Polar Biol (2009) 32:1507–1519
DOI 10.1007/s00300-009-0648-8

ORIGINAL PAPER

Taxonomic review of *Haliclystus antarcticus* Pfeffer, 1889 (Stauromedusae, Staurozoa, Cnidaria), with remarks on the genus *Haliclystus* Clark, 1863

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Received: 12 February 2009 / Accepted: 19 May 2009 / Published online: 17 June 2009

Abstract Difficulties concerning the taxonomy of stauromedusae are long known, and there is a clear need for taxonomic revision of the genus *Haliclystus*, as well as the reevaluation of some species. *Haliclystus antarcticus* Pfeffer, 1889 is recorded from Admiralty Bay, King George Island, Antarctic Peninsula. Due to the lack of detailed information on this species, we provide a redescription, presenting new data on the cnidome, morphometry, geographical distribution and intraspecific variation. Based on these characters, we propose that our specimens and *Haliclystus auricula* from Chile and Argentina are synonymous and should be classified as *H. antarcticus*. We also review the worldwide distribution of the genus *Haliclystus* Clark, 1863 and discuss taxonomic issues, concluding that some characters traditionally used in the taxonomy of the group should be used cautiously.

Keywords Southern Ocean · Antarctic Peninsula · Benthos · Lucernariidae · Stauromedusae

Introduction

Staurozoa was recently proposed as a distinct class of the phylum Cnidaria (Marques and Collins 2004). Phylogenetic analyses based on morphological and molecular data indicate its basal position or early divergence within Medusozoa (Marques and Collins 2004; Collins et al. 2006; Van Iten et al. 2006). The class Staurozoa has only one order, Stauromedusae, comprising six families, 15 genera and approximately 50 species (Daly et al. 2007; Bisby et al. 2008; Mills 2009). This traditional classification does not yet have a phylogenetic framework, and it includes some non-monophyletic groups (Collins and Daly 2005 for the Lucernariidae and Depastridae).

The stauromedusae, or stalked jellyfishes, have a cosmopolitan distribution (Lutz et al. 1998), but the latitudinal distribution of the species is unequal. Approximately 80% of the species are found in the northern hemisphere, viz. North Pacific, North Atlantic, Arctic Ocean and Mediterranean (maybe related to the fact that the northern hemisphere has about 80% of the land mass of the earth). Only 11 species have been recorded from the southern hemisphere (Grohmann et al. 1999; Bisby et al. 2008), and most of them are found in higher latitudes, both temperate and polar waters (Mayer 1910; Bisby et al. 2008).

Notwithstanding its broad distribution, the group has been scarcely studied and knowledge concerning its biology and ecology is limited, especially regarding the southern hemisphere (Davenport 1998; Zagal 2004a). Indeed, despite broader research programs focusing on the biodiversity of the Southern Ocean (Arntz 1997), the research effort applied to different taxonomic groups has not been uniform (López-Gonzáles and Gili 2000).

Eight formally described species and two commonly adopted names (*nomina nuda*, *Haliclystus "californiensis"* and *Haliclystus "sanjuanensis"*) of the genus *Haliclystus* are recorded for the northern hemisphere, and only three species for the southern hemisphere (Figs. 1, 2; see also Bisby et al. 2008). Among the austral species, *Haliclystus antarcticus* was originally described by Pfeffer (1889), and subsequently studied by Carlgren (1930, taxonomy and

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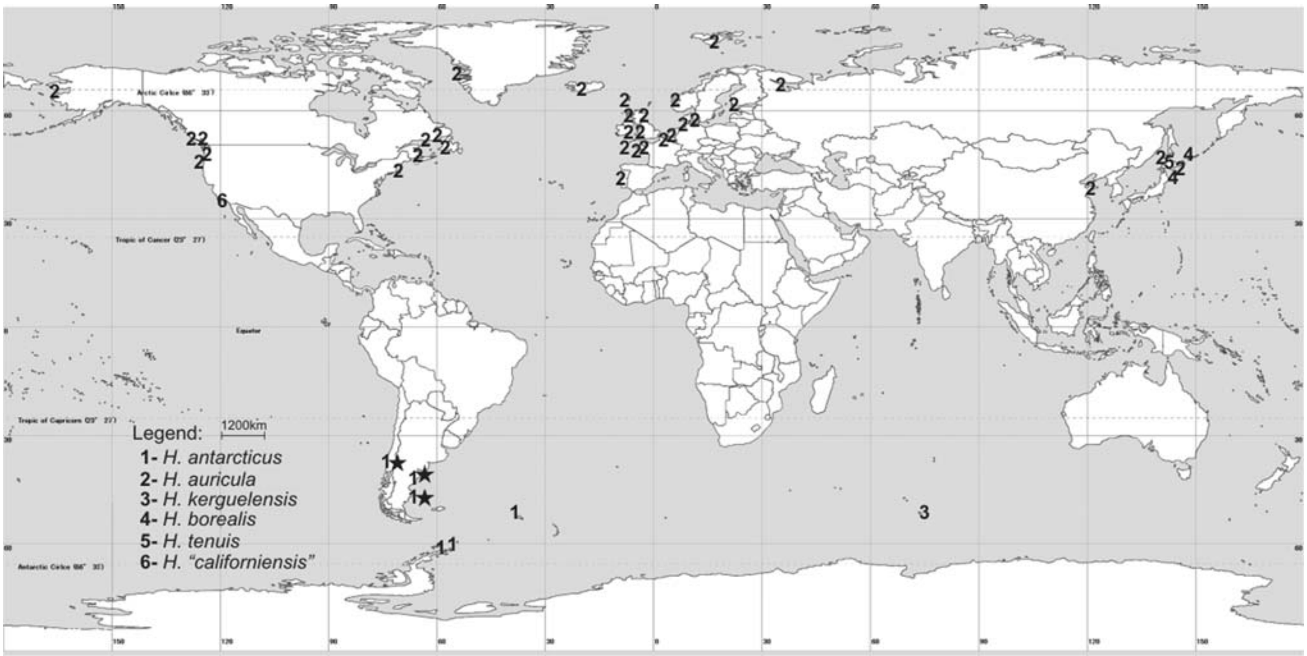

Fig. 1 Global distribution of selected species of the genus *Haliclystus* (part 1). *H. antarcticus*, *H. auricula* (unspecific locality for Greenland coast), *H. kerguelensis*, *H. borealis*, *H. tenuis* and *H. "californiensis"* (Pfeffer 1889; Kishinouye 1910; Mayer 1910; Uchida 1929; Carlgren 1930; Kramp 1961; Amor 1962; Corbin 1979; Hirano 1986, 1997; Mianzan 1989; Davenport 1998; Hansson 1998; Grohmann et al. 1999; Zagal 2004a, b, 2008; Mills and Larson 2007; and Smithsonian online database (http://nhbacsmith2.si.edu/emuwebizweb/pages/nmnh/iz/Query.php. Accessed 03 Jun 2008) *H. antarcticus* highlighted with a star were originally misidentified as *H. auricula*, see text

