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The ctenostome bryozoan family Clavoporidae: diversity and description of new taxa

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Abstract Deutsch

Diese Masterarbeit behandelt die Ctenostome-Bryozoenfamilie Clavoporidae und liefert die bislang umfassendste morphologische Revision der Gruppe. Basierend auf Museumsbelegen aus London und Paris sowie aktuellem Material aus dem Atlantik, dem Mittelmeer, Neuseeland, dem Pazifik und der Antarktis werden mehrere neue Gattungen und Arten beschrieben und unsichere Taxa neu zugeordnet. Die Arbeit etabliert messbare, reproduzierbare Merkmalssets für die speziellen morphologischen Anpassungen der Familie (Capitulum, Pedunkel-Kenozooid-Architektur) sowie für Ankermethoden (Rhizoide vs. Haftscheibe) und interpretiert diese im funktionellen Kontext der Tiefsee. Ein Bestimmungsschlüssel, standardisierte Artprofile sowie Abbildungen unterstützen zukünftige Arbeiten zur Systematik und ökologische Studien. Die Ergebnisse erweitern die Verbreitungs und Tiefenangaben, identifizieren Neuseeland als äußerst diversitätsreichen Lebensraum und beleuchten Hypothesen zur Reproduktion (Brutpflege oder mögliche capitulum-basierte Fragmentation). Die Arbeit dient als Erweiterung bereits bekannter Arten und als Rahmenwerk für künftige Forschungen zu den Clavoporidae.

Abstract English

This thesis offers a comprehensive morphological revision of the Ctenostome Bryozoan family Clavoporidae, integrating museum collections from London and Paris as well as newly collected material from the Atlantic, Mediterranean, New Zealand, the broader Pacific and Antarctica. Several new genera and species are described, targeted reassignments for problematic taxa are proposed, and standardized diagnostic features for the capitulum, peduncle (kenozooid architecture), and anchoring methods (rhizoids vs. basal discs) are introduced. A practical identification key, consistent species profiles, and high-quality imagery support reproducible taxonomy and subsequent ecological research. The findings extend distributional and bathymetric ranges, emphasize Zealandia as a diversity hotspot, and propose hypotheses regarding reproduction (brooding or potential capitular fragmentation). Overall, the thesis provides a solid foundation for future studies on Clavoporidae.

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1. Introduction

Bryozoans, also known as "moss animals," are colonial invertebrates with a fossil record extending back to the Early Ordovician, around 480 million years ago (Taylor, 2020; Waeschenbach & Taylor, 2012). Despite their small individual size — usually less than a millimeter — bryozoans form complex and extensive colonies capable of encrusting surfaces, developing branching structures, or forming gelatinous masses. The group encompasses approximately 6,000 extant and more than 17,800 fossil species, thriving across marine and freshwater ecosystems (Bock & Gordon 2013).

Their feeding relies on a specialized tentacle crown known as a lophophore, which is cone-shaped and creates currents with ciliated tentacles to swirl food inward. Also, the tentacles are utilized to capture food directly, depending on the morphological variation of the polypide. This places them in the same functional ecological group as sponges and other sessile filter feeders (Winston, 1978). Bryozoans play essential roles in their habitats, contributing substantially to reef construction and serving as sensitive bioindicators of environmental conditions, both present and historical. Bryozoans are especially valuable in paleontological research because their calcium carbonate skeletons frequently fossilize, forming abundant assemblages that provide crucial insights into past marine ecosystems (Taylor, 2020). Notably, early bryozoans likely lacked mineralized skeletons, explaining the ambiguity in their Cambrian fossil record. Nevertheless, the considerable morphological diversity observed in Ordovician fossils indicates that bryozoans had a more extensive evolutionary history preceding the emergence of skeletonization. Bryozoan colonies exhibit intricate specialization among their zooids, a phenomenon known as polymorphism (Schack et al. 2018).

The bryozoan clade Gymnolaemata is the most speciose and diverse, comprising two groups: the calcified Cheilostomata and the uncalcified Ctenostomata. Ctenostomata is a paraphyletic assemble within Gymnolaemata, and ctenostome-like bryozoans are ancestral to Cheilostomata and encompass all uncalcified marine bryozoans. Ctenostome zooids generally exhibit the highest variety of zooidal shape among bryozoans. Systematics currently divides the ~350 recent described species into approximately 7–8 superfamilies (Schwaha, 2020). More recent studies recovered 3 distinct clades (currently termed clades A, B, and C; Decker et al. 2024; Waeschenbach et al. 2025). Clade B is essentially represented by Alcyonidioidea, which has members showing various colonies morphologies ranging from encrusting sheets or large, erect forms. One family within Alcyonidioidea is Clavoporidae Osburn & Soule, 1953, which is characterized by pedunculate (stalked) colonies with a swollen capitulum (head) primarily composed of functional autozooids. Kenozooids, specialized zooids without feeding structures generally form the stalk. These structures potentially facilitate colony movements, including extension and contraction, in soft-sediment or deep-water environments due to the potential presence of muscular fibers within the kenozooids (d'Hondt, 1983).

Clavoporidae currently includes five genera: *Clavopora* Busk, 1874; *Ascorhiza* Fewkes, 1889; *Metalcyonidium* d'Hondt, 1975; *Pseudalcyonidium* d'Hondt, 1975; and *Cephaloalcyonidium* d'Hondt, 2006. The type genus *Clavopora* is monotypic and exhibits a globular capitulum attached to a thick peduncle anchored by rhizoids (Busk, 1874). *Ascorhiza* species possess distinctly annulated peduncles and muscular, rhomboidal kenozooids (Fewkes, 1889; Robertson, 1902). *Metalcyonidium* features peduncles composed of cylindrical kenozooids arranged in a single series, while *Pseudalcyonidium* colonies possess elongated peduncles formed by singular, thread-like kenozooids (d'Hondt, 1976). *Cephaloalcyonidium* is characterized by polypido-kenozooids containing rudimentary polypides and transverse muscle fibers (d'Hondt, 2006). Numerous undescribed samples of clavoporids were collected in the past decades that waited further species assessment and description. The aim of this study is to analyse the family, including museum samples and together with formal descriptions of new taxa, provide a general revision of the family. It thus also aims to significantly expand the current knowledge on clavoporid diversity and their geographic and ecological distribution.

2. Materials and Methods

2.1 Material

Samples from New Zeeland were collected by trawls, epibenthic sleds or box corers from NIWA (and its predecessor, the New Zealand Oceanographic Institute) over a depth range 570 - 3798 m between 1968 – 2014. The primary fixation was in seawater-formalin, followed by storage in small sample glass containers filled with ethanol. In total 36 samples were suitable for further analysis.

Further samples were provided by the Musée national d'Histoire naturelle Paris (collected between 1960-1993) and the Natural History Museum of London (collected between 1964-1984) as well as material collected from Antarctica in 2009. Additional samples collected at Kristineberg station, Sweden, over several years, and at Roscoff marine station, France, in 2025, were also analyzed. The latter samples were either fixed in absolute ethanol or in 2.5% glutaraldehyde in 0.05 M phosphate buffer containing 10% sucrose.

2.2 Methods

Specimen documentation and imaging was conducted using a Nikon SMZ25 (Nikon, Tokyo, Japan) stereomicroscope equipped with a Ds-Ri2 camera, a Hirox RH2000 microscope (Hirox, Tokyo, Japan) or an Olympus SZX16. Measurements were conducted using Fiji open-source software.

3. Results

3.1 Taxonomic Survey

3.1.1 Analysis of described species

Family Clavoporidae Osburn & Soule, 1953

3.1.1.1 Genus *Clavopora* Busk, 1874

Type species: *Clavopora hystricis* Busk, 1874

Diagnosis: Small club-shaped colony ~3 mm high, with a small, globular capitulum, thick peduncle composed of multiserial, hexagonal to polygonal, proximo-distally flattend kenozooids. Peduncule proximally anchored via few, thick rhizoids. Transition of peduncle to capitulum smooth, not showing high angles.

Remarks: The type genus of the entire family is based on a single specimen that was initially considered as fully differentiated (Busk, 1874) but based on the small capitulum and number of autozooids, it appears more like a young specimen. A second, potential specimen was described closer to the French coast from 80m depth, and it is 3x the size of the original Busk specimen (3mm vs 1cm; Gautier, 1954). However, despite their close geographical location, the original sample is showing thick, rhizoids, whereas Gautier's specimen is broadly attached to a mollusc shell and shows no mention of rhizoids. Since the original substrate of Busk's specimen is unknown, it is impossible to assess whether different habitats and substrates affect the formation/presence of rhizoids. The assessment of Prenant and Bobin (1956) that the two specimens could represent different species based on the provided tentacle numbers (12-14 by Busk, and 22-24 by Gautier) can be ignored since Busk's original assessment was based on a single specimen with retracted zooids. In contrast, Gautier's number is potentially based on section information or again an estimated guess, which is fitting more into the general regime of the superfamily Alcyonidiodea (Schwaha, 2020).

Distribution: Recent, Europe, Mediterranean Sea, Deep water off African coast. Second specimen possibly also 80m close to coast of Marseille.

3.1.1.2. Genus *Ascorhiza* Fewkes, 1889

Type species: *Ascorhiza occidentalis* Fewkes, 1889

Diagnosis: Colony attached to substrate with large attachment disc lacking and rhizoids. Peduncle thin, elongate, consisting or serial, parallelly arranged kenozooids giving the stalk an annulated appearance. Muscle fibres present in peduncle kenozooids. Transition from peduncle to stalk abrupt, showing high angle at transition. Transition zone composed of kenozooidal budding zone.

Remarks: Although geographically quite distinct, some early authors considered *A. occidentalis* to be synonymous to *C. hystricis* (see Gautier 1954 for a summary). However, as

also summarized in previous assessments, beside the wide geographical separation (Mediterranean vs. East Pacific); 1) the peduncle is attached via a baseplate and not via rhizoids as in *Clavopora*, 2) the peduncle has a unique arrangement of rows of parallel, muscular kenozooids, 3) the transition zone to the capitulum is sharp and composed of a budding region of new kenozooids, which has not been reported for *Clavopora*. A second species from West Pacific waters (Mawatari 1968) was also assigned to this genus as *A. mawatarii* (d'Hondt, 1983), but in fact lacks most of the definitive characters described of the genus *Ascorhiza* and will be require a new genus (see below).

Distribution: Recent, East Pacific coast, California, North American Pacific 36 meters. First collected from 36–40 m depths near Santa Barbara, California (Fewkes 1889, Robertson 1902). Also from Vancouver area (O'Donoghue, 1926).

3.1.1.3. Genus *Metalcyonidium* d'Hondt, 1975

Type species: *Metalcyonidium gautieri d'Hondt,* 1976

Material analysed: MNHN-IB-2008-6704; NHMUK 1984.2.19.1

Diagnosis: Peduncle composed of uniserial kenozooids, proximal kenozooid anchored by multiple rhizoids. Capitulum globular to elongated.

Description: One specimen sample with smaller capitulum from Paris (MNHN-IB-2008-6704) (Fig.1 A, B) and one with a larger more rounded capitulum from London (NHMUK 1984.2.19.1) (Fig1. C, D, E). Overall colony length ranges ~3.5mm to ~6.6 mm (mean 4360.677 µm, SD 1647.025 µm). Capitulum globular. Autozooids elongated, almost triagonal with apex directed toward peduncle. Rhizoids arising from terminal peduncle segment. Rhizoid fibers fine and covered with substrate grains (Fig.1 A, E). Capitulum length 1242.478 µm to 2832.310 µm (mean 2202.398 µm, SD 844.731 µm), width 871.113 µm to 2333.333 µm (mean 1736.096 µm, SD 766.999 µm). Peduncle length 2213.211 µm to 3742.226 µm (mean 3118.199 µm, SD 802.294 µm), width of 440.507 µm to 600.664 µm (mean 515.013 µm, SD 80.658 µm). Capitulum kenozooid length 196.554 µm, width 118.710 µm. Peduncle kenozooid length 328.798 µm to 750.783 µm, (mean 465.751 µm, SD 194.033 µm), width 98.264 µm to 492.314 µm (mean 365.481 µm, SD 180.178 µm). Autozooid length 401.509 µm to 708.348 µm (mean 572.943 µm, SD 156.560 µm), width 155.369 µm to 338.470 µm (mean 262.636 µm, SD 95.512 µm). Capitulum-peduncle length ratio of 0.561 – 0.757:1. Cystid wall transparent.

Distribution: Recent, Europe (Bay of Biscay, western Mediterranean), depths of 463–1250 m. First collected from 507m in the Northeast Atlantic Ocean in the West Bretagne region

3.1.1.4. Genus *Pseudalcyonidium* d'Hondt, 1976

Type species: *Pseudalcyonidium bobinae d'Hondt*, 1976

Analysed Material: NHMUK 1984.2.19.5; NHMUK 1983.11.22.28

Diagnosis: Clavoporid with elongated peduncle consisting of single kenozooid, rarely more, never in regular arrangement. Attachment to substrate via rhizoids. Capitulum pear-shaped or elongated (Fig.2 A, B).

Description: Colony ~3.9 mm high (Fig.2 A). Capitulum broadly pear-shaped, with densely arranged autozooids of pentagonal or hexagonal outline and of different sizes, enlarging toward apex. Zooids usually symmetrical along longitudinal axis, arranged in irregular alternating pattern within longitudinal rows. Orifice circular, typically situated about one-quarter of the zooid length. Basal autozooids approximately hemispherical with no apertural opening. Early buds at capitulum apex (Fig.2 B). Peduncle with consistent diameter, with slight constrictions at irregular intervals (Fig.2 C). Rhizoids differ in diameter and length, relatively thick and short (Fig.2 D). Capitulum length 1259.259 µm to 2139.661 µm (mean 1668.363 µm, SD 362.554 µm), width 757.629 µm to 991.228 µm (mean 882.903 µm, SD 125.284 µm). Peduncle length 2215.385 µm, width 144.737 µm to 284.249 µm (mean 214.493 µm, SD 98.650 µm). Capitulum kenozooid length 135.965 µm to 272.250 µm (mean 235.726 µm, SD 66.639 µm), width 120.614 µm to 201.523 µm (mean 179.571 µm, SD 39.390 µm). Peduncle kenozooid length 157.025 µm to 794.139 µm (mean 550.429 µm, SD 277.097 µm), width 126.144 µm to 452.782 µm (mean 229.250 µm, SD 150.464 µm). Rhizoid region 620.673 µm in length. Autozooid length 498.369 µm to 538.272 µm (mean 512.819 µm, SD 17.678 µm), width 268.530 µm to 427.999 µm (mean 342.138 µm, SD 71.242 µm). Capitulum-peduncle length ratio 0.568 to 0.966:1 (mean 0.753).

Distribution: Recent, Europe (North Atlantic), bathyal to abyssal depths of 1200–3100 m.

3.1.1.5. Genus *Cephaloalcyonidium* d'Hondt, 2006

Type species: *Cephaloalcyonidium morchellanum* d'Hondt, 2006

Analysed material: MNHN-IB-2008-20246 (holotype), MNHN-IB-2008-20256 (paratype)

Diagnosis: Clavoporid with peduncle composed of regular series of small, hexagonal kenozooids (Fig.3 D). Peduncle cylindrical, anchored to substrate vis several rhizoids on proximal of peduncle (Fig.3 C). Capitulum globular with sharp with high angle insertion to peduncle (Fig.3 A, B).

Description: Capitulum length 2225 µm, width 2262.5 µm. Peduncle length 3450 µm, width 462.5 µm. Capitulum-peduncle length ratio 0.644:1. Rhizoid length 1575 µm. Autozooid length 313.397 µm, width 344.498 µm. Capitulum kenozooids length 169.059 µm, width 149.92 µm. Peduncle kenozooid length 153.11 µm, width 140.351 µm.

Distribution: Recent, Pacific (New Caledonia), collection depth approximately 164 m.

3.2. Description of new taxa

3.2.1. New genera and species

3.2.1.1. Genus *Bomburozoon* gen. nov.

Type species: *Bomburozoon* gen. nov. *bulbosus* sp. nov.

Etymology: from *Bombur*, the obese dwarf in the “The Hobbit” film series, based on the large, massive capitulum.

Diagnosis: Peduncle affixed to substrate by attachment disc, lacking any rhizoids. Peduncle composed of irregular arrangement of kenozooids or various sizes. Capitulum massive with gradual or sharp border to peducule. Capitulum consisting of polygonal autozooids and intercalated small kenozooids. Orifice of autozooids usually centrally located.

***Bomburozoon* gen. nov. *bulbosus* sp. nov**

Analysed material: NIWA 98074 (holotype)

Diagnosis: Peduncle-capitulum transition gradual (Fig.4 B, D). Capitulum expanded, massive, sac-like (Fig.4 A). Autozooid orifice with short apertural papilla (Fig.4 E, F). Kenozooids of peduncle larger than kenozooids of capitulum (Fig.4 B, D). Attachment disc expanded towards substrate, wider than remaining peduncle (Fig.4 C).

Description: Colony ~12,3 mm in length. Capitulum massive, lobular and sac-like. Capitulum length 6386.291 µm to 7318 µm (mean 6756.765 µm, SD 424.726 µm); width 5182.166 µm to 5698.925 µm (mean 5504.218 µm, SD 257.759 µm). Peduncle cone shaped, length 5906.25 µm to 7122 µm (mean 6623.76 µm, SD 513.868 µm). Peduncle width 2073 µm to 2493.882 µm, (mean 2195.916 µm, SD 173.301µm.). Peduncle structure starting thick at gradual transition to capitulum narrowing toward baseplate. Capitulum-peduncle length ratio 1: 1.020080 width. Capitulum kenozooid length 244.586 µm to 308.475 µm (mean 273.572 µm, SD 20.702 µm), width 167.741 µm to 385.475 µm (mean 279.571µm, SD, 76.462 µm). Peduncle kenozooid length 318.072 µm to 893.030 µm (mean 571.877 µm, SD 183.967 µm), width 296.474 µm to 579.706 µm (mean 409.633 µm, SD 93.989 µm). Capitulum autozooid (lower, central parts) length 491.691 µm to 669.401 µm (mean 547.123 µm, SD 56.371 µm), e width 397.811 µm to 721.389 µm (mean 513.796 µm, SD 95.521 µm). Attachment disc almost circular, mean length 2776.060 µm, mean width 2762.090 µm.

Distribution: New Zealand, 250m depth

***Bomburozoon* gen. nov. *antarcticus* sp. nov.**

Analysed material: MNHN IB-2009-165 (syntypes)

Diagnosis: Capitulum massive, sac like with sharp transition to much thinner peduncle (Fig.5 A, D). Peduncle of consistent thickness, narrow without distinct expansion into attachment disc (Fig.5 C, D).

Etymology: antarcticus, referring to its sampling locality from Antarctica.

Description: Colonies ~12 – 25 mm high. Capitulum length 8719.194–22925.122 µm (mean 11706.353 µm, SD 3422.122 µm), width 4605.120–10802.966 µm (mean 7498.467 µm, SD 1540.311 µm). Peduncle length 5461.674–17768.894 µm (mean 9850.594 µm, SD 3437.438 µm), width 1540.623–2744.742 µm (mean 2069.710 µm, SD 323.690 µm). Angle between capitulum and peduncle varies from almost 90 degrees steep on both sides to almost flat (Fig.5 D). Capitulum kenozooid length 145.095 µm to 445.196 µm (mean 284.593 µm, SD 94.156 µm), width 143.039 µm to 419.263 µm (mean 253.666 µm, SD 75.395 µm). Peduncle kenozooid length 308.248 µm to 1473.980 µm (mean 987.067 µm, SD 293.189 µm), width 471.211 µm to 948.789 µm (mean 698.754 µm, SD 131.968 µm). Pattern of kenozooids in peduncle vary between big hexagonal cells meandering in serpentines to small triagonal kenozooids wedged in between (Fig.5 C, D). Autozooid length 406.586–887.905 µm (mean 631.895 µm, SD 146.670 µm), width 388.909–824.259 µm (mean 533.273 µm, SD 121.010 µm). Cystid wall yellow to brownish in coloration. Capitulum- peduncle length ratio between 1.596 and 1.290:1 (mean 0.885, SD 2.537).

Remarks: Form of capitulum variable due to transportation and possible differences in ontogenesis but overall colony structure coherent.

Distribution: Antarctica, Adélie Land. Station unknown, but other sampling localities of the CeaMarc 2008 Aurora Australis cruise usually range between 200-800m depth.

3.2.1.2. *Zigzagpedunculus* gen nov.

***Type species*:** *Zigzagpedunculus* gen nov. *gracilis* sp. nov.

Diagnosis: Clavoporid with peduncle composed of alternating row of kenozooids arranged in a zig-zag pattern.

Etymology: Zigzag refers to the typical arrangement of kenozooids and pedunculus for their presence in the peduncle.

Remarks: in many instances, the pattern of kenozooid arrangement is hard to distinguish and requires observation from the right angle. Observed perpendicular to the zig—zag axis would rather appear like a uniserial kenozooid arrangement as typical for *Metalcyonidium*.

Zigzagpedunculus gen nov. *gracilis* sp. nov.

Analysed material: NIWA 133682 (holotype), NIWA 133634 (paratype 1), NIWA 133635 (paratype 2), NIWA 13369 (paratype 3), NIWA 133672 (paratype 4), NIWA 133676 (paratype 5), NIWA 133677 (paratype 6), NIWA 133680 (paratype 7), NIWA 133693 (paratype 8)

Etymology: *gracilis* referring to the rather slender capitulum

Diagnosis: colony spindle-shaped, capitulum elongated, oval to tube shaped (Fig.6 A). Autozooids oval round to pentagonal. Angle between capitulum and peduncle rather flat (Fig.6 B). Kenozooids towards capitulum smaller before distinct zig-zag pattern (Fig.6 C, D). Peduncle always several times longer than capitulum. Rhizoid with few massive to very fine fibers originating from last kenozooid of peduncle (Fig.6 E).

Description: Colony ~7.1 mm high. Capitulum length 1109.785 µm to 2285.906 µm (mean 1617.981 µm, SD 317.804 µm), width 505.662 µm to 697.354 µm (mean 591.402 µm, SD 62.588 µm). Peduncle narrow, length 2021.341 µm to 12036.319 µm (mean 5510.754 µm, SD 2600.118 µm), width 141.421 µm to 283.332 µm (mean 218.805 µm, SD 34.132 µm), always slightly smaller in width than capitulum. Capitulum-peduncle length ratio averages 0.294:1 (SD 0.122), peduncle generally several times longer than capitulum. Capitulum kenozooids length measure 40.404 µm to 161.224 µm (mean 86.123 µm, SD 32.681 µm), width 32.183 µm to 119.226 µm (mean 73.378 µm, SD 26.872 µm). Peduncle kenozooids larger, length 125.243 µm to 469.362 µm (mean 275.924 µm, SD 108.666 µm), width 61.054 µm to 213.080 µm (mean 136.110 µm, SD 45.013 µm). Autozooid length 84.427 µm to 190.165 µm (mean 129.608 µm, SD 56.235 µm), width 147.030 µm to 320.000 µm (mean 239.071 µm, SD 53.609 µm). Rhizoid length 209.472 µm to 2644.827 µm (mean 745.228 µm, SD 825.052 µm). Cystid wall transparent.

Remarks: rhizoid measurement display certain degree of heterogeneity, suggesting considerable morphological variability in this zone, but sometimes lacking due to damaged structures.

Distribution: New Zealand, depth 568-1552m

***Zigzagpedunculus* gen. nov. *pyriformis* sp. nov.**

Analysed Material: NIWA 133622 (holotype), NIWA 133623 (paratype 1), NIWA 133683 (paratype 2), NIWA 133654 (paratype 3)

Etymology: pyriformis reflecting the more pear-shaped capitulum.

Diagnosis: capitulum oval shaped with steep angle between capitulum and peduncle (Fig.7 B; Fig. 8 B). Several thick and thin rhizoid fibers originating from multiple kenozooids at proximal end of peduncle (Fig.7 D; Fig.8 C). Rhizoid always massive (Fig.7 A; Fig.8 A, C).

Description: colony ~7.4 mm high. Capitulum robust, length 1229.251 µm to 3137.048 µm (mean: 1590.926 µm, SD: 712.682 µm), width 586.328 µm to 1423.956 µm (mean: 821.574 µm, SD: 281.384 µm). Peduncle length 1931.908 µm to 17,517.698 µm (mean: 5821.703 µm, SD: 6433.742 µm), width 229.786 µm to 343.426 µm (mean: 282.579 µm, SD: 38.664 µm). Capitulum-peduncle length ratio 0.273:1 on average (range: 0.179 – 0.636, SD:

0.111), indicating high variability in peduncle size among specimens. Capitulum kenozooid length 56.927 µm to 143.511 µm (mean: 91.751 µm, SD: 28.183 µm), width 53.214 µm to 148.018 µm (mean: 99.222 µm, SD: 41.180 µm). Peduncle kenozooid length 94.691 µm to 361.790 µm (mean: 178.618 µm, SD: 84.323 µm), width 58.987 µm to 187.966 µm (mean: 131.197 µm, SD: 39.544 µm). Autozooid length 116.611 µm and 508.321 µm (mean: 274.509 µm, SD: 111.718 µm), width from 92.338 µm to 341.225 µm (mean: 166.379 µm, SD: 75.032 µm). Cystid wall slightly colored but transparent. Rhizoid fibre length 453.817 µm to 2882.150 µm (mean: 1087.938 µm, SD: 704.202 µm).

Remarks: The main differences between *Z. gracilis* and *Z. pyrigormis* being a slightly more massive and pear shaped capitulum, and multiple rhizoids in *Z. pyriformis* from several kenozooids (Fig.6 A, E; Fig.7 B, D; Fig.8 D, C) The peduncle is showing proportionally greater length. Kenozooids in the peduncle are generally larger (Fig.7 C, D; Fig.8 C). Finally, the rhizoid region displays considerable variation due to its bristling and coiled up structure with many fine substrate particles attached, implying the colony had been attached to sandy bottoms before collection (Fig.8 C).

Distribution: New Zealand, depth 693m

3.2.1.3. *Michelinopedunculus* gen. nov.

Type species: *Michelinopedunculus* gen. nov. *microcephalus* sp. nov.

Etymology: from the Michelin man reflecting the peculiar 'tire-stack' arrangement of the kenozooids in the peduncle.

Diagnosis: Clavoporid with thick peduncle consisting of short rings of kenozooids (Fig.9 E). Rhizoid process originating sideways of basal region irregularly of peduncle spanning approximately 20 kenozooid rings. Rhizoid thick at origin close to peduncle and thinning out very finely (Fig.9 C).

Michelinopedunculus gen. nov. *microcephalus* sp. nov.

Analysed material: NIWA 133660 (holotype)

Etymology: micro for small and cephalon for head, reflecting the small capitulum of the species.

Diagnosis: same as for the family

Description: colony large and erect ~9 mm high, with small autozooidal capitulum (Fig.9 A). Autozooids flat with round apertural area. Angle between capitulum flat, capitulum and peduncle almost invariant in width (Fig.9 B, D). Capitulum small, length 716.883 µm and 750.192 µm (mean 733.538 µm, SD 23.553 µm), width 475.325 µm to 532.231 µm (mean 503.778 µm, SD 40.239 µm). Peduncle long, length 7853.558 µm to 8447.955 µm (mean 8150.757 µm, SD 420.302 µm), width 378.302 µm to 405.195 µm (mean 391.749 µm, SD 19.016 µm). Capitulum-peduncle length ratio of 0.088:1 (SD 1.706). Capitulum kenozooids

length 40.482 µm to 45.205 µm (mean 42.844 µm, SD 3.340 µm), width 56.507 µm to 405.195 µm (mean 230.851 µm, SD 246.560 µm). Peduncle kenozooid length 75.000 µm to 80.583 µm, (mean 77.792 µm, SD 3.948 µm), width 190.291 µm to 342.458 µm (mean 266.375 µm, SD 107.598 µm). Autozooid length 118.151 µm to 124.643 µm (mean 121.397 µm, SD 4.591 µm). width 115.068 µm to 133.434 µm (mean 124.251 µm, SD 12.987 µm). Rhizoid region spans 766.119 µm to 1332.945 µm (mean 1049.532 µm, SD 400.807 µm).

