Ernst Haeckel’s mysterious species, Part I: the validity of Carybdea murrayana Haeckel, 1880 (Cubomedusae) and revisional notes on Haeckel’s other Carybdeidae

ILKA STRAHELER-POHL*

Medusa(’s) nursery, Private Laboratory of Developmental, Evolutionary Biology and Life Cycle Research, Almmarkstr. 25, 21864 Stade-Hagen, Germany

Received 26 February 2019; Accepted 30 September 2019 Responsible Editor: Dhugal Lindsay

doi: 10.3800/pbr.15.1

Abstract: The type material of the species Carybdea murrayana Haeckel, 1880 was rediscovered in the Cubozoa collection of the Natural History Museum in London. A comparison of C. murrayana with Carybdea marsupialis (Linnaeus, 1758) and with Carybdea branchi Gershwin & Gibbons, 2009 was performed because the validity of the species has been doubted for over a century and because C. murrayana had been declared a synonym of C. marsupialis by authors like Mayer, Bigelow and Kramp, due to an apparent overlapping distribution range. The results demonstrate that C. murrayana is different from C. marsupialis but identical to C. branchi. Therefore, C. branchi is declared a junior synonym of the valid species C. murrayana Haeckel, 1880 according to the International Code of Zoological Nomenclature.

Additionally, the line drawings and/or descriptions of the carybdeid species Procharagma prototypus Haeckel, 1880 and Procharybdis cuboides Haeckel, 1880 were translated, diagnosed, compared to well-known carybdeid species and revised.

Key words: box jellyfish, carybdeid species, Carybdea marsupialis, museum collection, John Murray Expedition

Introduction

Ernst Haeckel is one of the most disputed scientists of the 19th century due to his partial support of Darwin’s theory and their friendship, of further developing his own recapitulation theory (“ontogeny recapitulates phylogeny”) of evolution and for establishing the disputed and nowadays disproved biogenetic law or embryological parallelism (Haeckel 1899, Blechschmidt 1977, Krauße 1987). Haeckel’s ideas were often speculative and mostly lacked empirical support, which tarnished his scientific credentials (Haeckel 1899, Bowler 1989, Milner 1990, Krauße 1987). Additionally, he was accused of falsification concerning drawings (Rütimeyer 1868, Teudt 1909, Richards 2008) commented on and denied several times by Haeckel himself (Haeckel 1891, Haeckel 1910, Richards 2008), which might have led also to general doubt concerning his descriptions of new species.

Haeckel described about 18 new cubomedusan species in his 2nd part of “System der Acraspeden, Medusen” at the end of the 19th century (Haeckel 1880) (see Table 1).

Nearly all of the species newly described by Haeckel (1880) were doubted or declared invalid by many authors in the past into the present (e.g. Mayer 1910, Kramp 1961, Gershwin 2005a+b, 2006a, Collins et al. 2011 Bentlage & Lewis 2012). The main reasons were: nearly all described species seemed to have never turned up again; some were based on doubtful material (e.g. juvenile, partly destroyed specimens); and others were seen as synonyms of already described species from other locations.

Carybdea murrayana Haeckel, 1880 is one example of such a doubtful species. It was sampled by the naturalist John Murray during the H.M.S. Challenger Expedition in 1876, named by Haeckel in 1880 (described and drawn in more detail by him in 1882) but was never officially
| No. | Original species name (according to Haeckel 1880) | Reference for synonyms | Synonym (change)/ Status | Size: BH×BW (mm) | Sampling location/ Collector | Actual Suborder | Actual Family |
|-----|--------------------------------------------------|------------------------|--------------------------|-----------------|-----------------------------|-----------------|--------------|
| 1   | Charybdea obeliscus                               | Bentlage & Lewis (2012): | Alatina obeliscus (Haeckel, 1880) / nomen dubium | 35 × 20          | West coast of Africa; Cape Verde Islands / Museum Godffroy, Germany | Carybdeida      | Alatinida    |
| 2   | Charybdea philippina                              | Bentlage & Lewis (2012): | Alatina philippina (Haeckel, 1880) / nomen dubium | 30 × 20          | Pelew Islands (Palau), The Philippines / Semper   | Carybdeida      | Alatinida    |
| 3   | Charybdea pyramis                                 | Gershwin (2005a, b):     | Alatina pyramis (Haeckel, 1880) / valid          | 30 × 20          | Tropic belt of Atlantic Ocean; Antilles / Museum Godffroy, Germany | Carybdeida      | Alatinida    |
| 4   | Procharybdis securigera                           | Mayer (1910):            | Maybe juvenile of Carybdea rastonii Haacke, 1887 / not valid | 40 × 40          | Pacific Coast of Central America / Fuchs  | Carybdeida      | Alatinida    |
| 5   | Procharybdis tetraptera                           | Mayer (1910):            | Procharybdis tetraptera / maybe a Carybdea species and/or immature | 30 × 20          | Indian Ocean; Sunda-Archipelago (Sunda Strait)-Java/ Sumatra/ Rabbe | Carybdeida      | Alatinida    |
| 6   | Procharybdis turricula                            | Bentlage & Lewis (2012): | Alatina turricula (Haeckel, 1880) / nomen dubium | 170 × 70         | Pelew Islands (Palau), The Philippines/ Semper | Carybdeida      | Alatinida    |
| 7   | Charybdea murrayana                               | Kramp (1961):            | Carybdea marsupialis (Linnaeus, 1758) / not valid | 60 × 50          | West coast of Africa, not far from Sierra Leone/John Murray | Carybdeida      | Carybdeida   |
| 8   | Procharagma prototypus                            | Mayer (1910):            | Carybdea rastonii (Haacke, 1887) / not valid    | 8 × 8            | Chinese Sea/Weber            | Carybdeida      | Carybdeida   |
| 9   | Procharybdis cuboides                             | Mayer (1910):            | Carybdea rastonii (Haacke, 1880), nomen dubium  | 35 × 35          | Sandwich Islands/n/a        | Carybdeida      | Carybdeida   |
| 10  | Tamoya prismatica                                 | Mayer (1910):            | Tamoya haplonema / not valid                    | 80 × 40          | West Indian Ocean, Antilles / Schnehagen | Carybdeida      | Tamoyida     |
| 11  | Procharybdis flagellata                           | Mayer (1910), Southcott (1956): | Procharybdis flagellata / not valid | 40 × 20          | North coast of Australia; Torres-Straits / Weber (New-Guinea / Lesson?) | Carybdeida      | ?            |
| 12  | Procharagma aurea                                 | Gershwin 2005a           | Copula aurea / ?                               | 10 × ?           | Pelew Islands (Palau), The Philippines / Semper | Carybdeida      | Tripedaliida |
| 13  | Tamoya bursaria                                   | Bentlage & Lewis (2012): | Tamoya bursaria (Lesson, 1829) / nomen dubium   | 100 × 70         | New-Guinea, Rawack, Waigiou / Lesson  | Carybdeida      | ?            |
| 14  | Tamoya gargantua                                  | Bentlage & Lewis (2012): | Tamoya haecckeli Southcott, 1967 = Tamoya gargantua / valid | 160-200 × 80-100 | Tropical Part of Pacific Ocean; Tahiti / Lesson; Samoa / Weber | Carybdeida      | ?            |
| 15  | Chirodropus gorilla                               | Uchida (1929):           | Chirodropus gorilla / valid                     | 150 × 120        | Coast of Lower Guinea (Equatorial Guinea), Chinchozo, Loango / Falkenstein | Chirodripida    | Chirodripida |
Validity of Carybdea murrayana Haeckel, 1880

