A New Cheilostome Bryozoan with Gigantic Zooids from the North-West Pacific

Andrei V. Grischenko1*, Paul D. Taylor2 and Shunsuke F. Mawatari1

1Laboratory of Systematics and Evolution, Division of Biological Sciences, Graduate School of Science, Hokkaido University, Sapporo 060-0810, Japan
2Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

ABSTRACT—Gontarella gigantea gen. et sp. nov. is described from two stations, one in the Sea of Okhotsk and the second on the Pacific side of the Small Kuril Arc. This membraniporiform anascan cheilostome bryozoan has very large zooids, the largest known among extant sheet-like encrusting anascans. Comparative data on similar sheet-like cheilostomes gathered from the literature shows that the new species represents a conspicuous outlier in size, with the surface area of the zooid being approximately twice that of the next largest species. Skeletal evidence, including the lack of ovicells, indicates that G. gigantea belongs within the malacostegan family Electridae. The gigantic ancestrula suggests that the species has a cyphonautes larva about 1 mm in maximum dimension.

Key words: bryozoans, taxonomy, zooidal size

INTRODUCTION

Body size has long been a focus of interest among biologists. For example, research has sought to record and understand latitudinal gradients in body size, the implications of size for organismal physiology, and the relationships between size and life history strategy. Most studies have dealt with unitary, non-colonial animals; there has been very little research on the more complex modular, colonial organisms where body size is expressed at two hierarchical levels: the colony and the zooid. Intraspecific variations in colony size have received some attention (e.g., Grischenko et al., 1999; Barnes and Whittington, 1999). Interspecific variation in bryozoan colony size covers more than three orders of magnitude, the smallest colonies being about 1 mm (e.g., Cook, 1981) and the largest over 1 metre in diameter (e.g., Cocito et al., 1998). Most of this variance is accounted for by differences in the number of zooids in the colony, and not by differences in the size of these zooids. Zooid size, as measured by length and width on the surface of the colony, is relatively uniform within the phylum, especially among marine species.

Temperature-related, intraspecific variation in zooid size among cheilostome bryozoans, the most diverse group of living bryozoans, has attracted recent interest (O’Dea and Okamura, 1999), as has the genetic vs environmental components of size variation within species (Hageman et al., 1999). However, zooid size variation between species has been relatively neglected, although comparative lophophore size in marine bryozoan populations has been studied (e.g., Ryland, 1975), while McKinney and Jackson (1989) noted correlations between zooid length and colony growth-form. The bryozoan colony growth-form containing the greatest number of species consists of a sheet-like encrustation sometimes referred to as ‘membraniporiform’. Zooid length and width in membraniporiform cheilostomes are typically less than 1 and 0.5 mm respectively. Here we describe a new cheilostome genus and species with gigantic zooids up to 1.85 mm long and 1.20 mm wide. Data from the literature on similar sheet-like cheilostomes demonstrates that the new species forms a striking outlier in size – the surface area of zooids in the new species is approximately twice those of zooids in the next largest species.

MATERIALS AND METHODS

Most of the material was collected by AVG in September 1992 during a short cruise on the Middle Fishery Refrigerator Trawler Rodino in the Western Kamchatka shelf of the Sea of Okhotsk. Additional material was collected by the Pacific Institute of Bio-Organic Chemistry during the 14th Expedition of the RV Akademic Oparin, in September 1991, in north-west Pacific coastal waters of the Habomai Islands (Small Kuril Arc).

Colonies were cleaned in sodium hypochlorite solution, rinsed
with tap-water and dried in air prior to their measurement under a
binocular microscope (Nikon SNZ–10). Some dried colonies were
coated with Pd–Pt by an ion sputter (Hitachi E–1030) and observed
under a scanning electron microscope (Hitachi S–2380N) at 10–20
kV accelerating voltage. Other coated specimens were studied for
skeletal ultrastructure using an Hitachi S–2500, and uncoated
material, both bleached and unbleached, was examined at low
magnifications with an ISI ABT–55 equipped with an environmental
chamber and back-scattered electron imager. Mineralogical analy-
sis was performed using an X-ray diffractometer with curved posi-
tion sensitive detector of 120 degrees arc (Enraf Nonius CPS120).