Remarks: Kenozooids show considerable variability in width due to irregular constrictions in the peduncle. The kenozooid rings have constrictions at the side giving them a tire stack appearance, as well as ridges running in the middle of the kenozooid rings witch in some regions of the peduncle appear to be alternating like a spring coil. The lateral rhizoid extension seems unique for this genus and species. Since there are additional short rhizoids from the basal end of the peduncle as well as the extension, it does not seem to be artificial. Fully understanding the internal structure of the kenozooids would require histology or perhaps CT imaging.

Distribution: New Zealand, depth 1124m

3.2.1.4. *Heteropedunuculus* gen. nov.

Type species: *Heteropedunuculus* gen. nov. *fewkesi* sp. nov.

Etymology: hetero- referring to the heterogenous, unique composition of kenozooids in the peduncle of the genus.

Diagnosis: peduncle heterogenous and very long consisting of two rows of kenozooids in meandering zig-zag pattern. Peduncle showing variation in thickness and terminal thin filament at proximal end (Fig.10 B, D). Rhizoid fibres emanating from entire filament length, partially also from more distal peduncle areas. Rhizoid fibres thin and rather short (Fig.10 C). Capitulum with 3-4 rings of autozooids, laterally slimmer, of cylindrical form. Central autozooids round and larger (Fig.10 A, B). Lowest ring of autozooids near transition to peduncle small zooids. Angle between peduncle and capitulum steep, capitulum wider than peduncle (Fig.10 B).

Remarks: although the general kenozooidal arrangement of the peduncle is reminiscent of the genus *Zigzagpedunculus* gen. nov., it shows a high heterogeneity over it size in *Heteropedunculus* gen. nov. whereas it is rather consistent over the entire range of the peduncle in *Zigzagpedunculus* gen. nov. (Fig. 8 A).

***Heteropedunuculus* gen. nov. *fewkesi* sp. nov**

Analysed material: NIWA 133642 (holotype)

Diagnosis: same as for the genus

Etymology: named after J. Walter Fewkes who described the clavoporid genus *Ascorhiza*

Description: colony long, erect, approximately 8.5 mm high. Capitulum length 729.153 µm to 800.407 µm (mean 764.041 µm, SD 50.384 µm), width 771.625 µm to 824.456 µm (mean 798.041 µm, SD 37.357 µm). Peduncle length 7628.275 µm to 7961.046 µm (mean 7794.661 µm, SD 235.305 µm), width 228.681 to 257.291 µm (mean 242.986 µm, SD 20.230 µm). Capitulum-peduncle length ratio of 0.094:1. Capitulum kenozooid length 56.948 µm to 88.608 µm (mean 72.778 µm, SD 22.387 µm), width 42.711 µm to 86.076 µm (mean 64.394 µm, SD 30.664 µm). Peduncle kenozooid length 126.218 µm to 156.880 µm (mean 141.549 µm, SD 21.681 µm), width 133.345 µm to 152.366 µm (mean 142.856 µm, SD 13.450 µm). Autozooid length 377.215 µm to 463.087 µm (mean 420.151 µm, SD 60.721 µm), width 275.949 µm to 382.550 µm (mean 329.250 µm, SD 75.378 µm). Rhizoid region spans 617.681 µm to 699.079 µm (mean 658.380 µm, SD 57.557 µm).

Distribution: New Zealand, depth 1552m

3.2.1.5. *Calyssozoon* gen. nov.

Type species: *Calyssozoon* gen. nov. *minusculum* sp. nov.

Etymology: from *calysso*-, chalice, reflecting the general chalice-shape of the colony.

Diagnosis: Capitulum massive lobular. Angle between capitulum and peduncle high spanning between 45 and 90 degrees. Capitulum wider than peduncle (Fig.11 A, B, D). Peduncle longer and narrower than capitulum (Fig.11 C) with thick rhizoid region from proximal end. Rhizoids originate from several kenozooids (Fig.11 A, E).

***Calyssozoon* gen. nov. *minusculum* sp. nov.**

Analysed material: NIWA 133809 (holotype)

Diagnosis: same as the genus

Etymology: *minusculum* reflecting the generally very small size of the colony

Description: colony small and erect about 3.1 mm high (Fig.11 A). Capitulum length 1264.091 µm to 1916.000 µm (mean 1590.460 µm, SD 490.969 µm), width 1739.000 µm to 1984.049 µm (mean 1861.525 µm, SD 173.276 µm). Peduncle length 1553.000 µm to 2266.129 µm (mean 1909.565 µm, SD 504.258 µm), width 469.000 µm to 605.454 µm (mean 537.227 µm, SD 96.488 µm). Capitulum-peduncle length ratio 0.662:1. Capitulum kenozooids length 96.237–263.288 µm (mean 179.763 µm, SD 118.123 µm), width 59.365–237.693 µm (mean 148.529 µm, SD 126.097 µm). Peduncle kenozooids length 51.697–298.032 µm (mean 174.865 µm, SD 174.185 µm); width 51.643–297.772 µm (mean 174.708 µm, SD 174.039 µm). Autozooid length 262.181 µm to 310.438 µm (mean 286.310 µm, SD 34.123 µm), widths 197.215 µm to 222.075 µm (mean 209.645 µm, SD 17.579 µm). Autozooids oval in younger

parts of capitulum, rectangular to polygonal in older ones (Fig.11 B, C, D). Cystid wall transparent with yellowish coloration. Rhizoid region measured 871.294 µm in length.

Remarks: the specimen has an epiphyte located at the tip of the capitulum, which was not regarded in its analysis (Fig.11 B). The specimen is shrivelled, which makes measurement data not totally accurate. Capitulum relatively broad, peduncle consisting of rings to cells of irregular size. At the upper part of the capitulum an old autozooid with cone shape and a low apertural papilla and rectangular aperture. Polypides are partially visible due to the semi-translucent cuticle.

Distribution: New Zealand, depth 3480m

3.2.1.6. *Metamichelinopedunculus* gen. nov.

Type species: *Metamichelinopedunculus* gen. nov. *paradoxus* sp. nov.

Etymology: combination of names of *Metalcyonidium* and *Michelinopedunculus* gen. nov. reflecting its two-partite composition of the peduncle.Diagnosis: peduncle composed of proximal area of elongated uniserial stacks of kenozooids with a distal area comprised of tight, dense rings close to capitulum (Fig.12 B, D). Capitulum torpedo shaped (Fig.12 A). Autozooids small, round to oval elongated (Fig.12 B). Rhizoid from several kenozooids of proximal area, thick and few in number (Fig.12 C).

Remarks: distinction of proximal kenozooids in the stalk is very difficult.

***Metamichelinopedunculus* gen. nov. *paradoxus* sp. nov.**

Analysed material: NIWA 133629 (holotype)

Etymology: paradoxus reflecting the bizarre combination of characters in the specimen.

Diagnosis: same as for genus.

Description: colony ~11 mm high. Capitulum length 2125.000 µm to 2231.331 µm (mean: 2178.166 µm, SD: 75.187 µm), width 684.021 µm and 695.312 µm (mean: 689.667 µm, SD: 7.984 µm). Peduncle length 9168.974 µm to 9220.734 µm (mean: 9194.854 µm, SD: 36.600 µm), width 298.365 µm to 351.562 µm (mean: 324.964 µm, SD: 37.616 µm). Capitulum-peduncle length ratio averaged 0.237:1 (range: 0.232–0.242, SD: 2.054). Capitulum kenozooid length 50.651 µm to 162.078 µm (mean: 106.365 µm, SD: 78.791 µm), width 56.319 µm to 79.856 µm (mean: 68.088 µm, SD: 16.643 µm). Peduncle kenozooid length 83.133 µm to 215.107 µm (mean: 149.120 µm, SD: 93.320 µm), width 106.375 µm to 150.922 µm (mean: 128.649 µm, SD: 31.499 µm). Autozooid length 347.864 µm and 383.744 µm (mean: 365.804 µm, SD: 25.371 µm), width 192.801 µm and 201.410 µm (mean: 197.106 µm, SD: 6.087 µm). Rhizoids extended between 957.131 µm to 990.806 µm (mean: 973.969 µm, SD:

23.812 µm). Rhizoids always consisting out of very few fine but notably long single strands originating from several points at the base of the peduncle.

Remarks: capitulum kenozooids vary considerably and the peduncle kenozooids are similarly variable. Overall, these values highlight the pronounced disparity between the relatively large capitulum and the substantially elongated peduncle, as well as considerable kenozooid variation within both regions.

Distribution: New Zealand, depth 1113m

3.2.1.7. *Buskozoon* gen. nov.

Type species: *Buskozoon* gen. nov. *vadum* sp. nov.

Etymology: named after George Busk, who described the first clavoporid.

Diagnosis: Clavoporid with peduncle composed of regular, small, poly- to hexagonal kenozooids (Fig.15 C, D). Peduncle firmly attached to substrate via broad attachment disc (Fig.13 D; Fig.14 D; Fig 15 C). Capitulum-peduncle transition gradual. Colony of dark, brown appearance.

Remarks: This genus differs from other non-rhizoidal clavoporids in having regular, small kenozooids forming the peduncle and a smooth, gradual transition from the peduncle to the capitulum.

Buskozoon gen. nov. *vadum* sp. nov.

Analysed material: KB24_6A; KB24_23G; KB24_24A; KB24_38F; KB24_45A; KB09; RC25

Etymology**:** vadum meaning shallow, alluding to the shallow sampling locations of the species.

Diagnosis: same as for genus.

Description. Capitulum 3.535–12,576.503 µm length and 4.589–3,381.820 µm width. In KB24 set 3.535–9,766.790 µm long (means reported: 4,885.163 µm and 6,903.664 µm) and 4.589–3,381.820 µm wide (mean 1,693.205 µm, SD 2,388.063 µm)(Fig.13 A); in KB09 2,919.117–8,981.024 µm long (mean 5,612.695 µm, SD 3,086.769 µm) and 1,327.586–2,163.089 µm wide (mean 1,824.037 µm, SD 439.428 µm)(Fig.14 A). In RC25 4,341.072–12,576.503 µm long (mean 8,115.216 µm, SD 4,160.493 µm) and 1,454.175–2,363.793 µm wide (mean 2,052.720 µm, SD 518.489 µm), with capitulum often appearing bumpy or dented (Fig.15 A, B). Peduncle 4.501–9,035.631 µm length and 8.558–2,527.070 µm width. KB24 4.501–8,210.683 µm long (mean 4,107.592 µm, SD 5,802.647 µm) and 8.558–2,527.070 µm wide (means 1,267.814 µm and 1,780.857 µm); in KB09 4,719.364–9,035.631 µm long (mean 6,199.053 µm, SD 2,457.316 µm) and 481.737–826.629 µm wide (mean 602.300 µm, SD 194.456 µm); in RC25 2,460.046–4,003.558 µm long (mean 3,259.029 µm, SD 773.196 µm) and 902.213–1,185.000 µm wide (mean 1,009.017 µm, SD 153.562 µm). Capitulum:peduncle ratio is in KB24 between 0.785–1.190:1 (mean 1.189, SD 1.190); in KB09 between 0.905:1

(range 0.619–0.994, SD 1.256); and in RC25 between 2.490:1 (range 1.765–3.141, SD 5.381).Capitulum kenozooids: in KB24 132.846–244.472 µm long (mean 188.659 µm, SD 78.932 µm) and 139.844–341.262 µm wide (mean 240.553 µm, SD 142.424 µm); in KB09 100.074–193.162 µm long (mean 152.705 µm, SD 47.723 µm) and 89.789–205.490 µm wide (mean 143.595 µm, SD 58.273 µm); in RC25 115.350–217.629 µm long (mean 164.435 µm, SD 51.263 µm) and 87.346–232.621 µm wide (mean 142.168 µm, SD 78.920 µm). Peduncular kenozooids: in KB24 set 146.015–264.249 µm long (mean 205.132 µm, SD 83.604 µm) and 110.221–209.124 µm wide (mean 159.673 µm, SD 69.935 µm); in KB09 161.961–254.971 µm long (mean 207.058 µm, SD 46.569 µm) and 78.494–175.136 µm wide (mean 115.110 µm, SD 52.402 µm); in RC25 124.807–221.250 µm long (mean 184.104 µm, SD 51.897 µm) and 105.461–127.555 µm wide (mean 113.695 µm, SD 12.074 µm). Autozooids hexagonal, measuring in KB24 189.986–316.062 µm length (mean 253.024 µm, SD 89.149 µm) and 163.541–292.098 µm width (mean 227.820 µm, SD 90.904 µm) (Fig.14 B). In KB09 269.704–654.351 µm length (mean 452.695 µm, SD 193.002 µm) and width 218.530–362.483 µm (mean 308.343 µm, SD 78.327 µm) (Fig.13 C); in RC25 150.073–442.754 µm length (mean 296.414 µm, SD 206.957 µm). Baseplate (attachment disk) rounded, sometimes with small marginal indentations (Fig.14 D; Fig 15 C). In KB09 385.844–1,728.170 µm length (mean 1,136.395 µm, SD 685.104 µm) and 758.577–1,267.014 µm in width (mean 948.328 µm, SD 277.660 µm), in RC25 495.800–2,921.170 µm length (mean 1,435.005 µm, SD 1,301.913 µm) and 293.364–2,096.128 µm width (mean 1,225.663 µm, SD 902.971 µm).

Distribution: Atlantic Ocean, North Sea, Skagerrak (20-32m) and English Channel, Bretagne (77-80 m).

Remarks: the comparatively high abundance and shallow sampling locations renders this species ideal for future studies concerning ontogeny and plasticity in clavoporids.

3.2.1.8 New species of *Metalcyonidium*

***Metalcyonidium elongatum* sp. nov.**

Analysed material: NIWA 133677 (holotype); NIWA 133633 (paratype 1); NIWA 133673 (paratype 2); NIWA 133687 (paratype 3); NIWA 133801 (paratype 4)

Etymology: *elongatum* referring to the highly elongated kenozooids

Diagnosis: peduncle comprised of uniserial and highly elongated and long kenozooids (Fig.16 E), Capitulum highly elongated (Fig.16 A, B). Rhizoid comprised of few, short and thick fibres (Fig.16 C).

Description: colony ~10 mm high. Capitulum 1469.456 µm - 4100.085 µm length (mean 2440.458 µm, SD 808.869 µm) and 464.105 µm - 1148.699 µm width (mean 724.860 µm, SD 183.546 µm). Autozooids arranged in 2-3 rows, with few small kenozooids in between. Peduncle 3862.221 µm - 14582.239 µm length (mean 8638.145 µm, SD 4213.860 µm) and

203.125 µm - 697.987 µm width (mean 397.658 µm, SD 132.150 µm). Capitulum-peduncle ratio 0.170:1. Capitulum kenozooids 63.447 µm to 212.686 µm length (mean 138.578 µm, SD 46.966 µm) and 56.143 µm to 234.318 µm width (mean 120.058 µm, SD 58.845 µm). Peduncle kenozooids 126.918 µm to 1006.017 µm length (mean 480.483 µm, SD 309.300 µm) and 99.963 µm to 658.786 µm width (mean 245.556 µm, SD 165.526 µm). Autozooids 320.456 µm to 649.418 µm length (mean 470.637 µm, SD 103.436 µm) and 144.133 µm and 390.797 µm width (mean 272.226µm, SD 77.854 µm). Rhizoid region 493.478 µm to 1925.436 µm (mean 1113.097µm, SD 538.853 µm). Fibers thick and thinning proximal, originate from last kenozooid.

Distribution: New Zealand, depth 785-1024m

***Metalcyonidium compressum* sp. nov.**

Analysed material: NIWA 133658 (holotype); NIWA 133644 (paratype 1); NIWA 133639 (paratype 2); NIWA 133651 (paratype 3)

Diagnosis: uniserial peduncle kenozooids very narrow, sometimes annular in appearance (Fig.17 D). Capitulum large, almost length of peduncle and only slightly wider than peduncle (Fig.17 A). Autozooids pik shaped (Fig.17. B) . Rhizoid only from last kenozooid, spindle-shaped (Fig.18 C).

Etymology: compressa reflecting the stout peduncle of narrow kenozooids.

Description: capitulum length 923.791 µm to 4300.000 µm (mean: 3051.694 µm, SD: 1251.795 µm), width 469.674 µm to 1064.286 µm (mean: 754.544 µm, SD: 231.491 µm). Peduncle length 979.975 µm to 4644.063 µm (mean: 3145.904 µm, SD: 1196.475 µm), width 260.376 µm to 541.362 µm (mean: 377.400 µm, SD: 96.111 µm). Capitulum-peduncle ratio averaged 0.970:1 (range: 0.926–0.943, SD: 1.046). Capitulum kenozooids few but distinct, length 55.660 µm to 138.158 µm (mean: 90.190 µm, SD: 30.935 µm), width 42.453 µm to 136.650 µm (mean: 82.468 µm, SD: 36.475 µm). Peduncle kenozooids length 97.227 µm to 382.734 µm (mean: 262.980 µm, SD: 94.091 µm), widths of 46.093 µm to 537.705 µm (mean: 287.818 µm, SD: 163.402 µm). Autozooid length 203.704 µm to 744.878 µm (mean: 463.668 µm, SD: 181.312 µm), width 143.656 µm to 493.904 µm (mean: 290.557 µm, SD: 129.408 µm). Autozooids pike shape, often with distinct apertural papilla or slight peristome. Rhizoid length 123.500 µm to 1243.377 µm (mean: 699.492 µm, SD: 424.168 µm).

Distribution: New Zealand, depth 1109-1386m

***Metalcyonidium absurdum* sp. nov.**

Analysed material: NIWA 133650 (holotype)

Etymology: absurd for the bizarre colony structure consisting almost entirely of a peduncle.

Diagnosis: colony highly elongated peduncle comprised of several, elongated kenozooids (Fig.18 C, D). Rhizoid region short with only few short fibers (Fig.18 A, D). Capitulum miniscule, comprised only of few zooids (Fig.18 B).

Description: colony ~11mm in length, with oval capitulum distinctly shorter than peduncle. Rhizoids from proximal part of peduncle. Capitulum length 1025.082 µm to 1087.912 µm (mean: 1056.497 µm, SD: 44.428 µm), width 424.056 µm to 449.176 µm (mean: 436.616 µm, SD: 17.763 µm). Peduncle slender and long, length 9975.089 µm to 11044.728 µm (mean: 10509.909 µm, SD: 756.349 µm), width 324.662 µm to 329.670 µm (mean: 327.166 µm, SD: 3.541 µm). Capitulum-peduncle length ratio average at 0.098:1 (range: 0.099–0.103, SD: 1.355). Capitulum kenozooid length 112.690 µm, width 83.756 µm (n=1). Peduncle kenozooids length 285.235 µm to 291.328 µm (mean: 288.282 µm, SD: 4.308 µm), width 294.805 µm to 903.987 µm (mean: 599.396 µm, SD: 430.757 µm). Autozooid length 606.091 µm, width 214.721 µm (n=1). Autozooids oval shaped, transparent, orifice distal (Fig.18 B). Rhizoids few, thick and long, spindle-shaped (Fig.18 D). Rhizoid length 1139.302 µm to 1660.337 µm (mean: 1399.820 µm, SD: 368.427 µm).

Distribution: New Zealand, depth 1126m

3.2.1.9 New species of *Pseudalcyonidium*

Pseudalcyonidium sp. nov. 1

Analysed material: NIWA 133643 (holotype); NIWA 133646 (paratype 1); NIWA 133697 (paratype 2); NIWA 133812 (paratype 3).

Diagnosis: colony slender ~7mm high. The peduncle consists of one slender kenozooid, often twisted (Fig.19 B). Rhizoid massive, consisting of many fine bristle-like fibres (Fig.19 A) Capitulum pear-shaped (Fig.19 C).

Description: capitulum length 834.811 µm to 4056.670 µm (mean: 2123.051 µm, SD: 1037.882 µm), width 290.847 µm to 812.640 µm (mean: 589.776 µm, SD: 208.536 µm). Capitulo-peduncular transition narrows with smooth transition into peduncle with low angle. Peduncle composed of single kenozooid, length 2343.891 µm to 12,079.601 µm (mean: 6592.684 µm, SD: 3040.798 µm), width 95.831 µm to 529.915 µm (mean: 347.472 µm, SD: 152.865 µm). Capitulum-peduncle length ratio averaged 0.322:1 (range: 0.336 – 0.356, SD: 0.341), reflecting predominance of peduncle. Capitulum kenozooid length 31.351 µm and 112.805 µm (mean: 72.078 µm, SD: 57.597 µm), width 25.428 µm to 93.496 µm (mean: 59.462 µm, SD: 48.131 µm). Autozooids with a slightly raised apertural papilla. Autozooid length 73.712 µm to 521.341 µm (mean: 270.094 µm, SD: 162.735 µm), width 52.296 µm to 371.951 µm (mean: 168.481 µm, SD: 122.021 µm). Rhizoid thick and long, from multiple points

at proximal part of peduncle, consisting of several bristle-like fibers, usually heavily coiled. Rhizoid length 835.523 µm to 1610.067 µm in length (mean: 1179.786 µm, SD: 394.372 µm).
Distribution: New Zealand, depth 790-1676m

***Pseudoalcyonidium* sp. nov. 2**

Analysed material: NIWA 133666 (holotype)

Diagnosis: colony small erect ~ 3.1 mm high. Capitulum short and narrow, almost emerald-shaped with intermediate autozooids (Fig.20 B). Peduncle consists of a single kenozoid with a long spindle shaped rhizoid (Fig.20 B).

Description: capitulum length 649.608 µm to 667.683 µm (mean: 658.646 µm, SD: 12.781 µm), width 396.444 µm to 411.585 µm (mean: 404.015 µm, SD: 10.706 µm). Peduncle length 2397.767 µm to 2641.166 µm (mean: 2519.467 µm, SD: 172.109 µm), width 219.512 µm to 222.065 µm (mean: 220.789 µm, SD: 1.805 µm). Capitulum- peduncle length ratio averaged 0.261:1 (range: 0.253–0.271, SD: 0.074). Capitulum kenozooid length 15.590 µm, width 13.363 µm (n=1). The peduncle consists of one very elongated tube. It is relatively narrow right underneath the capitulum, enlarges subsequently until it starts narrowing down again approximately halfway down in the direction of the Rhizoid, giving it the approximate form of an eel tail (Fig.20 A, B, D). Autozooid length 137.525 µm to 205.806 µm (mean: 171.666 µm, SD: 48.282 µm), width 108.015 µm to 157.907 µm (mean: 132.961 µm, SD: 35.279 µm). Apertural papilla present in the upper region of the capitulum (Fig.20 B). Rhizoid lengths varied from 360.625 µm to 529.736 µm (mean: 445.181 µm, SD: 119.580 µm).

Distribution: New Zealand, depth 1109m

3.2.2. Reassignment of described species to new genera

3.2.2.1 *Pseudascorhiza* gen. nov.

Metalcyonidium morum Hirose, 2022

Type species: *Pseudascorhiza* gen. nov. *morum* (Hirose, 2022) comb. nov.

Etymology: pseudo- in reference to its high similarity to the genus *Ascorhiza* via a similar peduncle structure and attachment method.

Diagnosis: clavoporid with uniserial chain of kenozooids attached to substrate via attachment disc.

Diagnosis: small, pedunculate clavoporid in which the entire colony is organized into a two-part capitulum borne on a long, cylindrical stalk of short kenozooids. The capitulum is distinctly bipartite, comprising an elongate, brownish upper region packed with older, neatly orthogonal autozooids and a shorter, white, conical lower region bearing larger, younger autozooids. The

two parts are separated by a conspicuous constriction that functions as a natural fracture plane.

Description: colonies stand 13.6–17.9 mm high and attach to a single sand grain 1–2 mm in diameter by a basal disc. The head reaches about 3.9 mm in total length: the upper capitulum is ~2.5 × 1.6 mm, cylindrical and rounded distally, with densely set autozooids 0.18–0.29 mm across whose small, papilliform orifices face outward; the lower capitulum is conical, 1.3–2.0 mm long and 1.2–1.7 mm in diameter, often slightly depressed at the apex, and carries larger autozooids (0.29–0.41 mm) with less distinct boundaries and orifices. The neck at the junction narrows to ~1.1 mm in diameter. The peduncle is white, 9.7–15.9 mm long, and composed of roughly 42–50 short, mostly uniform, cylindrical kenozooids 0.24–0.29 mm in length and 0.28–0.32 mm in diameter; in mature colonies the subcapitular elements become conspicuously elongate (to ~0.92 mm), whereas the basal few are slightly reduced (0.14–0.15 mm long, ~0.22–0.23 mm wide) and broaden into the attachment region (measured ~0.10 mm long, ~0.30 mm wide). Each kenozooid contains ~four white myofibrils that span its length (0.06–0.08 mm thick), consistent with a contractile, posture-adjusting stalk. The larval type and reproductive mode remain unknown, but the frequent separation of the upper capitulum at the constriction, together with its older zooids and distinct pigmentation, suggests a dispersal strategy in which a reproductive head detaches and drifts before settlement.

Distribution: recent, Northwest Pacific (Japan), depths ~180–230 m.

Remarks: contrary to its original genus, *Metalcyonidium* is always attaches via rhizoids to the substrate. Despite the possibility plasticity of attachment discs on hard substrates vs. rhizoids to small sand particles (Ramalho et al. 2020), *P. morum* also attaches to small sand grains via a disc and not rhizoids. The structure of the peduncle shown in Hirose (2022, p. 94, Fig. 9) appears to be composed of rings of several kenozooids and not single, uniserial ones as in *Metalcyonidium*. Ultimately clarifying the true structure of the peduncle kenozooids could transfer this species in the genus *Ascorhiza*. This would also geographically fit with the only valid species of the genus *Ascorhiza*, A. occidentalis from the North-East Pacific coast.

3.3. Unassigned taxa

3.3.1 NIWA 133688 (specimen nr. 5)

Analysed material: NIWA 113688 (**specimen** nr.5)

Diagnosis: colony big and erect ~23 mm high. Capitulum in trapezoid form, almost uniformly overflowing in the stalk widthwise (Fig.21 B, D9). Peduncle strongly heterogenous consisting of two rows of alternating kenozooids in the region beneath the capitulum, transitioning to a translucent fibrous form approximately 300 µm of the peduncle length (Fig.21 B, C).

Description: capitulum length 2052.532 µm, 547.571 µm width. Peduncle elongated, reaching 21325.236 µm length, 371.134 µm width. Capitulum-peduncle ratio approximately 0.096:1. Rhizoid length 1252.779 µm (Fig.21 A). Capitulum kenozooid legnth 45.395 µm, width 54.858 µm. Peduncle kenozooids length 150 µm, width 182.895 µm. Autozooid length 298.531 µm, width 186.861 µm . Orifice slightly elevated (Fig.21 B).
Distribution: New Zealand, depth 1103m.
Remarks: unclear whereas the kenozooid appearance is truly formed by colony traits or if this is a convincing deformation due to transportation and storage.

