and shape reported for *Apodera vas* suggests the existence of a complex of distinct species (Penard, 1911; Zapata & Fernandez, 2008). Although, the size of the larger

morphotype (mean length: 208 µm) (Table 2) falls within the range recorded for *Apodera vas*, it can be easily differentiated by the presence of a distinct hollow keel surrounding the main body, as in genus *Gibbocarina*. The margins of the neck range from almost straight to slightly concave with a bulge at the base. The margins of the neck are compressed, except in the basal bulge region, as an extension of the hollow keel. This is easily visible on SEM images but is less obvious, and possibly overlooked in light microscopy. This morphology matches well with the line drawing of the original description of *Nebela penardi* Brehm, 1928 (hereafter *Apodera angatakere*), which unfortunately lacked a scale or indication of size. The tests of *Apodera vas* were found in forest litter samples, brown mosses, and *Sphagnum* whereas tests of *Apodera angatakere* were almost exclusively found in *Sphagnum* samples collected in peatlands but also brown mosses in an alpine fen and mosses in low *Metrosideros* forest on Auckland Island.

## Phylogenetic placement within Hyalospheniformes and paraphyly of *Apodera vas*

We obtained partial COI sequences of 655 nucleotides from three specimens of *Apodera vas* and three of *Apodera angatakere*. Sequences of genus *Apodera* form a moderately supported clade (bs: 66; pp: 58; Figure 3) and together with the genera *Alocodera* and *Padaungiella* they form a highly supported clade that is sister to the clade formed by all the other genera of Hyalospheniformes used to build the tree.

While sequences of *Apodera angatakere* form a highly supported monophyletic clade, *A. vas* appears to be paraphyletic with one sequence branching at the base of *A. angatakere* and two other sequences forming a distinct clade within *Apodera*. Interestingly the two specimens of *A. vas* branching together were found in the same sample from Taranaki Maunga, New Zealand's North Island, whereas the one that branches at the base of *A. angatakere* was found on Macquarie Island. This strongly supports the hypothesis that *Apodera vas* is currently a complex of distinct species, possibly with distinct distribution patterns.

## Taxonomic status of *Apodera angatakere* (*Nebela penardi)*

*Apodera angatakere* was first briefly reported as *Nebela penardi* in a publication focusing mostly on copepods (Brehm, 1928). Only two drawings were shown (Figure 2D) and no indication of size or scale was provided. Brehm had sent a moss sample containing testate amoebae to Eugène Penard who described the finding as follows: "It is similar to *Nebela vas* Certes (now *Apodera vas*), but differs therefrom in that the shell possesses a broad, hollow, and characteristic keel, which is always present and might well be regarded as a sufficient character to distinguish a new species. I have not been able to identify it with any known species." (Brehm, 1928). As a result, Brehm proposed to name the species *Nebela penardi*.

To our knowledge there is no further mention of this species in the scientific literature and the species has been overlooked since then. Notably, Deflandre did not mention it in his 1936 monograph of the genus *Nebela* (Deflandre, 1936). Moreover, at the time of its description, the name *Nebela penardi* Brehm, 1928 was preoccupied by *Nebela penardi* Heinis, 1914. It is therefore a junior homonym of this species, which implies that *Nebela penardi* Brehm was unavailable and thus invalid.

As there is no known synonym for this taxon, we therefore rename it in agreement with ICZN article 60.3, and as we transfer it to a new genus both a new generic name and a new species epithet are required. Furthermore, as a side note, Heinis (Heinis, 1914) used the name *Nebela penardi* to erroneously rename a taxon that, according to Deflandre (1936), corresponds to *Nebela martiali* (now *Certesella martiali*). *Nebela penardi* Heinis is therefore a junior synonym of *Certesella martiali*.

A very similar species was described under the name *Nebela kenyana* by Didier Chardez from mountain lakes in Kenya at over 4000 m a.s.l. (Chardez, 1982). This species has a similar size and overall morphology including a hollow keel surrounding the fundus of the test and a distinct neck with swollen sides. However, it lacks the characteristic constriction at the base of the neck which defines *Apodera* and, in that, it is more similar to genus *Padaungiella*.