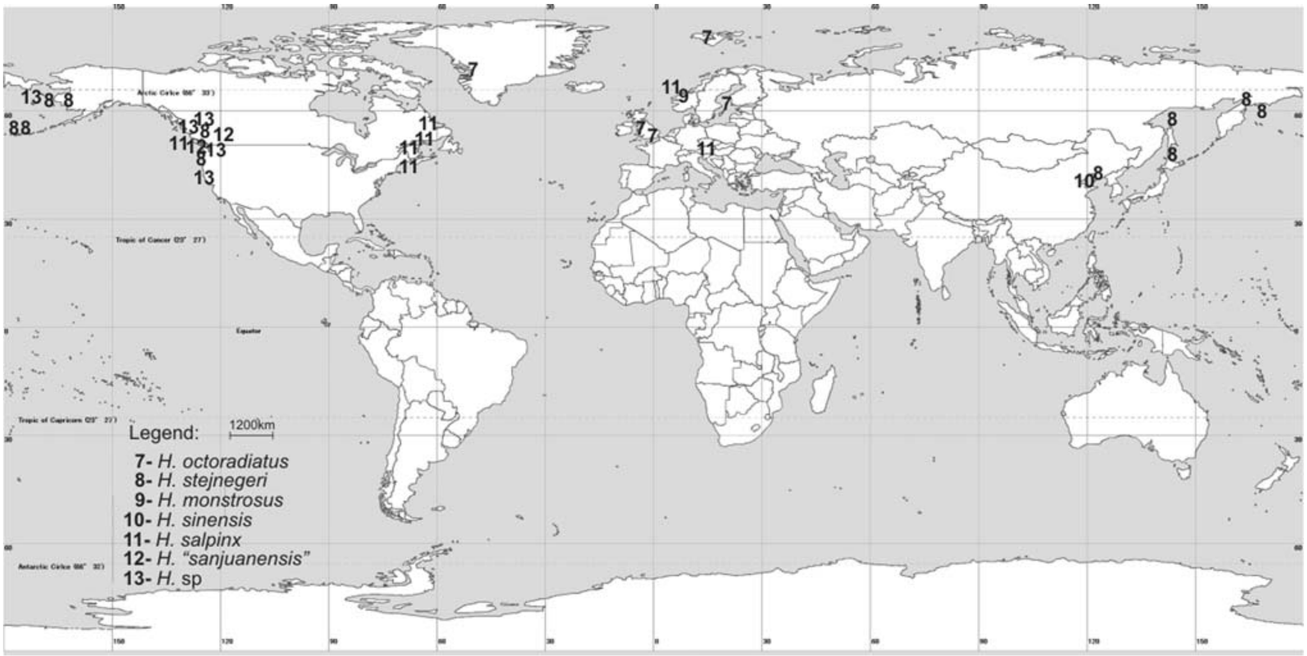

Fig. 2 Global distribution of selected species of the genus *Haliclystus* (part 2). *H. octoradiatus* (unspecific locality for Greenland coast), *H. stejnegeri*, *H. monstrosus*, *H. sinensis*, *H. salpinx*, *H. "sanjuanensis"* and *Haliclystus* sp. (Browne 1895; Mayer 1910; Uchida 1929; Ling 1937; Hirano 1986; Kramp 1961; Otto 1976; Hansson 1998; and Smithsonian online database (http://nhbacsmith2.si.edu/emuwebizweb/pages/nmnh/iz/Query.php. Accessed 03 Jun 2008)

histology) and Davenport (1998, trophic relationships). Other literature dealing with *H. antarcticus* consists only of compilations (Mayer 1910; Thiel 1936; Kramp 1961).

Hirano (1997:251) discussed some taxonomic issues of *Haliclystus*, noting the importance of more detailed studies that include southern species. Indeed, we consider further

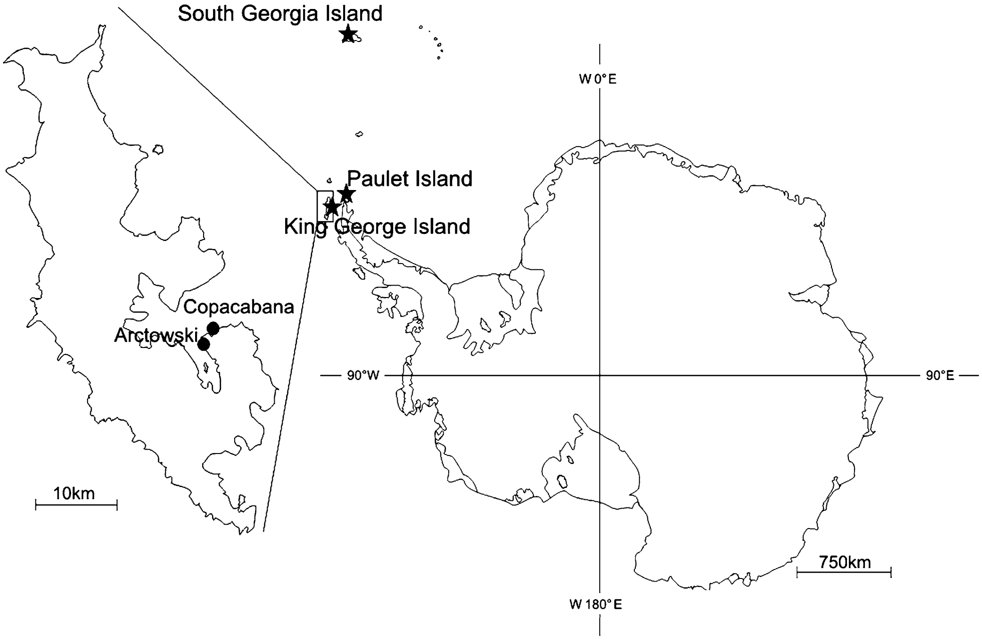

Fig. 3 Map of Antarctica, highlighting the South Georgia Island, type locality of *Haliclystus antarcticus*, Paulet Island, and King George Island, new record for the species. Detail of King George Island, evidencing the collection points of *H. antarcticus*, Polish Arctowski Station and the US Copacabana Refuge

studies on the biology, morphological intraspecific diversity and geographical distribution of *H. antarcticus* to be of utmost importance in understanding the genus. Therefore, the goal of this study is to fully redescribe the species, presenting new data on its cnidome, morphometry and distribution.

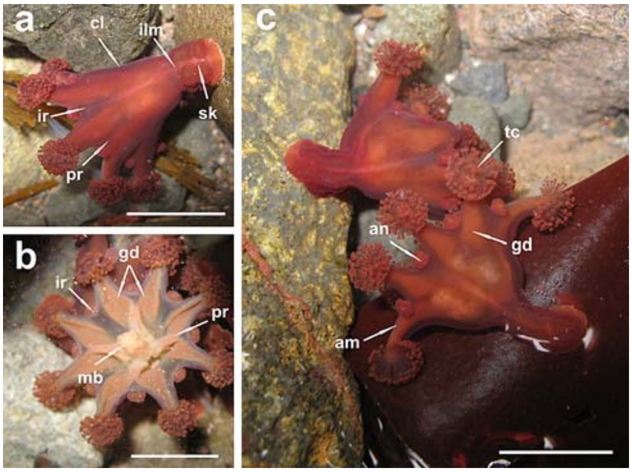

Fig. 4 Living specimens of *Haliclystus antarcticus* in the field. **a** Specimen in side view with contracted stalk, attached to rock: *cl* calyx, *ilm* interradial longitudinal muscle, *ir* interradius, *pr* perradius, *sk* stalk; **b** specimen in oral view: *gd* gonads, *ir* interradius, *mb* manubrium, *pr* perradius; **c** specimens in side view attached to rock and algae (Rhodophyta *Iridaea cordata*): *am* arms, *an* anchors, *gd* gonads, *tc* tentacle cluster. Scale = 1.2 cm