3.4 Specimens of questionable assignment

Ascorhiza mawatarii d'Hondt, 1983
Clavopora hystricis Mawatari, 1968
not *Ascorhiza mawatarii* Harmelin & d'Hondt, 1992
not *Ascorhiza mawatarii* Ramalho et al. 2020

Remarks: This species was erected based on specimen without locality (coll Reyss, d'Hondt 1983). Since the holotype (MNHN-IB-2008-8500) is dry and unrecognizable, this species is a *nomen nudum* and cannot be recollected without type locality. The supposed paratype of the clavoporid studied by Mawatari (1968) is from Antarctica and from its kenozooidal peduncle arrangement does not belong to the genus *Ascorhiza*. The types of these samples need to be located and studied to obtain more information on their sampling locality and their true affinity. Specimens designated as *A. mawatarii* by Harmelin & d'Hondt (1992) are from the Deep-Sea collections from the Atlantic coast close to Gibraltar. These samples supposedly correspond to a specimen from Corsica in the Mediterranean (MNHN-IB-2008-9597). Another specimen from Corsica (MNHN-IB-2008-8729) differs significantly, however. Descriptions of the specimen are given below. Both are non-rhizoidal clavoporids with attachment discs, but both differ in their kenozooidal arrangement from the genus *Ascorhiza*.

Clavoporid indet. (cf. *Ascorhiza mawatarii* d'Hondt, 1983)
Ascorhiza mawatarii Harmelin & d'Hondt, 1992
?*Ascorhiza mawatarii* Ramalho et al. 2020

Analysed material: MNHN-IB-2008-9597
Locality: Corsica, Mediterranean Sea.
Description: colony erect ~21mm in height. Distinct peduncle widening progressively toward capitulum, clear boundary visible at transition (Fig.22 C). Capitulum massive, elongated, oval.

Zooids hexagonal, commonly rising toward periphery. Autozooids clustered (Fig.22 B, D). Disk-like base at terminal end of peduncle attaching colony to substrate, with subtle indentations around circumference. Peduncle transparent, with basal portion showing slight white coloration. Kenozooids of peduncle distinct, in numerous parallel rows, variable in size (Fig.22 D). Capitulum length 11 424.000 µm, width 6025.974 µm to 6640.000 µm (mean 6332.987 µm, SD 434.182 µm). Peduncle length 9985.192 µm, width 2146.782 µm to 3405.622 µm (mean 2619.005 µm, SD 559.256 µm). Capitulum kenozooid length 306.124 µm to 628.079 µm (mean 403.673 µm, SD 131.764 µm), width 224.026 µm to 487.181 µm (mean 322.991 µm, SD 102.024 µm). Peduncle kenozooid length 753.027 µm to 996.575 µm (mean 834.871 µm, SD 114.520 µm), width of 434.923 µm to 707.900 µm (mean 589.794 µm, SD 113.533 µm). Autozooid length 249.514 µm to 643.495 µm (mean 482.504 µm, SD 149.221 µm), width 199.482 µm to 532.981 µm (mean 379.914 µm, SD 120.653 µm). Attachment disc round, 2881.818 µm in diameter. Capitulum-peduncle length ratio 1.144:1.

Clavoporid indet. (as *Clavopora* sp.)
***Clavopora hystricis* (Gautier, 1954)**

Analysed material: MNHN-IB-2008-8729
Locality: strait of Bonifacio, Mediterranean Sea from 75 meters depth.
Description: tripartite club-shaped colony ~6,2 mm high, with a globular to slightly pear shaped capitulum and a thick peduncle (Fig.23 A). Peduncle composed of kenozooids. Zoarium, simple claviform, subcapitulate, composed of distinct cells (Fig.23 B). Colony yellowish to translucent in coloration. Capitulum roughly pear shaped with a length 2373.093 µm and a width 1943.307 µm. Peduncle length is 3784.568 µm and with a width of 591.132 µm. Kenozooids in the capitulum range in length from 131.241 to 179.487 µm (mean 149.935 µm, SD 22.400), width ranges from 79.613 µm to 156.368 µm (mean 105.994 µm, SD 34.577 µm). Peduncle kenozooids length ranges from 157.025 µm to 271.511 µm, (mean 214.268 µm, SD 80.954 µm) width measures uniform 82.725 µm. Autozooid length 247.863 µm to 316.346 µm (mean 279.273, SD 28.589 µm), width 247.863 µm to 316.346 µm (mean 279.273, SD 28.589 µm). Length ratio capitulum to peduncle of 1: 0.627.

4. Discussion

This chapter seeks to contextualize and interpret the findings of this study within a broader framework of bryozoan taxonomy. Building upon the preceding results, the discussion synthesizes the morphological and the preliminary studies to explore the taxonomic

positioning, diversity, and adaptations of the analysed specimens. The primary research goal is, as previously stated, to clarifying the taxonomy and diversity of clavoporids. This was conducted by morphological characterization of specimens from sampling areas with no previous records of the family, which, not surprisingly, led to description of new genera and species.

4.1 Methodological comparisons and challenges

Clavoporid studies are restricted to morphological observations owing to the lack of molecular sequence data. Most studies were only conducted based on superficial observations of colonies, sometimes on single specimens (Busk, 1874; Fewkes, 1889), whereas only Robertson (1902) appeared to have done sectioning for studying details of *Ascorhiza occidentalis*. Later studies applied more measurements for the description and study of new taxa (d'Hondt, 1976, 2006), most recently Hirose (2022) on Japanese clavoporids.

The difficulties are especially pronounced in ctenostome bryozoans, where the limited number of diagnostic characters complicates species identification (Schwaha, 2020). Due to their uncalcified nature, soft tissue morphology is essential. For some species of the closely related genus *Alcyonidium* even data on the reproductive mode is often critical for species determination (see e.g. Porter et al. 2001; Ryland & Porter 2003; Porter 2004). However, so far, we only have little data available on clavoporid reproduction and no indications for its applicability in species determination.

Despite the importance of soft body morphology in ctenostome systematics, clavoporids remain little explored in this aspect, owing to the number of specimens – frequently a single per species – which limits the use of destructive morphological techniques. However, non-destructive imaging might such as µCT would be interesting to apply in clavoporid research to obtain more detailed information on internal structures.

Although, extraction of DNA was attempted on some of the fresher, more appropriately preserved clavoporid samples, only a small fragment could be obtained and of little value.

4.2 Species delimitation and comparison to other alcyonidioideans

The family Clavoporidae Osburn & Soule, 1953, represents a morphologically distinct lineage within the superfamily Alcyonidioidea, characterized by unique club shaped colonies and specialized peduncular structures composed of kenozooids (d'Hondt, 1975, 2006; Schwaha, 2020). These features appear to be adaptations for deep-sea and soft-sediment environments, contrary to most species of Alcyonidiidae. Members of both families share a flexible, but thick cuticle in their colonies, potentially enabling colonization of habitats less accessible to calcified bryozoans (Waeschenbach et al., 2012; Schwaha, 2020).

The diagnostic characteristic of Clavoporidae is their club-shaped colony shape, featuring swollen capitula transitioning to specialized peduncles, with autozooids exclusively located within the capitulum (Osburn & Soule, 1953). Although there are several species of the genus forming erect colonies, the kenozooidal peduncle seems to be only proper distinctive feature of clavoporids. Erect species of the genus *Alcyonidium* such as *A. torpedo* exhibits flat, lobate colonies attached via a short cylindrical peduncle, with autozooids distributed uniformly across its entire surface (d'Hondt, 2006). *A. diaphanum* colonies are erect, flexible, and variably branched, lacking clear differentiation between a capitulum and peduncle (Porter et al. 2001). *A. pedunculatum* was originally considered as intermediate of *Alcyonidum* and *Ascorhiza* (Robertson 1902), and, although, it is also pedunculate, the preduncle is short and the 'capitulum' is a flattened disc. The general morphology, thus, is quite coinciding with *A. flabelliforme*, but their geographic distribution clearly separates these species, the former being found in the Northern Hemisphere and the later in Antarctica.

The attachment strategies within Clavoporidae also differ significantly. Genera differences are mainly based on variation in colonial attachment strategies and peduncle composition. *Clavopora*, *Pseudalcyonidium*, *Metalcyonidium*, and *Cephaloalcyonidium* utilize rhizoids emerging from kenozooidal peduncles, while *Ascorhiza* has a direct, firm attachment (Fewkes, 1889; d'Hondt, 1975, 2006).

4.3 Comparative analyses of focal clades and species

Clavoporids are easiest to separate by their attachment method (baseplate-/rhizoidal attachment) and in the following chapters all members included in this study are discussed subdivided by how they anchor and how the peduncle is composed (multiple kenozooids / uniserial / single kenozooid). Anchoring mechanisms between taxa differ by extensive rooting systems and those with basal attachments based on their primary attachment strategy (Cook, 1981; Schack et al. 2018). Other characters suitable for systematic purposes are: the shape of the capitulum and its transitional angle to the peduncle, structure of the peduncle, the shape and packing of autozooids and kenozooids in the capitulum, the distribution and pattern of kenozooids in the peduncle, and potential budding zones in the capitulum and/or peduncle.

4.3.1 Comparative analysis of taxa with baseplate anchorage

As a result of this study, there are four genera with five species with non-rhizoidal attachment mechanisms: *Bomburozoon* gen. nov. (*B. bulbosus* sp. nov. and *B. antarcticus* sp. nov.) (Fig.24 A, B), *Ascorhiza occidentalis* Fewkes, 1889, *Buskozoon gen. nov.* (*B. vadum sp. nov.*) (Fig.24 C), and *Pseudascorhiza* gen. nov. *morum* comb. nov.

Bomburozoon bulbosus has a massive, lobular sac-like capitulum with a gradual transition angle and a cone-shaped peduncle that narrows toward a wide baseplate. *Bomburozoon*

antarcticus also bears a massive head but with a steeper, sharp neck onto a uniformly narrow peduncle without an expanded disc. Both are consistently head-dominant (Cap:Ped ≈ 1 in B. *bulbosus*; >1 in most B. *antarcticus*). In contrast, *A. occidentalis* has an annulated and slender peduncle, with a very sharp high-angle transition at a budding collar. The head is relatively small to moderate. *Buskozoon vadum* sits between these: cap shapes vary from globular to elongated, but the transition is always smooth and gradual. Cap:Ped varies (≈0.8–>2), indicating pronounced environmental inflation of the head atop a conservative stalk micro-architecture.

Capitula of *Bomburozoon* intermix polygonal autozooids with small kenozooids. Apertures are central, with a short apertural papilla (*B. bulbosus*). In *Ascorhiza occidentalis*, autozooids form distal to the budding collar. Basal autozooids are less informative because the neck is sharply differentiated by the collar itself (Fewkes*,* 1889). *Buskozoon* autozooids are hexagonal, often arching upwards and the size variance is moderate, dependent on colony size. The clearest separator between them is stalk architecture. *Ascorhiza occidentalis* was described with rows of parallel, muscular kenozooids and an annulated budding collar region at the peduncle-capitulum transition (Fewkes*,* 1889). The kenozooid composition of Clavoporid indent. is composed of numerous parallel rows (Fig.24 D) but differs in appearance from depictions of of other descriptions (d'Hondt, 1983; Harmelin & d'Hondt, 1992; Mawatari ,1968) so the true affiliation remains unclear (see above) but differs significantly from the peduncle composition of the other baseplate attached species.

Buskozoon displays apical early buds like other alcyonidioideans but lacks evidence for a collar. *Buskozoon vadum* shows regular, small poly- to hexagonal autozooids. *Pseudascorhiza morum* is a peduncle-dominant, bipartite-headed form with a basal attachment disc, a constricted neck, and a stalk built from short multiserial ringlets of kenozooids rather than a uniserial chain. Its upper vs. lower capitulum contrast (older, brownish upper; larger, paler, younger lower) and easy separation at the constriction are unique and suggest a dispersal mechanism via detachable, reproductive upper heads. It is peduncle dominant (capitulum ≈ 3.9 mm; peduncle 9.7–15.9 mm), unlike *Bomburozoon* species. It differs from *Ascorhiza occidentalis* by lacking a true annulated, budding collar and from *Buskozoon vadum* by lacking a fine, regular polygonal mosaic arrangement of autozooids and by its bipartite head. Genus *Bomburozoon* is irregular multiserial, with coarser kenozooids than the head (especially *bulbosus*). *Bomburozoon antarcticus* variably displays meandering hexagonal to small triangular intercalations.

In general, non-rhizoidal clavoporids seem to be more restricted to shallower depths, compared to the deeper rhizoidal ones: *B. bulbosus* around 250m, *B. antarcticus* at 200 – 800 m, *A. occidentalis* at 36–40 m, *B. vadum* at 30-50m, *P. morum* at 180-230m. Also, the indeterminate specimens from the collection of MNHN (Paris) are shallower. In addition, large

capitulum and a more moderate capitulum-peduncle ratio seem to more common in non-rhizoidal clavoporids, potentially reflecting more stable substrates.

4.3.2 Comparative analysis of taxa with multiserial peduncle and rhizoid

Multiserial peduncle clavoporids recognized in the present study: *Zigzagpedunculus* gen. nov. (*Z. gracilis* sp. nov., *Z. pyriformis* sp. nov.), *Michelinopedunculus* gen. nov. (*M. microcephalus* sp. nov.), *Heteropedunculus* gen. nov. (*H. fewkesi* sp. nov.), *Calyssozoon* gen. nov. (*C. minusculum sp. nov.*), *Metamichelinopedunculus* gen. nov. *(M. paradoxus* sp. nov.*), Cephaloalcyonidium morchellanum* (Fig.25).

Zigzagpedunculus (both *Z. gracilis* and *Z. pyriformis*) is defined by a strict, zipper-like peduncle built from two alternating longitudinal series of kenozooids along the entire length. When observed obliquely, kenozooids can be mistaken for a uniserial chain typical for *Metalcyonidium*. Capitula are translucent and relatively small. *Z. gracilis* bears an elongated oval head and typically a few massive to very fine rhizoids from the terminal kenozooid, whereas *Z. pyriformis* carries a more pear-shaped head, a consistently stouter stalk, and multiple rhizoid bundles arising from several proximal kenozooids. Both have intermediate neck angles (neither abrupt collars nor long tapering necks). Difficulties arise with specimens showing heterogeneous biserial stalks and *Metalcyonidium* with long uniserial kenozooids: these lack the continuous alternating arrangement of *Zigzagpedunculus* and show either uniserial segmentation or modifications of the zig-zag motif.

Michelinopedunculus microcephalus has a stack of short, broad kenozooid rings, many with shallow lateral constrictions and a median ridge. The small head sits on a penducle of nearly constant width and the whole colony appears rather as a column with cap than a club. Also, a proximal filament emanates from the lower peduncle and bears its own short rhizoids for ~20 rings before tapering, a structure not observed in any other clavoporid. This combination ring-stack, microcephalous head, and lateral rhizoid process, precludes confusion with any zigzag or mosaic stalk.

Heteropedunculus fewkesi shares with *Zigzagpedunculus* the basic plan of two longitudinal series but differs: segments of clean zig-zag alternate with thinner, filiform runs where kenozooids narrow and spacing loosens. The capitulum is laterally narrow and encircled by 3–4 low rings of autozooids, with a crown of larger, round central zooids. Fine, short rhizoids can arise along the lower third of the stalk, not just at its base, which is also diagnostic.

Calyssozoon minusculum is the smallest colony among the studied taxa and should not be dismissed as juvenile of anything else. The capitulum is a chalice with autozooids that are oval in the youngest sectors and become rectangular to polygonal in older patches. The peduncle is proportionally long but narrow and shows an irregular small cell mosaic rather than rings or a two-row zipper. Several thick rhizoids originate from multiple proximal kenozooids. Thicker

and shorter rhizoids were interpreted for firm point attachment, while fine or spindle-extended rhizoids are adapted to spread loads into softer, grainy substrates (Schack et al., 2018).

Metamichelinopedunculus paradoxus has a long stalk with two distinct areas in the peduncle, one just below the neck and one near the base, separated by a slightly narrower, more translucent mid-shaft of smaller, irregular kenozooids. The head is moderately large and torpedo shaped and few very long, fine rhizoids arise from several basal points.

Cephaloalcyonidium morchellanum differs from other genera in a peduncle of very small, hexagonal kenozooids and also its globular head composed of many autozooids.

4.2.3 Comparative analysis of *Metalcyonidium* species

Differences in the species are present in their capitulum-peduncle ratio and peduncular kenozooid elongation with associated rhizoid architecture (Fig.26). *M. gautieri* is moderately peduncle dominant, of medium-sized uniserial stalk with fine rhizoids arising from the terminal element, a globular head, and elongate, trapezoid autozooids. *M. elongatum* sp. nov. has much more elongated kenzooids in the peduncle, and also the largest peduncle with few, short but thick rhizoid fibres concentrated at the basal kenozooid. Its autozooids are conspicuously large with clear distal papilla, and the capitulum is tall, semicrescent to semicircular, separating it from the more globular one of *M. gautieri*.

Metalcyonidium absurdum sp. nov. is also strongly peduncle dominant but differs from *elongatum* in having narrow, very uniform stalk width with moderately long peduncular kenozooids and few, thick, spindle-like long rhizoids. Its capitulum is minute and possibly reflects an early ontogenetic stage and potential could be *M. elongatum*, but owing to the lack of comparative ontogenetic stages, remains distinct.

In contrast, *Metalcyonidium compressum* sp. nov. has almost an equal ratio of capitulum to ratio and thus also the largest capitula in the genus. The stalk is only slightly narrower than the head. Peduncular kenozooids are shorter on average (mean~263 µm) than in *M. elongatum* and *gautieri*.

4.2.4 Comparative analysis of new species of *Pseudalcyonidium*

Across the material, all three species share a single, tubular peduncular kenozooid (occasionally with weak constrictions), rhizoidal anchorage, and a pear-to-oval capitulum carrying the autozooids (Fig.27). *P. bobinae* sits near the intermediate condition (Cap:Ped ≈ mean ≈ 0.75:1), whereas the two new species are strongly stalk-dominant: *sp. nov. 1* average (0.32:1), and *sp. nov. 2* (0.26:1). Thus, the new species extend the variety of *Pseudalcyonidium* colonies to tall, elevated forms with relatively small heads.

The rhizoid shape in *P. bobinae* bears relatively thick, short fibres clustered at the basal end of the peduncle. *P.* sp. nov. 1 develops a massive, many-filament, bristle-like coil of rhizoids with multiple origins along the proximal shaft (often heavily entangled with sediment), suggesting spread in softer or shifting substrates. *P.* sp. nov. *2* differs by a single, long spindle-shaped rhizoid from the terminal kenozooid which consist of few, thick strands implying point anchorage on firmer patches.

The capitulum of *P. bobinae* is broadly pear-shaped with irregularly alternating autozooids (round to hexagonal), a low apertural papilla, and early buds at the apex. *P.* sp. nov. 1 shows variable capitulum size but remains narrow, with slightly raised apertural papillae and moderate autozooid size variation. P. sp. nov. 2 carries only a minute capitulum with an emerald like outline, small, uniform autozooids and occasional low apertural papilla.

4.3 Implications for taxonomy and ecology

The analysis of the specimens provides a detailed view of potential ecological specializations and geographical distribution of Clavoporidae. The family has successfully colonized a wide range of benthic environments, mostly from deep sea habitats, with a remarkable bathymetric range up to 3100 m, but also shallower subtidal depths (Busk 1874, Robertson 1902, this study). The characteristic colony shape of clavoporid with its elongated peduncle could be an adaptation for life on soft substrates, which are typical for deep sea sediments. Most clavoporid genera exhibit elongated peduncles that elevate the feeding capitulum above silty or muddy bottoms, to optimize feeding and avoid burial (d'Hondt, 2006). The deep-sea bryozoan family Pachyzoidae anchors in soft sediments with non-kenozooidal cystid appendages (Schwaha & Gordon, 2024). This contrasts sharply with shallow-water species which are predominantly encrusting forms adapted to hard substrates like rocks and algae (Gordon, 2009). The specialized stalks are highly modified kenozooids that fulfill a support function, exemplifying the modularity that allows bryozoans to adapt to diverse ecological niches (Schack et al., 2018).

Kenozooidal peduncles of clavoporids suggest a capacity for posture adjustment or anchorage. Muscle fibers were originally described in the kenozooids of *Ascorhiza occidentalis* enabling potential movement (Robertson 1902), also distinguishing the family from the related Alcyonidiidae, whose peduncles lack such specialization. However, since active coiling or strongly bent peduncles were not observed in this study, active movement of peduncles appears unlikely, making it more likely to be a feature of structural support. In other deep-sea bryozoans, such as Pachyzoidae, active colonial movement is rather unlikely or limited, although muscular rhizoids have been observed (Schwaha & Gordon, 2024).

Nothing is known about ontogeny of clavoporids, which complicates species comparisons, particularly if data is restricted to single specimens. The higher abundance of *B. vadum*

sampes in shallow European habitats provides the first opportunity to study specimens of different sizes and proportions. Based on first observations, it appears that young colonies still have a high peduncle dominance that rapidly, in older colonies, shifts to large capitula than peduncula.

Clavoporids show a broad distribution with representatives in the Atlantic, Pacific, Mediterranean, and Antarctic waters. New Zealand waters currently appear as a hot spot for clavoporid diversity with several novel genera. This pattern conincides with the deep-sea ctenostome family Pachyzoidae, which show a variety of species in Zelandia (Schwaha & Gordon, 2024). This generally reflects the high endemism of bryozoan diversity in the area (Gordon, 2010), although sampling bias represents a problem. This wide distribution and localized endemism may be a consequence of the reproductive strategy. Clavoporids and pachyzoids brood embryos. Brooding in general has been considered a major influence in bryozoans for species diversification, at least in cheilostomes (Taylor, 1988).

Evidence of reproduction in clavoporids is sparse, but clear patterns can be inferred. Budding of new zooids has been observed at the capitulum peduncle junction in *Metalcyonidium gautieri* and at the capitulum apex in *Pseudalcyonidium bobinae*. A proximal budding zone, in relation to zooidal orientation is unique or rare and probably an adaptation to potential capitulum fragmentation, as observed in *P. morum* (Hirose 2022).

Sexual reproduction involved brooding from all observations of this study, which is similar in the deep-sea ctenostome family *Pachyzoidae* (Schwaha & Gordon, 2024), but differs to Aethozoidae. The latter is an understudied group of solitary, predominantly deep-sea ctenostomes that have been shown to produce many oligiolecithal oocytes, which along with the presence of an intertentacular organ strongly suggest broadcasting and planktotrophic larvae (Schwaha et al. 2019).

5. Conclusion

This comparative analysis has resulted in the description of eight new genera (*Bomburozoon*, *Michelinopedunculus*, *Metamichelinopedunculus*, *Zigzagpedunculus*, *Heteropedunculus*, *Calyssozoon*, *Buskozoon*, and *Pseudascorhiza*) and numerous new species. The findings reveal profound morphological heterogeneity within the family, particularly in the architecture of the kenozooidal peduncle and varied colony attachment strategies.

In conclusion, this thesis establishes a new, more robust taxonomic framework for Clavoporidae. It highlights the importance of morphological analysis in systematics and lays the essential groundwork for future phylogenetic and ecological studies of the family.

The newly proposed taxa of Clavoporidea are as follows:

Ascorhiza Fewkes, 1889

Ascorhiza occidentalis Fewkes, 1889

Bomburozoon gen. nov
Bomburozoon antarcticus sp. nov.
Bomburozoon bulbosus sp. nov.

Buskozoon gen. nov
Buskozoon vadum sp. nov.

Calyssozoon gen. nov.
Calyssozoon minusculum sp. nov.

Cephaloalcyonidium d'Hondt, 2006
Cephaloalcyonidium morchellanum d'Hondt, 2006

Clavopora Busk, 1874
Clavopora hystricis Busk, 1874

Heteropedunuculus gen. nov
Heteropedunuculus fewkesi sp. nov.
Metalcyonidium d'Hondt, 1976
Metalcyonidium gautieri d'Hondt, 1976
Metalcyonidium elongatum sp. nov.
Metalcyonidium compressum sp. nov.
Metalcyonidium absurdum sp. nov.

Metamichelinopedunculus gen. nov.
Metamichelinopedunculus paradoxus sp. nov

Michelinopedunculus gen. nov
Michelinopedunculus microcephalus sp. nov.

Pseudalcyonidium d'Hondt, 1976
Pseudalcyonidium bobinae d'Hondt, 1976
Pseudalcyonidium sp. nov. 1
Pseudalcyonidium sp. nov. 2

Pseudascorhiza gen. nov.
Pseudascorhiza morum (Hirose, 2022) comb. nov.

Zigzagpedunculus gen. nov.
Zigzagpedunculus gracilis sp. nov.
Zigzagpedunculus pyriformis sp. nov.

6. Clavoporidae – Practical Determination Guide

Key and comparative notes for all described and newly analyzed members in „The ctenostome bryozoan family Clavoporidae: diversity and description of new taxa. “

How to use this guide

1. **Look at anchorage first** – baseplate vs. rhizoids.
2. **Stalk (peduncle) architecture** – continuous kenozooid vs. multiple kenozooids; uniserial vs. multiserial; ringed vs. polygonal blocks; special patterns (zig-zag, meandering, alternating, “tire-stack”).
3. **Capitulum** – shape (globular, pear, 2-part, torpedo), size vs. stalk (ratio), apertural papilla/orifice, tentacle counts (when known).
4. **Confirm with key characters** – depth/region, base morphology (disk/gear), and zooid dimensions measurement.

Glossary

- **Capitulum:** Upper part (head) of the colony
- **Peduncle:** Lower part (stalk) of the colony
- **Autozooid**: A feeding zooid which has a retractable, introverted lophophore, often identical within a colony.
- **Aperture/orifice:** Colony opening bordered by soft tissue
- **Baseplate**: disk-like expansion at the base of the peduncle (always without rhizoids).
- **Rhizoids**: filaments from peduncle base; few thick vs. many fine.

- **Kenozooid**: non-feeding structural zooid which possess neither orifices nor feeding organs and have a connective or strengthening function stalk/capitulum (shapes: polygonal, rhomboidal, ring-like).
- **Cuticle**: Outer body wall (ectocyst) – translucent, thick untransparent or leather like.
- **Uniserial peduncle**: one column of kenozooids; **multiserial**: several rows around axis. **single kenozooid:** peduncle lacking distinctive cell separations (e.g. *Pseudalcyonidium*).

I. Dichotomous Key

Order Ctenostomata paraphyletic group of Gymnolamenata that always lack calcified cystid walls

> **Family Clavoporidae Soule, 1953** erect colonies **differentiated in club shaped capitulum** (head) carrying **functional autozooids** and **peduncle** (stalk) with hollow or fibre filled **kenozooids** for structural support or movement. Mostly abyssal but occasionally in shallow waters.

