***Rossella podagrosa* Kirkpatrick, 1907—A valid species after all**

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Abstract

In this study we provide evidence that the species *Rossella podagrosa* Kirkpatrick, 1907, commonly considered a synonym of *Rossella racovitzae* Topsent, 1901, is truly a valid species. We show that it can be clearly distinguished from other species especially when taking into consideration the *in situ* habitus of the sponge in combination with the spicules. Furthermore we demonstrate the weaknesses in the so far published synonymy concept for the very complicated genus *Rossella* Carter, 1872. From this we conclude that the best strategy for further analysis of *Rossella* and establishment of acceptable synonymies will need to be based on detailed examination of the spicules, the holotypes, and *in situ* habitus. When possible it will be useful to analyze specimens from all Antarctic oceanographic regions.

Key words: Porifera, Hexactinellida, Rossellidae, Synonymy, Antarctica, Ross Sea

Introduction

The sponges of the genus *Rossella* Carter, 1872 are amongst the most remarkable invertebrates of the Antarctic shelf. They reach enormous sizes and show a distinctive habitus, being commonly barrel-shaped with one wide central osculum, with the outer surface in most species bearing conules. Often long and thick bundles of spicules protrude from the conules (Barthel & Tendal 1994). Budding has been regularly reported (Barthel & Tendal 1994; Teixidó *et al.* 2006) but without definitive patterns. Classically thought to be rather slow growing, *Rossella* and *Anoxycalyx* (*Scolymastra*) *joubini* have recently been shown to be capable of fast growth and proliferation in the case of favourable environmental conditions (Dayton *et al.* 2013; Fillinger *et al.* 2013). *Rossella* spp. reach high abundance in undisturbed areas of the Antarctic shelf, where they appear as a structuring benthic element. Dayton *et al.* (1974) documented a sponge assemblage which was highly dominated by what they called *R. racovitzae*, making up 42 % of the ground cover and 71 % of the sponge biomass. These sponges, forming the basis of this present study, are here re-identified as representatives of the species *R. podagrosa*. Similar densities have been documented by Gutt & Koltun (1995), Gutt & Piepenburg (2003), and Teixidó *et al.* (2004). *Rossella* spp. are also important as substrate and habitat for several benthic invertebrates and juvenile fishes (Kunzmann 1996; Barthel 1997; Gutt & Schickan 1998; Kersken *et al.* 2014). Still, despite the unquestionable high ecological importance of *Rossella* in the Antarctic and nearly 150 years of research, the taxonomy of *Rossella* and its many species remains complicated and not fully understood.

The taxonomic history of *Rossella* is long and complicated: the genus was established by Carter (1872), followed by rather quick descriptions of a large number of additional species (e.g. by Topsent 1901; Kirkpatrick 1907; Schulze & Kirkpatrick 1910 (in fact, 25 species and varieties: Ijima 1927; Reiswig 1990). Soon after, doubts arose whether all these species are truly valid, and, synonymies were postulated. The first revision of the genus was done by Burton (1929); this led to a reduction into five Antarctic species and included the synonymization of the genus *Aulorossella* Kirkpatrick, 1907 with *Rossella*. A further reduction was proposed by Koltun (1976), who also

synonymized the genus *Gymnorossella* Topsent, 1916. He accepted only the two species *Rossella antarctica* Carter, 1872 and *Rossella racovitzae*. This yielded an extremely vague definition of *R. racovitzae*, which simply comprised all *Rossella* not identifiable as *R. antarctica*. Later Barthel & Tendal (1994) established a new system, according to which *Rossella* comprises seven species: *R. antarctica*, *R. racovitzae*, *R. villosa* Burton, 1929, *R. fibulata* Schulze & Kirkpatrick, 1910, *R. nuda* Topsent, 1901, *R. levis* (Kirkpatrick, 1907) and *R. vanhoeffeni* (Schulze & Kirkpatrick, 1910). This system was recently applied by Göcke & Janussen (2013). It has many advantages as it aims to define clearly distinguishable species. Still it has some flaws as it is based mainly on material sampled in the Weddell Sea, neglecting *Rossella* from other parts of the Antarctic and it also is mainly based on spicule characters, partly neglecting the external morphology of the sponges. The drawbacks of the different synonymy concepts will be discussed in detail later in this paper. Additional to the Antarctic *Rossella* spp., a species from the northern Atlantic was described as *Rossella nodastrella* by Topsent (1915). Dohrmann *et al.* (2012) however could show that this species is morphologically and genetically distinguished from Antarctic *Rossella* spp. and erected a new genus called *Nodastrella* Dohrmann, Göcke, Reed & Janussen, 2012, which so far contains two species. *Rossella* thus is an exclusively Antarctic genus.