Materials and methods

Specimens of *H. antarcticus* were collected manually during low tide (tide prediction between 0.2 and 0.4 m) on two beaches in Admiralty Bay, King George Island, Antarctic Peninsula (Fig. 3): (A) Pieter Lenie, in Copacabana (North American Refuge, 62°10′S, 58°26′W) and (B) Shag Point, in Arctowski (Polish Station, 62°10′S, 58°31′W). Material was collected on 16 and 17 February, and 1 March 2007, during the XXV Brazilian Antarctic Program. Individuals of *H. antarcticus* were attached to algae *Iridaea cordata* (Rhodophyta) or rocks (Fig. 4) around 0.1–1.0 m deep. Specimens of *Haliclystus* from Chile were also collected manually, during low tide, on Los Molinos beach, Valdivia, Chile. Material was collected on 11 March 2009. Individuals were attached to algae *Gracilaria chilensis* (Rhodophyta) and *Ulva lactuca* (Chlorophyta). They were all preserved directly in 4% formaldehyde solution in seawater or in 80% ethanol. Qualitative observations were made based on 184 individuals (134 from Antarctica and 50 from Chile) and measurements of material were made with 60 individuals (50 from Antarctica and 10 from Chile) preserved in formaldehyde solution. Nematocyst types and distribution were determined using a light microscope. Only capsules of undischarged nematocysts were measured (*n* = 10). Selected parts of individuals for scanning electron microscopy were dehydrated in a graded series of ethanol, dried in a critical point dryer, and sputter-coated with gold (modified from Migotto and Marques 1999). Studied materials were deposited in the Cnidarian Collection of the Museu de Zoologia of the Universidade de São Paulo (MZUSP), São Paulo, Brazil; in the Cnidarian Collection of Zoology Department of the Universidade Federal do Rio de Janeiro (DZUFRJ), and in the Cnidarian Collection of the Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro, Brazil.

Taxonomy

Haliclystus antarcticus Pfeffer, 1889 (Figs. 4–8)

Haliclystus antarcticus, Pfeffer 1889:52–53; Mayer 1910:536; Thiel 1936:167; Uchida 1929:154; Carlgren 1930:1–6, Figures 1–9; Kramp 1961:292; Davenport 1998:663–664; Grohmann et al. 1999:386.

Haliclystus auricula, Amor 1962:89–96, Figures 1–2; Zagal 2004a:331–336; 2004b:337–340; 2008:259–262, Figure 1 [non *Lucernaria auricula* Rathke, 1806, = *Haliclystus auricula* (Rathke, 1806)]

Type series

The material used by Pfeffer (1889) to describe the species is lost. We also did not find other materials from South Georgia Island studied by Carlgren (1930, no reference in the paper) and Davenport (1998, no reference in the paper and no reply to our contacts). We, therefore, designate as Neotype of the species the specimen MZUSP 1551, from Pieter Lenie Beach, Copacabana Refuge (USA), Admiralty Bay, King George Island, Antarctic Peninsula, 62°10′S 58°26′W, 17 Feb 2007, depth 0.5 m (tide prediction 0.2–0.4 m), fertile specimen on alga *Iridaea cordata*, formaldehyde solution, col. and det. A.C. Morandini.

Type locality

South Georgia Island, Antarctica (Pfeffer 1889).

Material examined

Pieter Lenie Beach, Copacabana Refuge (USA), Admiralty Bay, King George Island, Antarctic Peninsula, 62°10′S 58°26′W, 17 Feb 2007, depth 0.5 m (tide prediction 0.2–0.4 m), fertile specimen on algae *Iridaea cordata*, formaldehyde solution, col. and det. A.C. Morandini, NEOTYPE MZUSP 1551; Shag Point, Arctowski Polish Station, Admiralty Bay, King George Island, Antarctic Peninsula, 62°10′S 58°31′W, 16 Feb 2007, depth 0.5 m (tide prediction 0.2–0.4 m), fertile specimens on algae *Iridaea cordata*, formaldehyde solution, col. and det. A.C. Morandini, 3 individuals MZUSP 1552; Shag Point, Arctowski Polish Station, Admiralty Bay, King George Island, Antarctic Peninsula, 62°10′S 58°31′W, 16 Feb 2007, depth 0.5 m (tide prediction 0.2–0.4 m), fertile specimens on algae *Iridaea cordata*, ethanol, col. and det. A.C. Morandini, 2 individuals MZUSP 1553; Pieter Lenie Beach, Copacabana Refuge (USA), Admiralty Bay, King George Island, Antarctic Peninsula, 62°10′S 58°26′W, 17 Feb 2007, depth 0.5 m (tide prediction 0.2–0.4m), fertile specimens on algae *Iridaea cordata* or rocks, formaldehyde solution, col. and det. A.C. Morandini, 5 individuals MZUSP 1554; Pieter Lenie Beach, Copacabana Refuge (USA), Admiralty Bay, King George Island, Antarctic Peninsula, 62°10′S 58°26′W, 17 Feb 2007, depth 0.5 m (tide prediction 0.2–0.4 m), fertile specimens on algae *Iridaea cordata* or rocks, formaldehyde solution, col. and det. A.C. Morandini, 4 individuals MZUSP 1555; Pieter Lenie Beach, Copacabana Refuge (USA), Admiralty Bay, King George Island, Antarctic Peninsula, 62°10′S 58°26′W, 17 Feb 2007, depth 0.5 m (tide prediction 0.2–0.4 m), fertile specimens on algae *Iridaea cordata* or rocks, formaldehyde solution, col. and det. A.C. Morandini, 50 individuals MZUSP 1556; Pieter Lenie Beach, Copacabana Refuge (USA), Admiralty Bay, King George Island, Antarctic Peninsula, 62°10′S 58°26′W, 17 Feb 2007, depth 0.5 m (tide prediction 0.2–0.4 m), fertile specimens on algae *Iridaea cordata* or rocks, formaldehyde solution, col. and det. A.C. Morandini, 35 individuals MZUSP 1557; Pieter Lenie Beach, Copacabana Refuge (USA), Admiralty Bay, King George Island, Antarctic Peninsula, 62°10′S 58°26′W, 17 Feb 2007, depth 0.5 m (tide prediction 0.2–0.4 m), fertile specimens on algae *Iridaea cordata* or rocks, ethanol, col. and det. A.C. Morandini, 30 individuals MZUSP 1558; Pieter Lenie Beach, Copacabana Refuge (USA), Admiralty Bay, King George Island, Antarctic Peninsula, 62°10′S 58°26′W, 17 Feb 2007, depth 0.2 m (tide prediction 0.2–0.4 m), fertile specimens on rocks, formaldehyde solution, col. and det. A.C. Morandini, 2 individuals DZUFRJ 1-047; Pieter Lenie Beach, Copacabana Refuge (USA), Admiralty Bay, King George Island, Antarctic Peninsula, 62°10′S 58°26′W, 01 Mar 2007, depth 0.2 m (tide prediction 0.2–0.4 m), fertile specimens on rocks, formaldehyde solution, col. and det. A.C. Morandini, 2 individuals MNRJ 7671; Los Molinos, Valdivia, Chile, 11 Mar 2009, specimens on algae *Gracilaria chilensis* (Rhodophyta) and *Ulva lactuca* (Chlorophyta), formaldehyde solution, col. J.P. Didier, 20 individuals MZUSP 1559; Los Molinos, Valdivia, Chile, 11 Mar 2009, specimens on algae *Gracilaria chilensis* (Rhodophyta) and *Ulva lactuca* (Chlorophyta), ethanol solution, col. J.P. Didier, 30 individuals MZUSP 1560.