The specimens described here are deposited in the Zoological
Institute, Russian Academy of Sciences (ZIRAS), Saint Petersburg,
Russia; Department of Zoology, The Natural History Museum (NHM),
London, UK; the Zoological Institute, Faculty of Science, Hokkaido
University (ZIHU), Sapporo, Japan; and the National Institute of
Water and Atmospheric Research (NIWA), Wellington, New
Zealand.

RESULTS

Systematics
Order Cheilostomata Busk, 1852
Suborder Malacostega Levinsen, 1902
Superfamily Membraniporoidea Busk, 1852
Family Electridae Stach, 1937
Genus Gontarella gen. nov.

Diagnosis: Colony encrusting. Zooids monomorphic, very
large in size, irregularly rhombic to oval in shape; opesia
longitudinally ovoidal, extensive, occupying most of frontal
area; gymnocyst lacking; cryptocyst a narrow unornamented
shelf, widest proximally, tapering distally, depressed; mural
rim irregularly beaded, forming raised zooidal boundary,
some zooids having a distal gap in mural rim; basal wall
incompletely calcified, containing an oval uncalcified
window; pore chambers lacking; vertical walls exterior (i.e.
containing a cuticular layer); lateral walls usually with four
septulae having an iris-like structure; distal wall with
numerous, irregularly arranged rosette plates, some uni-
porous, others containing up to four pores. Ancestrula
single, large, oval; opesia occupying nearly all frontal area;
gymnocyst lacking; cryptocyst limited to very narrow
proximal shelf; mural rim with sparse, irregular tubercles;
pore chambers absent; vertical walls containing numerous
pores, 14–16 present in proximal half of zooid, concave,
those on left and right sides divided by a narrow median
septum; basal wall with oval uncalcified window. Periances-
trular buds at least three in number (distal and two disto-lat-
eral), possibly with additional lateral buds forming after-
wards; early budded zooids smaller than ancestrula.
Skeletal walls calcitic, incorporating a fabric of wedge-
shaped granular crystallites.

Table 1. Measurements of zooids of Gontarella gigantea gen. et sp. nov. (in mm, except for Nz; all post-ancestrular zooids were measured from the holotype, ZIRAS 1/49944; ancestrulae measured from holotype and NHM 2002.1.7.2)

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>Range</th>
<th>S.D.</th>
<th>Nz</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zooids</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>L</td>
<td>1.55</td>
<td>1.15–1.85</td>
<td>0.197</td>
<td>30</td>
</tr>
<tr>
<td>W</td>
<td>0.97</td>
<td>0.70–1.20</td>
<td>0.147</td>
<td>30</td>
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<tr>
<td>Opesia</td>
<td></td>
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<td></td>
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<tr>
<td>L</td>
<td>1.15</td>
<td>0.92–1.37</td>
<td>0.135</td>
<td>30</td>
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<tr>
<td>W</td>
<td>0.82</td>
<td>0.57–1.05</td>
<td>0.121</td>
<td>30</td>
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<tr>
<td>Operculum</td>
<td></td>
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<tr>
<td>W</td>
<td>0.39</td>
<td>0.36–0.45</td>
<td>0.028</td>
<td>30</td>
</tr>
<tr>
<td>H</td>
<td>0.24</td>
<td>0.21–0.28</td>
<td>0.025</td>
<td>30</td>
</tr>
<tr>
<td>Ancestrula</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>1.07</td>
<td>1.02–1.11</td>
<td>–</td>
<td>2</td>
</tr>
<tr>
<td>W</td>
<td>0.73</td>
<td>0.70–0.75</td>
<td>–</td>
<td>2</td>
</tr>
<tr>
<td>Ancestral opesia</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>0.91</td>
<td>0.87–0.95</td>
<td>–</td>
<td>2</td>
</tr>
<tr>
<td>W</td>
<td>0.63</td>
<td>0.57–0.68</td>
<td>–</td>
<td>2</td>
</tr>
<tr>
<td>Ancestral operculum</td>
<td></td>
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<tr>
<td>W</td>
<td>0.33</td>
<td>–</td>
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<td>1</td>
</tr>
<tr>
<td>H</td>
<td>0.22</td>
<td>–</td>
<td>–</td>
<td>1</td>
</tr>
</tbody>
</table>

* Abbreviations: L. length; W. width; H. height; Nz. number of zooids; S.D. standard deviation.