sighted again and was, therefore, doubted and seen as a probable variety of Carybdea marsupialis (Linnaeus, 1758) (Mayer 1910, Bigelow 1938, Kramp 1961). Gershwin & Gibbons (2009) were the first to argue for the validity of the species. Bentlage & Lewis (2012) listed C. murrayana in their Carybdeidae species list.

The type material of C. murrayana was rediscovered in 2016 in the cubomedusan collection of the Natural History Museum of London. It consisted of two mature female medusae, one was dissected and broken into three pieces, and the other one was only cut open on one side. These specimens show all the features that Haeckel (1880, 1882) drew and described. As there was always doubt concerning the validity of this species, the goal of this paper is to provide more information on C. murrayana by comparing it with specimens of C. marsupialis and Carybdea branchi Gershwin & Gibbons, 2009 this last one with overlapping distribution range.

Additionally, two other species of the family Carybdeidae described by Haeckel (1880) as Procharagma prototypus Haeckel, 1880 and Procharybdis cuboides Haeckel, 1880 are diagnosed and revised.

### Material and Methods

All medusae specimens observed were preserved in 5% formalin and water.

### Morphological comparison

The rediscovered type specimens of Carybdea murrayana were preserved in 5%–7% formalin; therefore, no molecular analysis could be performed. However, as all anatomical structures were excellently preserved a direct comparison with the structures of the Carybdea species from Africa and Spain was possible. Therefore, only morphological characters were used to identify the species, a valid approach even in the age of molecular phylogenies (Páll-Gergely 2017).

### Species observed

**Project 1: Carybdea murrayana:**

As the statement that Carybdea murrayana from West Africa is considered to be a synonym of “Carybdea marsupialis” by Mayer (1910), Bigelow (1938) and Kramp (1961) was based on descriptions by Linnaeus (1758) and Claus (1878), specimens of C. marsupialis from the Mediterranean Sea were also examined. As the distributional range of Carybdea branchi overlaps with that of C. murrayana,
the holotype, paratypes, additional registered museum material and specimens of *C. branchi* recently sampled in South Africa were also examined.

All information about the specimens observed and the referring museum collections are listed in Tables 2a, b. Additionally, all data were compared to the original line drawings made by Haeckel in 1879 (with courtesy of the collections of Ernst-Haeckel-Haus, Friedrich-Schiller-Universität Jena Institut für Geschichte der Medizin, Naturwissenschaft und Technik) and to the detailed descriptions and line drawings of Haeckel (1880, 1882).

Project 2: *Procharagma prototypus* and *Procharybdis cuboides*

As the type materials of *Procharagma prototypus* and *Procharybdis cuboides* could not be found in the European museum collections that were visited, only data from the literature (Haeckel 1880, 1904) and the original line drawings of Haeckel (between 1877 and 1880, with courtesy of the collections of the Ernst-Haeckel-Haus, Friedrich-Schiller-Universität Jena Institut für Geschichte der Medizin, Naturwissenschaft und Technik) were used to diagnose the validity and identity of the species.

Species used for comparison were *Carybdea arborifera* Maas, 1903, *Carybdea brevipedalia* Kishinouye, 1891, and *Carybdea rastonii* Haacke, 1887 due to type localities and proposed synonymy by Mayer (1910).

All information about the specimens observed and the museum collections are listed in Tables 2a, b.

**Measurements**

Standard measurements were used (Gershwin & Gibbons 2009, Straehler-Pohl 2014, Acevedo et al. 2019): bell height (BH) as length between bell turn-over (velarium excluded from measurement) and top of apex; interpedalial diameter (IPD) as distance between opposite pedalia (outer pedalial wing edges) at the level of the bell turn-over; interrhopalial width (IRW) was measured between adjacent rhopalia, with the specimen flattened; pedalia length (PL) was measured from attachment to bell (pedalial base) to the tentacle insertion, as a proportion in relation to bell height.

Photographs were taken under the same conditions with digital cameras (Canon Powershot G12 and Canon Eos 550D).