Description

Calyx conical (Fig. 4a), maximum diameter 1.25 times wider than high, height 3.5–16.2 mm (mean 9.9 ± 3.2 mm, $n = 50$) excluding tentacular clusters, width 4.1–23.4 mm (12.4 ± 4.4 mm), semi-translucent, separated from stalk. Stalk morphologically distinct from calyx (umbrella) (Fig. 4a), sometimes marked by thin stria, sometimes with no constriction at all. Outer surface of calyx (exumbrella) smooth (Fig. 4).

Eight adradial arms (Figs. 4c, 5) (abnormal specimens with 7–12), length 0.3–6.0 mm (2.3 ± 1.1 mm) excluding tentacular clusters. Distal internal region of arms thicker in

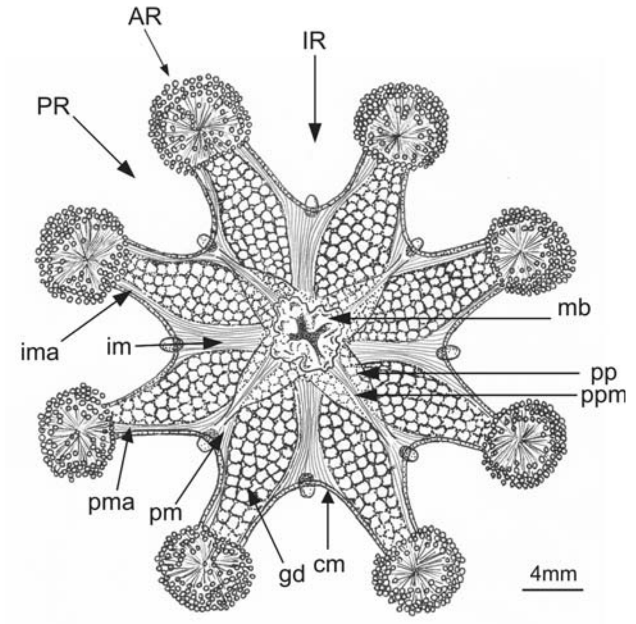

Fig. 5 Representation of the oral view of *Haliclystus antarcticus*: *AR* adradius, *IR* interradius, *PR* perradius, *im* interradial muscle, *ima* interradial muscles extending to the tip of the arm, *pm* perradial muscle, *pma* perradial muscle extending to the tip of the arm, *gd* gonads, *cm* coronal muscle, *mb* manubrium, *pp* perradial pouches, *ppm* perradial pouches muscle

mature specimens due to gonadal content, forming a groove about half of an arm midline (Fig. 6b). Arms generally equidistant (Fig. 5), distance from the distal end of arms (base of tentacular cluster) to anchors 0.3–6.6 mm (2.7 ± 1.3 mm). Distal region of each arm with 6-224 (97 ± 40) capitate tentacles (Figs. 4c, 6a, g); centripetal (towards mouth/subumbrella) tentacles smaller, larger tentacles at the central area of the cluster, centrifugal tentacles (towards margin/exumbrella) of intermediate size (Figs. 6h, 8a, b). Each tentacle with hollow stem and distal globular end (Fig. 6i) covered with nematocysts. Internal base of tentacular cluster with intertentacular lobules (Fig. 6j, k).

"U"-shaped coronal muscle in eight segments, each segment extending between distal regions of successive arms (Figs. 5, 7b, 8i). Radial muscle arranged in eight bands (four perradial and four interradial), centripetal to the coronal muscle, from the subumbrellar rim to the manubrium (Figs. 5, 8a).

One anchor centered between successive arms (abnormal specimens with 0–3) (Fig. 4c), located at the umbrellar rim, projecting towards the exumbrella, height 0.3–3.1 mm (1.6 ± 0.6 mm), width 0.4–2.7 mm (1.2 ± 0.4 mm), totaling eight anchors, four perradial and four interradial (Fig. 6g). Anchors stalked, height of cylindrical stalk 0.05–0.51 mm (0.2 ± 0.1 mm) (Figs. 7a, 8g). The anchor morphology varies during ontogeny: at early ontogenetic stage (after metamorphosis to medusae) the anchors are circular, sometimes with a tentacular knob; juvenile anchors triangular, with a shallow groove at the basal region; median to late ontogenetic stages apparently cross constricted at the central region, approximately "8"-shaped, forming a longitudinal groove at the central region (Figs. 7d–g, 8d–f). Adult anchors generally with wrinkled aspect.

Aboral stalk (Fig. 4a) four-chambered internally over the entire length; length 2.3–10.7 mm (6.5 ± 2.0 mm), externally divided into four regions (four furrows, not necessarily clear in juveniles) by four interradial longitudinal muscles (Fig. 4a), which extend all along the stalk upwards, reaching the manubrium, and subdivided towards the subumbrellar rim of the arms (Figs. 4, 5, 6m). Base of stalk with adhesive disc of wrinkled aspect, diameter 1.5–8.0 mm (4.2 ± 1.5 mm) (Figs. 6n, 8j).

Manubrium (Figs. 4b, 5) four-sided in cross section, each interradial face cross-striated from base of manubrium up to three-fourths of its height; each face separated by four bands of perradial muscles extending from mouth corners to perradial anchors (Fig. 5). Mouth four-sided, delicately pleated and frilled lips; interradial face projected outwards at the buccal rim, which is cut out in the area corresponding to the cross striations of the manubrium (Fig. 6a, c, e, f).

Four perradial pouches at the gastrovascular cavity (not visible in juveniles), extending from the manubrium to the perradial anchors, separated from each other by four interradial septa (Figs. 4b, 5, 6c). Pouches with gonads on the inner wall. Numerous gastric cirri at the perradial corner (=pouch centrifugal end) of the gastrovascular cavity (Fig. 6d).

Eight adradial gonads extending from the manubrium to the distal end of arms (Fig. 5), visible through translucent calyx (Fig. 4c), organized into four pairs (Figs. 4b, 5). Gonadal length 1.6–12.9 mm (6.9 ± 2.2 mm). Each pair of gonads arising centripetally at perradii, gonads somewhat parallel up to half of their length, then separating adradially (Figs. 4b, 5, 6a). Successive pairs of gonads completely separated at the interradii by interradial septa (Figs. 4b, 5). Gonads comprised of numerous small vesicles, organized in 6–12 rows, each vesicle circular to hexagonal in shape (probably due to tightly packed arrangement), maximum width 0.5–0.65 mm (0.6 ± 0.04 mm) (Figs. 6d, 8c). Gonads mature in specimens with calyx height of about 11.72 mm and above.

Living specimens red-orange in colour with light-red gonads (Fig. 4) in King George Island, Antarctica; and specimens red or/and green in colour (some individuals presented calyx and stalk green and tentacles red, for example, others are completely green or red) in Valdivia, Chile. Oral surface largely unpigmented. Preserved individuals rosy-cream in colour.