Primary anchorage

1. Colony fixed by a **broad attachment disc (baseplate)**; **rhizoids absent** **2**

1'. Colony fixed by **rhizoids** (few thick strands or many fine/bristly fibers) **7**

Baseplate-anchored taxa

2. Peduncle–capitulum **transition sharp/high-angle**; stalk formed by **parallel serial kenozooids** that give a distinctly **annulated** look; budding zone at transition; East Pacific .....***Ascorhiza occidentalis***

2'. Two-part capitulum separated by a constriction; peduncle of **40–50 short cylindrical** kenozooids **regular**; upper cap often brownish and **detachable**.....***Pseudascorhiza morum***

2''. Peduncle–capitulum **transition gradual**; stalk **not** strictly parallel-serial; colonies Atlantic/NZ/Antarctic or shallow NE Atlantic; **dark to brownish** possible **3**

3. Peduncle composed of **regular, small poly- to hexagonal kenozooids**; colony**dark brown** ; **gradual** transition; **shallow Atlantic / Channel / Skagerrak**.....***Buskozoon vadum***

3'. Peduncle kenozooids **irregular in size/arrangement** (cone-shaped stalk possible); cap often **massive/sac-like**; NZ or Antarctic deep water **4**

4. Attachment **disc broad and clearly wider** than basal stalk; peduncle **cone-shaped**, narrowing toward base; cap **massive, lobular**; New Zealand (~250 m) ..... ***Bomburozoon bulbosus***

4'. Attachment **disc not expanded** (stalk of **fairly constant narrow width** to the base); cap **massive, sac-like**, often thick yellow-brown cuticle; **Antarctica, abyssal**.....***Bomburozoon antarcticus***

Rhizoid-anchored taxa

7. Peduncle built of **regular small hexagonal kenozooids**; cap **globular**, high-angle insertion ..... ***Cephaloalcyonidium morchellanum***

7'. Peduncle other architectures **8**

8. Peduncle a **single continuous kenozooid** (no transverse partitions); **annulated or twisted cord**; axis of musculature visible; **pear to elongate cap**.....**9**

8'. Peduncle **segmented into kenozooids** (uniserial, multiserial, or ring-like stacks) **11**

Continuous/"single-tube" peduncles (*Pseudalcyonidium*)

9. Peduncle **single slender tube**, often **twisted**; rhizoid **massive bristly coil** from **multiple points**; cap 0.8–4.1 mm, pear-shaped .....***Pseudalcyonidium* sp. nov. 1**

9'. Peduncle **single very elongated tube** with **eel-tail profile** (widens then narrows toward rhizoid); rhizoid **long, spindle-shaped**, few fibers; **small emerald-like cap**.....***Pseudalcyonidium* sp. nov. *2***

9" . Peduncle **continuous regular kenozooids** with muscular fiber visible, annulated externally; cap **pear-shaped 1.3–1.5 mm**; rhizoids **few–several, short–medium**; bathyal–abyssal N. Atlantic ..... ***Pseudalcyonidium bobinae***

Segmented peduncles

11. Peduncle **uniserial** from base to cap; rhizoids **few, thick or fine** from terminal unit **12**

11'. Peduncle **multiserial** (two rows or more) or **stacked rings**; special **zig-zag/meander** or **tire-stack** patterns present **15**

11" Peduncle **thick** almost as broad as cap, kenozooid segmentation slightly irregular, with **very few** and **thick rhizooids** ……..**17**

Uniserial peduncles – *Metalcyonidium*

12. Peduncle made of **~9 large segments**(~0.5–0.7 mm each); cap small (~1 mm); rhizoids **fine, ringed**; NE Atlantic (463–1250 m) .....***Metalcyonidium gautieri***

12'. Peduncle of **many short rings** (dozens) or **highly elongated blocks**; cap proportion and rhizoids as below **13**

13. Capitulum not two-part; choose on **kenozooid elongation** and **cap:ped** proportion **14**

14. Peduncle kenozooids **highly elongated and long**; colony to ~10 mm; rhizoids **few, short, thick**; cap relatively small (cap:ped ≈ **0.17:1**) .....***Metalcyonidium elongatum***

14'. Peduncle with **shorter kenozooids**; choose on overall **cap vs stalk length** and **rhizoid shape**:

- Cap length ≈ peduncle length (ratio **~0.97:1**); colony **digitate**; terminal unit **spindle-like** with few thick rhizoids .....***Metalcyonidium compressum***
- Cap tiny vs **very long slender peduncle** (ratio **~0.10:1**); rhizoids **few, thick, long**; peduncle width near-constant .....***Metalcyonidium absurdum***

Multiserial / ring-stack peduncles

15. Peduncle shows **two alternating rows** of kenozooids forming a clear **zig-zag** immediately beneath the capitulum; stalk generally slender; choose on **rhizoid mass** and **cap shape**.....**16**

15'. Peduncle **ring-like short kenozooids** giving a **tire-stack** impression, with **lateral rhizoid origin** along ~20 rings; cap **very small**; stalk thick and long .....***Michelinopedunculus microcephalus***

15" . Peduncle **two-row meandering zig-zag** but **heterogeneous** over penducle; terminal **thin filament** bearing **many short fine rhizoids** along lower third; cap **cylindrical with 3–4 rings** of autozooids .....***Heteropedunuculus fewkesi***

16. Cap **elongate oval to tube-shaped** (slender “spindle” habit); rhizoid a **long spindle** of **few to very fine fibers** from the **last peduncular kenozooid**; peduncle several × longer than cap (mean cap:ped ~0.29:1) .....***Zigzagpedunculus gracilis***

16'. Cap **oval to pear-shaped**, angle to stalk **steep**; **rhizoids numerous, thick + thin**, arising from **multiple** basal kenozooids; rhizoid region **massive**; cap:ped on average **0.27: 1....Zigzagpedunculus *pyriformis***

16" . Peduncle **heterogeneous with three zones** (distal/base with short wide rings; central irregular translucent section); rhizoids **few, very long, fine** from several basal points; cap **torpedo-shaped**; cap:ped **~0.24:1……. *Metamichelinopedunculus paradoxus***

Small-cap, thick-stalk multiserial (*Clavopora*)

17. Colony very small (~3 mm); cap **small globular**; peduncle **thick**, **multiserial hexagonal–polygonal kenozooids**, **flattened proximo-distally**; **few thick rhizoids**; transition smooth, low angle
.....***Clavopora hystricis***

Taxon	Attachment	Peduncle architecture	Transition angle	Capitulum shape	Cap:Ped (L)	Rhizoids	Autozooids (shape/size)	Colony size	Region/Depth
Clavopora hystricis	Rhizoids	Multiserial hex–poly (thick)	Low	Small globular	~1:<1	Few, thick (proximal)	Hex/pent; small	~3–10 mm	Mediterranean; deep off Africa; ~80 m
Ascorhiza occidentalis	Disc	Parallel muscular rows (annulated)	High	Globular–oval	≥0.66	None	—	—	NE Pacific, 36–40 m
Metalcyonidium gautieri	Rhizoids	Uniserial	Low–intermediate	Globular–oval	0.56–0.76	Terminal; fine sandy	Elongate triangular	~3.5–6.6 mm	Bay of Biscay–W Med; 463–1250 m

Pseudalcyonidium bobinae	Rhizoids	Single (rarely >1)	Low	Pear/elong-pear	0.57–0.97	Thick, short	498–538×269–428 µm	~3.9 mm	N Atlantic 1200–3100 m
Cephaloalcyonidium morchellanum	Rhizoids	Regular small hex series	High	Globular	0.64	Several proximal	~313×344 µm	—	New Caledonia ~164 m
Bomburozoon bulbosus	Disc	Irregular cells; cone to baseplate	Low	Massive sac-like	~1.0	None	492–669×398–721 µm; short papilla	~12 mm	NZ ~250 m
Bomburozoon antarcticus	Disc	Thin uniform; heterogeneous	High intermediate	Massive sac-like	≈0.89	None	407–888×389–824 µm	12–25 mm	Antarctic abyssal
Zigzagpeduncul us gracilis	Rhizoids	Zig-zag alternating rows	Intermediate	Elongate tube	~0.29	Few →very fine; last cell	Small–mod; oval–pent	~2.1 mm	NZ 568–1552 m
Zigzagpeduncul us pyriformis	Rhizoids	Zig-zag; larger kenoz.	High	Pear-shaped robust	~0.27 (var.)	Multiple; several cells	117–508×92–341 µm	~1.8 mm	NZ ~693 m

Micheli nopedu nculus microce phalus	Rhizo ids	Ring-stac k (short rings)	Lo w	Ver y sm all hea d	0.0 88	Later al proce ss + basal	~118–125×11 5–133 µm	~9 mm	NZ 1124 m
Heterop eduncul us fewkesi	Rhizo ids	Two-row meanders + filament	Hig h	Cyli ndri cal (3–4 ring s)	0.0 94	Thin, short along filame nt	377–463×27 6–383 µm	~8.5 mm	NZ 1552 m
Calysso zoon minusc ulum	Rhizo ids	Rings→irr egular cells	Hig h (45–90°)	Lob ular /ch alic e	0.6 6	Thick proxi mal bundl e	262–310×19 7–222 µm	~3.1 mm	NZ 3480 m
Metami chelino pedunc ulus paradox us	Rhizo ids	Ringed distal+ba sal; irregular center	Lo w	Tor ped o-s hap ed	0.2 37	Very few, long & fine	~348–384×19 3–201 µm	~11 mm	NZ 1113 m
Buskoz oon vadum	Disc	Regular small poly/hex	Lo w	Glo bul ar →el ong .; ofte n sph	0.6 2–3.1 4 (sit e-v ar.)	None	Hex bounda ries; low papilla	8–18 mm	N Sea/Sk agerrak /Chann el

				erical					
Metalcyonidium elongatum	Rhizoids	Uniserial (very long cells)	Low	Highly elongate	0.170	Few; short & thick	320–649×144–391 µm	~10 mm	NZ 785–1024 m
Metalcyonidium compressum	Rhizoids	Uniserial (short cells)	Low	Capitulum ≈ stalk	~0.97	Few; thick (spindle last cell)	204–745×144–494 µm	~6 mm	NZ 1109–1386 m
Metalcyonidium absurdum	Rhizoids	Uniserial (very long stalk)	Low	Small oval	0.10	Few; thick & long	~606×215 µm (n=1)	~11 mm	NZ 1126 m
Pseudalcyonidium sp. nov. 1	Rhizoids	Single; often twisted	Low	Pear; narrows into stalk	0.32	Massive bristling bundle	74–521×52–372 µm; low papilla	~7 mm	NZ 790–1676 m
Pseudalcyonidium sp. nov. 2	Rhizoids	Single; eel-tail profile	Low	Small emerald-like	0.26	Long spindle	138–206×108–158 µm	~3.1 mm	NZ 1109 m
Pseudascorhiza morum	Disc	Multi-ring (not uniserial)	High	Chalice-like	≥0.66	None	—	—	Japan 180–230 m

NIWA 133688	Rhizoids	2-row zig-zag under head → fibrous	Low	Trapezoid; overhang	0.096	Rhizoid ~1253 µm	≈299×187 µm; pentagonal orifice	~23 mm	NZ (deep) – uncertain
Clavoporid indet. (MNHN-9597)	Disc	Many parallel rows; large cells	High	Large elongated oval	1.14	None	250–643×199–533 µm	~21 mm	Corsica
Clavoporid indet. (MNHN-8729)	Rhizoids?	Rows → muscular strand mid-peduncle	Low	Globular–pear	~1:0.63	Likely rhizoidal	≈248–316 µm	~6.2 mm	Bonifacio, 75 m

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8. Figures of analysed species

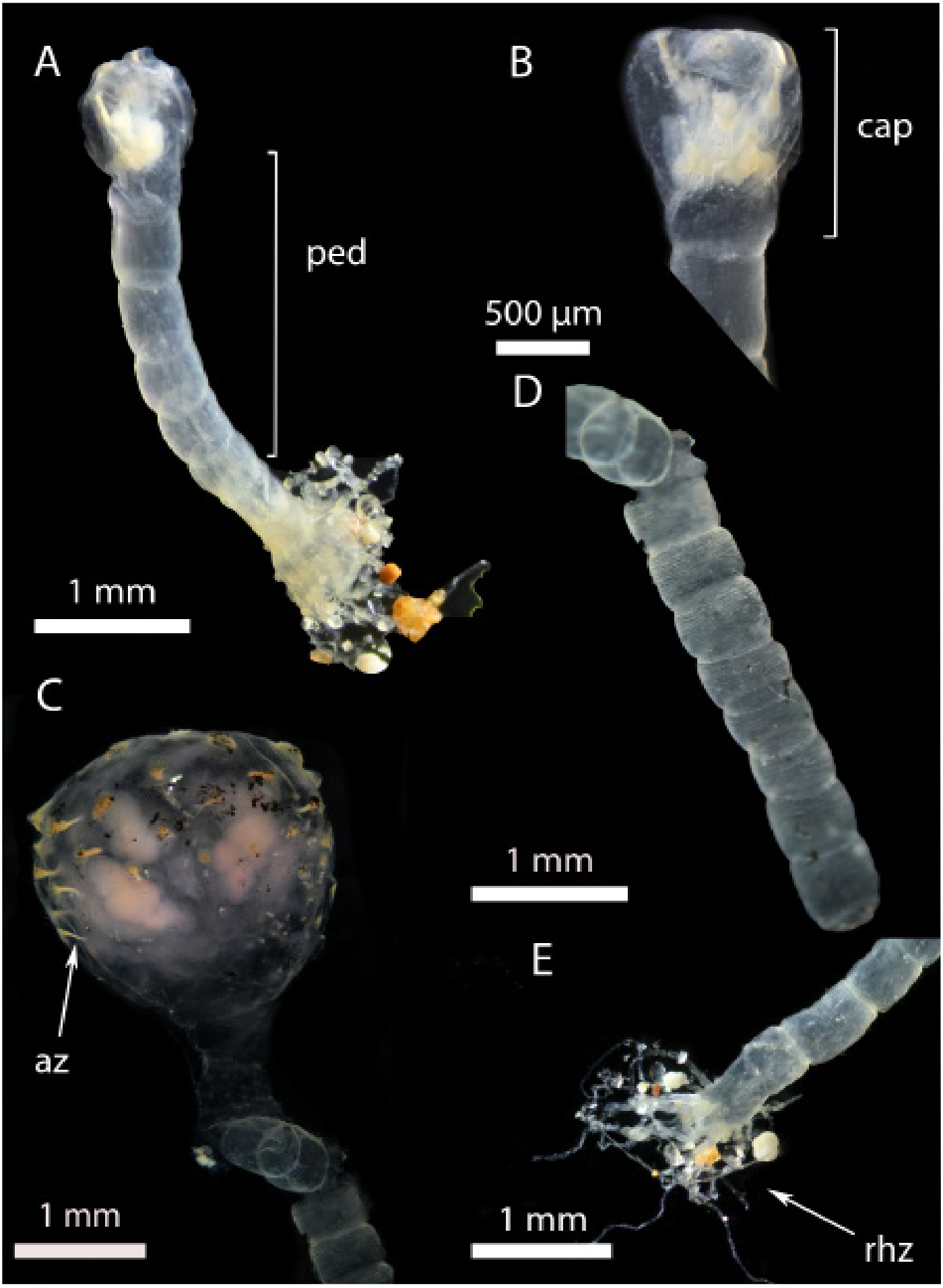

Fig.1 ***Metalcyonidium gautieri d'Hondt,*** **1976**
MNHN-IB-2008-6704 A: Overview of Colony B: Capitulum close up
NHMUK 1984.2.19.1 C: Capitulum and upper peduncle close up D: Peduncle with kenozooids close up
E: Rhizoid structure. Abbrv. cap – capitulum; ped – peduncle; az – autozooid; rhz – rhizioid

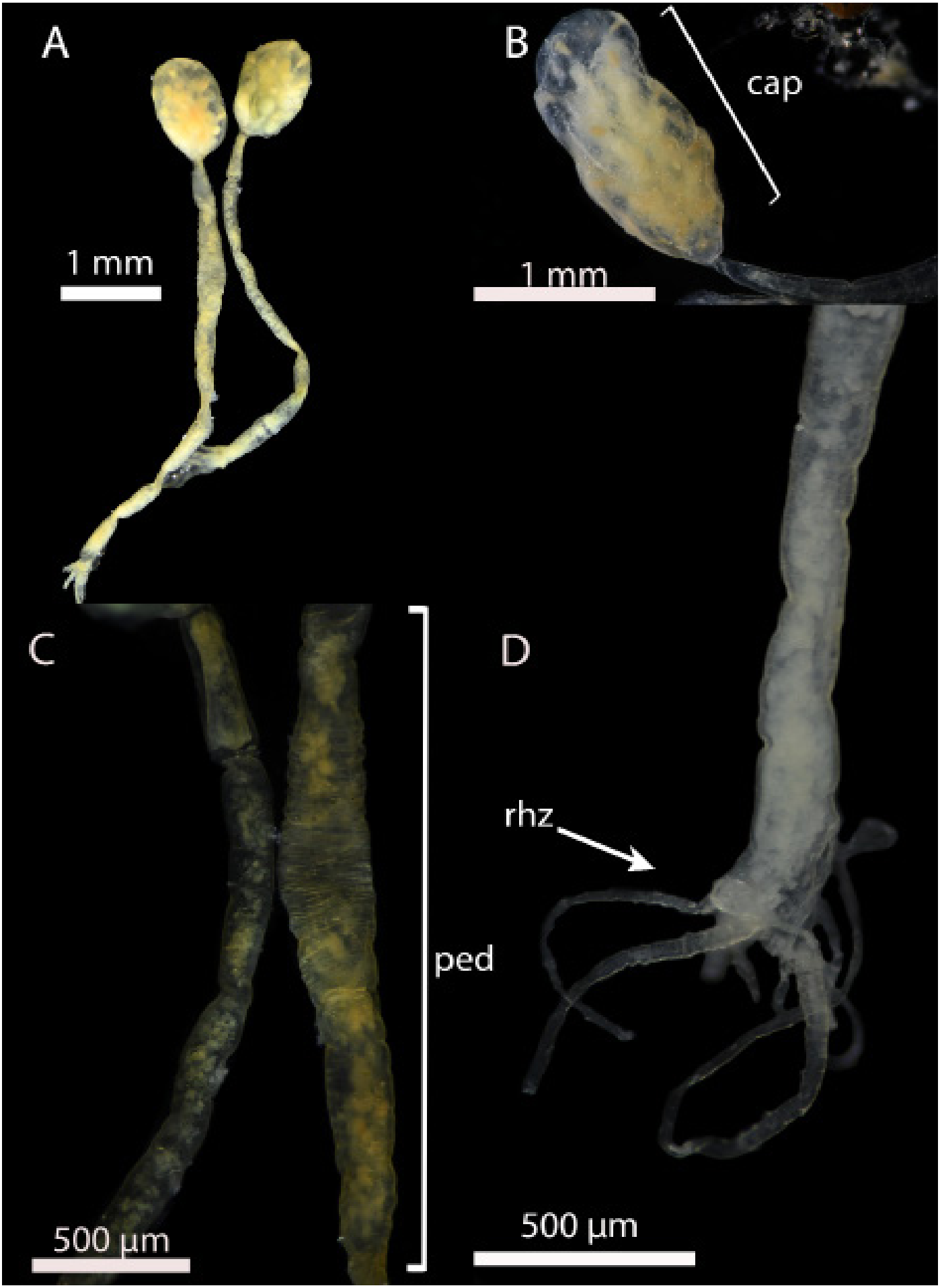

Fig.2 *Pseudalcyonidium bobinae d'Hondt,* 1976
NHMUK 1984.2.19.5 A: Colony overviw C: Peduncle composition
NHMUK 1983.11.22.28 B: Capitulum close up C: Peduncle composition as single kenozooid D: Rhizoid
Abbrv. cap – capitulum; ped – peduncle; rhz – rhizoid

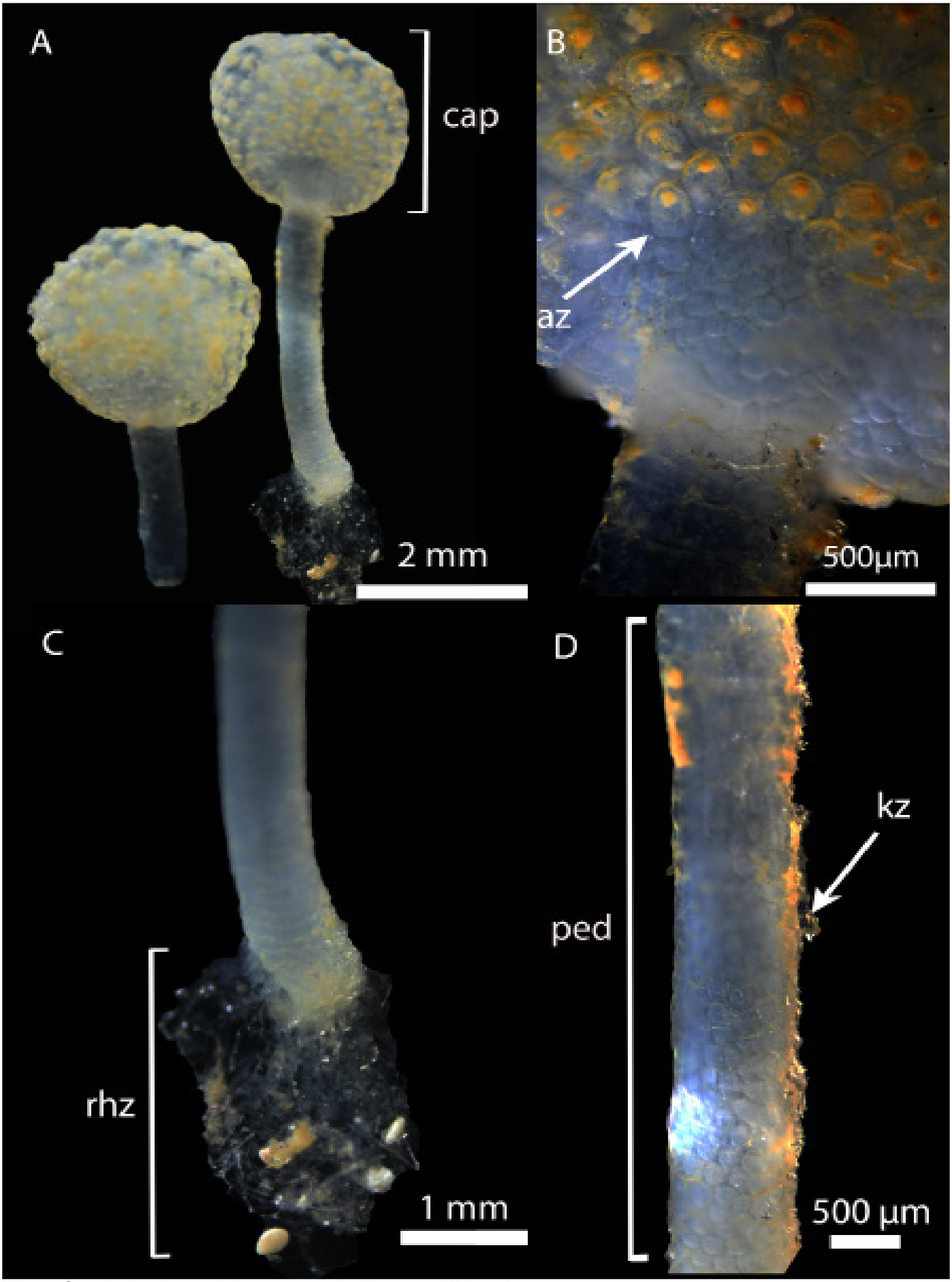

Fig.3 ***Cephaloalcyonidium morchellanum d'Hondt,*** **2006**
MNHN-IB-2008-20246 (holotype), MNHN-IB-2008-20256 (paratype) A: Colony overview B: Close up of lower capitulum to upper stalk with marked autozooide C: Rhizoid and lower penduncle close up D: Peduncle composition of regular multiserial rows kenozooids
Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; rhz – rhizioid

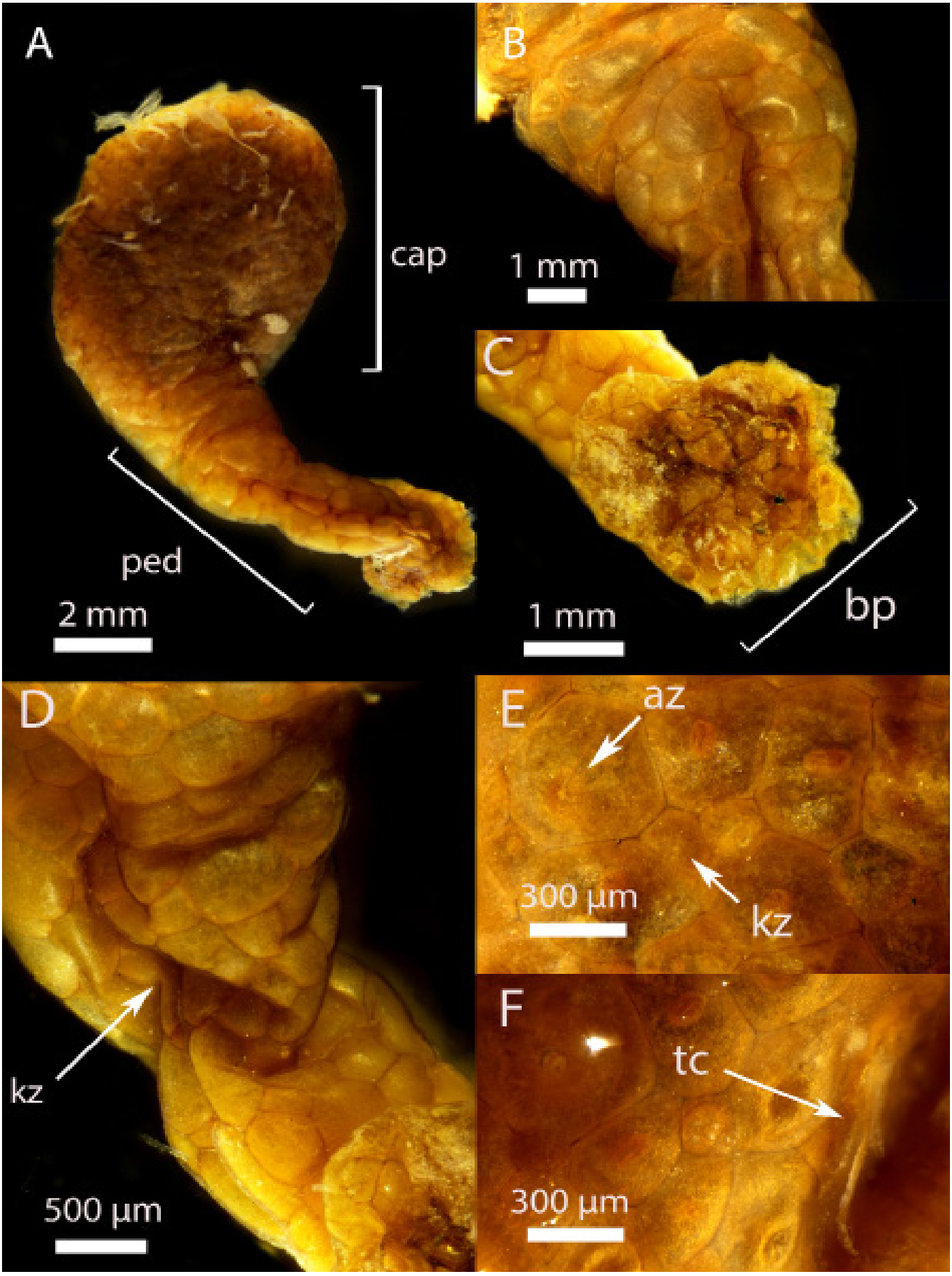

Fig.4 ***Bomburozoon gen. nov. bulbosus sp. nov.***
NIWA 98074 (holotype) A: Overview of Colony B: Transition lower capitulum to upper peduncle C: Baseplate D: Close view of the irregular compasition in peduncle kenozooids E-F: Detailed view of autozooids and kenozooids of the capitulum
Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; bp – baseplate; tc – tentacle