Table 2. Astrogenetic size variation in Gontarella gigantea gen. et sp. nov. (in mm, except for Nz), NHM 2002.1.7.2

<table>
<thead>
<tr>
<th>Generations</th>
<th>L (zooids)</th>
<th>W (zooids)</th>
<th>L (opesia)</th>
<th>W (opesia)</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Range</td>
<td>Mean</td>
<td>Range</td>
<td>Mean</td>
</tr>
<tr>
<td>ancestrula</td>
<td>–</td>
<td>1.02</td>
<td>–</td>
<td>0.75</td>
</tr>
<tr>
<td>1 (Nz = 3)</td>
<td>0.81–0.87</td>
<td>0.84</td>
<td>0.63–0.69</td>
<td>0.65</td>
</tr>
<tr>
<td>2 (Nz = 3)</td>
<td>0.93–1.00</td>
<td>0.97</td>
<td>0.66–0.69</td>
<td>0.67</td>
</tr>
<tr>
<td>3 (Nz = 4)</td>
<td>1.08–1.14</td>
<td>1.11</td>
<td>0.69–0.75</td>
<td>0.73</td>
</tr>
<tr>
<td>4 (Nz = 5)</td>
<td>1.14–1.23</td>
<td>1.19</td>
<td>0.63–0.75</td>
<td>0.69</td>
</tr>
</tbody>
</table>

* Abbreviations: L. length; W. width; Nz. number of zooids.
Type species: Gontarella gigantea sp. nov.

Etymology: The new genus is named in honour of Dr Valentina I. Gontar (Zoological Institute, Russian Academy of Science, St Petersburg) in recognition of her contributions to bryozoology.

Remarks: This monotypic new genus can be distinguished from existing genera using characters detailed below in the Remarks section of the species description. Principal non-metric characters important in discriminating Gontarella from other malacostegan anascans are the lack of gymnocyst and spines, non-granular cryptocyst forming a narrow sunken shelf proximally, absence of pore chambers, ancestrula with numerous septular pores around the perimeter, distal and two distolateral periancestrular buds but no proximal periancestrular bud, periancestrular zooids smaller than the ancestrula, and calcitic skeleton with wedge-like granular ultrastructure.

Gontarella gigantea sp. nov.
(Figs 1–18)

Material examined: Holotype: ZIRAS 1/49944 (one colony on polychaete tube; preserved in alcohol), Pacific Institute of Bio-Organic Chemistry Collection dredged during the 14th Expedition of the RV Akademic Oparin, Stn 94, 10 September 1991, north-west Pacific Ocean in the coastal waters of the Habomai Islands, Small Kuril Arc (43°10.2'N, 146°18.2'E), depth 535 m, bottom silty sand, Trawl Sigsby, collector A.V. Smirnov. Paratypes: NHM 2002.1.7.1 (large colony on a stone), NHM 2002.1.7.2 (small ancestrulate colony on a stone), ZIHU–02049 (one colony on a stone), ZIHU–02050 (colony fragment detached from hydrocoral Allopora sp.), NIWA P–1273 (one colony fragment on a stone); sorted from a crab trap by A.V. Grischenko on the Middle Fishery Refrigerator Trawler Rodino, 12 September 1992, Western Kamchatka Shelf of the Sea of Okhotsk, about 32 km from Cape Hayruyuova (57°36.2'N, 156°09.0'E), depth 78–81 m, bottom silt, sand and gravel.

Measurements: See Tables 1 and 2.

Description: Colony encrusting, multiserial (Figs 1, 5), unilamellar, rarely multilamellar, bright yellow in colour when alive, sallow or white when dry. Zooids extremely large (Figs 4, 6; Table 1), irregularly rhombic to oval, about 1.5 times longer than wide, approximately 500 µm deep, arranged more or less quincuncially; row bifurcations preceded by a wide zooid and followed by two narrow zooids, one of which is longer than the other (Fig. 2), re-establishing alternating arrangement of zooids. Zooidal boundaries in bleached specimens marked by fine sutures (Fig. 7), indicating position of cuticle between juxtaposed vertical exterior walls of adjacent zooids (Figs 15, 17, 18). Gymnocyst lacking. Cryp-
tocyst smooth, without granulation, depressed beneath level
of zooidal boundary (Figs 7, 8), a narrow proximal shelf
tapering distally, sometimes with a complete gap at distal
extremity of zooid; irregular, convex, wart-like structures
(Figs 5, 7) occasionally present on proximal cryptocyst.
Opesia longitudinally oval in outline (Fig. 5), occupying most
of frontal area. Mural rim irregularly beaded. Pore chambers
lacking. Vertical walls exterior (overbleached colonies split
into single zooids); lateral vertical walls containing four,
sometimes five, septulae with iris-like structure (Fig. 10); dis-
tal vertical walls containing numerous, rosette plates (Fig.
9), arranged in an irregular line, some uniporous, others