*Gonads* in Cubozoa

The study follows Acevedo et al. (2019) in using the

---

**Table 2a.** Unregistered specimens examined for this study.

| Provider | No. of specimens | Species ID on label | Sampling location** | Collector | Sampling date |
|----------|------------------|---------------------|---------------------|-----------|---------------|
| André C. Morandini | 7 | *Carybdea branchi* Gershwin & Gibbons, 2009* | South Africa, Hout Bay (34°03′4.8″S, 18°20′53.99″E), swimming at surface near pier | A.C. Morandini & S.N. Stampar | 05 May 2013 |
| Melisa J. Acevedo | 5 | *Carybdea marsupialis* (Linnaeus, 1758) | Spain, Denia, Almadavra Beach (38°51′50″N, 0°1′24″E), surface, dipnet | M. J. Acevedo | 10, 29 Sep 2010 |
| Angel Yanagihara | 10 | *Carybdea arborifera* Maas, 1897 | Hawaii, Kewalo Basin (21°17.564′N, 157°51.462′W) | A. Yanagihara | 29 May 2013 |
| Sho Toshino | 3 | *Carybdea brevipedalia* Kishinouye, 1891 | Japan, Kanagawa Prefecture, Aburatsubo Bay (35°09′35.2″N, 139°36′56.0″E) | S. Toshino | 24 Oct 2011 |
| Sho Toshino | 3 | *Carybdea brevipedalia* Kishinouye, 1891 (juvenile medusae of different sizes and developmental stages) | Japan, Oita Prefecture, Oita City, Hoso fishing port (33°14′37″N, 131°46′34″E) | S. Toshino | Sep 2017 |
| Sho Toshino | 1 | *Carybdea brevipedalia* Kishinouye, 1891 | Japan, Wakayama Prefecture, Shirahama (33°40′54″N, 135°20′40″E) | S. Kubota | 1995 |
| Jamie Seymour | 1 | *Carybdea rastonii* Haacke, 1887 | Australia, Victoria, Mirimbula (36°53′53″S, 149°54′04″E) | G. Hood | 03 Mar 2000 |
| Jamie Seymour | 1 | *Carybdea rastonii* Haacke, 1887 | South Australia, Waterloo Bay (33 39′ 00″S, 134 54′ 00″E) | J. Seymour | Feb 1999 |
| George I. Matsumoto | 8 | *Carybdea confusa* Straehler-Pohl, Matsumoto & Acevedo, 2017* | USA, California, Santa Barbara, 20 m West of Goleta Pier, 5 m depth (34°24′58″N, 119°49′43″W) | S. Anderson | 21 Oct 1998 |

*Identifications were done in 2013, **longitudes and latitudes taken from: http://latitude.to or http://google.de/maps
Table 2b. Specimens from museum collections examined for this study.

| Collection | Code No. | No. specimens | Species identification | Original identification | Sampling location | Collector | Sampling date |
|------------|----------|---------------|------------------------|-------------------------|-------------------|-----------|---------------|
| NHM        | 1882.10.9.2a+b (lecto- & paralectotype) | 2 | Carybdea murrayana Haeckel, 1880*** | Charybdea murrayana Haeckel, 1880 (type species) | West Africa, 20°10′N, 14°51′W | John Murray | 04 Apr 1876 |
| NHM        | 2000.1800–1803 | 4 | Carybdea murrayana Haeckel, 1880*** | 1938: Medusae; Gershwin 2000: Carybdea robsonae | South Africa, Simonstown docks; Hand net, surface | Discovery Expedition | 17 Nov 1938 |
| NHMD       | —        | 1 | Carybdea murrayana Haeckel, 1880*** | Carybdea alata Reynaud 1830 | South Africa, False Bay | G.F. Papenfuss | 27 Oct 1937 |
| RBINS      | I.G. 11204 | 1 | Carybdea murrayana Haeckel, 1880*** | Dr. G. Ranson, 1945: Tamoya haplonema Müller, 1859 | 4 miles off Lüderitz Bay (Namibia, Africa) | Cruise of "Mercator" | 18 Jan 1938 |
| NHM        | 1983.4.25.1 | 1 | Carybdea arborifera Maas 1897** | Carybdea marsupialis (Linnaeus, 1758) | Durban Museum (South Africa) | E.T. Brown beq. | Dec 1914 |
| MCNB       | MZB 2015-4807 | 1 | Carybdea murrayana Haeckel, 1880*** | Carybdea branchi Gershwin & Gibbons, 2009 | South Africa, Hout Bay (34°03′4.8″S, 18°20′53.99″E), swimming at surface near pier | A.C. Morandini & S.N. Stampar | 05 May 2013 |
| SAM        | H4863 (holotype C. branchi) | 1 | Carybdea murrayana Haeckel, 1880**** | Carybdea branchi Gershwin & Gibbons, 2009 | SE corner of Alfred Basin, in front of the Two Oceans Aquarium, V&A Waterfront, Cape Town [33°54.527′S, 018°25.074′E], surface | L. Gershwin & L. Hoensen | 18 Jan 2001 |
| SAM        | H4864a+b (paratypes C. branchi) | 2 | Carybdea murrayana Haeckel, 1880**** | Carybdea branchi Gershwin & Gibbons, 2009 | SE corner of Alfred Basin, in front of the Two Oceans Aquarium, V&A Waterfront, Cape Town [33°54.527′S, 018°25.074′E], surface | L. Gershwin & L. Hoensen | 18 Jan 2001 |
| NHM        | 21.11.16.14 | 3 | Carybdea brevipedalia Kishinouye, 1891** | Carybdea rastonii Haacke, 1887 | Japan, Mesaki | ?, collected for Exhibition | 1921 |
| CAS        | CASIZ 197981 | 1 | Carybdea confusa Strachler-Pohl, Matsumoto & Acevedo, 2017 | Carybdea marsupialis (Linnaeus, 1758) | California, Santa Barbara, 20 meters west of Goleta Pier (34°24′58″N, 119°49′43″W), 5 m depth | Shane Anderson | 21 Oct 1998 |
| CAS        | CASIZ 197982 | 2 | Carybdea confusa Strachler-Pohl, Matsumoto & Acevedo, 2017 | Carybdea marsupialis (Linnaeus, 1758) | California, Santa Barbara, 20 meters west of Goleta Pier (34°24′58″N, 119°49′43″W), 5 m depth | Shane Anderson | 21 Oct 1998 |
term gonads to refer to areas where gametes are formed.

**Results**

**Project 1—Carybdea murrayana**

There were two errors noted in Acevedo (2016: pp. 30, 32, 41, 42, 43) and Straehler-Pohl et al. (2017: p. 131, 136) concerning the structures of the velarial canal system in *C. branchi* and *C. murrayana*, partly corrected by Acevedo et al. (2019: 526–527, 539) both were described to possess 3 velarial canal roots per octant. Additional inspections confirmed the results of Gershwin & Gibbons (2009) that *C. branchi* possesses only 2 velarial canal roots per octant and revealed that *C. murrayana* also possesses only 2 velarial canal roots per octant. Herewithin, the errors by Acevedo (2016) and Straehler-Pohl et al. (2017) are corrected within Table 3 and Figures 4S, T, U, 5G, M.