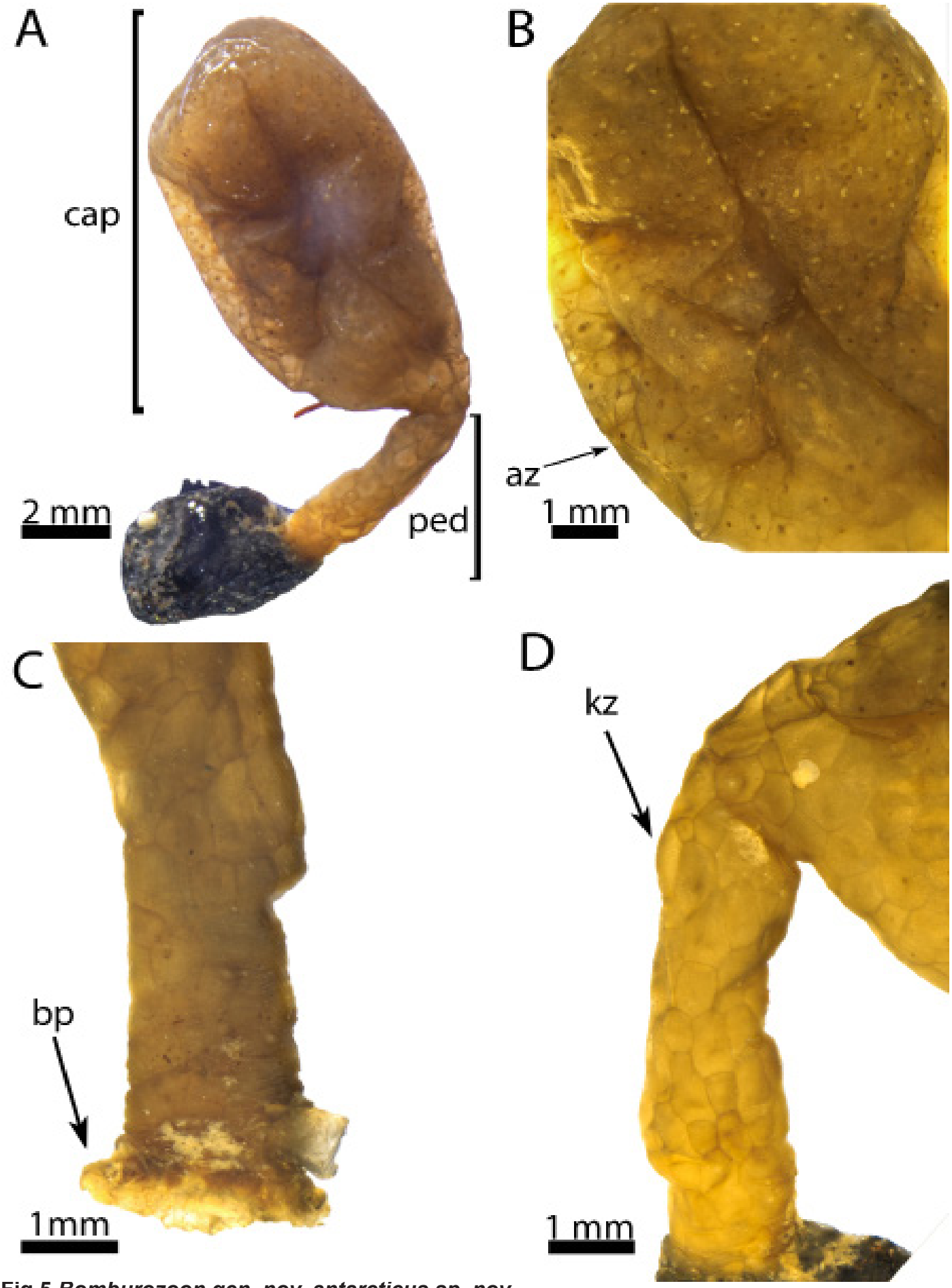

Fig.5 ***Bomburozoon gen. nov. antarcticus sp. nov.***
MNHN IB-2009-165 (syntypes) A: Colony overview attached to a small rock pebble B: Close view of upper capitulum with marked autozooid C: Lower peduncle and close up of baseplate D: Transition of lower capitulum to the peduncle close up with marked big kenozooid.
Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; bp – baseplate

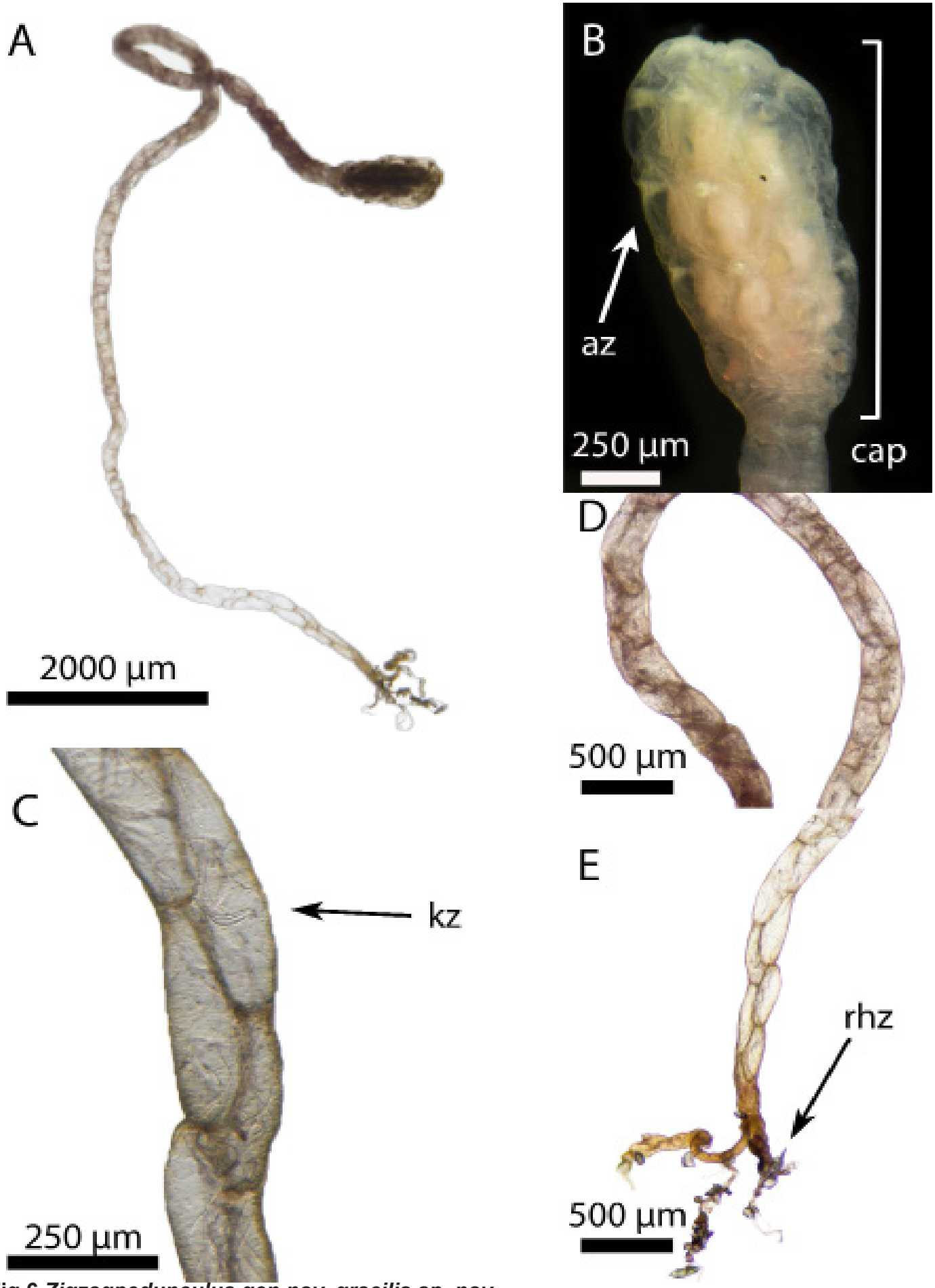

Fig.6 ***Zigzagpedunculus gen nov. gracilis sp. nov.***
NIWA 133682 A: Colony overview B: Close up of capitulum with mareked autozooid C: Peduncle composition of alternating kenozooids „zigzag“ D-E Lower Peduncle with rhizoid close up
Abbrv. cap – capitulum; kz – kenozooid; az – autozooid; rhz – rhizioid

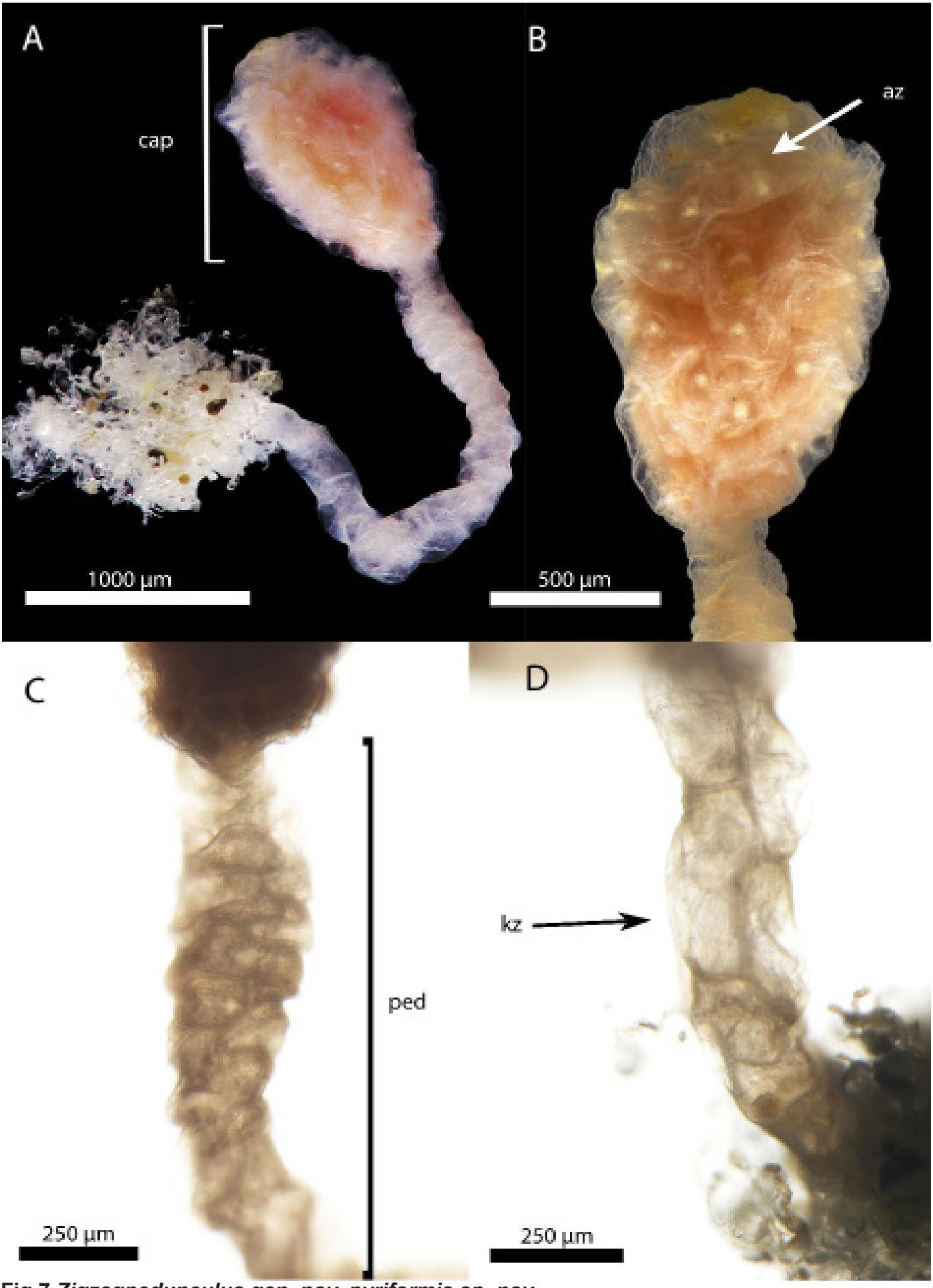

Fig.7 ***Zigzagpedunculus gen. nov. pyriformis sp. nov.***
NIWA 133622 (holotype 1) A: Colony overview B: Close up of capitulum with mareked autozooid C: Transition between lower capitulum and upper peduncle D Lower Peduncle and rhizoid close up with marked kenozooid. Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; rhz – rhizioid

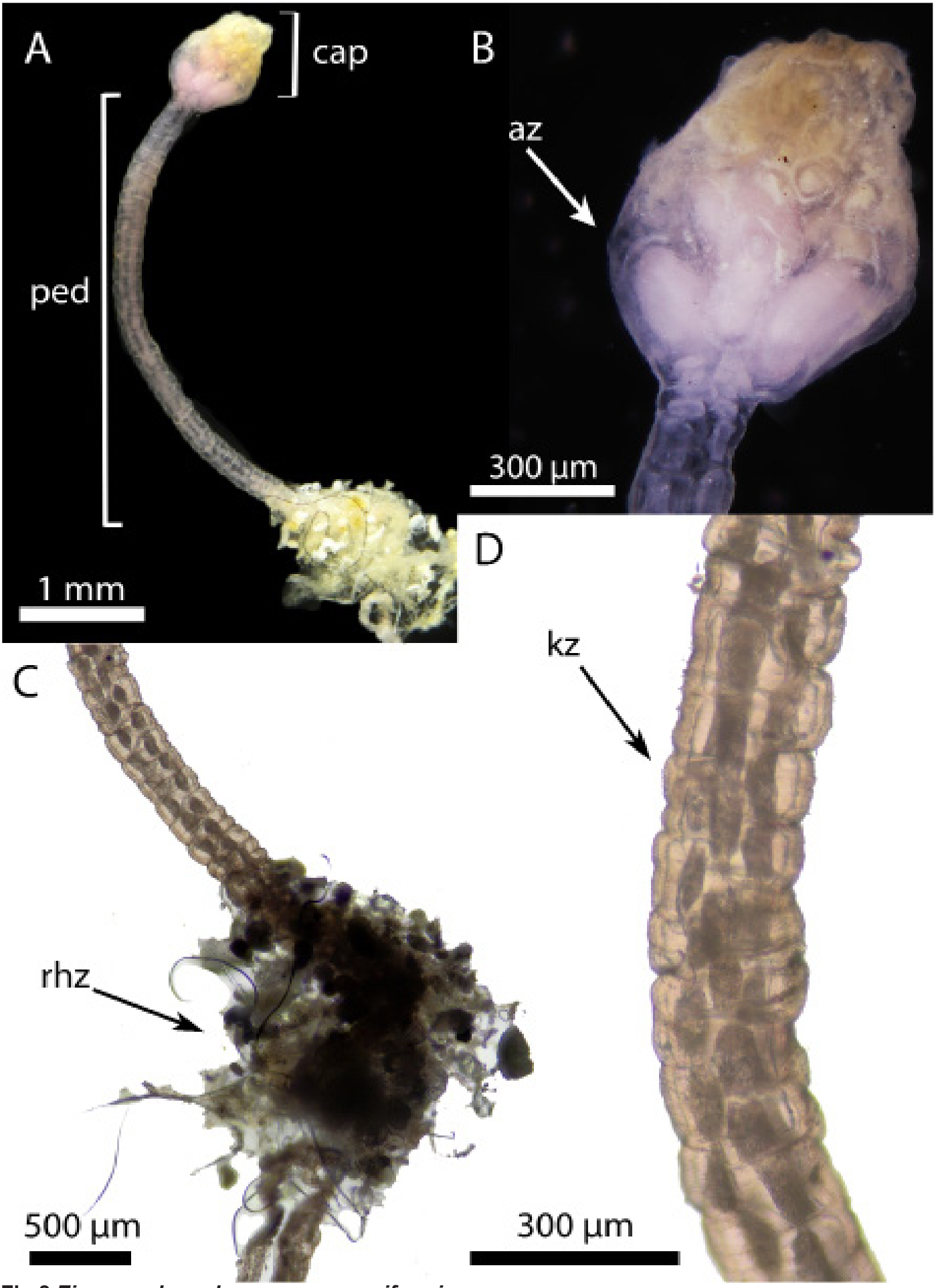

Fig.8 ***Zigzagpedunculus gen. nov. pyriformis sp. nov.***
NIWA 133654 (paratype 3) A: Colony overview B: Close up of capitulum with mareked autozooid C: Lower Peduncle and rhizoid close up marked with „rhz“ D: Alternating bipard kenozooidal peduncle composition
Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; rhz – rhizioid

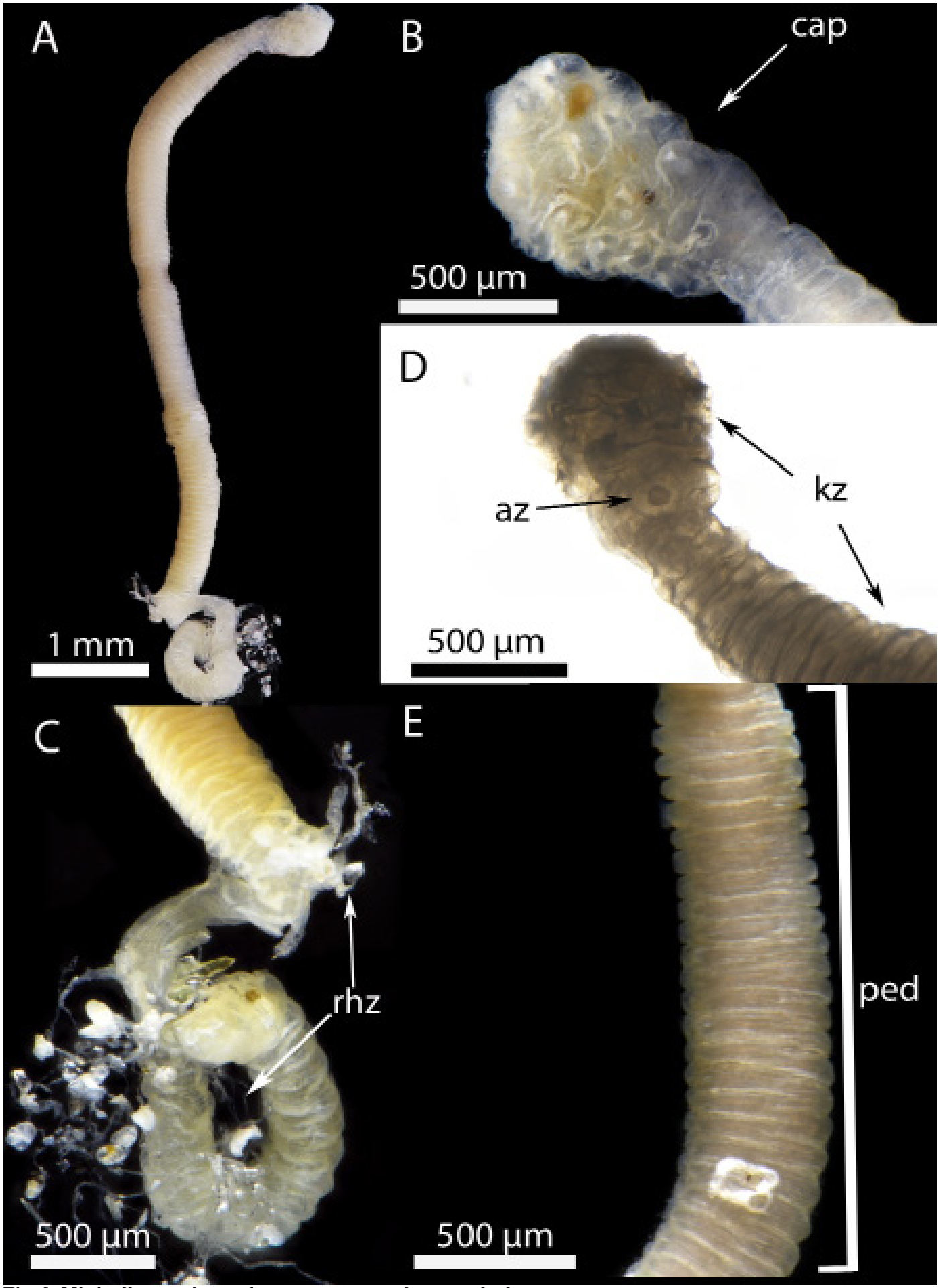

Fig.9 ***Michelinopedunculus gen. nov. microcephalus sp. nov.***
NIWA 133660 (holotype) A: Colony overview B & D Close up of capitulum with mareked autozooid and kenozooids of the capitulum and peduncle C: Rhizoid with multi-kenozooid origin E: kenozooid composition of peduncle. Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; rhz – rhizioid

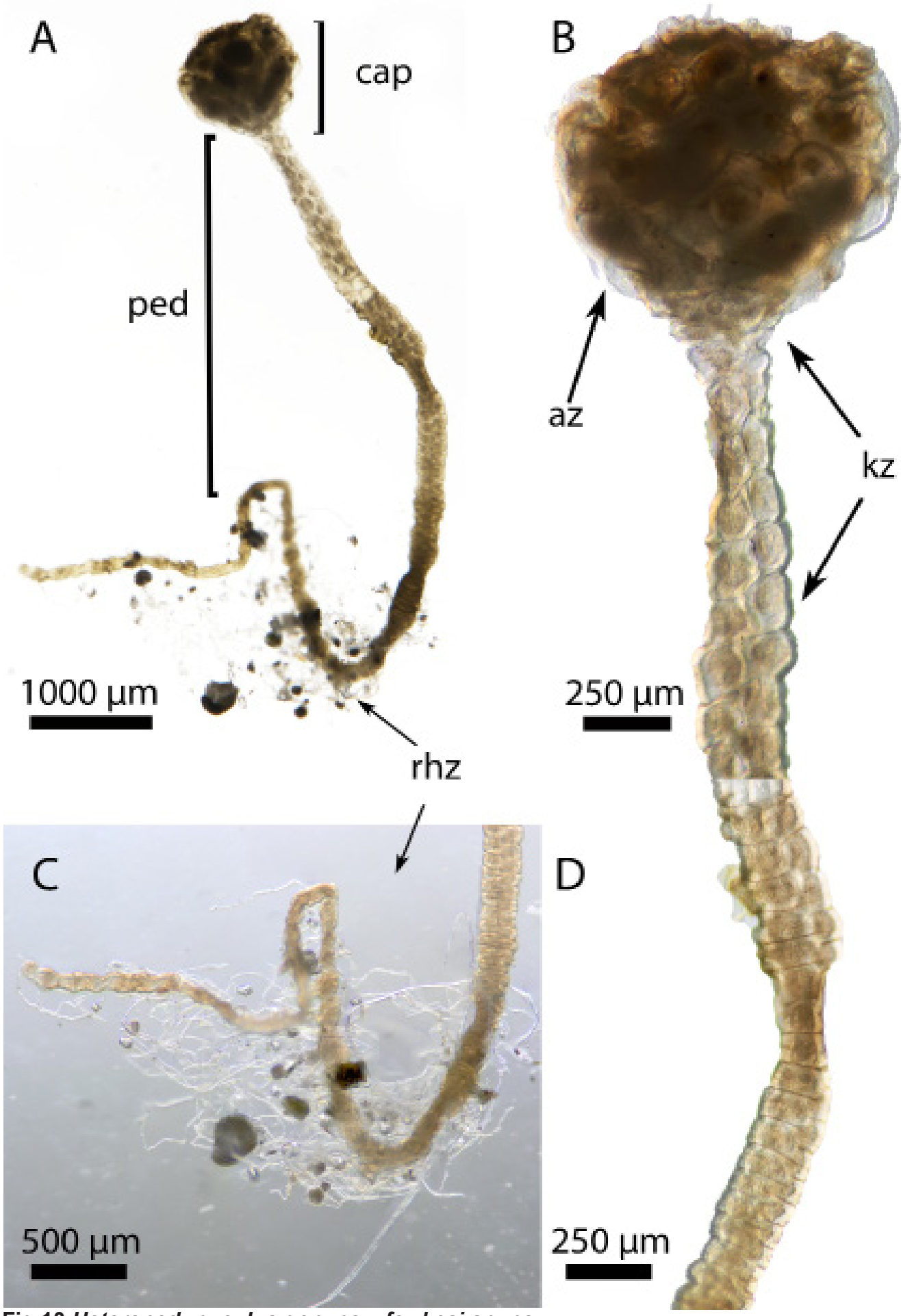

Fig.10 ***Heteropedunuculus gen. nov. fewkesi sp. nov***

NIWA 133642 (holotype) A: Colony overview B&D Close up of capitulum and upper peduncle with mareked autozooid and kenozooids C: Origin of rhizoid in multiple kenozooids

Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; rhz – rhizioid

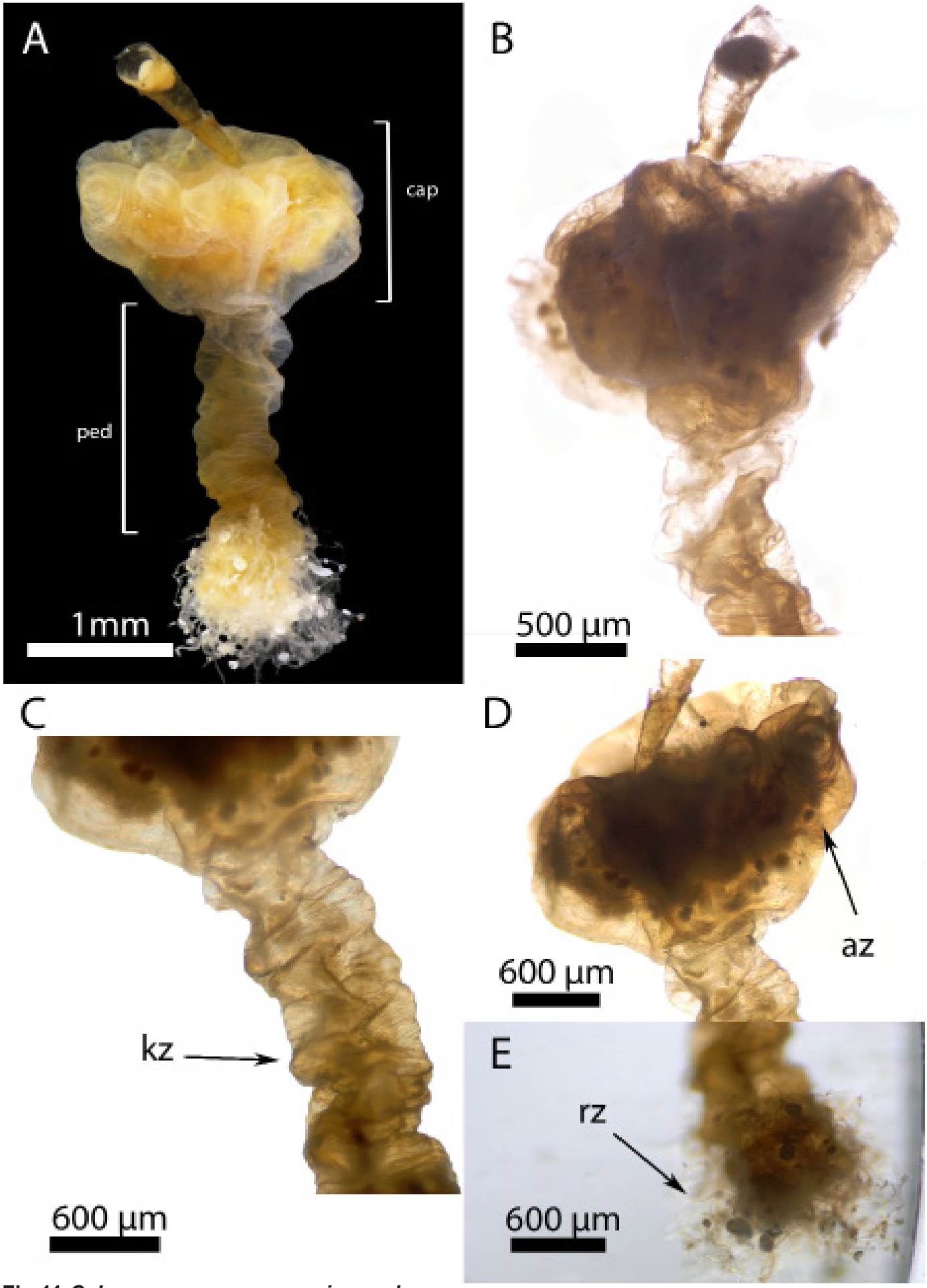

Fig.11 ***Calyssozoon gen. nov. minusculum sp. nov.***
NIWA 133809 (holotype) A: Colony overview B Close up of capitulum C: Transition between lower capitulum and upper peduncle with marked kenozooid D Sideview of capitulum close up with marked autozooid E: Rhizoid. Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; rhz – rhizioid