Figs. 5–10. *Gontarella gigantea* gen. et sp. nov. (5–8, NHM 2002.1.7.1; 9–10, ZIHU–02050), bleached. 5. Astogenetically mature zooids, ×
11. 6. Colony margin with zooids overgrowing *Cauloramphus spiniferum* (Johnston, 1832) illustrating the enormous size of the *G. gigantea*
zooids, × 24. 7. Detail of astogenetically mature zooids showing beaded mural rims and narrow cryptocysts, × 38. 8. Growing edge of the col-
yony showing developing zooids with thin lateral walls, partially calcified basal walls, and no pore chambers, × 37. 9. Interior of the distal wall of
a zooid, showing multiporous and uniporous septulae, × 200. 10. Group of zooids becoming split through their independent vertical walls after
overbleaching destroyed the intercalary cuticle, × 60.
multiporous with up to four separate pores. Basal wall of zooids incompletely calcified (Fig. 8), an oval uncalcified window present. No ovicells, avicularia, or other polymorphs.

Frontal membrane translucent (Figs 1–3). Operculum semicircular, with pale brown marginal thickening (Fig. 2). Polypides yellow in alcohol-preserved specimen (Figs 1–3); tentacle number unknown.

Ancestrula single, very large (Figs 11–14; Table 1), oval, lacking gymnocyst and with cryptocyst developed only as a very narrow proximal shelf, opesia occupying most of surface area. Mural rim beaded. Vertical walls concave, a narrow median septum at proximal extremity separating left and right sides of ancestrula; 7–8 pores present in each proximolateral vertical wall (Fig. 14). Basal wall containing uncalcified window. Ancestrula budding three zooids, one distal and two distolateral; additional zooids possibly budded laterally. Periancestrular zooids (Fig. 13) smaller than ancestrula, initiating a zone of astogenetic change with progressively increasing zooid size (Table 2).

Skeleton calcitic, moderately high in Mg, with estimated 8 per cent Mg substitution of Ca. Ultrastructural fabric finely granular, some walls comprising wedge-shaped crystallites (Fig. 16) with fibrillar substructures. Ropey fabric (Fig. 18) visible at junction with cuticle in fractured compound vertical walls.

Remarks: Gontarella gigantea exhibits the simple skeletal morphology, including most notably a lack of ovicells and usually of avicularia, that is characteristic of the Malacostega (see Taylor, 1987). Species belonging to this primitive, paraphyletic group of cheilostomes possess non-brooded cyphonautes larvae. Although the larva of Gontarella is yet unknown, it can be inferred that it is of this type. Malacostegans are generally classified into two families, Electridae and Membraniporidae. The Electridae as currently understood is a paraphyletic family that includes the oldest known cheilostomes. In contrast, the Membraniporidae are monophyletic and can be distinguished by the derived character of having a twinned ancestrula. The ancestrula of G. gigantea is single, excluding it from the Membraniporidae and placing the new genus and species in the Electridae.