Here we describe some recently sampled specimens of *Rossella podagrosa*, a species commonly considered a synonym of *R. racovitzae*. In comparison with the original type material we show that *R. podagrosa* is actually well-founded. In particular the *in situ* habitus of the species was extensively documented by underwater photography and repeated growth measurements in McMurdo Sound, in the Ross Sea.

Materials & Methods, study area

The sponges used as basis for this study were observed and collected in essentially the same location as the type material collected near Winter Quarters Bay, McMurdo Sound, by the Discovery expedition. In addition, the type material from Natural History Museum London was analyzed.

Spicule preparations were made following the standard procedure (Boury-Esnault & Rützler 1997) by dissolving small amounts of tissue in concentrated nitric acid and cleaning them three times in deionized water. For light microscopy (LM), spicules were placed on glass slides and fixed in Euparal or UV-sensitive glue. For scanning electron microscopy (SEM), spicules were placed on stubs and sputter-coated. Measurements of spicules were done using a high-resolution light microscope with an ocular micrometer. When possible, 30 spicules of each type were measured. Only in very few cases of rare spicules the number was lower. Numbers of measured spicules are always indicated. Values are given as: “minimum – mean – maximum (number of spicules measured)”. In calycomes often single rays had to be measured, as they were often fragmentary. The measurements of these complex spicules were done as illustrated in Göcke & Janussen (2013).

Results

Analyzing several underwater *in situ*-photographs in combination with careful inspection of the spicule material of a certain type of rossellid sponge, which occurs as one of the most abundant and biomass-rich sponges in the Ross Sea, led to the recognition that this is in fact a representative of the species *Rossella podagrosa*. This species is currently considered a junior synonym of *R. racovitzae*, but after re-evaluating the specific characters of the species on the basis of new material as well as on the type, we now re-establish the species *Rossella podagrosa*.

Class Hexactinellida Schmidt, 1870

Subclass Hexasterophora Schulze, 1886

Order Lyssacinosida Zittel, 1877

Family Rossellidae Schulze, 1885

Subfamily Rossellinae Schulze, 1885

Genus *Rossella* Carter, 1872

Rossella podagrosa Kirkpatrick, 1907

(Fig. 1–2, Tab. 1)

Rossella podagrosa Kirkpatrick, 1907: 11, pl. 3, figs. 2–3, pl. 5, fig. 1. Topsent 1917: 14. Tabachnick 2002: 1447.

Rossella podagrosa tenuis Topsent, 1916: 4; 1917: 15.

Not *Rossella racovitzae* Burton 1929: 407–409, fig. 1, pl. 1; 1932: 256–257; 1934: 7. Koltun 1976: 165 (pars). Barthel & Tendal 1994: 92–95, figs. 35–36, pl. 3–4. Göcke & Janussen 2013: 116–120, fig. 2 F, 7, tab. 6).

Material. 1 Specimen (P 1635) from 30 m depth at Cape Armitage, Ross Island, McMurdo Sound, Antarctica; BMNH 1908.2.5.6 (type) from Discovery Collection, Winter Quarters Bay, Hut Point, D Net, 15.12.1902.

Description. The sponge body is of a slender, upright shape with one round osculum at the top. It usually bears numerous buds that originate from the basal region of the mother and grow from ~ 3–5 mm to > 3 cm prior to separation. The sponges show an unusual fast growth rate increasing their length by as much as 16 cm in a decade and have been shown to increase their volume by almost 300% in just three years. Moreover, newly separated buds themselves can grow new buds within one year (Dayton, 1979). This mode of reproduction leads to a typical appearance of dense colonies with several specimens growing close to each other (Fig. 1 A). Colonies are often densely covered by sediment including loads of (foreign) loose spicular material, so that in many cases only the tips of the sponges with the oscules are visible within the sediment (Fig 1B–D). The single specimen (Fig. 1E) can reach a height of approximately 20 cm. The surface bears no conules, but it can be covered by a narrow veil of protruding pentactines. Protruding diactins are not prominent. The sponge has a basal root tuft of long pentactines as it is usual for the genus. The inner cavity has a dense surface; its basal part in rare cases bears large round cavernous openings. In contrast to other *Rossella* species, the texture of the sponge is soft, and it is too fragile for handling without damaging it. In fact the measurements in Dayton (1979) were made by supporting the sponges with a spoon because the sponge collapses very easily.