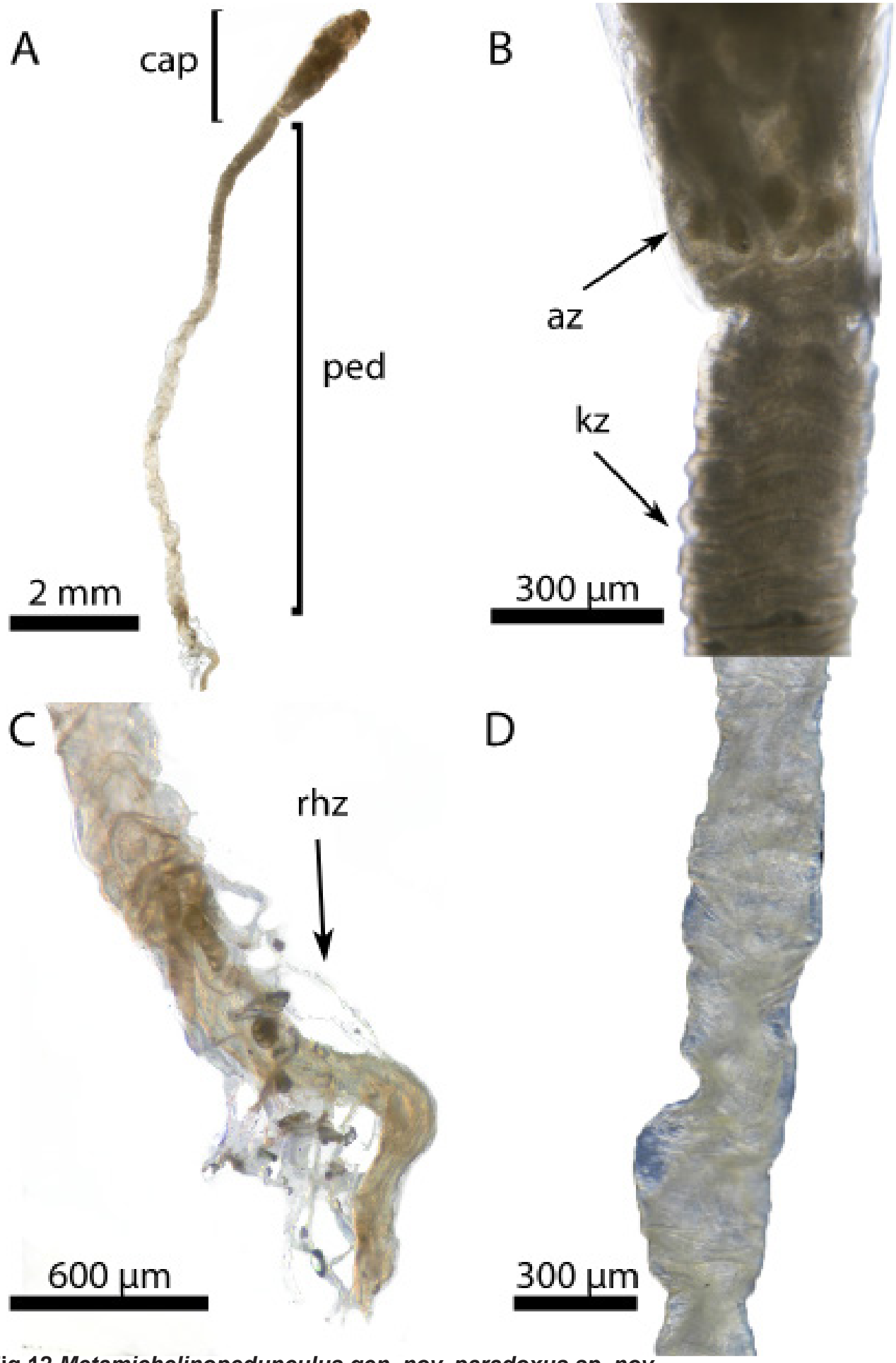

Fig.12 ***Metamichelinopedunculus gen. nov. paradoxus sp. nov.***
NIWA 133629 (holotype) A: Colony overview B Close up of capitulum to peduncle transition with marked kenozooids and autozooids C: Rhizoid multikenozooidal in origin D: komposition of the lower peduncle
Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; rhz – rhizioid

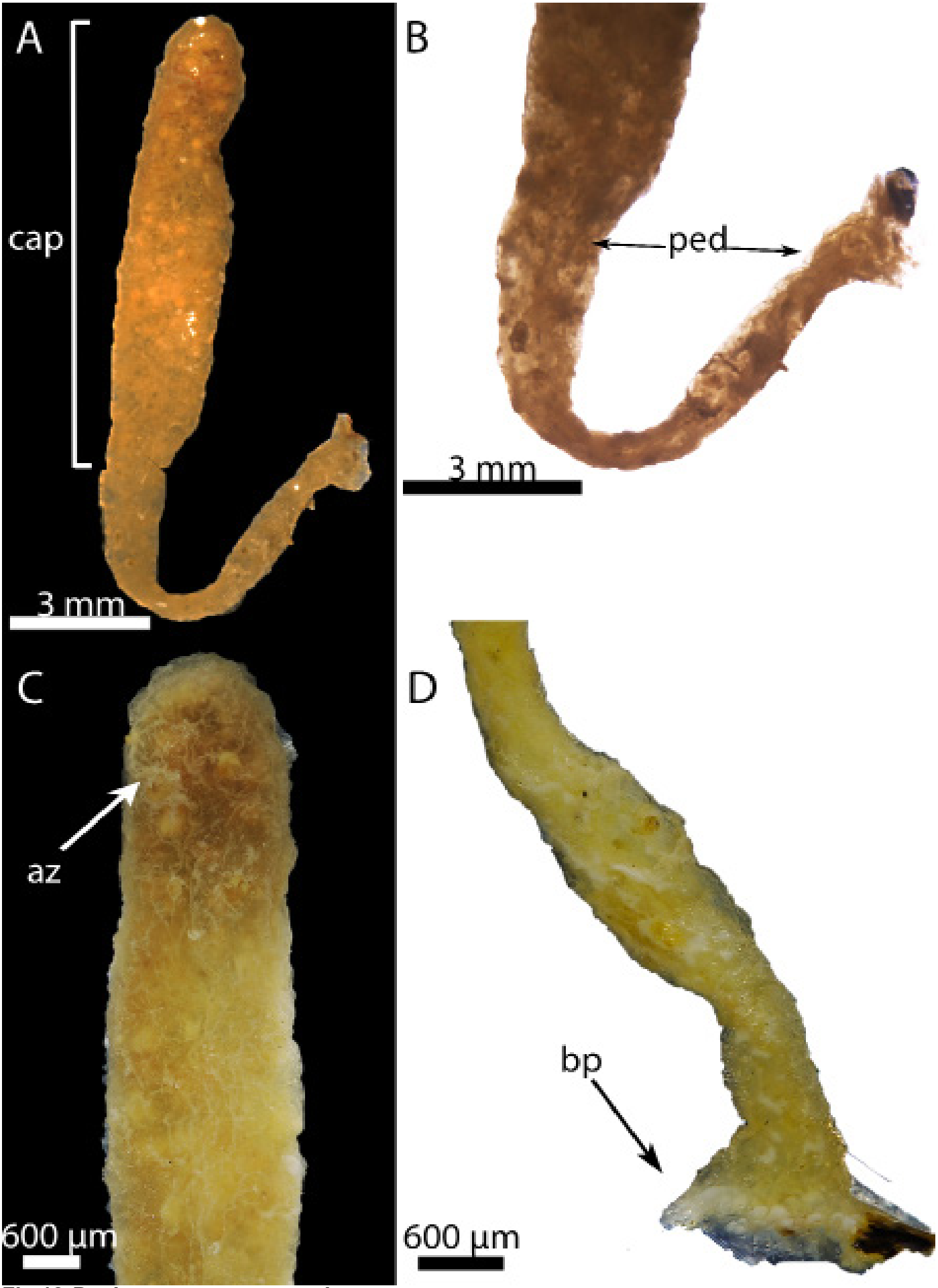

Fig.13 ***Buskozoon gen. nov. vadum sp. nov.***

KB09 (ind.3) A: Colony overview B Close up of capitulum to peduncle transition C: Capitulum close up with marked autozooid D: Close up of lower peduncle and baseplate

Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; rhz – rhizioid

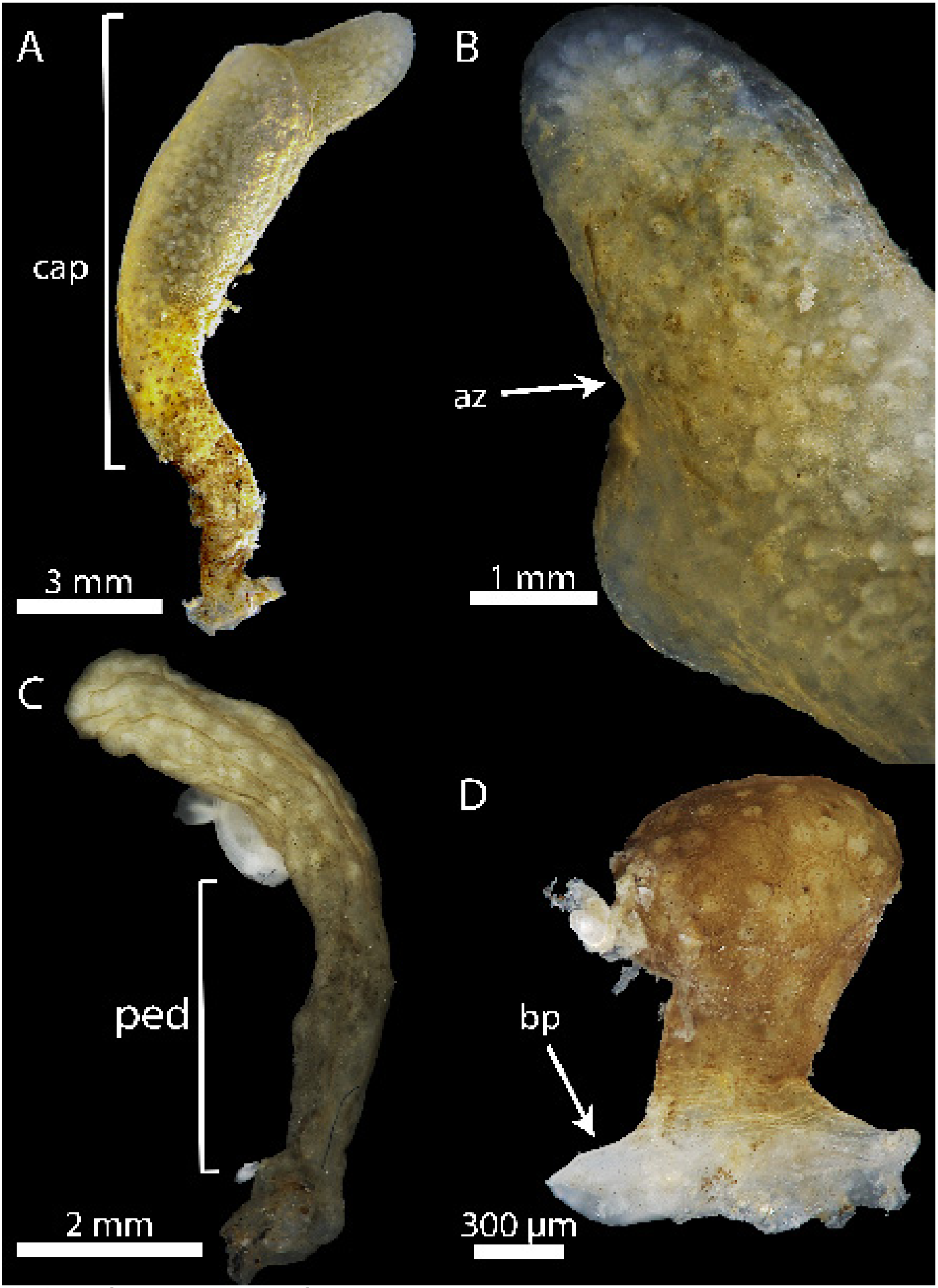

Fig.14 ***Buskozoon gen. nov. vadum sp. nov.***

KB24 38F A: Colony overview B Close up of capitulum to peduncle transition D: Colony overview with marked baseplate 24A C: Colony overview

Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; bp – baseplate

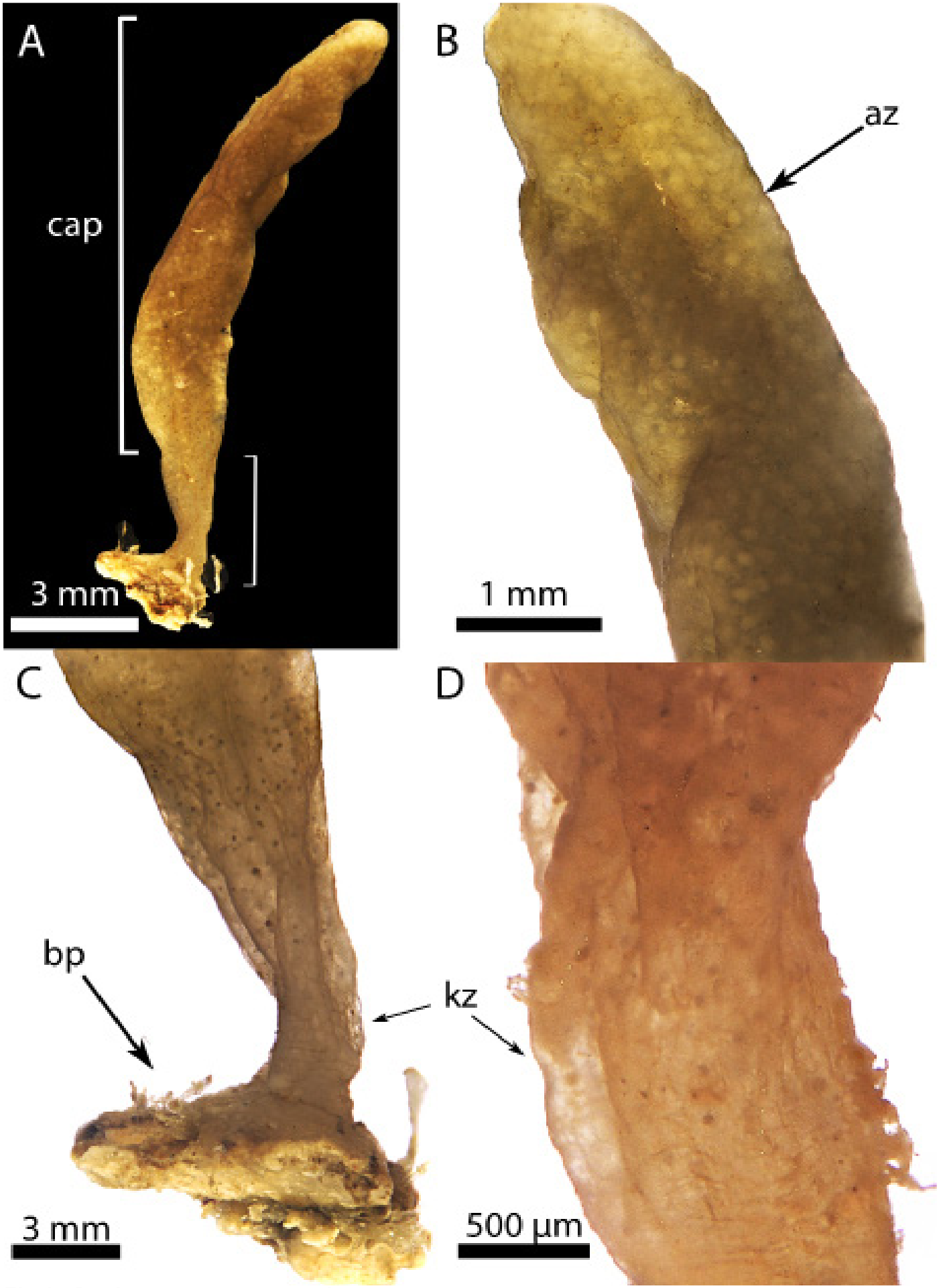

Fig.15 ***Buskozoon gen. nov. vadum sp. nov.***
RC25 (ind.3) A: Colony overview B Close up of capitulum with marked autozooid C: Lower peduncle and baseplate D: Close up of kenozooid composition of the pedunce
Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; bp – baseplate

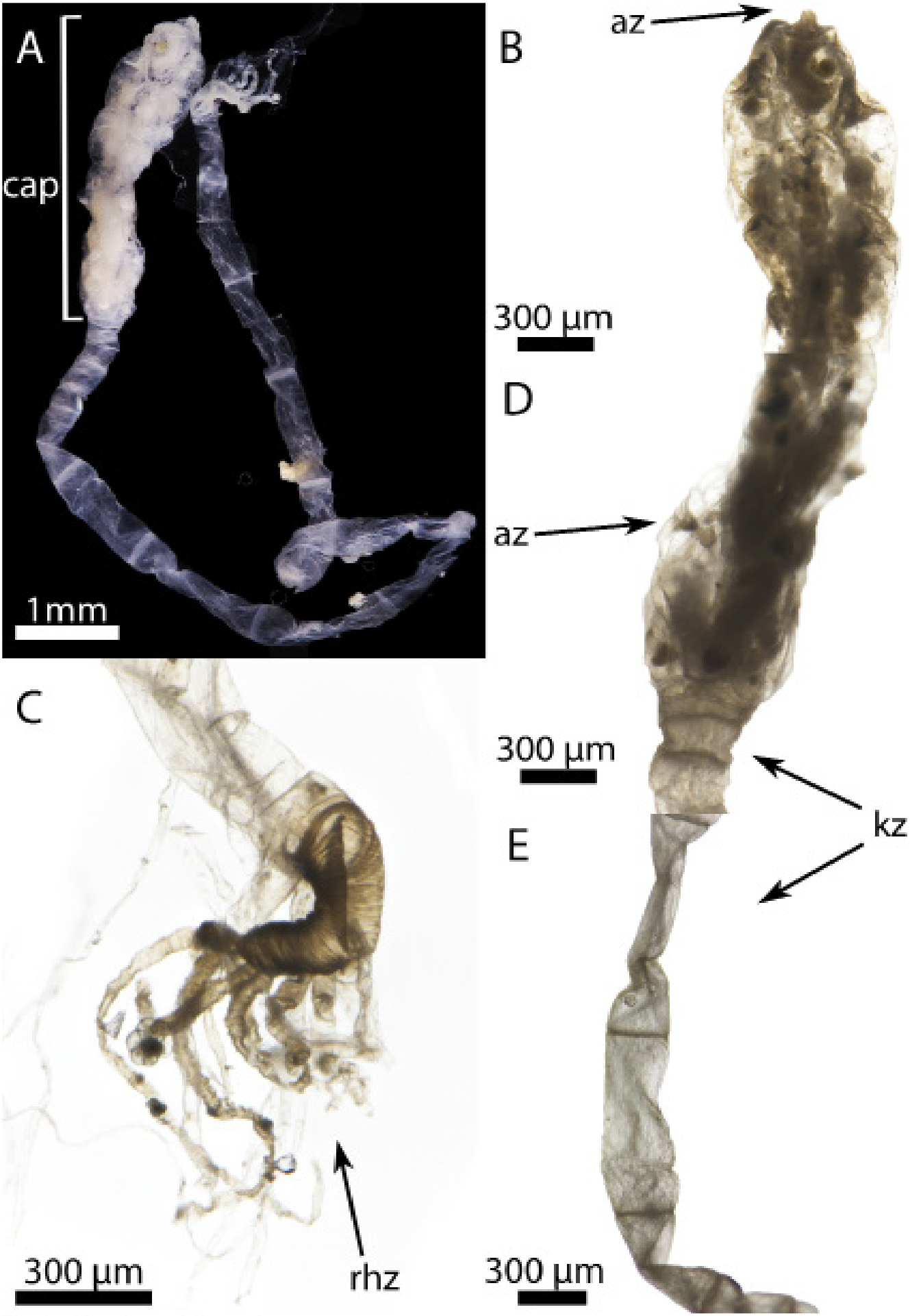

Fig.16 ***Metalcyonidium elongatum sp. nov.***
NIWA 133677 A: Colony overview B: Close up of upper capitulum with marked autozooid C: Close up of rhizoid D: Close up of lower capitulum and upper peduncle D: Close up of uniserial peduncle kenozooids Abbrv. cap – capitulum; kz – kenozooid; az – autozooid; rhz – rhizioid

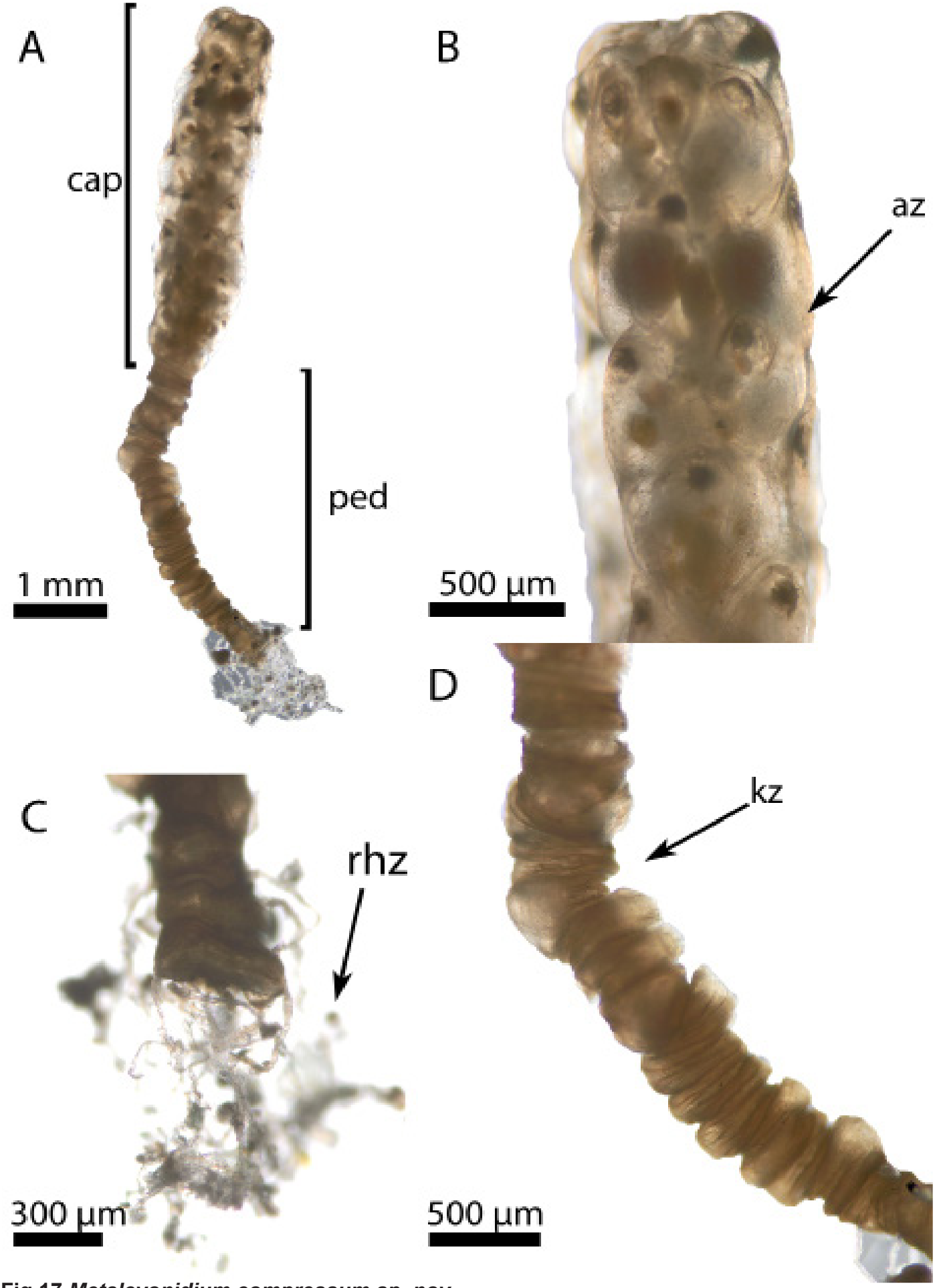

Fig.17 ***Metalcyonidium compressum sp. nov.***
NIWA 133658 A: Colony overview B: Close up of upper capitulum with marked autozooid C: Close up of rhizoid D: Close up of peduncle
Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; rhz – rhizioid

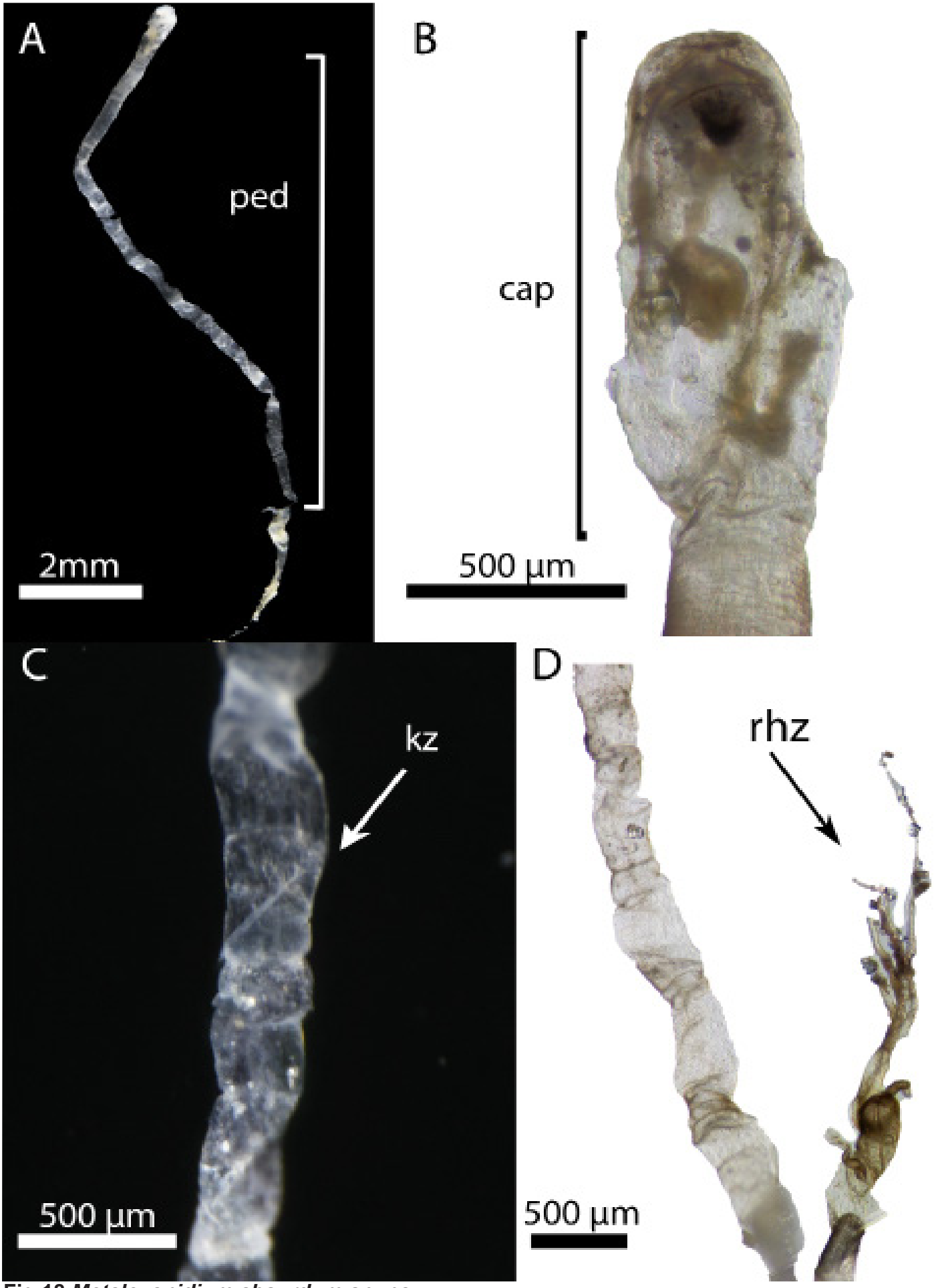

Fig.18 ***Metalcyonidium absurdum sp. nov.***
NIWA 133650 (holotype) A: Colony overview B: Close up of upper capitulum C: Composition of uniserial peduncle kenozooids close up D: Close up of rhizoid
Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; rhz – rhizioid