Three genera of Membraniporidae – Membraniopora de Blainville, 1830, Jellyella Taylor and Monks, 1997, and
Acanthodesia Canu and Bassler, 1920 (often synonymised with Biflustra d’Orbigny, 1852 (Fig. 19) but, in the absence of data on the ancestrula in Biflustra, Acanthodesia is here retained) – have sheet-like encrusting colonies similar to Gontarella. All, however, can be distinguished from Gontarella by their twinned ancestrulae. In addition, the type species of Membranipora de Blainville, 1830, M. membranacea (Linnaeus, 1767) (Fig. 24), which is a specialized epiphyte, has: (1) lightly calcified rectangular zooids with tubercles at the corners; (2) a granulated but slight cryptocyst; (3) uncalcified bands in the lateral vertical walls; (4) multiporous septulae, two in each transverse wall, and four in each lateral wall; (5) ‘tower’ zooids; and (6) an aragonitic skeleton. The type species of Jellyella Taylor and Monks, 1997, J. eburnea (Hincks, 1891) (Fig. 20), has: (1) a moderately to well-developed gymnocyst produced into tubercles and/or spines proximally and around the opesium; (2) cryptocyst absent or forming a narrow, pustulose proximal shelf; (3) long spinules growing into the zooidal chamber; and (4) skeletal walls of calcite including a layer of spindle-shaped crystallites.
arranged transversely to wall growth direction. The third membraniporid, *Acanthodesia* Canu and Bassler, 1920, the type species *A. savartii* (Audouin, 1826) (Fig. 21), has: (1) a well-developed, granulated, proximal; (2) no gymnocyst; (3) lateral walls with multiporous septulae; and (4) a lamellar calcitic skeleton.

Two common genera of extant electrids – *Conopeum* Gray, 1848, and *Electra* Lamouroux, 1816 – have sheet-like encrusting colonies. Both can be distinguished from *Gontarella* in possessing pore chambers. In the type species of *Conopeum* Gray, 1848, *C. reticulum* (Linnaeus, 1767) (Fig. 22), additional differences from *Gontarella* include: (1) the gymnocyst and cryptocyst are narrow, the latter finely granular; (2) a variable number of small spines may sometimes be present, disposed regularly around the periphery of the zooid; (3) a pair of triangular chambers (kenozoooids) are

usually present at the distal angles of each zooid; and (4) the ancestrula buds two disto-lateral zooids, followed by a proximal zooid. The type species of *Electra* Lamouroux, 1816, *Electra pilosa* (Linnaeus, 1767) [= *E. verticillata* (Ellis and Solander, 1786)] (Fig. 23), has: (1) a moderately to well-developed gymnocyst containing apparent pores which are actually internal pits roofed by very thin calcification; (2) reduced, non-granular cryptocyst; (3) spines bordering the opesia, including a long median proximal spine. A third living electrid – *Aspidelectra* Levinsen, 1909 – is immediately distinguished from *Gontarella* by its costate frontal shield. Another electrid – *Villicharixa* Gordon, 1989 – has opesia ringed by articulated spines. Some additional electrid genera with sheet-like colonies are known only as fossils, including *Charixa* Lang, 1915, *Spinicharixa* Taylor, 1986, *Eokotosokum* Taylor and Cutfey, 1992, and *Bullaconopeum* Taylor, 1995. All are either spinose or have prominent gymnocyst tubercles, providing clear distinctions from *Gontarella*.

Ecology and Distribution: *Gontarella gigantea* is currently known from two widely-separated localities in the north-west Pacific: (1) the oceanic side of the Habomai Islands, Small Kuril Arc, (north-east of Hokkaido Island) and (2) the Western Kamchatka Shelf of the Sea of Okhotsk. Therefore, *G. gigantea* ranges at least between the latitudes of 43°10.2′ and 67°37.0′N, and can be categorized as a Pacific Asiatic Wide-Boreal species.

*G. gigantea* has been recorded within areas of soft and mixed sea-bed (silt, sand, gravel) attached to hard substrata (stones, tubes of polychaetes and the hydrocoral *Allopora* sp.). Known depth range is 78–535 m, with the more southerly occurrence being in deeper water.

**DISCUSSION**

The most remarkable feature of *Gontarella gigantea* is the enormous size of the zooids which average 1.55×0.97 mm in the holotype and can attain a length of 1.85 mm and width of 1.20 mm. To illustrate this we have compiled data from the literature (Kluge, 1975; Gostilovskaya, 1978; Ryland and Hayward, 1977; Winston, 1982; Gordon, 1984; Dick and Ross, 1988; Hayward, 1994, 1995; Hayward and Ryland, 1995; Soule et al., 1995; Tilbrook, 1998; Winston et al., 2000; Grischenko et al., 2000; Tilbrook et al., 2001) for a further 99 species of sheet-like encrusting anascan cheilostomes. These species were selected haphazardly from faunal studies describing bryozoans from different parts of the world. Values of mean or median (when range only was given) for zooid length and width were recorded as proxies for zooid size.