**Systematics** (based on Straehler-Pohl (2017), Jarms & Morandini (2019))

Phylum Cnidaria Verrill, 1865
Subphylum Medusozoa Petersen, 1979
Class Scyphozoa Goette, 1887
Order Cubomedusae Haeckel, 1880
Suborder Carybdeida Gegenbaur, 1857
Family Carybdeidae Gegenbaur, 1857
Genus Carybdea Péron & Lesueur, 1810

Genus Carybdea Péron & Lesueur, 1810
Definition: (after Acevedo et al. 2019, Straehler-Pohl 2019)

With heart-shaped rhopalial niche openings showing a single upper covering scale and no lower covering scale; lacking rhopalial horns. Gastric phacellae either brush to epaulette-shaped or brush-shaped filaments growing in horizontal rows. Polypoid stage and medusa production: only known for two species, *Carybdea xaymacana* Conant, 1897 and *Carybdea brevipedalia*. Medusa production: only known from *C. xaymacana* and *C. brevipedalia*.

Type species: *Carybdea marsupialis* (Linnaeus, 1758)

*Carybdea murrayana* Haeckel, 1880

Type locality: West Coast of Africa, not far from Sierra Leone (30°10′N, 14°51W), Challenger Expedition 1872-76 Station 348, from 400 m depth (Haeckel 1880, 1882).

**Inspection of Syntypes**

The “holotype” consisted of 2 specimens (=syntypes) of which one was dissected by Haeckel for his description and line drawings of structural details (Haeckel 1880, 1882) while the other was just cut open for the habitus line drawings by Haeckel (1882, 1904) but was not further dissected. Even if the first specimen is broken into 3 parts, the structures are in better condition than in the other one. I designate it as the lectotype (1882.10.9.2a) also because the first description is mainly based on this specimen, while the other is designated as a paralectotype (1882.10.9.2b) according to the International Code of Zoological Nomenclature (ICZN 1999).

The lectotype (NHM 1882.10.9.2a, Fig. 1B) was in good condition even if completely dissected; the bell was broken into three pieces (Fig. 1B) but the internal structures...
Table 3. Identification Table: Comparison of characters of specimens of *Carybdea marsupialis* from Spain, *Carybdea murrayana* from West Africa and *Carybdea branchi* from South Africa.

| *Carybdea marsupialis* (literal citation) | *Carybdea murrayana* (literal citation) | *Carybdea branchi* (literal citation) |
|-----------------------------------------|----------------------------------------|--------------------------------------|
| MZB 2015-1701 (neotype); MZB 2015-4806; BNHM 1972.5.24.1; 5 unregistered specimens from Denia; Spain; Acevedo et al. 2019; Figs. 5N–R | NMH 1882.10.9.2a+b (lecto- & paralecotype); Haeckel 1880, 1882; Figs. 1A–Q, 2A–F, 3A, B, 5H–M, 6 of present study | SAM-H4863 (holotype); SAM-H4864a+b (paratypes); NMH 2000.1800–1803; I.G. 11204; RBINS IG 11204; NHMD unregistered specimen; 7 unregistered specimens from Hout Bay, South Africa; MZB 2015-4807; unregistered living specimen from Lüderitz Bay, Namibia (Simon Elwen (Namibian Dolphin Project)), Gershwin & Gibbons 2009 (measurements of 28 specimens used for statistics); Figs. 4A–U, 5A–G |

Bell

- highly transparent, colourless, base of gastric phacellae, brownish-orange (freshly preserved, in-life; Fig. 5O, S); translucent whitish (preserved; Fig. 5N)
- transparent to translucent, colourless to reddish brown (preserved; Figs. 1B, I, J)
- highly transparent, base of gastric phacellae, yellowish to reddish-brown, pedalium, outer wing base, light brown, outer wing distal end, dark reddish brown (in-life (Figs. 4A, M): colouration fades fast after preservation); transparent to translucent, colourless to yellowish (preserved; Figs. 4B–E, 5A)

(Acevedo et al. 2019, p. 521: highly transparent with few whitish nematocyst warts sparsely scattered on bell from apex (very small warts) to bell margin (big warts along interradial furrows); [...] phacellae brownish-orange in colour, colour remains after preservation (Figs. 5C, D))

- mesogloea, thin
- mesogloea, firm, thick at interradial corners (Fig. 11, 2A, 3A2–3) (Haeckel 1882, p. 94: The gelatinous substance of the umbrella shows a considerable degree of firmness, [...] , thickest at the two sides of the pillars [...] )
- mesogloea, firm, thick at apex and interradial furrows (Figs. 4C–E, 5A) (Gershwin & Gibbons 2009, p. 43: with thick, rigid mesoglea, especially apically)

- cylindrical to pyramidal with rounded edges (Fig. 5N)
- almost cubical to truncate pyramidal with rounded edges (Figs. 11, 3A1–3) (Haeckel 1882, p. 93: [...] nearly cubical, [...] shape of a truncated, regular quadrilateral pyramid.)
- cubic to pyramidal with rounded edges (Figs. 4A–E, 5A)