Capitulum of tentacles with two types of nematocysts (Fig. 7k–m): isorhiza (atrichous or holotrichous—light microscopy was insufficient to distinguish the spines),

Fig. 6 Morphological characters of preserved *Haliclystus antarcticus*. **a** *gd* gonads, *ir* interradius, *pr* perradius, *tc* tentacular cluster; **b** *am* arm, *gv* groove over about half of arm midline; **c** *ir* interradii, *mb* manubrium, *pp* perradial pouches; **d** *gc* gastric cirri, *gd* gonads, *pp* perradial pouches with gonads at inner wall; **e** *lp* frilled lips of the mouth, *mb* manubrium; **f** *st* manubrium striations; **g** *ac* anchor, *am* arm, *tc* tentacular cluster; **h** *lt* larger tentacles, *st* smaller tentacles; **i** *ge* distal globular end of tentacle, *hs* hollow stem of tentacle; **j** longitudinal section of arm, showing internal space with intertentacular lobules (*il*); **k** detail of intertentacular lobules (*il*); **l** gonads (*gd*) extending until the end of the arms; **m** *sk* stalk; **n** *ad* adhesive disc at the base of stalk; **o** individual with two stalks (*sk*). *Scales*: **a**–**j** 1.2 mm, **k** 1.0 mm, **l** 0.60 mm, and **m**–**o** 1.05 mm

abundant, length 14.0–17.0 μm (15.3 ± 0.08 μm), diameter 4.0–6.0 μm (5.0 ± 0.05 μm); microbasic heterotrichous, scarce, length 15.0–20.0 μm (17.8 ± 0.15), diameter 8.0–10.0 μm (9.0 ± 0.05 μm). Gastric cirri with microbasic heterotrichous, abundant, length 10.0–12.0 μm (10.6 ± 0.06 μm), diameter 5.0–9.0 μm (6.3 ± 0.11 μm), and isorhiza (atrichous or holotrichous), scarce, length 11.0–14.0 μm (12.3 ± 0.12 μm), diameter 3.0–4.0 μm (3.5 ± 0.05 μm). Anchors with scarce microbasic heterotrichous, length 8.0–10.0 μm (9.0 ± 0.14 μm), diameter 5.0–6.0 μm (5.5 ± 0.07 μm). Exumbrella with scattered microbasic heterotrichous, abundant, length 7.0–10.0 μm (9.2 ± 0.12 μm), diameter 4.0–6.0 μm (4.9 ± 0.05 μm). Subumbrella with two types of nematocysts: isorhiza (atrichous or holotrichous), abundant, length 10.0–14.0 μm (12.4 ± 0.13 μm), diameter 3.0–4.0 μm (3.1 ± 0.03 μm); microbasic heterotrichous, scarce, length 10.0–20.0 μm (15.8 ± 0.44 μm), diameter 6.0–10.0 μm (9.2 ± 0.17 μm).

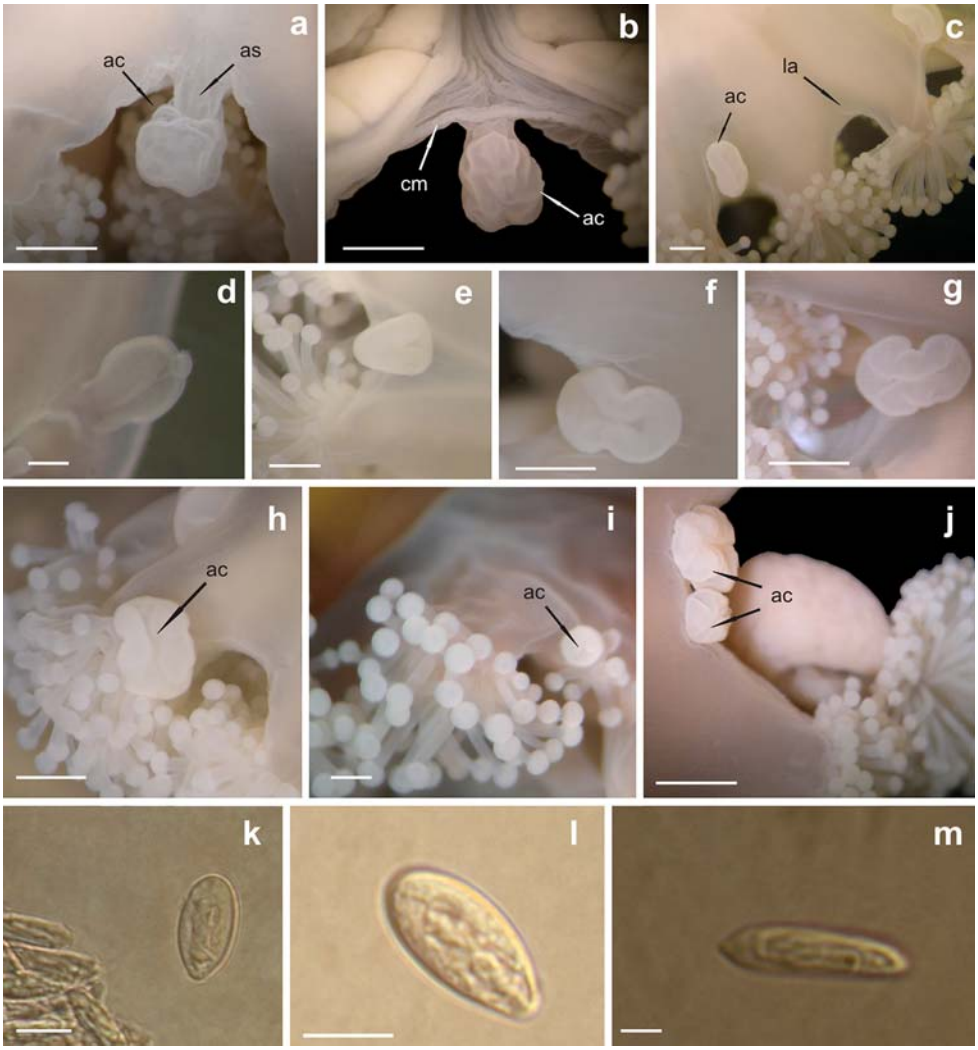

Fig. 7 Details of anchor, tentacle cluster and nematocysts of preserved *Haliclystus antarcticus*. **a** *ac* anchor, *as* anchor stalk; **b** *ac* anchor, *cm* coronal muscle; **c** *ac* anchor, *la* lacking anchor; **d**–**g** anchor development: **d** anchor with a tentacular knob at young specimen (without gonads); **e** triangular anchor, with a shallow groove at basal region; **f** median ontogenetic stage cross constricted at central region, approximately “8”-shaped, forming a longitudinal groove at central region; **g** mature specimen, with wrinkled aspect; **h** anchor (*ac*) together with tentacular cluster; **i** abnormal anchor (*ac*) together with tentacular cluster; **j** specimen with two anchors (*ac*); **k** nematocysts; **l** microbasic heterotrichous; **m** isorhiza (atrichous or holotrichous). *Scales* **a**–**c, f**–**h**, **j** 2.3 mm, **d**, **i** 0.4 mm, **e** 1.0 mm, **k**, **l** 9.0 µm and **m** 5.0 µm

Distribution

Antarctica: South Georgia Island (Pfeffer 1889; Carlgren 1930; Davenport 1998); King George Island, Admiralty Bay, Shag Point (this study); King George Island, Admiralty Bay, Pieter Lenie (this study); Graham Land, Paulet Island (Carlgren 1930). Argentina: Chubut and Santa Cruz (Amor 1962; Mianzan 1989; as *H. auricula*). Chile: Valdivia (this study and Zagal 2004a, b, 2008; as *H. auricula*).