## Choice of a species name—an iterative process involving the Māori Language Commission

The choice of a name was an iterative process involving all authors in collaboration with Te Taura Whiri I te Reo Māori. We aimed to find a species name that would be appropriate for the organism and ideally reflect the specific morphology which could be described in general words as a flattened gourd with a constriction at the base of the neck and a hollow "keel." We also aimed to represent the Mauri (life force) of this unique species that was named by Māori for them as kaitiaki (guardian) of Aotearoa (New Zealand).

The options considered were:

1. An amoeba with a hard shell. According to the Reed Dictionary of Modern Māori, the word "amoeba" is translated as "pūora hurikē" and a "hard shell" is translated as "anga." Combining the two with the word "whai" meaning "in possession of" leads to the name "Pūora hurikē whaianga."
2. Considering that a shelled amoeba is analogous to a miniature snail, the second option was "A snail with a keel-like shell." Snail and keel being respectively translated as "ngata" and "takere," this would then form "Ngata anga whaitakere."
3. An amoeba with a keel-like hull: pūora anga whaitakere.
4. An amoeba with a keel: pūora whaitakere.
5. A shell with a keel: Anga whaitakere.

The fifth option was chosen both for the way it sounded and the fact that the name would describe well the morphology of the amoeba. However, in a final discussion, Mr. Ngahiwi Apanui from the Māori Language Commission suggested that the "whai" could be dropped to shorten the name. The final chosen name was then «Angatakere», to be pronounced æŋætɑkɛrɛ (AN-GAH-TAH-KEH-REH).

## Implications for biodiversity estimates and conservation

It is estimated that 10% of the New Zealand mainland was covered by wetlands before human arrival around 780 cal. Yr BP (Ausseil et al., 2011; McGlone, 2009), and while testate amoebae were too small to be recognized by Māori until the introduction of the microscope, the wetland habitats that supported these organisms were highly valued by Māori for centuries, as mahinga kai/hauanga kai (food gathering areas), rongoā (gathering plants for medicinal use) and for material resources. Wetland extent was minimally affected by early Māori settlers, although extensive deforestation of dryland forest by burning transformed the landscape (Argiriadis et al., 2018; McWethy et al., 2010; Perry et al., 2014). Wetland loss rapidly accelerated after European arrival in the 1800s, largely for agricultural development, and is now only 10% of the original extent (Ausseil et al., 2011). It is estimated that the 250,000 ha of wetlands that remain are under increasing pressure from drainage, area loss, fragmentation, grazing, fire, pollution, and climate change (Meyer et al., 2013; Robertson et al., 2019). The fact that we can still find novel diversity or diversity that has been very poorly described in such habitats makes them even more precious and worthier of conservation.

Describing the still mostly unknown diversity of protists requires a major effort in basic taxonomy (Heger et al., 2014). The magnitude of land-use changes and natural habitat destruction occurring throughout the world and the now well-established existence of restricted geographical distribution patterns in free-living protists (Foissner, 2008) implies that a large proportion of protist diversity will likely disappear before it can be described, and thus the conservation of protists should indeed be a priority (Cotterill et al., 2008; Qin et al., 2016). *Apodera angatakere* is a highly conspicuous genus of testate amoeba and has to date only been found in New Zealand. Large species are more likely to have restricted geographical distribution as shown empirically for terrestrial and subaquatic testate amoebae in the southern temperate and Antarctic zones (Wilkinson, 1994), at the global scale (Wilkinson, 2001; Yang et al., 2010) and confirmed by an atmospheric circulation modeling study (Wilkinson et al., 2012). Given its large size it is likely an endemic taxon and as such could represent the first documented microbial species for which New Zealand has a conservation responsibility at the global scale. *Apodera angatakere* could therefore be considered as a flagship species for microbial biogeography and conservation.