- apex, very thick mesogloea, domed, with horizontal constriction (Fig. 5N)
- apex, mesogloea, slightly thicker than in other parts, slightly arched, no horizontal constriction visible (Figs. 2A, 3A1–4) (Haeckel 1882, p. 94: The gelatinous substance of the umbrella [...] thickest [...] above in the cap-shaped apical cover of the umbrella)
- apex, thick mesogloea, slightly arched, with slight horizontal constriction (Fig. 4C–E) (Gershwin & Gibbons 2009, pp. 43, 44: [...] with thick, rigid mesoglea, especially apically; [...] Coronal indentation shallow just below apex. [...] Fig. 1A)
| Table 3. Continued. |
|---------------------|
| **Carybdea marsupialis** (literal citation) | **Carybdea murrayana** (literal citation) | **Carybdea branchi** (literal citation) |
| • nematocyst warts, small, densely scattered, flat on bell sides, prominent on apex, round to oval, whitish to brownish (in-life; Fig. 5S), from apex to velarium | • nematocyst warts, none visible in NMH 1882.10.9.2a+b (according to Haeckel 1882, pp. 93–94: The exumbrella appears finely granulated, numerous urticating warts or round groups of thread cells are scattered freely over it) | • nematocyst warts, different sizes (interradial furrows, bell margin, bigger nematocyst warts, bell sides, apex smaller nematocyst warts), densely scattered from apex to bell-turnover (Fig. 4A), flat to prominent, irregularly shaped, white (Fig. 4L, M); easily rubbed off when handled, preserved and sent to other labs (own observation; Figs. 4E, 5A) (Gershwin & Gibbons 2009, p. 43: [...] with numerous oblong to amorphous small unraised or slightly raised nematocyst warts scattered densely over entire exumbrella) |

**Size**

|BH: up to 30 mm (preserved; Fig. 5N) | BH: up to 60 mm (preserved: Haeckel 1882) | BH: up to 82 mm (preserved) |
|---|---|---|
(mean: 28.2 mm, SD: 2.49, n=5) | (actual mean: 53.0, SD: 4.243, n=2) | (mean: 45.58, SD: 10.498, n=35) |
| IRW: no data | IRW: 29 mm (preserved: Haeckel 1880) | IRW: up to 51 mm |
(mean: 32.6 mm, SD: 2.51, n=5) | (actual mean: 46.5, SD: 4.95, n=2) | (mean: 28.55, SD: 7.566, n=35) |
| IPD: up to 35 mm | IPD: up to 68 mm | IPD: up to 99 mm (preserved) |
(mean: 32.6 mm, SD: 2.51, n=5) | (actual mean: 65.00, SD: 4.243, n=2) | (mean: 57.53, SD: 14.410, n=35) |
| IPD/BH: 1.16 (mean, SD: 0.099, n=5) | IPD/BH: 1.23 (mean, SD: 0.018, n=2) | IPD/BH: 1.26 (mean; SD: 0.076, n=35) |
| IRD/BH: no data | IRW/BH: 0.66 (mean; SD: 0.011, n=2) | IRW/BH: 0.62 (mean; SD: 0.053, n=35) |
| PL: up to 13 mm (mean: 11.4 mm, SD: 1.14, n=5) | PL: 32 mm, 25 mm (n=2) | PL: up to 40 mm (mean: 31.20, SD: 7.079, n=5) |
| PW: up to 7 mm (mean: 6.6 mm, SD: 0.89, n=5) | PW: 18 mm, 14 mm (n=2) | PW: up to 23 mm (mean: 17.60, SD: 3.286, n=5) |
(Haeckel 1882, p. 93: Horizontal diameter of the umbrella, 50 mm; vertical diameter, 60 mm.) |

**Gonads**

| Interradial | Interradial | Interradial |
|---|---|---|
| paired, 4 | paired, 4 | paired, 4 |
| size, covering area of gastric pouch from bell margin to 3/4 of bell height below stomach (Fig. 5N) | size, length covering entire area of gastric pouch from stomach to bell margin | size, length covering entire area of gastric pouch from stomach to bell margin |
| narrow leaf-shaped, very thin tissue, separated by perforated interradial septum, attached at entire length of septum | broad leaf-shaped (Figs. 1E, J), very thin tissue, pleated, separated by unperforated septum, attached along entire length of septum | narrow to broad leaf-shaped, thin tissue, pleated, separated by unperforated septum, attached at entire length of septum, outer margins of adjacent gonad leaves might touch or overlap (Figs. 4E) |
Table 3. Continued.