Expressed as the square root of length x width, the frequency plot of zooid size is strongly right-skewed (Fig. 25). Most species have small zooids, the modal value is closer to the minimum than maximum value, and a steadily declining number of species have large zooids. The long right tail of the distribution includes a gap between the second largest species and *G. gigantea* which has approximately twice the surface area. Therefore, for this data at least, *G. gigantea* forms a significant outlier of exceptional size.

Although beyond the scope of the present paper and

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**Fig. 25.** Frequency distribution of zooidal size, expressed as the square root of length x width (in µm²), in 100 species of anascan bryozoans with sheet-like encrusting colonies. Note the conspicuous outlier represented by *Gontarella gigantea* gen. et sp. nov.
warranting a much more detailed study, the form of the size frequency distribution deserves comment as we are unaware of any comparable analysis elsewhere for bryozoan zooid size. The pattern is very similar to that noted previously for body size in non-colonial organisms, as summarized by Brown (1995). In non-colonial groups as diverse as bacteria, trees, insects, fishes and mammals, Brown noted how there are: (1) many more species with small than large body sizes; and (2) that the distribution is highly right-skewed, with a sharp decline in number of species with progressively smaller body sizes from the mode, and a gradual decline in those with progressively larger body sizes.

In spite of the remarkably large zooid size of *G. gigantea*, it does not possess the largest zooids known for all fossil and extant cheilostome Bryozoa. The Cretaceous anascan *Herpetopora laxata* (d’Orbigny, 1852), with runner-like encrusting colonies has autozooids ranging up to 8.28 mm in length (Taylor, 1988). However, most of this length is taken up to be a very narrow proximal part (cauda) whereas the ‘functional’ part of the autozooid containing the opesia is of normal dimensions. Autozooids of some recent cheilostomes with erect colonies can also attain a gigantic size. For instance, the erect Antarctic ascophoran *Antarcticaetos tubecata* (Rogick, 1955) produces zooids 1.5–3.0 mm long by 0.5 mm wide (Hayward, 1995). Another Antarctic ascophoran with erect branching bilaminar colonies, *Cellarinelloides crassus* Moyano, 1970, has zooids 1.8–3.0 mm long by 0.5–0.6 mm wide (Hayward, 1995). Zooids in some Antarctic erect anascans are only a little smaller. Those of *Camptopilites rectilineari* Hastings, 1943 are 2.3–2.5 mm long by 0.2 mm wide (Hayward, 1995), and *Klugelflustra antarctica* (Hastings, 1943) has zooids 1.5–2.5 mm long by 0.4 mm wide (Hayward, 1995).

Not only are the zooids from the zone of astogenetic repetition very large in *G. gigantea*, but the ancestrula is also gigantic. Table 3 lists ancestrular dimensions in some comparative anascan species with non-twinned ancestrulae. The linear dimensions of the *G. gigantea* ancestrula are almost twice the size of those of the next biggest species.

The larva of *Gontarella* is not yet known. However, on the basis of adult characters and the consequent systematic placement of the genus, the larva is inferred to be of the cyphonautes type, i.e. a bivalved, planktotrophic, non-brooded larva. In view of the large size of the ancestrula in *Gontarella* it is expected that the larva will also be large. The relationship between ancestrular size and the size of the mature cyphonautes larva for some malacostegan species shows that ancestrular length and larval maximum dimension are similar (Cook, 1962, 1964; Cook and Hayward, 1966). Therefore, the larva of *Gontarella* may be about 1 mm in maximum dimension, a size somewhat greater than the value of 850 µm for the largest cyphonautes (*Membranipora membranacea* (Linnaeus, 1767)) recorded in the British fauna (Ryland and Hayward, 1977) and which produces a twinned ancestrula on metamorphosis unlike the single ancestrula of *Gontarella*.

The physiological and ecological significance of large zooid size in *G. gigantea* is not understood. Observations of the limited material available suggest that *G. gigantea* is a good competitor for substrate space: colonies were frequently observed overgrowing other species of bryozoans but were never seen to be overgrown themselves. This matches the observations and predictions made by other authors. For bryozoans in general, competition for substrate space is aided by having large zooids, partly because large zooids have more powerful feeding currents potentially

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**Table 3.** Comparison of ancestrula size in *Gontarella gigantea* gen. et sp. nov. with some other anascan membraniporiform cheilostome species having non-twinned ancestrulae.