In here we restrict the analysis of spicules (Tab. 1, Fig. 2) to the characters of highest taxonomical importance, which means that these are the spicules with the highest significance for distinguishing *R. podagrosa* from other *Rossella* spp.. The spicules of the new specimen P1635 are in full accordance with those of the type (see comparison in Fig. 2, Tab. 1) and with the typical spicule inventory of the genus. Most characteristic spicules are the calyccomes and mesodiscohexasters. Calyccomes (Fig. 2A, D) are about 190 to 250 µm in diameter, they have short primary rays (in mean about 10 µm) and middle pieces (mean about 11 µm), but long secondary rays (mean about 90 µm). The number of secondary rays on each ray ranges from 2 to 6, but is most commonly 4 and very rarely higher than 5. Secondary rays are almost straight, only slightly bent outwards in the proximal region. Calyccomes are densely covered by fine spines. Mesodiscohexasters (Fig. 2B, E) have a very typical shape; they strongly resemble the calyccomes, but are only about half the size (mean about 129 µm) and much thinner with almost absent middle pieces. Each ray bears two to four secondary rays; there are no hemi-forms with non-split rays. Mesodiscohexasters are quite rare, but occur regularly. Microdiscohexasters (Fig. 2C, F) have secondary rays of two different lengths and distinct disc-shaped middle-parts. They are about 30 to 55 µm in diameter. Remarkably large oxyhexactines (mean diameter about 180 µm) and oxyhexasters (mean diameter about 174 µm), commonly as mono- or dioxyhexasters, which have only one or two primary rays split into two secondary rays, occur in about the same frequency. Dermal pentactines have smooth surfaces without hooks.

Remarks. The species *Rossella podagrosa* is clearly characterized by the combination of its typical habitus with numerous buds and its rather small calyccomes with normally only 4 to 5 secondary rays on each ray. Furthermore, oxyhexactines and oxyhexasters are quite large for *Rossella* (see Barthel & Tendal 1992), although Göcke & Janussen (2013) reported similar sizes from several well-known species in the eastern Wedell Sea. The appearance *in situ* resembles that of *R. antarctica* (Fig. 1D) in strongly sediment-covered specimens. A clear character for differentiation *in situ* is that *R. podagrosa* usually grows partly within the sediment, while *R. antarctica* occurs on the sediment. Also, *R. podagrosa* has a more elongate body form, whereas that of *R. antarctica* is strongly rounded. In terms of spicules, the difference is clear: *R. antarctica* has dermal pentactines with strong lateral hooks (as shown by Carter 1872) and much smaller calyccomes with different shape; primary

FIGURE 1. Habit of *Rossella podagrosa*. A: Clean colony of strongly budding *R. podagrosa*, used by some comatulids as substrate. Scale bar: 10 cm. B: Close-up of *R. podagrosa* covered with sediment. Scale bar: 10 cm. C: Ground covered by dense mass of *R. podagrosa*, mostly concealed by sediment. Two clean specimens of *R. cf. levis* grow over the *R. podagrosa*-ground. Scale bar: 20 cm. D: Assemblage of large *R. podagrosa* coverage and one specimen of *R. antarctica* (to the upper left). Scale bar: 20 cm. E: Type of *R. podagrosa* (BMNH 1908.2.5.6). Scale bar: 50 mm.

FIGURE 2. Spicules of *R. podagrosa*. A–C: Specimen P1635, A: Calycocom, scale bar 30 μm , B: Mesodiscohexaster, scale bar 30 μm , C: Microdiscohexaster, scale bar 10 μm . D–F Specimen BMNH 1908.2.5.6 (type), D: Calycocom, scale bar 30 μm , E: Mesodiscohexaster, scale bar 30 μm , F: Microdiscohexaster, scale bar 10 μm .