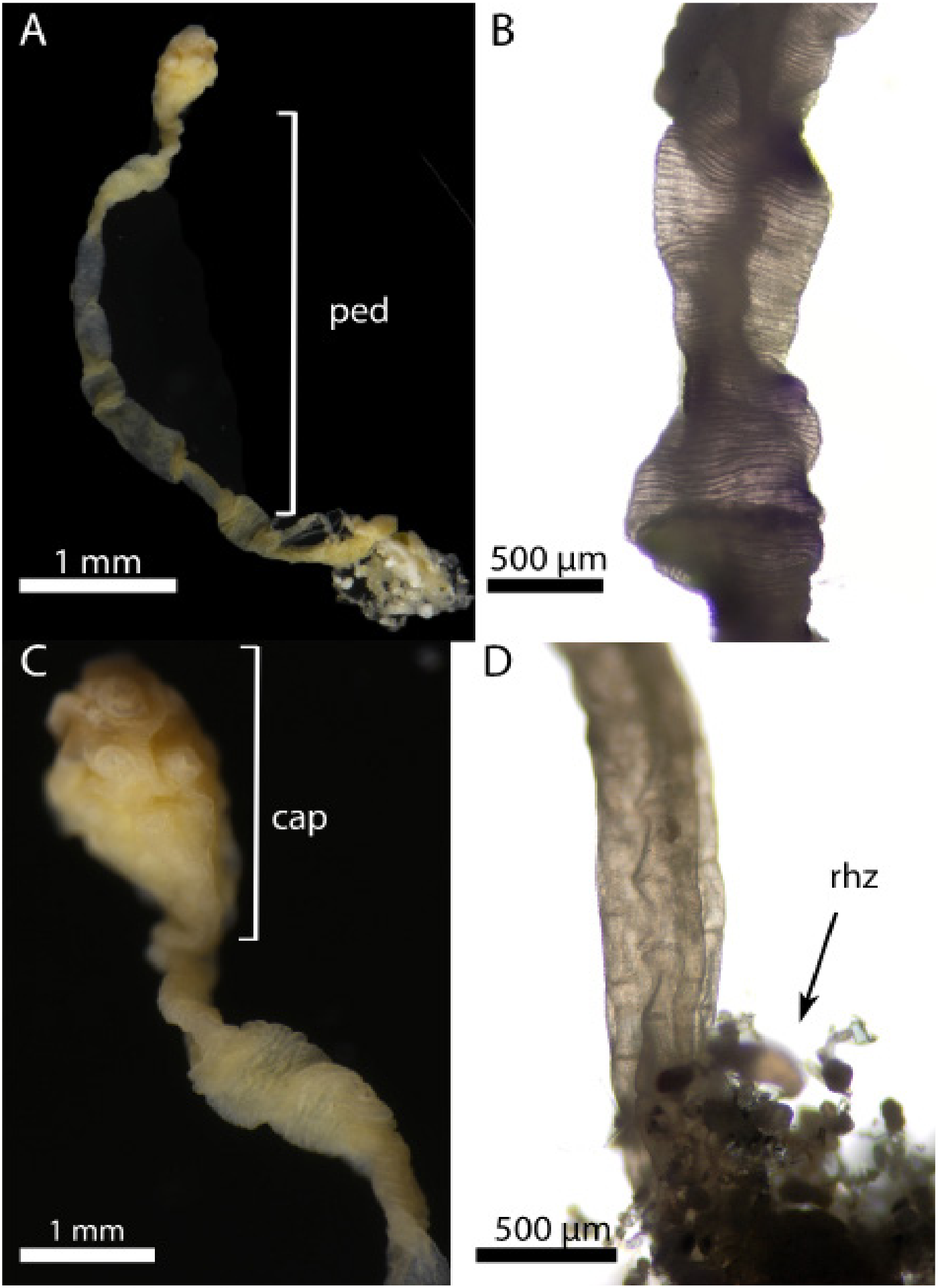

Fig.19 ***Pseudalcyonidium sp. nov. 1***

NIWNIWA 133643 (holotype) A: Colony overview with marked peduncle lenght B: Close up of upper peduncle C: Capitulum close up D: Close up of rhizoid and lower peduncle

Abbrv. cap – capitulum; ped – peduncle; rhz – rhizioid

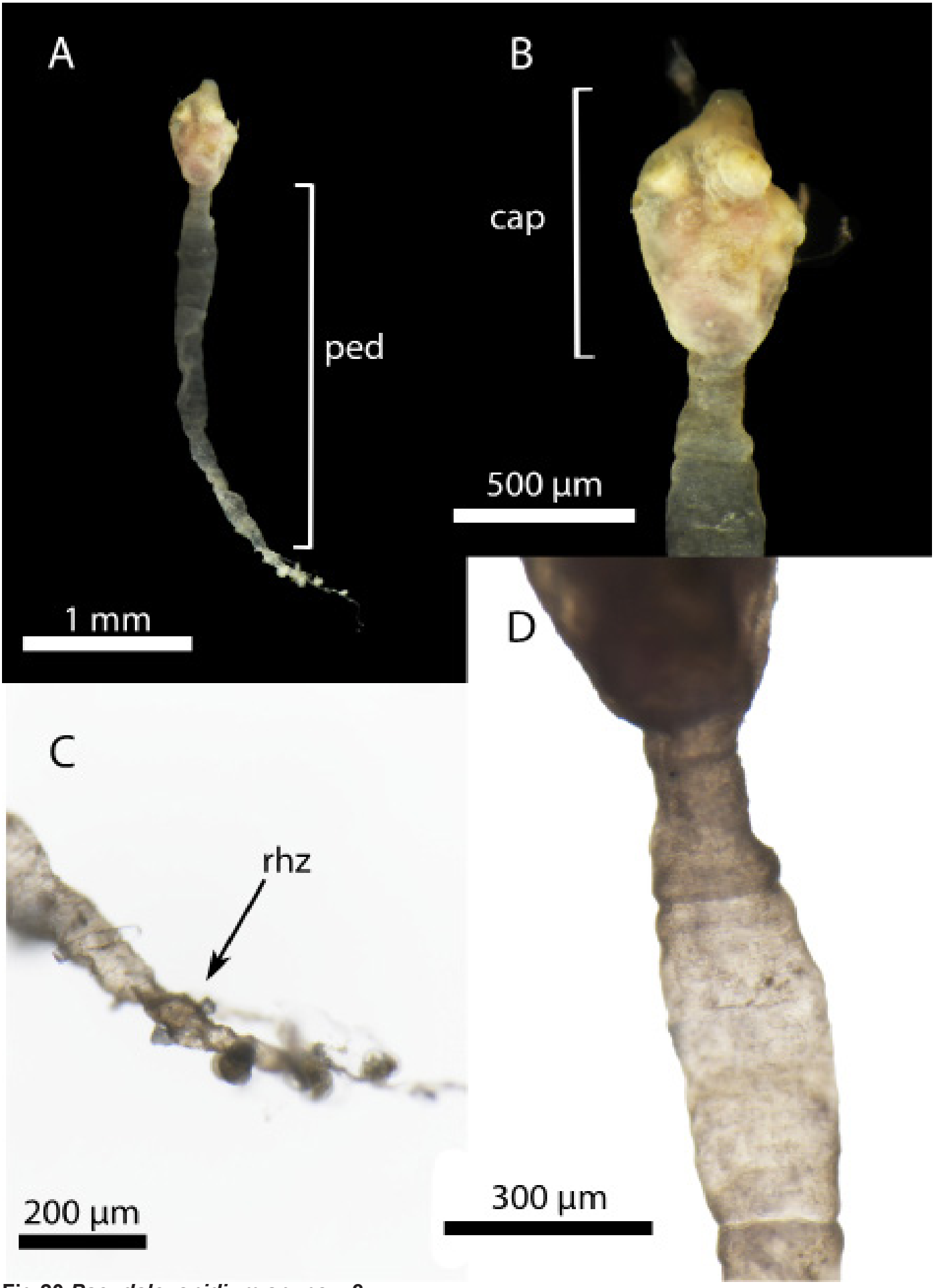

Fig.20 ***Pseudalcyonidium sp. nov. 2***
NIWA 133666 (holotype) A: Colony overview with marked peduncle lenght B: Close up of capitulum C: Rhizoid close up D: Close up of transition between lower capitulum and upper peduncle
Abbrv. cap – capitulum; ped – peduncle; rhz – rhizioid

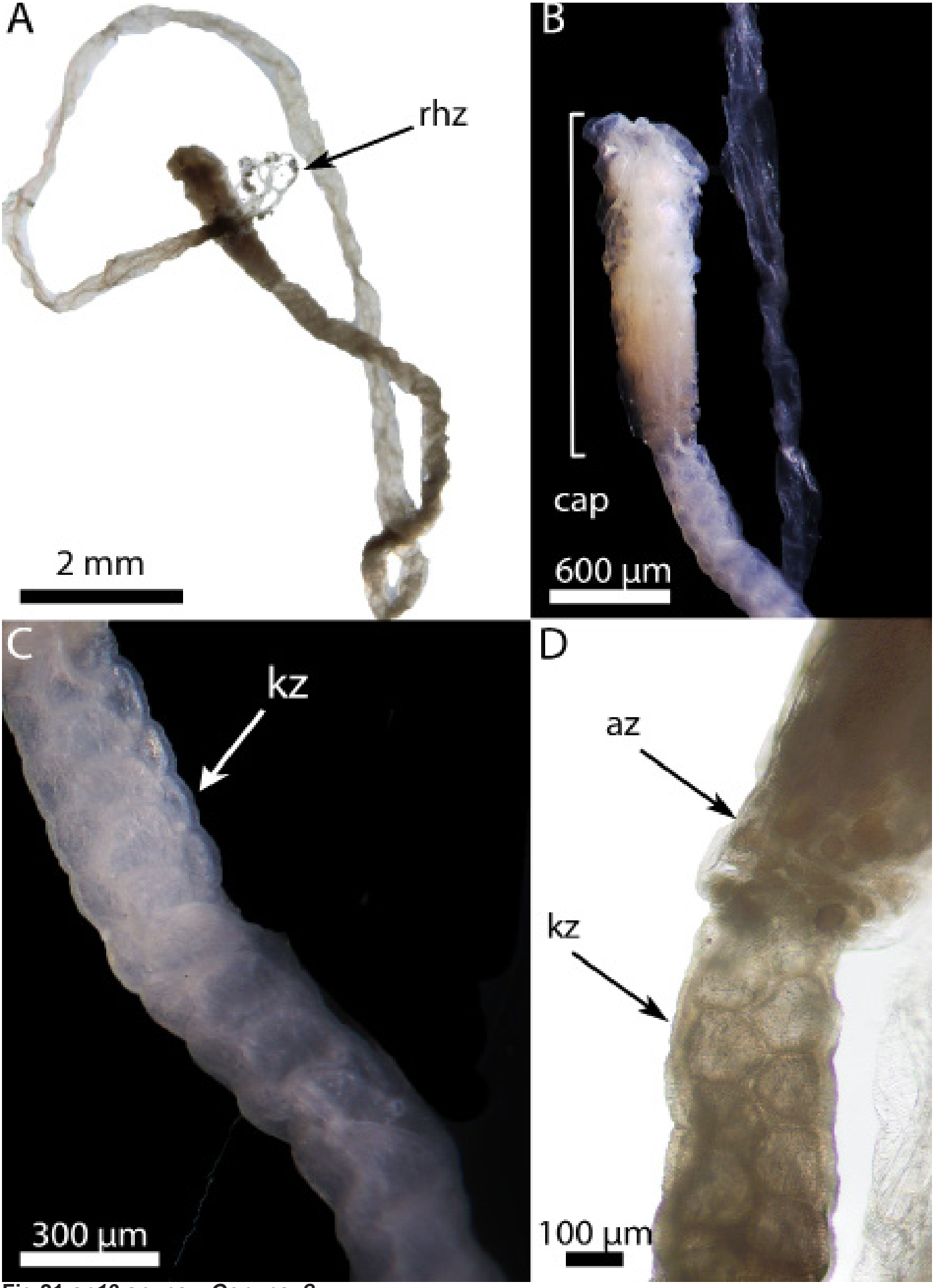

Fig.21 ***sp13 sp. nov. Gen. nov?***

NIWA 133688 (individuum nr. 5) A: Colony overview with marked rhizoid B: Close up of capitulum C: Close view of kenozooid komposition in peduncle D: Close up of transition between lower capitulum and upper peduncle. Abbrv. cap – capitulum; kz – kenozooid; az – autozooid; rhz – rhizioid

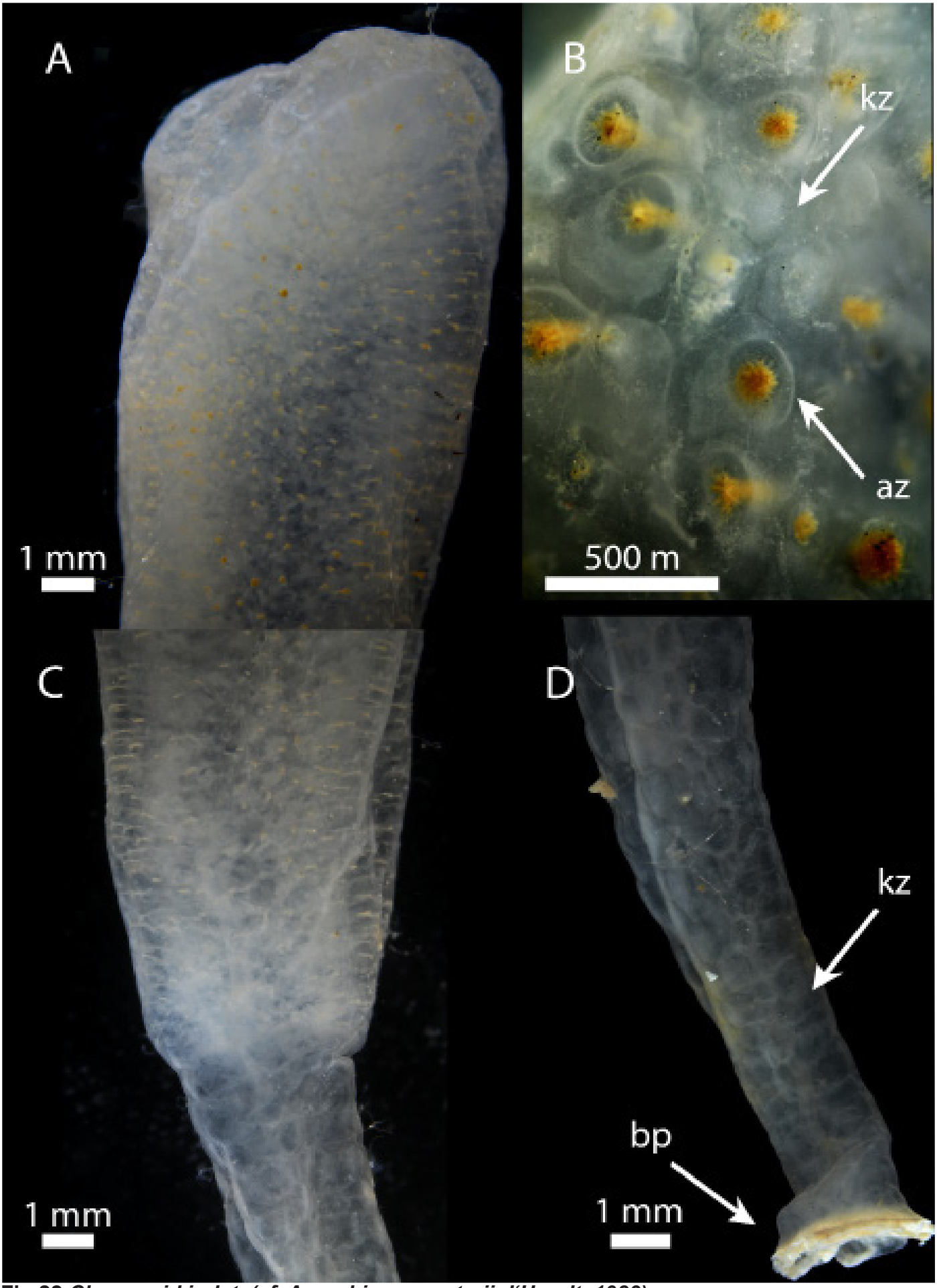

Fig.22 ***Clavoporid indet. (cf. Ascorhiza mawatarii d'Hondt, 1983)***
MNHN-IB-2008-9597A: Upper part of capitulum B: Detail view of kenozooids and autozooids in the capaitulum C: Lower part of capitulum with transition to upper peduncle D: Lower part of peduncle with baseplate
Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; bp – baseplate

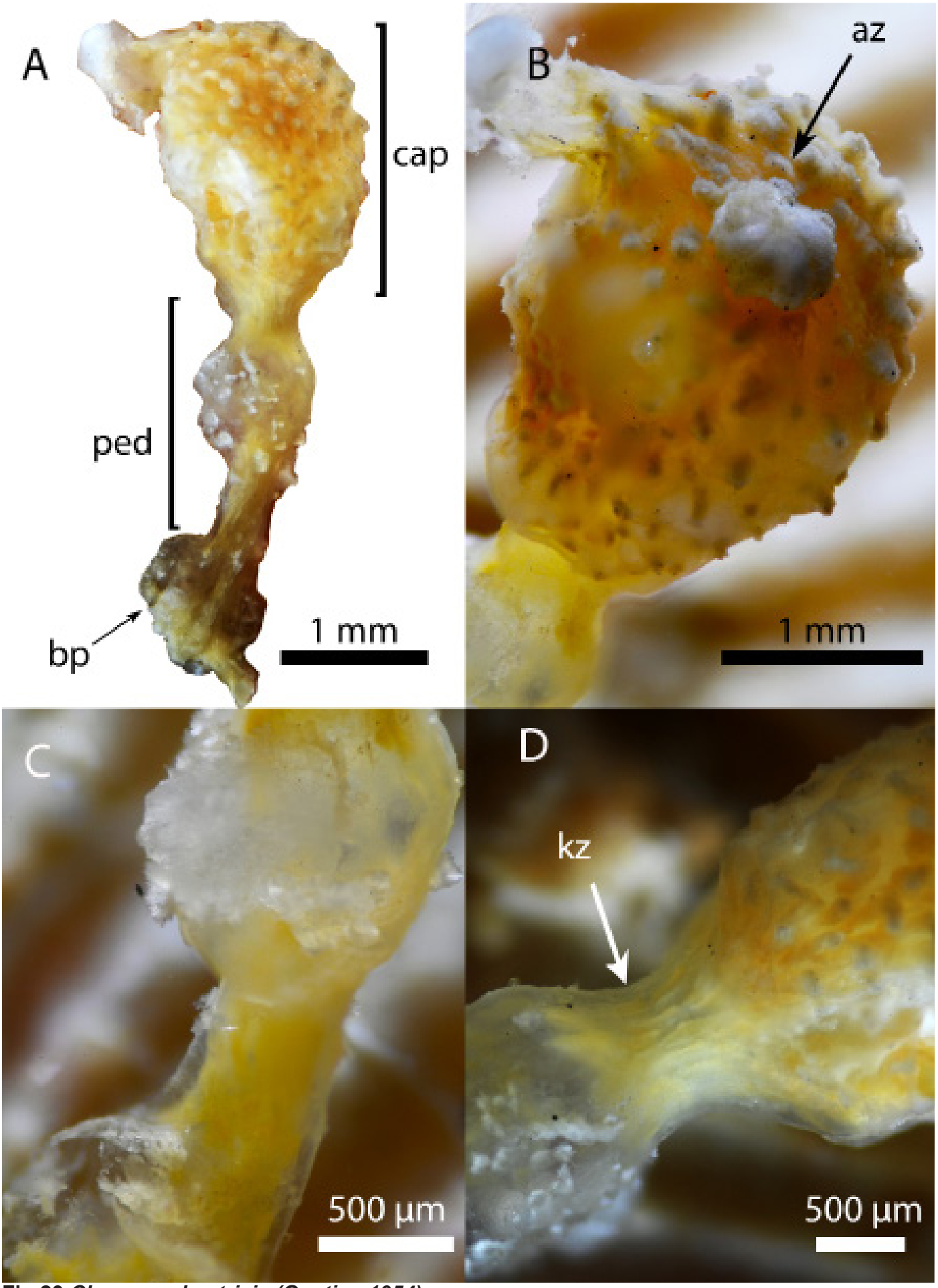

Fig.23 ***Clavopora hystricis (Gautier, 1954)***
MNHN-IB-2008-8729 A: Colony overview B: Detail view of the capaitulum
C: Lower part of the peduncle D: Transition between lower capitulum and upper peduncle Abbrv. cap – capitulum; ped – peduncle; kz – kenozooid; az – autozooid; bp – baseplate

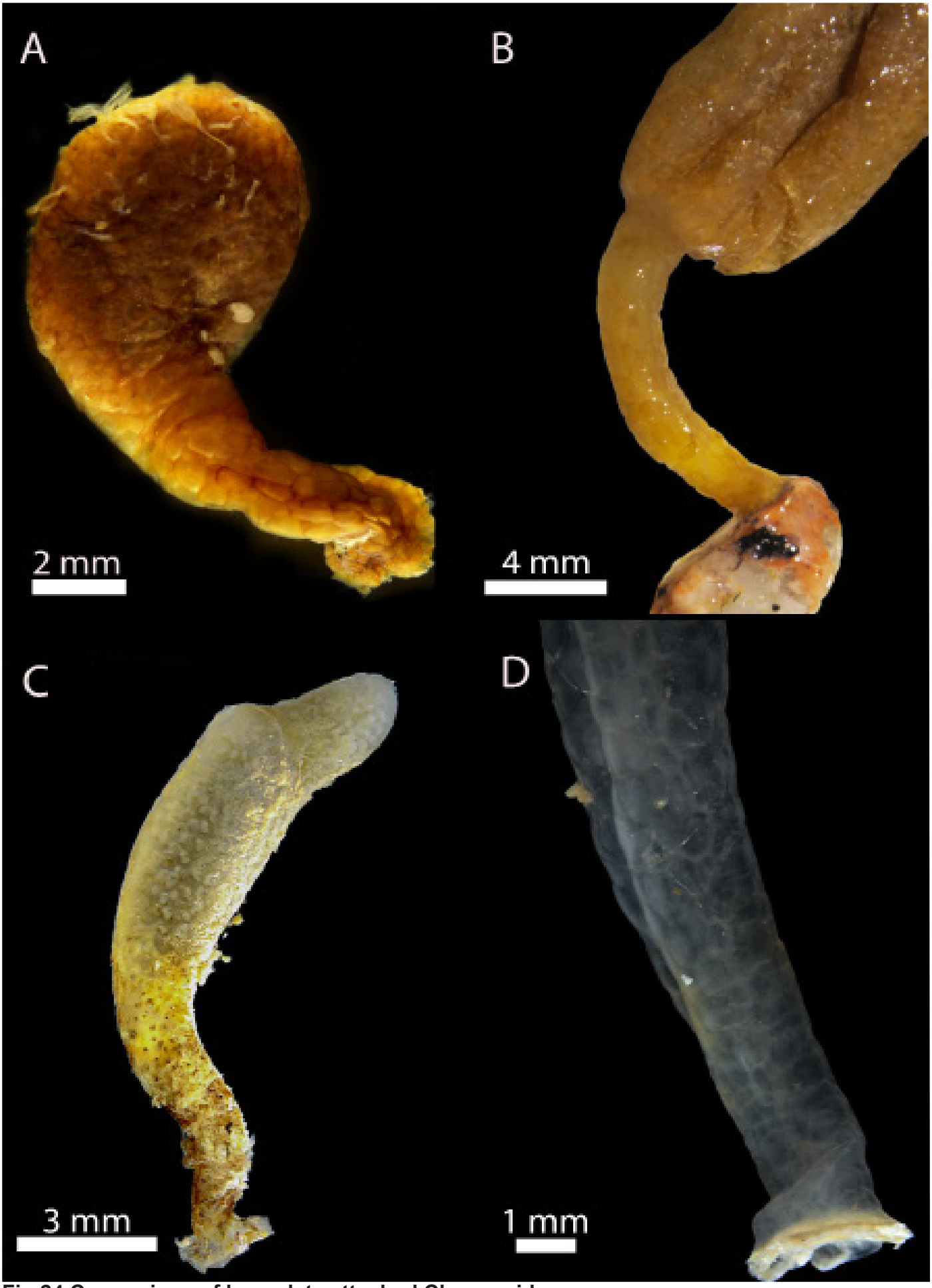

Fig.24 Comparison of baseplate attached Clavoporidae
A: Colony overview of *Bomburozoon. bulbosus* B: Colony overview of *Bomburozoon. antarcticus* C: Colony overview of *Buskozoon vadum* D: Peduncle composition and baseplate of *Clavoporid indet.*