<table>
<thead>
<tr>
<th>Species</th>
<th>Ancestrula size, µm</th>
<th>Reference</th>
</tr>
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<tbody>
<tr>
<td><em>Gontarella gigantea</em> gen. et sp. nov.</td>
<td>1100×700</td>
<td>herein</td>
</tr>
<tr>
<td><em>Smithipora abyssicola</em> (Smitt, 1873)</td>
<td>650×300</td>
<td>Ristedt, 1991: 379</td>
</tr>
<tr>
<td><em>Calpensia nobilis</em> (Esper, 1796)</td>
<td>600×300</td>
<td>Ristedt, 1991: 373</td>
</tr>
<tr>
<td><em>Antropora granulifera</em> (Hincks, 1880)</td>
<td>500×250</td>
<td>Ristedt, 1991: 372</td>
</tr>
<tr>
<td><em>Amphiblestrum inermis</em> (Kluge, 1914)</td>
<td>400×400</td>
<td>Ristedt, 1991: 372</td>
</tr>
<tr>
<td><em>Gregarinidra gregaria</em> (Heller, 1867)</td>
<td>400×300</td>
<td>Ristedt, 1991: 378</td>
</tr>
<tr>
<td><em>Cranoisina coronata</em> (Hincks, 1881)</td>
<td>400×240</td>
<td>Ristedt, 1991: 378</td>
</tr>
<tr>
<td><em>Alderina imbellis</em> (Hincks, 1860)</td>
<td>380×300</td>
<td>Ryland and Hayward, 1977: 96</td>
</tr>
<tr>
<td><em>Micropora brevissima</em> Waters, 1904</td>
<td>350×300</td>
<td>Ristedt, 1991: 379</td>
</tr>
<tr>
<td><em>Andreaella uncifera</em> (Busk, 1884)</td>
<td>350×300</td>
<td>Ristedt, 1991: 372</td>
</tr>
<tr>
<td><em>Ellisia antarctica</em> Hastings, 1945</td>
<td>300×250</td>
<td>Ristedt, 1991: 378</td>
</tr>
<tr>
<td><em>Callopora dumerilii</em> (Audouin, 1826)</td>
<td>300×240</td>
<td>Ristedt, 1991: 373</td>
</tr>
<tr>
<td><em>Electra monostachys</em> (Busk, 1854)</td>
<td>240×180</td>
<td>Ryland and Hayward, 1977: 70</td>
</tr>
<tr>
<td><em>Conopeum reticulum</em> (Linnaeus, 1767)</td>
<td>220×130</td>
<td>Ryland and Hayward, 1977: 60</td>
</tr>
<tr>
<td><em>Conopeum seuri</em> (Canu, 1928)</td>
<td>210×145</td>
<td>Ryland and Hayward, 1977: 62</td>
</tr>
</tbody>
</table>

* Indicates a malacostegan species known to have a cyphonautes larva.
capable of depleting food resources available to competitors (McKinney, 1993), and partly because the increased height of large zooids can present a greater physical obstacle to overgrowth by competitors (Buss, 1986).

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Dr Gordon Cressey (Department of Mineralogy, NHM) kindly undertook the mineralogical analysis. This study was partially supported by a Grant-in-Aid for International Scientific Research (No 12575008) from the Japanese Ministry of Education, Science, Sports and Culture (Shunsuke F. Mawatari, principal investigator).

REFERENCES

Audouin JV (1826) Explication sommaire des planches de polypes de l’Egype et de la Syrie, publiées par Jules-César Savigny. Descr Egypte Hist Nat 1: 225–244


Blainville HMD de (1830) Zoophytes. In “Dictionnaire des Sciences naturelles, dans lequel on traite méthodiquement des différents êtres de la nature Vol 60” Ed by GF Cuvier, FG Levrault, Paris, pp 1–546


Lamouroux JVF (1816) Histoire des Polyplumes Corralligenes Flexibles, vulgairement nommes Zoophytes. F Poisson, Caen

Lang WD (1915) On some new uniserial Cretaceous cheilostome Polyzoa. Geol Mag 6: 496–504


Levinsen GMR (1909) Morphological and systematic studies on the chelostomatous Bryozoa. Nationale Forfatteres Forlag, Copenhagen


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