rays and middle pieces are much more prominent and the number of secondary rays per ray is higher (compare Schulze & Kirkpatrick 1910; Barthel & Tendal 1992; Göcke & Janussen 2013). *Rossella racovitzae* differs from *R. podagrosa* by a larger body size, lack of buds and the presence of clear conules on the surface. Furthermore, it has much bigger calycomomes (400 µm) with a higher number of secondary rays (see Topsent 1901; Göcke & Janussen 2013). Similar sizes of calycomomes are found in *R. levis*, which nonetheless differs from *R. podagrosa* in some key points: it has a surface covered by numerous and very distinct conules (compare Fig. 1C), which in the lower part of the body bear bundles of protruding diactines. Calycomomes have considerably larger middle pieces and primary rays, and secondary rays have a stronger bending than in *R. podagrosa*. Microdiscohexasters have secondary rays of only one length without differentiated middle pieces (compare Kirkpatrick 1907; Göcke & Janussen 2013). Calycomomes with low numbers of secondary rays are also found in *R. nuda*. Compared to those of *R. podagrosa* these are almost twice as big. Also, the number of secondary rays never exceeds 4, which is lower than in *R. podagrosa* (see Göcke & Janussen 2013). The habitus differs as well: *R. nuda* is very smooth and appears always very clear and visible in underwater-photographs, whereas *R. podagrosa* is usually sediment-covered. *Rossella nuda* has been reported to grow buds of similar shape as those of *R. podagrosa* (Barthel & Tendal 1992), but they are much more rare and never form such dense aggregations of sponges as shown in Fig. 1A for *R. podagrosa*.

TABLE 1. Spicule sizes of *Rossella podagrosa* Kirkpatrick, 1907. Values in µm are given as follows: minimum - mean - maximum (number of spicules measured).

Parameter	P 1635	BMNH 1908.2.5.6 (type)
Rough Pentactine		
tangential ray (L)	50- <u>112.2</u> -150 (30)	60- <u>89.3</u> -120 (30)
proximal ray (L)	70- <u>91.4</u> -120 (7)	60- <u>83.3</u> -130 (9)
Rough Hexactine (D)	60- <u>205.2</u> -280 (30)	150- <u>195.3</u> -270 (30)
Oxyhexactine (D)	150- <u>181</u> -230 (30)	140- <u>192.7</u> -250 (30)
Oxyhexaster (D)	130- <u>173.3</u> -230 (30)	140- <u>174.8</u> -200 (30)
Microdiscohexaster (D)	30- <u>37.3</u> -45 (30)	35- <u>44.9</u> -55 (30)
Mesodiscohexaster (D)	105- <u>129.3</u> -150 (7)	105- <u>118.9</u> -140 (7)
Calycomome		
(D)	190- <u>215</u> -250 (9)	200- <u>225</u> -250 (6)
complete ray (L)	85- <u>110.1</u> -130 (30)	100- <u>115.7</u> -140 (30)
primary ray (L)	5- <u>9.6</u> -15 (30)	7.5- <u>12.3</u> -25 (30)
middle piece (L)	10- <u>13.8</u> -20 (30)	7.5- <u>11.8</u> -20 (30)
secondary ray (L)	62.5- <u>87.1</u> -110 (30)	80- <u>91.4</u> -105 (30)
number of sec. rays	2- <u>4</u> -6 (30)	2- <u>4.3</u> -6 (30)

Discussion

The long and complicated taxonomic history of the genus *Rossella* is summarized in the introduction. It can be brought down to two basic attempts of synonymies, which attempted to bring some order into the high amount of often similar species ascribed to the genus: The first was done by Burton (1929) and later continued by Koltun (1976). The second attempt was done by Barthel & Tendal (1992), which was followed by Göcke & Janussen (2013). It is now obvious that both concepts contain basic systematic weaknesses that compromise the results. Burton (1929) used an attempt that was basically concentrating on the external shape and neglected most spicule information which he discounted as being of minor importance. Furthermore he was led by a strong will to reduce the number of species and therefore would rather join two species than separate them if synonymy was questionable. Koltun (1976) obviously had the same will to reduce species numbers, and was furthermore confused when he re-introduced spicule information into Burton's spicule-less system. As Burton joined species with clearly different spicule inventory, e.g. *R. levis* and *R. nuda*, under one taxon name, the resulting "species" could not have