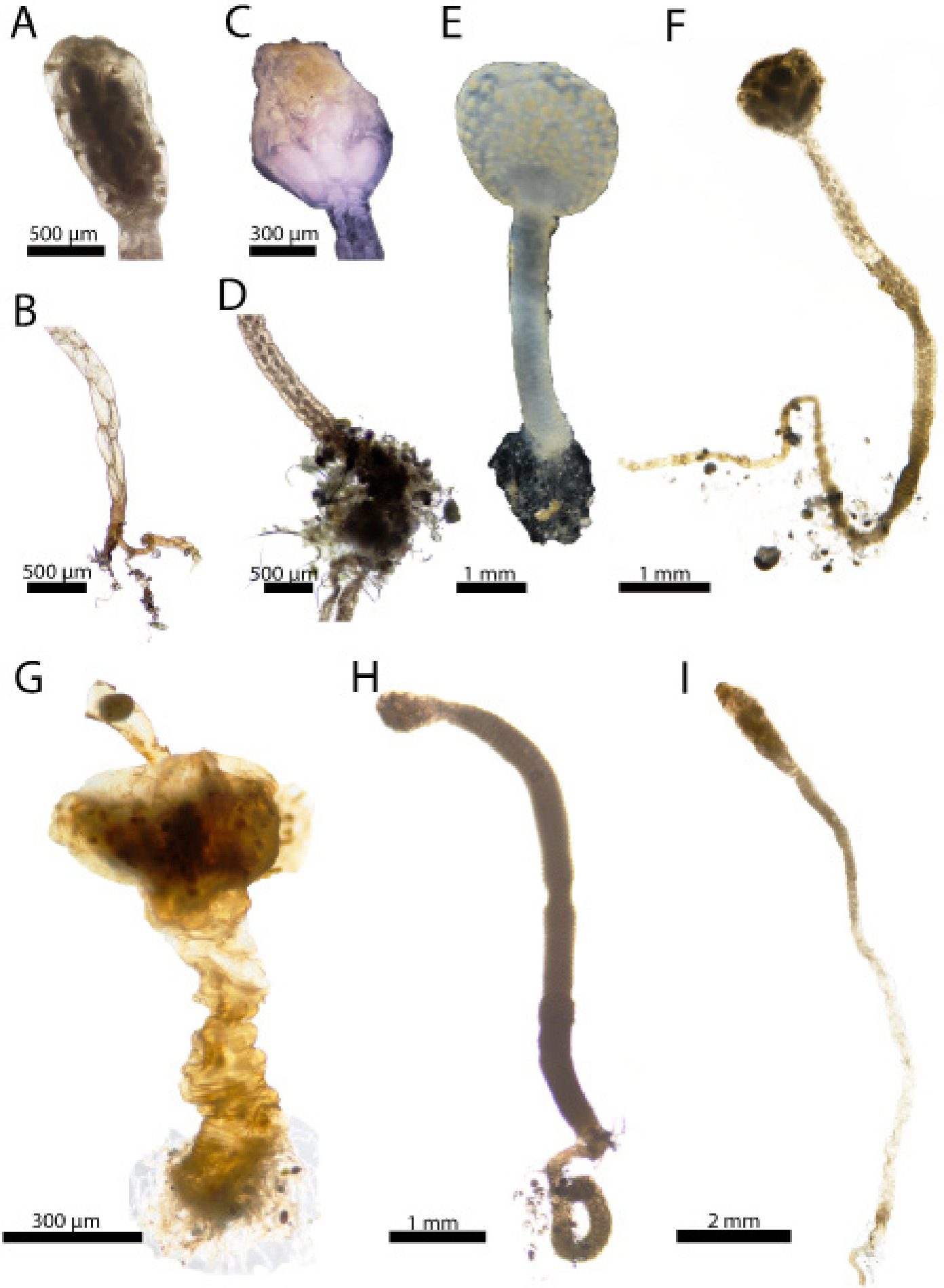

Fig.25 Comparison of multiserial peduncle and rhizoid attached Clavoporidae
A-B: Capitulum and lower peduncle of *Z. gracilis* C-D Capitulum and lower peduncle of *Z. pyriformis* E: C*ephaloalcyonidium morchellanum* F: *H. fewkesi* G: *Calyssozoon minusculum* H: *M.microcephalus* I: G*en6 sp7*

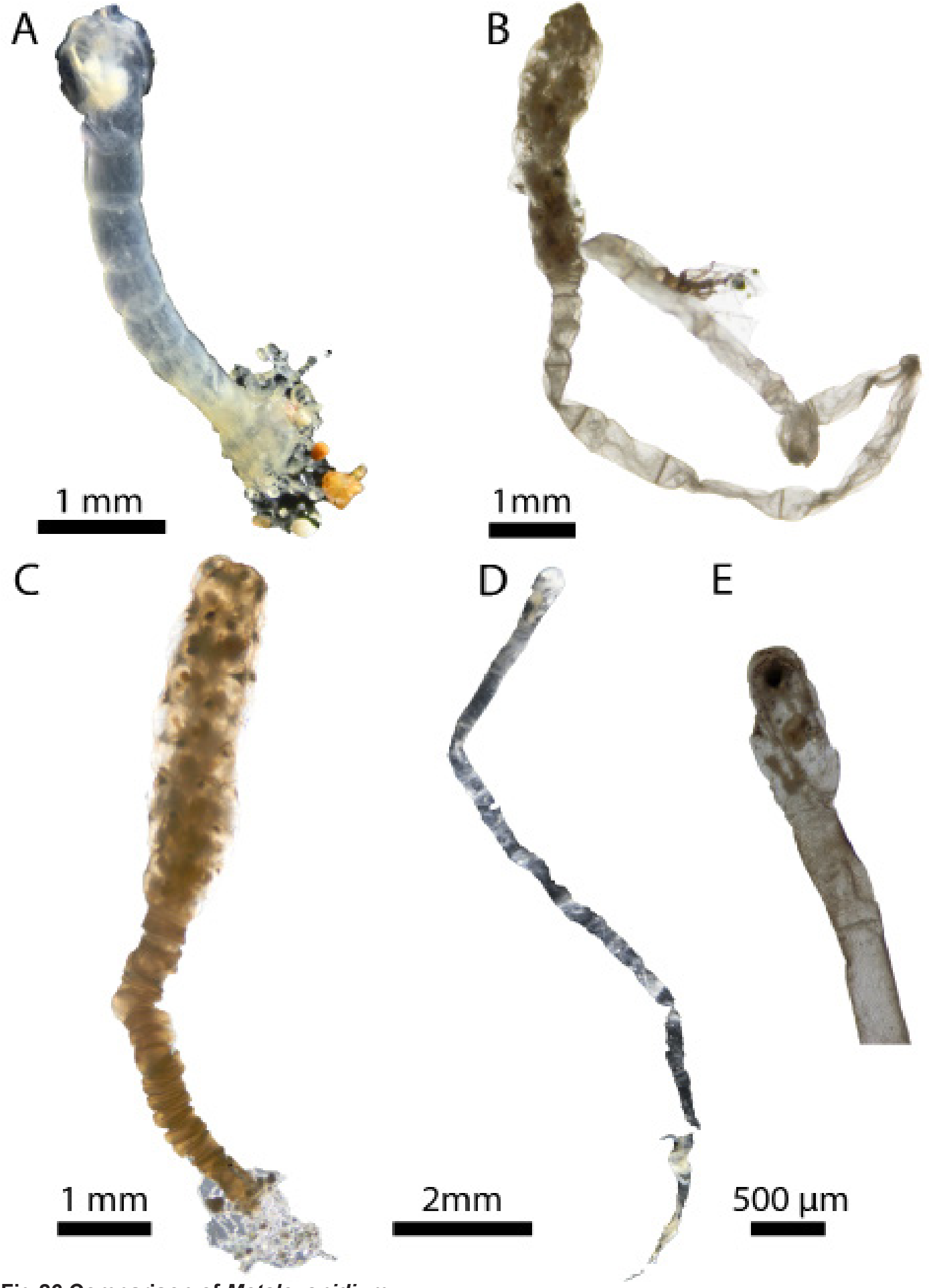

Fig.26 Comparison of *Metalcyonidium*

A: Colony overview of *M. gautieri* B: Colony overview of *M. elongatum* C: Colony overview of *M. sp. nov. 2* D: Colony overview of *M. sp. nov. 3* E: Close up of *M. sp. nov. 3* capitulum

Fig.27 Comparison of *Pseudalcyonidium*

A: Colony overview of *Pseudalcyonidium sp. nov 1* B: Colony overview of *P. sp. nov 2* C: Colony overview of *P. bobinae*

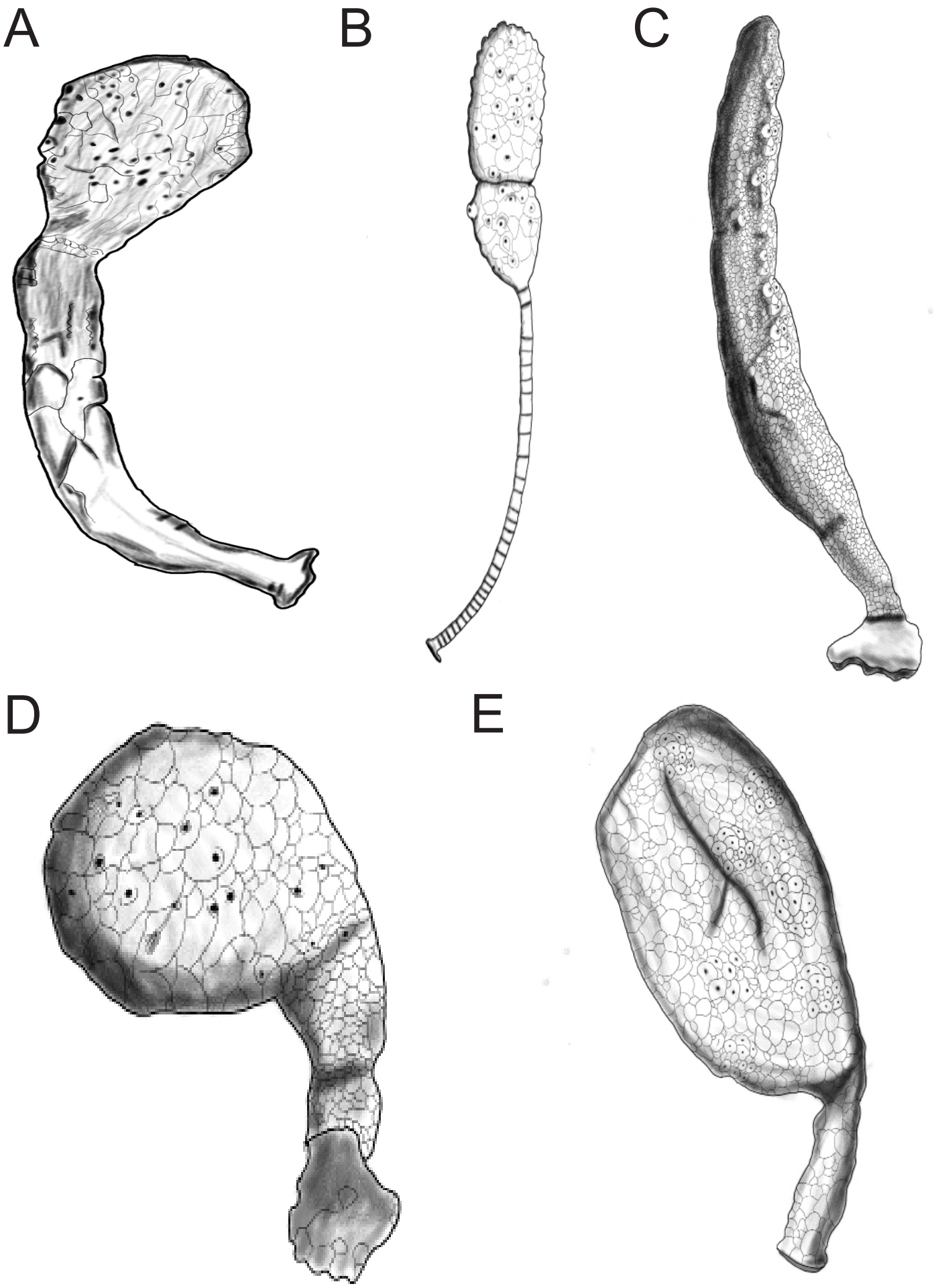

Fig.28 Shematic drawings of baseplate attached Clavoporidae - Dichotomous Key Part 1
A: *Ascorhiza occidentalis* drawn after d'Hondt, J.-L. (1983) B: *Pseudascorhiza / Metalcyonidium morum* after Hirose, M. (2022) C: *Buskozoon vadum* drawn after sample RC25 D: *Bomburozoon bulbosus* after sample 98074 E: *Bomburozoon antarcticus* after IB-2009-165

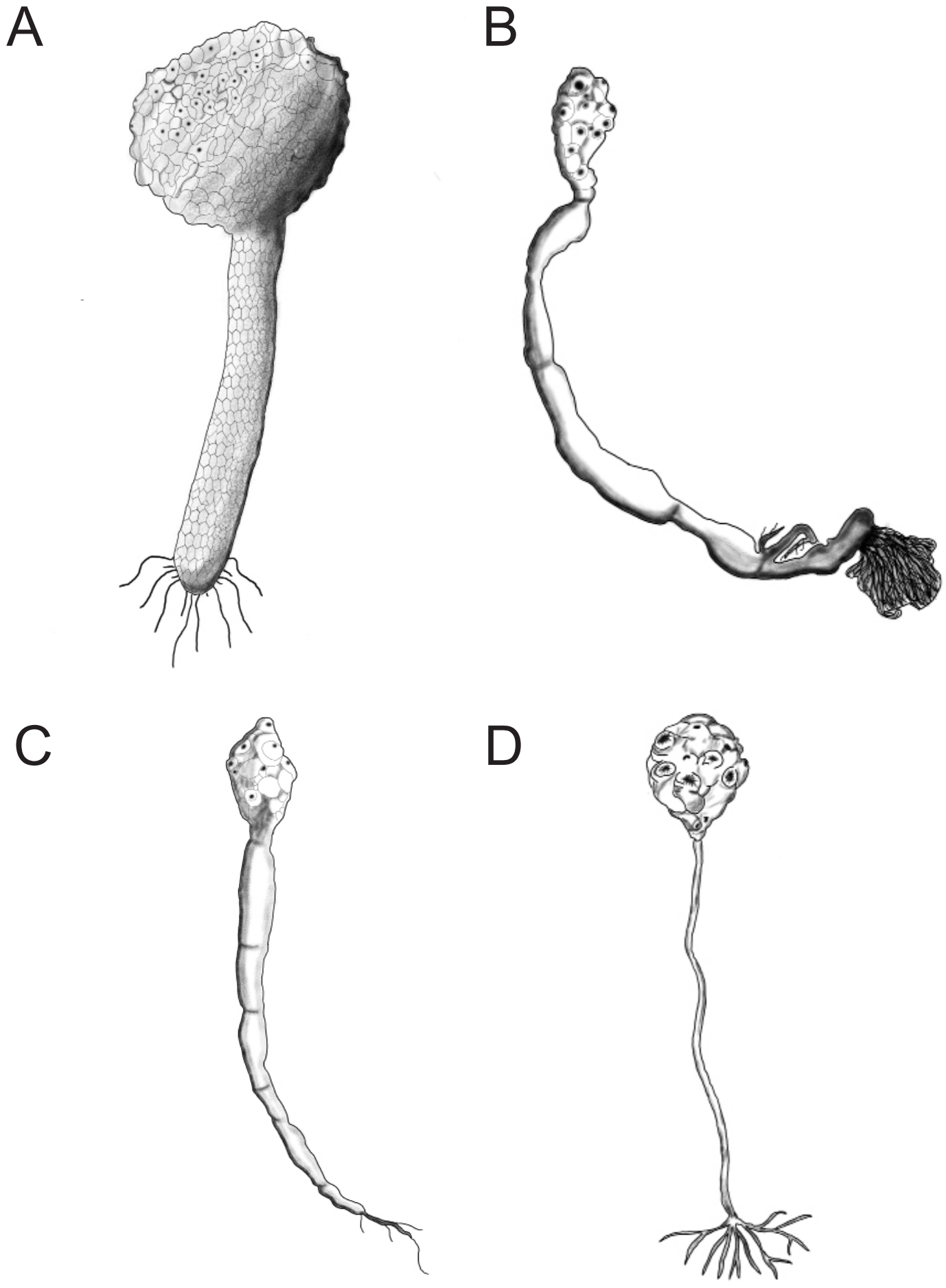

Fig.29 Shematic drawings of rhizoid anchored Clavoporidae taxa - Dichotomous Key Part 2
A: Cephaloalcyonidium morchellanum (7.) drawn after d'Hondt, (2006) B: *Pseudalcyonidium sp. nov. 1* (9.) after sample NIWA133643 *C: Pseudalcyonidium sp. nov. 2* (9') after NIWA133666 *2* D: *P. bobinae* (9'') after d'Hondt, J.-L. (1983)

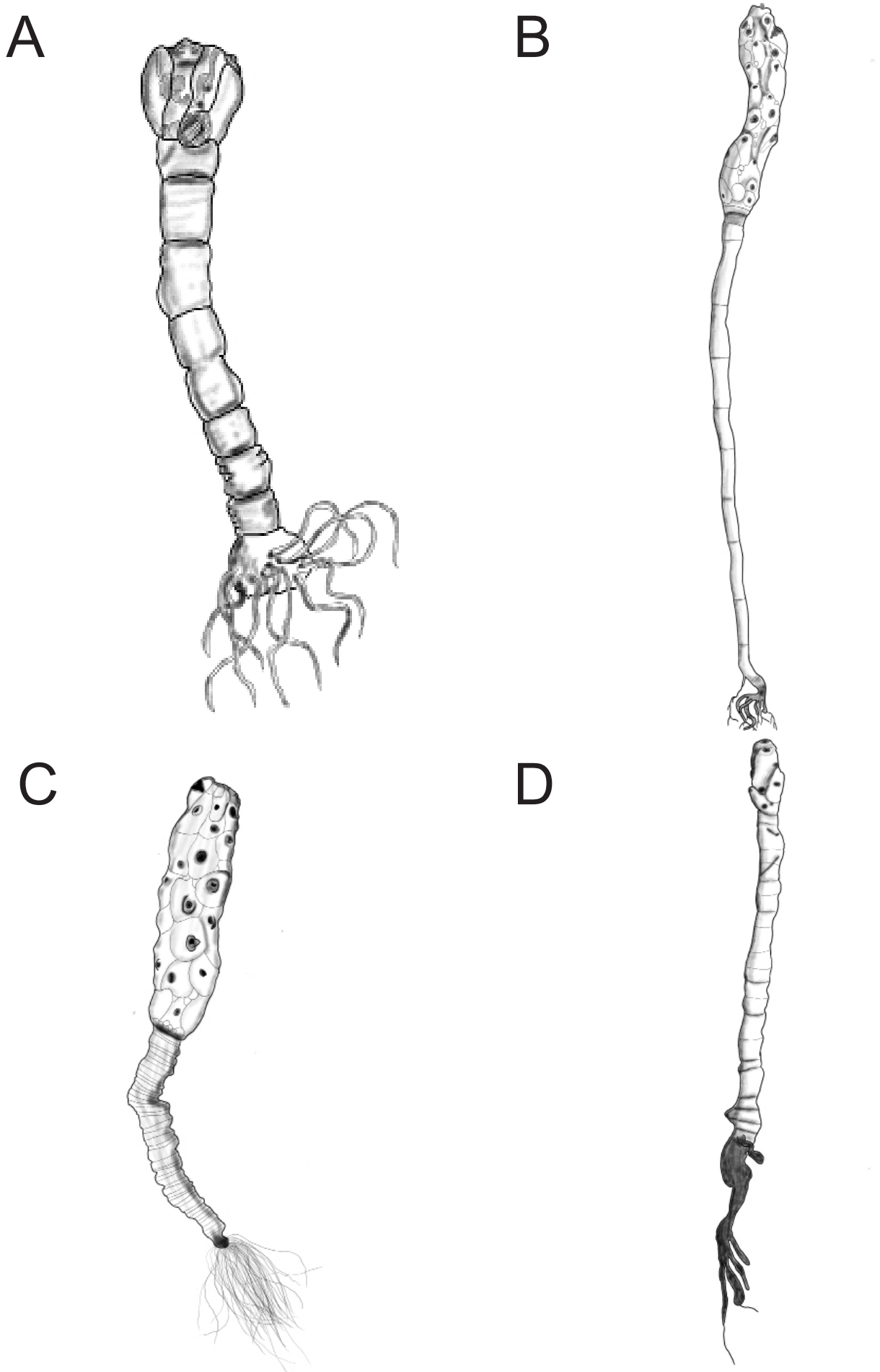

Fig.30 Shematic drawings of Metalcyonidium complex - Dichotomous Key Part 3
A: *Metalcyonidium gautieri* (12.) drawn after d'Hondt, (2006) B: *Metalcyonidium elongatum* (14.) drawn after sample NIWA133677 *C: Metalcyonidium sp. nov. 2 (*14') drawn after NIWA133658 *2* D: *Metalcyonidium sp. nov. 3* (14'') drawn after NIWA133650

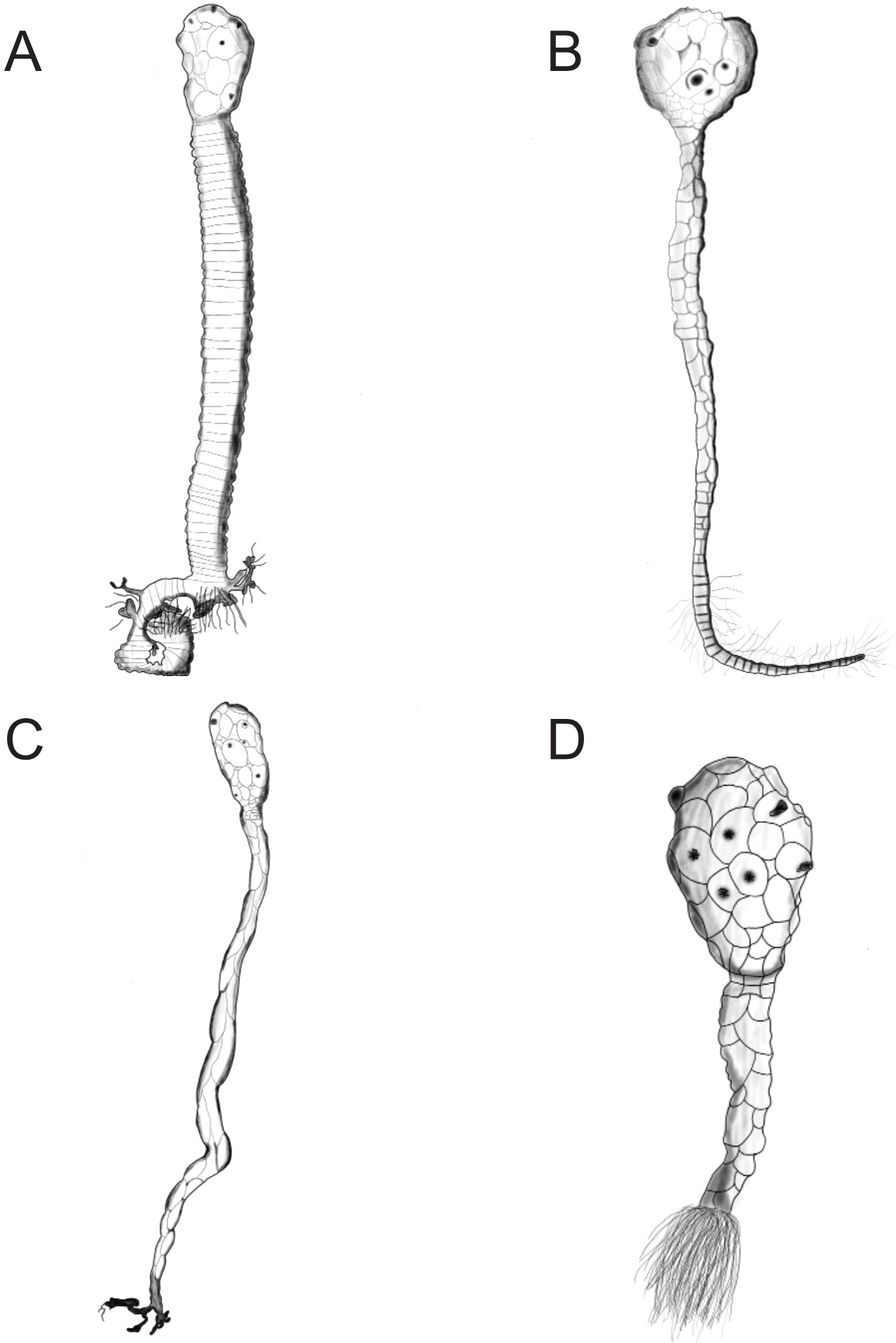

Fig.31 Shematic drawings of multiserial peduncle Clavoporidae - Dichotomous Key Part 4
A: *Michelinopedunculus microcephalus* (15‘) drawn after NIWA133660 B: *Heteropedunuculus fewkesi* (15‘‘) after sample NIWA133642 *C: Zigzagpedunculus gracilis (16.*) after NIWA133682 *2* D: *Zigzagpedunculus pyriformis* (16‘) after NIWA133654

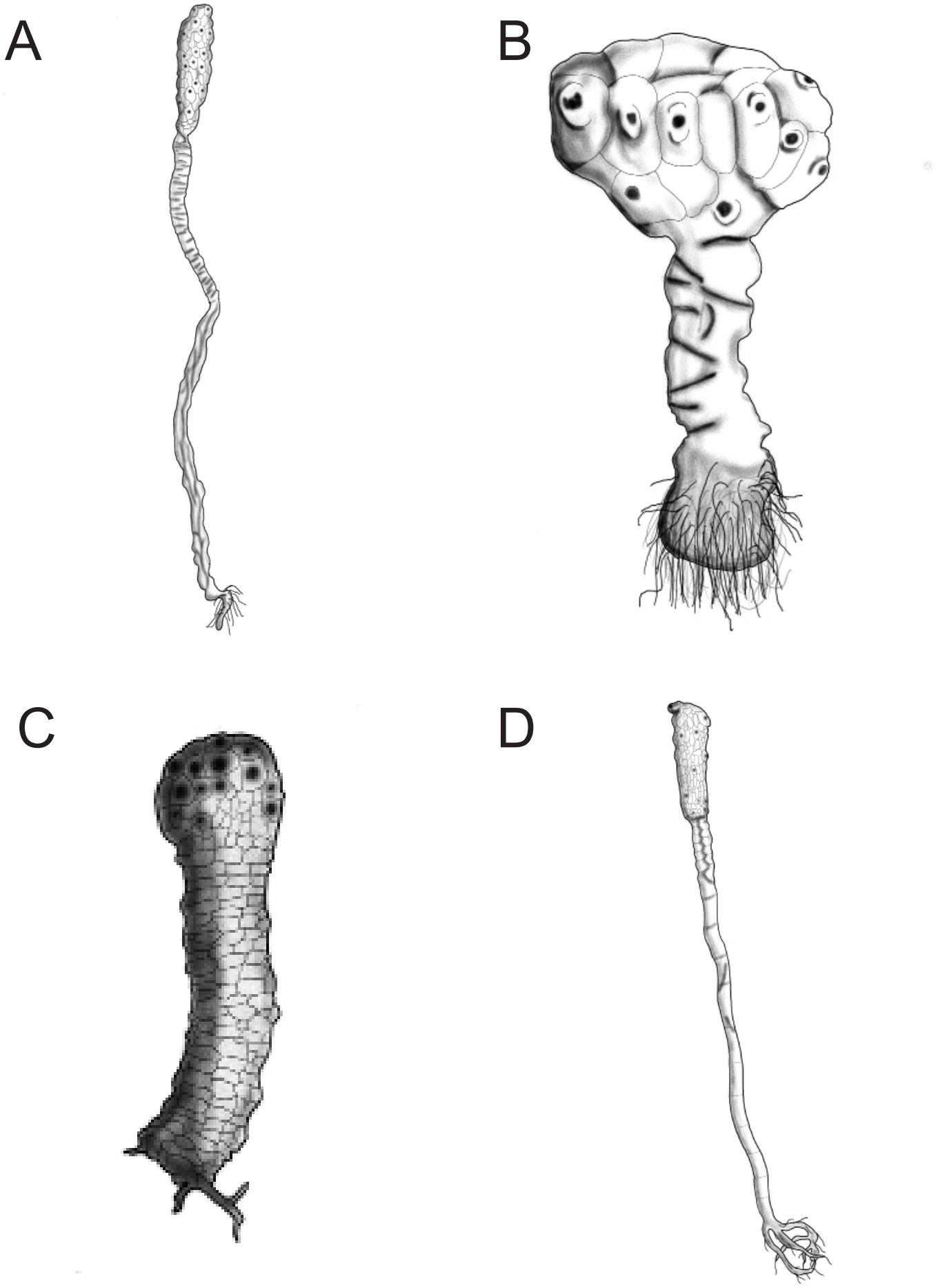

Fig.32 Multiserial peduncle Clavoporidae and unassigned taxa - Dichotomous Key Part 5
A: *Gen6 sp7 sp. nov.* (16‘‘) after NIWA 133629 (individuum nr. 5) B: *Calyssozoon minusculum* (16‘‘‘) after NIWA133809 C: *Clavopora hystricis* (17.) after d’Hondt, J.-L. (1983) D: *Sp13 sp. nov. Gen. nov?* after NIWA133688