## To discover, or not to discover: that is the question

Columbus thought he had discovered a new world hitherto unknown to Europeans. But it was later established that the Vikings had already made this discovery before him. And of course, the sheer notion of this major discovery disregarded the fact that native populations had already colonized the Americas millennia before Europeans were even able to conceive of the idea of sailing across the ocean.

This history is mirrored in the story of *Apodera angatakere*: Just like Columbus one of us (EM) thought he had discovered a new species only to be brought to the attention by another one of us (SL) that it had been previously described in a publication on microcrustaceans which had escaped the attention of previous researchers studying testate amoebae in New Zealand. But just as the Vikings did not establish a permanent settlement in America, Brehm's discovery was lost to science, or almost so.

The microbial world remains unknown for most of the people but charismatic groups such as testate amoebae are useful as messengers of the invisible dimension of nature's wonders and our impact on the biosphere. The fact that *A. angatakere* is known only from New Zealand and is restricted to ecosystems that have been almost entirely destroyed since European colonization is a perfect illustration of the fact that many species are being lost before we even have a chance to describe them.

## Taxonomic actions

Taxonomic summary:
Amorphea Adl et al. 2021
Amoebozoa Lühe 1913, sensu Cavalier-Smith 1998
Tubulinea Smirnov et al. 2005
Elardia Kang et al. 2017
Arcellinida Kent 1880
Difflugina Meisterfeld 2002, sensu Kosakyan et al., 2016
Hyalospheniformes Lahr et al., 2019
Hyalospheniidae (Schultze 1877) Kosakyan et Lara 2012
***Apodera angatakere*** (Brehm, 1928) Mitchell, Blandenier & Duckert 2021
1928 *Nebela penardi* Brehm
Icon: Brehm, 1928 Fig. 52

### Description

Test composed of two clearly distinct parts, a subcircular, oval, or ellipsoidal, compressed posterior part (body) and a neck. The two parts 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. The margins of the neck sometimes compressed. Body almost circular. Dimensions based on 63 specimens: 53 individuals from Taranaki Maunga, North Island, four from the Old Ghost Road, South Island, and six from the Keppler Track, South Island: Length (min.–average–max.): 186–208–226 µm, width: 120–148–167 µm, pseudostome: 39–44–50 µm. Circa 80 µm in breadth.

### Etymology

In the Māori language "angatakere" can be translated to "a keeled shell," referring to the conspicuous keel present on the outline of the test.

### Neotype

Brehm did not preserve any specimen, and the original type material is only represented by two simple drawings without indication of size. Because small variations 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 and reliably distinguish it from taxa yet to be described (Duckert et al., 2020; Kosakyan et al., 2016). 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 Taranaki Maunga, New Zealand's North Island. However, tests from the previous type locality and the ones from Taranaki Maunga were similar in all points. A permanent slide has been deposited at the Natural History Museum of Neuchâtel (Switzerland) with the ID 95-1.

### New type locality

Ahukawakawa swamp, along the Pouakai crossing trail, on the saddle between Taranaki Maunga and Pouakai Hut, New Zealand's North Island. Coord: −39.255058°, 174.043106°, Elevation: 921 m a.s.l.

## Geographical distribution

Known from New Zealand North and South Islands and Auckland Island. Likely also Campbell and Chatham Islands. We did not find it in Macquarie Island where all *Apodera* specimens lacked the characteristic hollow keel.

## Habitat

*Sphagnum* and brown mosses in peatlands and alpine wetlands in New Zealand's North and South Islands, mosses in low *Metrosideros* forest (Auckland Island).

## Remarks

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, we thus chose a specimen from Taranaki Maunga, New Zealand's North Island 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. The Auckland Island record is based only on microscopic observation (not illustrated) and is considered valid given the characteristic morphology. Nevertheless, it would need to be further confirmed by molecular data.

Three COI gene sequences of *Apodera angatakere* and *Apodera vas* (352–655 bp) were deposited in GenBank under the number MZ615186–MZ615188 and MZ615189–MZ615191, respectively.

## ZooBank registration number

urn:lsid:zoobank.org:act:921D8CE1-EF0F-4839-B264-97ED438B5694.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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