a distinct characteristic spicule inventory. Koltun realized this, but did not draw the conclusion that different species were joined under one taxon name. Instead he continued synonymizing until he found a working species concept, even though this lumped together many clearly recognizably different forms/species. Barthel & Tendal (1992) realized these problems and tried to establish a new system based on spicules that included habitus information. Thus, they resurrected several former species; however, they based their work mainly on the material sampled during the EPOS-expeditions of RV Polarstern in the Weddell Sea (1989), without much consideration of the type specimens or material from other parts of the Antarctic. Also, they did not put too much emphasis on the habitus information, probably because their material was trawled and therefore delicate specimens as *R. podagrosa* were not recovered in a condition that allowed for much habitus (or *in situ*) information. For this reason they ended up with a somewhat narrow perspective of the diversity of *Rossella* which e. g. did not incorporate *R. podagrosa*, which they still considered a synonym of *R. racovitzae*. However, Barthel & Tendal perceptively reported a strongly bud-producing variant of *R. racovitzae* that they state might be turned into a species at some point. The analysis of several *Rossella* species in Göcke & Janussen (2013) was based only on Weddell Sea material, just as the study of Barthel & Tendal (1992). Here we include material from the Ross Sea showing that *R. podagrosa* is a well-defined species when both habitus and spicule information are carefully considered. It is clear that a proper taxonomical analysis of *Rossella* should include as much material as possible from all around the Antarctic Ocean. More importantly, all information, such as habitus (best alive *in situ*) spicule inventory and molecular data (if available), must be included. *Rossella* once more has proven to be a complicated genus, more than previously thought, and it is still a long way to go to form a proper concept of valid *Rossella* species, including a full revision of holotypes (currently underway), analysis of further material from the whole southern ocean, and detailed molecular analysis.

Budding *Rossella* are not a new phenomenon; they have been reported several times, not only from the Ross Sea, but also from the Weddell Sea (Gutt & Piepenburg 2003; Teixido *et al.* 2006). Unfortunately, the original material of these studies could not be directly sampled, so it was always questionable which species really does this remarkable budding. As we have now re-established *R. podagrosa* and analyzed its budding habit, we come to the assumption, that in many of these cases, it might actually be the respective species, although so far not identified with its proper name due to the complicated synonymy history as shown above. Further inspection is needed to analyze its distribution and see how widespread the species really is, but it may be quite common around Antarctica, although it probably has its main occurrence range in the Ross Sea.

The mode of life of *R. podagrosa* is quite unique, as all other *Rossella* spp. live on, but never within, the sediment. This difference is well visible in Figs. 1C and D where *R. podagrosa* is visible only very slightly by its oscular regions sticking out of the mud, while the more typical *Rossella* appearance is visible in the adjacent large specimens of *R. cf. levis* and *R. antarctica*. *Rossella podagrosa* nonetheless clearly covers most ground in these pictures and is certainly the most abundant species in this area of the Ross Sea. In general, sponges consist of a complicated filtering apparatus with thin channels traversing its tissue, including chambers of flagellate cells which produce a strong current from which food particles are taken in and oscules just release the filtered water (van Soest *et al.* 2012). It is easy to imagine that such a delicate filtering system can easily be clogged by excessive sediment. In addition, some sponges even possess the capacity of self-cleaning, and some are able to shed sediment off their surfaces (Barthel & Wolfrath 1989; Bell, 2004; Schönberg & Suwa 2007). In her study on sponge-associated invertebrate faunas, Kunzmann (1996) showed that sponges with many protruding spicules and especially *R. antarctica* with its thick veil of pentactines shelter many animals from protozoans to large polychaetes and echinoderms. They also catch certain amounts of sediment. This is visible in Fig. 1D as well, where the specimen of *R. antarctica*, although growing clearly above the ground, is heavily covered by sediment and inhabiting invertebrates such as brittle stars. It can be assumed that these associations with presumably very complicated trophic interactions function as “microbial gardens”, in which bacteria settle and form the basic nourishment for the sponges. If this is true, similar processes may be assumed for *R. podagrosa* within the ground. Still, to test this hypothesis we will need much further work on microbes as well as on sponge-associated invertebrates. Another hypothesis is that the half-buried way of living might serve as a kind of hide-out for the sponge saving it from predators like *Acodontaster conspicuus* as proposed by Dayton (1979). If this assumption is true, it might also serve as an explanation for the very high abundances of this species, in combination with its high growth rates.

Conclusions. It is evident that *Rossella podagrosa* Kirkpatrick, 1907 is a valid species. It can be clearly

differentiated from other *Rossella* spp. Furthermore we show that a thorough revision of the genus *Rossella* will need detailed analysis of specimens from all areas of the Antarctic, and that it requires close examination of the habitus (at best based on *in situ* examination) as well as spicule analysis.

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