Discussion

Difficulties concerning the taxonomy of stauromedusae are long known (Mayer 1910:522; Gwilliam 1956:61; Kramp 1961:293), and the need for taxonomic revision of the genus *Haliclystus*, as well as the reevaluation of some species, has been urged by Hirano (1997). We have documented intraspecific and ontogenetic variation in the following characteristics that have been used in the taxonomy of Staurozoa: presence/absence of anchors and their morphology, arrangement of arms, number and shape of tentacles, relations between “size of stalk” and “size of calyx”, and morphological separation between calyx and stalk (Mayer 1910; Kramp 1961; Kikinger and Salvini-Plawen 1995), besides differences in number of gonadal sacs per gonad (Gwilliam 1956). These characters, then, must be carefully assessed when employed in the taxonomy of the group.

Hirano (1997:247) reviewed several species of *Haliclystus* having a circumboreal distribution and recognized two important characters defining groups (Table 1): the morphology of the base of the tentacle clusters and the location of white spots of nematocysts on the subumbrella. These characters led her to distinguish two complexes of species, those with intertentacular lobules located internally at the base of the tentacular cluster [*H. auricula*; *Haliclystus octoradiatus* (Lamarck, 1816); *H. “sanjuanensis”, nomen nudum*; *Haliclystus stejnegeri* Kishinouye, 1899] and those with a “U”-shaped interspace and without intertentacular

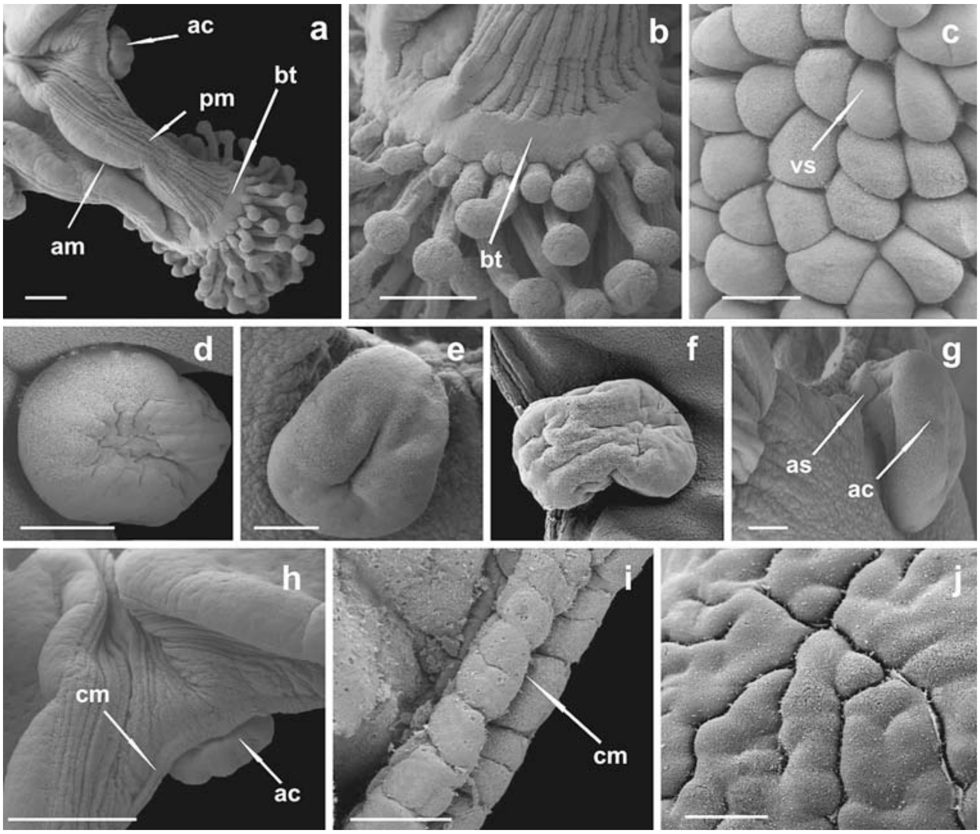

Fig. 8 Scanning electron micrographs of *Haliclystus antarcticus*. **a** *ac* anchor, *am* arm, *bt* rectangular internal space at the base of tentacular cluster, *pm* perradial muscles; **b** *bt* detail of rectangular internal space at the base of tentacular cluster; **c** *vs* gonadal vesicles; **d** circular anchor at young specimen (without gonads); **e** triangular anchor, with a shallow groove at basal region; **f** mature specimen, with wrinkled aspect; **g** *ac* anchor, *as* anchor stalk; **h** *ac* anchor, *cm* coronal muscle; **i** *cm* coronal muscle in detail; **j** base of stalk with adhesive disc of wrinkled aspect. *Scales* **a**, **b**, **f**, **h** 1.2 mm, **c** and **e** 0.6 mm, **d** 0.4 mm; **g** 0.2 mm; **i** 0.13 mm; and **j** 1.0 mm

lobules at that region (*Haliclystus tenuis* Kishinouye, 1910; *Haliclystus borealis* Uchida, 1933; *H. "californiensis"* of Gwilliam 1956). These two complexes are subdivided according to the location of white spots of nematocysts. *Haliclystus antarcticus* possesses the same pattern as *H. auricula*, with intertentacular lobules at the internal base of the tentacular cluster and without white spots of nematocysts.

Another character that seemed to divide the genus *Haliclystus* into two groups is the arrangement of the gonads. Apparently, according to the literature, there are two different patterns: the "Y-pattern" in which the two halves of each pair of gonads are close together at their perradial point of origin at the base of the bell (present in *H. antarcticus* and *H. octoradiatus*; see Browne 1895), and the pattern in which the proximal half of the gonads is connected in pairs at the interradii, but are completely separated in the perradii (present in *H. auricula*, *Haliclystus monstrosus* Naumov, 1961 and *H. borealis*; see Clark 1878; Hirano 1986; Kramp 1961; Naumov 1961). The pattern for *H. stejnegeri* is controversial: Hirano (1986) considers the pattern similar to that of *H. antarcticus*, and Uchida (1929) and Kramp (1961) consider it similar to that of *H. auricula*. However, in our observations of several specimens of the genus *Haliclystus* of the collection of the National Museum of Natural History, Smithsonian Institution, all species analysed [identified as *H. auricula* (USNM 54518), *H. stejnegeri* (USNM 1106655, USNM 1106935, USNM 1106936, USNM 1106937, USNM 1106938, USNM 1106939), *H. "sanjuanensis"* (USNM 1106653, 1106663, 1106664, 1106665), *H. borealis* (USNM 1106650) and *H. tenuis* (USNM 1106651, 1106652)] have the gonads united at the perradii. So that characteristic needs to be reevaluated for the different species of *Haliclystus*.