| Carybdea marsupialis (literal citation) | Carybdea murrayana (literal citation) | Carybdea branchi (literal citation) |
|----------------------------------------|---------------------------------------|-------------------------------------|
|            | (Haeckel 1882, p. 100: eight broad, thin, semi-oval leaves which are fastened in pairs along the four interradial septal selves, and project freely from these into the four radial pouches; they occupy the greater part of their hollow space so that the two reproductive leaves of each pouch touch each other or even overlap with their free margins in its middle; (present study Fig. 3A6)) | (Gershwin & Gibbons 2009, p. 47: Gonads attached along entire length of interradial septa; narrowly leaf-shaped, typically not overlapping along the interradius in present collection, pleated or simple. Interradial septa lacking perforations.) |
| • sexes unimorph; opaque white in preserved specimens (7% formalin) | • sexes—both specimens female (Fig. 1E), males unknown; opaque flesh coloured in preserved specimens (7% formalin) | • sexes unimorph; opaque yellowish white to brownish flesh-coloured in preserved specimens (7% formalin) |
| **Pedalia** | | |
| • 4, single, simple (Fig. 5Q) | • 4, single, simple | • 4, single, simple |
| • slightly stalked | • slightly stalked | • slightly stalked |
| • non-keeled at midline | • keeled at midline | • keeled at midline |
| • irregularly, broad leaf-shaped | • leaf-shaped (Figs. 1F, M, 2A2–3, 3A3) (Haeckel 1882, p. 95: [...] shaped like a thin longish oval leaf) | • leaf-shaped (Figs. 4M–P, 5E) |
| • PL ca. 40% of BH | • PL ca. 57% of BH (mean, SD: 0.002, n=2) (Haeckel 1882, p. 95: [...] nearly a third as long as the height of the umbrella) | • PL ca. 55% of BH (mean, SD: 0.039, n=7) (Gershwin & Gibbons 2009, p. 43: Pedalia about 1/2 bell height) |
| **Inner wing** | | |
| • flattened, nearly scalpel-shaped (Fig. 5Q) | • flattened, semi-oval shaped | • flattened, semi-oval |
| • not overhanging tentacle insertion; in some mature medusae margin sometimes undulated | • no incision above tentacle insertion, slightly overhanging tentacle insertion in one specimen (Fig. 5K, arrow) | • no incision above tentacle insertion, slightly overhanging tentacle insertion in large specimens (Figs. 4M, O, 5E, arrow) (Gershwin & Gibbons 2009, p. 43: [...] without tentacular overhang) |
| • nematocyst warts, none | • nematocyst warts, none | • nematocyst warts, none |
| **Outer wing** | | |
| • straight, narrower than inner wing, not overhanging tentacle insertion | • semi-oval shaped, narrower and longer than inner wing | • narrow semi-oval shaped, narrower and longer than inner wing |
| • nematocyst warts, irregular white nematocyst bands on outer keel, smaller warts scatter outer wing (Fig. 5Q) | • nematocyst warts, none visible in NMH 1882.10.9.2a+b | • nematocyst warts, irregularly shaped warts/bands from keel to pedalial canal border, scattered, (partly rubbed off in unregistered specimens from Hout Bay); in-life: light brown pigmentation at pedalial base, dark brown pigmentation above tentacle insertion (Fig. 4A (white arrows), M) |
|                        | *Carybdea marsupialis* | *Carybdea murrayana* | *Carybdea branchi* |
|------------------------|------------------------|----------------------|--------------------|
| **Pedial canal**       |                        |                      |                    |
| • cross section, diamond-shaped at base and midsection, flattened oval/ellipsoid towards distal end | • cross section, triangular at base, diamond-shaped from below knee bend towards distal end | • cross section, triangular at base, diamond-shaped from below knee bend towards distal end (Gershwin & Gibbons 2009, p. 43: Pedial canal strongly quadratic in cross section throughout length) |
| • same diameter from knee bend towards tentacle insertion, tentacle diameter wider than insertion | • same diameter from knee bend towards tentacle insertion, distal end broadly flared (Figs. 1F, 5K (arrow)) | • same diameter from knee bend towards tentacle insertion, distal end broadly flared (Figs. 4N–P, 5E) (Gershwin & Gibbons 2009, p. 43: flared slightly at tentacle insertion) |
| • straight after knee bend, after 1/3 curved towards inner wing, after 2/3 straight towards distal end | • straight | • straight |
| • very slightly, laterally keeled | • smooth edged/keeled at midline (Fig. 1F, 5K) | • smooth edged/keeled at midline (Figs. 4O, Q, 5E) |
| • knee bend rounded to rectangular, without any appendages (Fig. 5Q) | knee bend bulged to triangular volcano-shape (Figs. 1G, L, 5L) | knee bend bulged to triangular volcano-shape (Figs. 4Q, white arrow, 5F, white arrow) (Gershwin & Gibbons 2009, p. 43: [...] broadly rounded bulge or lateral-pointing thorn) |
| **Tentacles**          |                        |                      |                    |
| • 4, single | • 4, single | • 4, single |
| • light brownish pink, with white nematocyst-batteries (in-life: Fig. 5S); white (preserved: Fig. 5N) | • flesh coloured (preserved: Fig. 1I, J) | • flesh coloured (preserved: Figs. 4B–E, 5A), light pink (in-life: Figs. 4A, M, V) |
| • width, tapering slightly from below base to distal end | • width, broadly flared at base, tapering slightly below base to distal end (Figs. 1I, J) | • width broadly flared at base, tapering below base to distal end (Figs. 4A, J, 5A) |
| • broad, cross-section, round (in-life, preserved) | • filiform, broad, round in cross-section, (preserved) | • filiform, broad, round in cross section (preserved and in-life) |
| • “pearl-string”, “string” bearing series of “nematocyst-pearls” | • bearing series of dense nematocyst bands | • bearing series of dense, narrow nematocyst rings |
| **Rhopalial niches**   |                        |                      |                    |
| • 4, perradial, cavity, heart-shaped | • 4, perradial, cavity, oval heart-shaped | • cavity, oval heart-shaped |
| • orifice, rounded heart-shaped (Fig. 5P) | • orifice, oval heart-shaped (Figs. 1D, K, 3A8, 5I) | • orifice, oval heart-shaped (Figs. 4J–M, 5D) |
| • covering scales (preserved: Fig. 5P): upper, 1, triangular with sharp longish tip, lower, 0, orifice extends as narrow furrow running from cavity base to bell margin | • covering scales (preserved: Fig. 5J): upper, 1, broad triangular, lower, 0, orifice extends as a very broad furrow running from cavity base to bell margin (Haeckel 1882, p. 96: Each sense club [...] is partly covered externally by the protective scale, which projects like a roof over the ectodermal aperture of the rhopalial niche) | • covering scales (in-life: Fig. 4K; preserved: 4J, L, M, 5D): upper, 1, broad triangular, lower, 0, orifice extends as a very broad furrow running from cavity base to bell margin (Gershwin & Gibbons 2009, p. 43: 1 shallow covering scale above and 2 nearly imperceptible scales below) |
| • 1/5 up from margin | • 1/6 up from margin | • 1/6 up from margin |
| • number of eyes per rhopalium, 6 | • number of eyes per rhopalium, 6 | • number of eyes per rhopalium, 6 |
### Table 3. Identification Table: Comparison of characters of specimens of *Carybdea marsupialis* from Spain, *Carybdea murrayana* from West Africa and *Carybdea branchi* from South Africa.