The problem of finding clues to relationships among the stauromedusae is aggravated by the relatively few macromorphological characters that may be used for taxonomy (Hirano 1997). The species *H. octoradiatus*, *H. "sanjuanensis"*, *H. tenuis*, for example, have all been considered by some authors to be synonyms with *H. auricula* (Kramp 1961; Gwilliam 1956). However, from our point of view, there are enough characteristics to distinguish these species (Table 1), and they should be recognized as valid. Indeed, similarities between *H. antarcticus* and other species of the genus, such as *H. octoradiatus* (Carlgren 1930), *H. stejnegeri* (Hirano 1986) and *H. kerguelensis* Vanhöffen 1908 (Mayer 1910), have been noted in literature, with differences mainly based on morphometrical patterns (e.g. differences in proportions of the body parts). Among them, *H. kerguelensis* is the only other Antarctic species of the class (besides *H. antarcticus*, Fig. 1), and it was recorded from Kerguelen Island (Vanhöffen 1908; Kramp 1957). Mayer (1910:536) emphasized the similarities between *H. kerguelensis* and *H. antarcticus*, but they pointed out

Table 1 Comparisons of diagnostic characteristics of the species of *Haliclystus*

Species	White spots of nematocysts		Location of white spot of nematocysts	Number of tentacles per cluster	Stalk	Shape of anchors	Height of anchors × diameter of stalk	Rows of sacs per gonad	Internal base of tentacular cluster		References
	Present	Absent							“U-shaped”, without intertentacular lobules	Shallow internal space, with intertentacular lobules	
Haliclystus antarcticus	–	X	–	6–224	Half to two-thirds as long as the height of the calyx	Oval	Half to two-thirds as wide as the diameter of the stalk	6–12	–	X	Current data
Haliclystus auricula	–	X	–	30–120	About as long as the height of the calyx	Oval	One-third to one-fourth as wide as the diameter of the stalk	6–8	–	X	Rathke 1806; Clark 1863; Mayer 1910; Gwilliam 1956; Kramp 1961; Hirano 1997
Haliclystus borealis	X	–	Subumbrellar bell margin, in the perradii and interradii	20–30	Less than one-third as long as the height of the calyx	Circular	Two-thirds as wide as the diameter of the stalk	3–4	X	–	Uchida 1933; Uchida and Hanaoka 1934; Kramp 1961; Hirano 1986, 1997
Haliclystus “californiensis”	X	–	Subumbrellar bell margin in the perradii and interradii	60–70	Four to five times shorter than the calyx	Large cushion, imperfectly divided into two	Half as wide as the diameter of the stalk	3–4 abreast in the widest portion of the gonad	X	–	Gwilliam 1956; Hirano 1997
Haliclystus kerguelensis	?	?	?	Up to 50	Twice as long as height of calyx	Oval	One-third as wide as the diameter of the stalk	?	?	?	Vanhöffen 1908; Mayer 1910; Kramp 1957, 1961
Haliclystus monstrosus	?	?	?	100	Half as long as the height of the calyx	Trumpet shaped	Two-thirds to half as wide as the diameter of the stalk	4–6	?	?	Naumov 1961
Haliclystus octoradiatus	X	–	Subumbrellar bell margin in the interradii, and at the top of the gonads in the perradii	30–60	About as long as the height of the calyx	Oval	Half as wide as the diameter of the stalk	2	–	X	Lamarck 1816; Clark 1863; Browne 1895; Mayer 1910; Hirano 1997
Haliclystus salpinx	X	–	Subumbrellar bell margin and along the perradial margin of the gonads	60–250	Longer than the height of the calyx	Trumpet shaped	About as long and wide as the diameter of the stalk	4	X	–	Clark 1863; Mayer 1910; Gwilliam 1956; Kramp 1961
Haliclystus “sanjuanensis”	X	–	Perradially at the top of the gonads	Up to 130	Two-thirds as long as the height of the calyx	Oval	Half as wide as the diameter of the stalk	10–22 irregularly arranged (not in rows), abreast in the widest portion of the gonad	–	X	Hyman 1940; Hirano 1997; Mills and Larson 2007
Haliclystus sinensis	X	–	Subumbrellar bell margin	22	Half as long as the height of the calyx	Circular, wider than high	Half to one-third as wide as the diameter of the stalk	1	?	?	Ling 1937
Haliclystus stejnegeri	X	–	Subumbrellar bell margin, in perradii, and along the edge of the gonads	70–100	Half as long as the height of the calyx	Oval	Half as wide as the diameter of the stalk	6–8, irregularly arranged (not in rows), abreast in the widest portion of the gonad	–	X	Kishinouye 1899; Mayer 1910; Gwilliam 1956; Kramp 1961; Hirano 1986, 1997
Haliclystus tenuis	X	–	Subumbrellar bell margin in the interradii and perradii, and along subumbrella in the perradii	35–45	Half as long as the height of the calyx	Circular, slightly heart shaped	Diameter as long as that of the stalk	2	X	–	Kishinouye 1910; Hirano 1997

Table 2 Measures (maximum, minimum and mean; in mm) of morphological characters of *Haliclystus antarcticus* from Antarctica ($n = 50$), *Haliclystus* sp. from Chile ($n = 10$) and *H. auricula* from Argentina

	Calyx height	Calyx width	Anchors height	Anchors width	Arms lenght	Distance from the distal end of arms to anchors	Stalk length	Base of stalk
Haliclystus antarcticus	3.5–16.2 (9.9)	4.1–23.4 (12.4)	0.3–3.1 (1.6)	0.4–2.7 (1.2)	0.3–6.0 (2.3)	0.3–6.6 (2.7)	2.3–10.7 (6.5)	1.5–8.0 (4.2)
Haliclystus sp. (Chile)	4.1–7 (5.74)	6.9–13.8 (10.3)	0.7–1.5 (1.09)	0.6–1.3 (0.83)	1.0–2.5 (1.69)	1.2–3.0 (1.95)	2.9–5.0 (3.63)	1.7–3.1 (2.57)
Haliclystus auricula (Argentina)[a]	(9.0)	(17.0)	(2.0)	(1.5)	?	?	(6.0)	(4.0)

[a] Only mean, cf. Amor 1962

that *H. kerguelensis* has “fewer tentacles, smaller anchors and apparently a longer peduncle, although the stalk of *H. antarcticus* was probably contracted in Pfeffer’s preserved specimens”, and had different colours. Indeed, *H. kerguelensis* has up to 50 tentacles (Kramp 1961) and *H. antarcticus* has about 97 tentacles per cluster (Table 1), but as we pointed out, the number of tentacles can vary according to the life cycle stage (*H. antarcticus* presents a variation of 6-224 tentacles per cluster). In fact, anchors of *H. kerguelensis* seem to be smaller than anchors of *H. antarcticus*: the first one is one-third as wide as the diameter of the stalk (Mayer 1910) and the second one is about one-half to two-thirds as wide as the diameter of the stalk (Table 1). Concerning the stalk, *H. kerguelensis* has the “peduncle about twice as long as height of calyx” (Kramp 1961), and our analysis with relaxed individuals show that it is one-half to two-thirds as long as the height of the calyx for *H. antarcticus*. So, this is another difference that can be valid. The colours of *H. kerguelensis* can be rather different from those described by Vanhöffen (Kramp 1957), likewise colours in *H. antarcticus* can vary (same population of *H. antarcticus* in Chile presented individuals completely red or green), and this characteristic seems not to be useful in the taxonomy of the group. One “similarity” between the species is the arms that are 45° apart (Vanhöffen 1908; Mayer 1910; Kramp 1961), but as we observed for *H. antarcticus*, this characteristic can present intraspecific variation (see discussion below). According to these characteristics (relative size of the anchors and the stalk), we maintain the traditional view in distinguishing these species, but more detailed comparisons should be accomplished.