| Character                                      | *Carybdea marsupialis* | *Carybdea murrayana* | *Carybdea branchi* |
|-----------------------------------------------|------------------------|----------------------|--------------------|
| **Rhopalial horns**                           | • none                 | • none               | • none             |
| **Velarium**                                  | • narrow (≤1/4 of bell diameter) | • broad (≥1/4 of bell diameter) | (Gershwin & Gibbons 2009, p. 45: Velarium narrow) |
|                                               | • nematocyst warts, some, small, loosely scattered | • nematocyst warts, none | • nematocyst warts, none |
|                                               | • canal roots, 3 per octant (Fig. 5R) | • canal roots, 2 per octant (Figs. 1H, N–Q; 2C, F, 3B, 5M) | (Gershwin & Gibbons 2009, p. 45: [...] lacking nematocyst warts or freckles) |
|                                               | • canals, slim; next to frenulum, 1, simple to slightly forked; middle, 1–2, only single side branches; next to pedalium, 3–4, most complex, several side branches (Fig. 5R) | • canals, broad, 2–4 per root, canals dendritic, some side branches tend to grow in centripetal direction (Figs. 1H, O, Q) | (Gershwin & Gibbons 2009, p. 45: [...] Velarial canals 2 per octant) |
|                                               | • sharply pointed tips, deeply forked, slightly lobed • with smooth margin (Fig. 5R) | • very complexly patterned (Figs. 1H, 2C, F, 3B, 5M), canals flanking frenulum are as complexly branched as the ones flanking the pedalia; dendritic, lobed main branches and several dendritic, lobed side branches, all octants show a different pattern (Figs. 1 N–Q, 3B); not Anastomosing (Haeckel 1882, pp. 99–100: dendritic, caecal, velar canals run from their lower or distal margin into the "velarium". [...] Their ramification is delicately dendritic and is weaker towards the perradius, stronger towards interradius. There are forty-eight velar canals on the whole, so that twelve of them come on each quadrant. The largest velar canal lies nearest the interradial pedalia and shows 6 to 8 pairs of side branches, partly simple, partly cleft. [...] ) | • very complexly patterned (Figs. 4K, L), canals flanking frenulum are as complexly branched as the ones flanking the pedalia; dendritic, lobed main branches and several dendritic, lobed side branches, all octants show a different pattern (Figs. 4U, 5G); not Anastomosing (Gershwin & Gibbons 2009, p. 45: [...] with edges of branches bearing lateral lobations) |
| **Adradial lappendets**                        | • none                 | • none               | • none             |
| **Perradial lappendets**                      | • none                 | • none               | • none             |
| **Structures of digestive systems**           | • manubrium, short in length (1/4 of BH) not reaching lower bell half, mouth arms, 4, narrow, no nematocyst warts on mouth tube and lips | • manubrium, short in length (1/5 of BH) not reaching into lower bell half (preserved), mouth arms, 4, broad, large/long with rounded tips (Fig. 3A9) | • manubrium, intermediate in length (1/5–1/4 of BH) not reaching into lower bell half (preserved), mouth arms, 4, broad, long, rounded tips (Fig. 4R) |
were in very good condition. The paralectotype (NMH 1882.10.9.2b, Figs. 1I, J) was in good condition, the bell complete, only cut open at one side, but the internal structures were in worse condition than those of the lectotype. The internal structures of the lectotype and paralectotype were similar in their main characters (Fig. 1) but the velarial canal pattern varied for each specimen (Figs. 1H, N) as it was from octant to octant within one specimen (Figs. 1N–Q).

Next to the characters listed by Haeckel (1880, 1882; see Table 3), four additional morphological features concerning the pedalium and velarium were noted:

1. Pedial canal keeled at midline (Fig. 1F),
2. Pedial canal knee-bend of bulged volcano-shape (Figs. 1G, L),
3. Inner wing of pedial slightly overhanging tentacle insertion (Fig. 5K, white arrow) and
4. Each octant of the velarium shows 2 velarial canal roots from which various numbers of complexly branching velarial canals arise.

**Carybdea branchi** Gershwin & Gibbons, 2009

*Type locality:* South east corner of Alfred Basin, in front of the Two Oceans Aquarium, V&A Waterfront, Cape Town [33°54.527′S, 018°25.074′E] (Gershwin & Gibbons 2009).

*Inspection of holotype, paratypes and other registered material*

The holotype (SAM-H4863, Fig. 4B) was in quite good condition even if one pedalium was ripped off (but still present in the jar) and mostly opaque. The paratypes (Tables 2b, Fig. 4C) and other registered and unregistered material (Tables 2a, b, Figs. 4D, E, 5A) were in equally good or even better condition.

In the paratypes and additional material, the main characters were similar to those observed in the holotype by Gershwin & Gibbons (2009) (Table 3). They were also identical to the ones described above for *Carybdea murrayana* (Table 3) and are not repeated here. The domed apex, due to thick mesogloea with a circular constriction below as described (Gershwin & Gibbons 2009) and found...
Validity of *Carybdea murrayana* Haeckel, 1880

in *C. branchi* (Fig. 4C, E), is not visible anymore in the type material of *C. murrayana* (Fig. 2D) but that might be due to the long time of preservation and the withdrawal of water content by the preservation medium. Haeckel (1882) described and presented in his line drawings an obvious domed apex with a circular constriction at its base (Figs. 2A, 3A1–4). Slight differences between both species can also be found in the original bell sizes, nematocyst warts on the exumbrella/pedalia, the number of gastric filaments, and the distribution.

Otherwise, the characters listed in Table 3 show no significant differences in the morphological structures of *C. murrayana* compared to the ones of *C. branchi*.

*Carybdea marsupialis* (Linnaeus, 1758)
Type locality: Mediterranean Sea (Linnaeus 1758).
As before the 19th Century the declaration of a holotype was not usual (Daston 2004), there exists no holotype, therefore, a neotype (MZB 2015-1701) was declared in 2015 (Acevedo 2016, Acevedo et al. 2019).

The neotype and other registered collection material (Table 3) of *C. marsupialis* examined for this study were all in good condition. In the registered collection material the main characters were similar to those observed in the neotype (Acevedo 2016, Acevedo et al. 2019) and identical to the ones described in Table 3. They are therefore not repeated here.

The characters listed in Table 3 show distinct differences in the morphological structures of *Carybdea marsupialis* when compared to the observed West African species *C. murrayana* and *C. branchi*.