In this respect, specimens of *H. antarcticus* are similar to the specimens of *H. auricula* described by Amor (1962) and Zagal (2004a, b, 2008), from Argentina and Chile, respectively, which raised questions about their identification. Our observations of animals from Los Molinos, Valdivia, Chile (same locality as in Zagal 2004a, b, 2008) strongly suggest that these materials are misidentified and that their true identity is *H. antarcticus*. Support for the synonymy between *H. antarcticus* and “*H. auricula*” (from Chile and Argentina) is suggested by the relative size of the anchors, the average number of tentacles per cluster, the proportion of calyx/stalk and the arrangement of the gonads (see Tables 1, 2). However, usually the anchors of *H. antarcticus* from Chile have a tentacular knob, rarely observed in *H. antarcticus* from King George Island at about the same life cycle stage. This tentacular knob in the anchors was related to the earlier stages of *H. antarcticus* by Pfeffer (1889) and Carlgren (1930), and this difference might be an intraspecific and/or ontogenetic variation. Based on these characteristics, we propose that the species from Antarctica, Chile and possibly Argentina (although for this locality we do not have material and our conclusions are restricted to information from Amor 1962) are synonymous and should be classified as *H. antarcticus*. There is an apparent similarity between *H. auricula* and *H. antarcticus* (Table 1); however, the proportion between stalk and calyx, and the height of anchors × diameter of stalk are different (Table 1). Several authors attributed different characteristics for *H. auricula* (Rathke 1806; Clark 1863; Clark 1878; Uchida 1927; Gwilliam 1956; Hirano 1997) and it is possible that there are some misidentifications, raising problems about the taxonomy of the genus *Haliclystus*, and about its distribution.

Previous studies have proposed distinctive characters for *H. antarcticus* that have proven to be ineffective because of ontogenetic variation or high plasticity in the species (see below). Mayer (1910) distinguished *H. antarcticus* from *H. auricula* based on the arms being united in pairs in the former. However, in our large series of animals ($n = 184$), we have observed that the majority of *H. antarcticus* specimens have equidistant (45°) arms, though they are internally united “in pairs” by common bundles of interradial muscles. But we note that, in the early stages of development, the arms can be slightly united in pairs. According to Gwilliam for the genus *Haliclystus* (1956:52), “the arms pairing is not a consistent characteristic of the species and it is most probably an attitude caused by contractions of the marginal muscle.” Another putatively distinctive character, the number of tentacles, adopted by Mayer (1910) and Kramp (1961), is highly variable (6-224, for *H. antarcticus*), and its use should be employed cautiously in the taxonomy of the group (Table 1, see also Gwilliam 1956:53).

The morphological plasticity in the group also includes an array of abnormal features that have been described for other species of *Haliclystus* (Browne 1895:3, Plate 1), and these features are also present in *H. antarcticus* (as in Zagal 2008:260, tentatively identified as *H. auricula*), such as: variation in the number of arms; the morphology, number and location of anchors (Fig. 7c, h–j); the presence of two stalks (Fig. 6o). Earlier authors have hypothesized different environmental and biological causes of these abnormalities. Absence of arms, for instance, was proposed to be caused by physical disturbance such as wave action or predation (Zagal 2008). Browne (1895) reported cases of congenital variation and imperfect regeneration of organs damaged or completely destroyed by injury. Amor (1962) merged physical and biological reasons and pointed out that losses in body parts of stauromedusae due to their intertidal habit are compensated by their strong regeneration ability, occasionally leading to “supernumerary” members (see also Mayer 1910:522 and 532). However, it is unclear whether variation in symmetry is caused by genetic, environmental or developmental factors (variability in symmetric expression), or a combination of these factors (Gershwin 1999).

The cnidome found in our studies is similar to that described by Carlgren (1930), who reported oval and rod-shaped nematocysts in the tentacles and gastric cirri, with similar proportions to those we had observed. The “oval” nematocysts are probably the microbasic heterotrichous, and the “rod-shaped” ones are the isorhiza (atrichous or holotrichous). The type of nematocysts seems to be not helpful in distinguishing species because isorhizas and heterotrichous (euryteles) have already been described for other species of Staurozoa (Uchida 1929; Weill 1934; Larson 1980, 1988; Calder 1983; Hirano 1986; Larson and Fautin 1989; Collins and Daly 2005). However, Gwilliam (1956) used the morphometry of nematocysts to distinguish some species of *Haliclystus*, so their possible use in taxonomy needs further investigation.

Collins and Daly (2005:221) emphasized that evolutionary discussions of stauromedusae have largely focused on their relationship to other groups of Cnidaria rather than on those among its component subgroups. As a result, families and genera are recognized by a mosaic of features, many of which are not exclusive, or suggest contradictory groupings. In fact, the suprageneric affinities among stauromedusae are also not well founded (Daly et al. 2007), partly because of imprecise or incorrect information found in literature. Mayer (1910) described *H. antarcticus* with a single-chambered stalk, suggesting a close relationship between the genera *Haliclystus* (for which other species frequently have four-chambered stalks) and *Lucernaria* (species with single-chambered stalks). However, this apparent error by Mayer contrasts with the original description by Pfeffer (1889) and the subsequent study by Carlgren (1930), who also described a four-chambered stalk for the species. Our sections of the specimens corroborated the four-chambered stalk of the original description. This hypothesis of a close relationship between *Haliclystus* and *Lucernaria*, pointed out by Mayer (1910), was also refused based on molecular markers, since these genera do not form a clade corresponding to the family Lucernariidae (Collins and Daly 2005).

The lack of basic knowledge about most species of stauromedusae makes it difficult to address biogeographical questions, even though they are interesting animals for that approach, because of their life cycles and natural history. A possible justification for the lack of attention to this class is related to their cryptic habit and occurrence in specific habitats (Larson 1990; Salvini-Plawen 2006). Indeed, our specimens were found attached to rocks or to red or green algae, to which their coloration matches closely, effectively providing camouflage (see also information for other species in Larson 1980; Larson and Fautin 1989). It was most likely because of this lack of attention and taxonomic expertise that large populations of *H. antarcticus* have been overlooked in the Southern Ocean. Our study is the second record of the species outside its type locality, the previous record, by Carlgren (1930:2, for Paulet Island), was not noticed by several authors (Kramp 1961:292; Davenport 1998:663; Grohmann et al. 1999:386). To these, we also propose to encompass the materials from Argentina (Amor 1962) and Chile (Zagal 2004a, b, 2008).

Despite these difficulties discussed above, we have shown that what was thought to be a cosmopolitan species, *H. auricula*, appears not to be distributed in the southern hemisphere. Studies dealing with the distribution of these animals, mainly in the southern hemisphere, should be encouraged, since they contribute significantly to a better understanding of the evolution of the group.

Acknowledgments We are deeply grateful to: A.G. Collins (NMFS, National Systematics Laboratory, National Museum of Natural History, Smithsonian Institution) for corrections and comments on the manuscript and for providing support for the study of the Stauromedusae collection in the National Museum of Natural History, Smithsonian Institution; J.P. Didier, for her enormous support and commitment to the collection of material from Chile; A. Cunha, H.Y. Yamaguti, J. Bardi, M.M. Maronna, N. Mejía and T.P. Miranda (Instituto de Biociências, Universidade de São Paulo, USP) for discussions and suggestions on a previous version of the text and the figures; Enio Matos and Eduardo Matos (in memoriam) for their assistance on the SEM (Instituto de Biociências, Universidade de São Paulo, USP). We also thank the reviewers C. Mills, J. Gerhard and A.G. Collins, who have contributed to improve this paper. This work was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo, FAPESP (research grant 2004/09961-4), Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq (55.7333/2005-9, 490348/2006-8, 305735/2006-3, 47467-2007-7). A.C. Morandini had partial support from Conselho de Ensino para Graduados/Universidade Federal do Rio de Janeiro, Fundação Universitária José Bonifácio, CEPG/UFRJ–FUJB (ALV'2006 13126-1), CNPq (481399/2007-0), Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro, FAPERJ (E-26/171.150/2006) and Ministério da Ciência e Tecnologia/Financiadora de Estudos e Projetos MCT/FINEP/Ação Transversal-Cooperação ICTs- Empresas (Petrobras) - 06/2006 (3175/06).

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