Adult medusae of *C. marsupialis* are much smaller than the ones of *C. murrayana* or *C. branchi*. The rhopalial niche openings in all three species are heart-shaped and possess just 1 upper covering scale but in *C. marsupialis* the bottom niche channel, which runs towards the bell rim, is narrow while it is very broad in both African species. While in *C. branchi* and *C. murrayana* the pedalial canal knee bend shows a bulged, volcano-shaped appendage (Figs. 5F, L, arrows), the pedalial canal knee bend of *C. marsupialis* is rounded without any appendage (Fig. 5Q, arrow). The velarium shows 3 velarial canal roots per octant with 1–3 branched velarial canals per root, with sharp tips, in *C. marsupialis* (Fig. 5R), while the velarium in *C. murrayana* and *C. branchi* shows 2 velarial canal roots with 2–4 branched velarial canals per root and with rounded tips.
Validity of Carybdea murrayana Haeckel, 1880

Fig. 4. Carybdea branchi: A: adult medusa (in-life; photo by AC Morandini); B: Holotype SAM-H4863; C: Paratype SAM-H 4864b; D: NHM 2000.1800; E: adult medusa (preserved; photo by AC Morandini); F: apex (SAM-H 4863) with gastric phacellae (white arrows); G: apex (SAM-H 4864b) with gastric phacellae (white arrows); H: epaulette-shaped gastric phacellus; I: close up on phacellus base, note clustered, multiple stems, originating from 1 root; J: rhopalial niche (SAM-H 4863), note large, irregularly shaped nematocyst warts; K: rhopalial niche (in-life; photo by AC Morandini); L: rhopalial niche (NHM 2000.1800), note large, irregularly shaped nematocyst warts; M: rhopalial niche (preserved), note sham “lower scales” which are a preservation artefact; N: pedalium (SAM-H 4863); M: pedalium (in-life, blue colour due to background; photo by AC Morandini), note brownish coloured spots on base and tentacle insertion, note distinct pedalial knee bend with volcano-shaped appendage (arrow), note inner wing overhanging tentacle insertion; O: pedalium (NHM 2000.1800), note inner wing overhanging tentacle insertion; P: pedalium (SAM-H 4864b); Q: pedalial canal knee bend, note volcano-shaped appendage (arrow); R: manubrium (SAM-H 48064a), note long, broad, slightly frilled mouth arms (“frill” due to preservation); S: octant of velarium (SAM-H 4863; frenulum on the left border), numbers mark canal roots; T: octant of velarium (SAM-H 4864b; frenulum on the left border), numbers mark canal roots; U: quadrant of velarium (NHM 2000.1800; frenulum in the middle), numbers mark canal roots; V: C. branchi swimming next to Chirodropus gorilla in Lüderitz Bay, southern Namibia (after Straehler-Pohl (2019), p. 771, photo: Simon Elwen, Namibian Dolphin Project). f: frenulum; p: pedalium.
Fig. 5. Comparison of Carybdea branchi (A), Carybdea murrayana (H) and Carybdea marsupialis (N). Carybdea branchi: A: habitus, sampled by AC Morandini; B: gastric phacellus, note bush-like shape. C: gastric filaments (photo by AC Morandini), note tree-like shape with fused stalks originating from one root, branching several times towards the distal end; D: heart-shaped rhopalial niche, note long and broad niche channel running from niche towards bell rim; E: pedalium, note inner pedalial wing overhanging tentacle insertion (arrow; photo by AC Morandini); F: pedalial canal knee bend with volcano-shaped appendage (white arrow); G: velarium, octant, note 2 canal roots with up to 5 velarial canals of diverse shapes, lobations and branching, canal tips rounded; Carybdea murrayana: H: habitus of paralectotype; I: gastric phacellus, note bush-like shape, note single rooted attachment, and multiple branching of filaments; J: heart-shaped rhopalial niche, note broad niche channel running from niche towards bell rim; K: pedalium, note inner pedalial wing overhanging tentacle insertion (arrow); L: pedalial canal knee bend (dotted line) with volcano-shaped appendage (arrow); M: velarium, octant, note 2 canal roots with up to 5 velarial canals of diverse shapes, lobations and branching; Carybdea marsupialis: N: habitus, sampled by MJ Acevedo; O: gastric phacellus, note epaulette-shape; P: heart-shaped rhopalial niche (after Acevedo et al. 2019), note short, narrow niche channel; Q: pedalium, note that inner wing does not overhang tentacle insertion, note also rounded pedalial canal knee bend without appendage (arrow); R: velarium, octant, note 3 canal roots with 1 branching canal per root (after Acevedo et al. 2019); S: adult specimen, in-live, note brownish bases of gastric phacellae and nematocyst warts (photo by Eduardo Obis). f: frenulum; p: pedalium.
Project 2: Procharagma prototypus and Procharybdis cuboides

Procharagma prototypus Haeckel, 1880: (Figs. 6, 7)
Translation of original description (Haeckel 1880, pp. 436–437; Fig. 6A) from German to English:
"425. Species: Procharagma prototypus, Haeckel; nova species.

Plate XXV, Figures 1–2.

Species-diagnosis: Schärf würfelig-equal, equally high as wide; vent area (Comment by ISP: apex) as flattened as the 4 lateral planes, square. Stomach forms a flat square pouch, offset from the four-lobed mouth tube by a deep palatin-constriction; 4 linear phacellae, each split into 8 filaments. Bell margin with 8 flat adradial gelatin lobes (Comment by ISP: bell turn-over, velarium separated in 8 sections), 4 sense clubs small, in heart-shaped nichse, short way from bell margin. 4 tentacles simple, cylindrical, nearly as long as bell height.

Special description: Procharagma prototypus, which I could examine in two well-preserved spirit (Comment by ISP: ethanol) samples, is of high interest as being the cubo-medusa which shows, beyond all other known forms of this order, the simplest organization in form, and which can easily be phylogenetically derived from Tessera. The bell possesses a nearly perfect cubic shape, therefore, the flattened vent area has the same size and square shape as the 4 lateral planes; the sixth, oral plane of the cube is taken up by the square-shaped bell opening. The 4 lateral planes are marginally arched at the perradial midline and are offset from the rounded interradial edges only by a very flat, furrow-like depression.

The exumbrella is smooth, the gelatin of the bell is thin.
but solid. The subumbrella shows clearly the 4 perradial longitudinal muscles which divide the 4 square-panels of the ring muscles into halves and which rise from the sense niches to the mesogonia (Comment by ISP: gonads). The stomach forms a flat, square pouch at the base of the bell cavity; a deep palatine constriction separates it from the short, four-sided pyramidal mouth tube, which is drawn out into 4 short, triangular, perradial mouth arms. Inside the 4 interradial stomach corners 4 linear phacellae are set, each split into 8 digiform filaments that decrease in size from midline of the palm towards the borders on each side. The gonads are 8 rather narrow longish panels, their free margin irregularly lobate (Comment by ISP: folded); both samples were males. The bell margin bulgingly thickened and split into 8 flat, marginally salient, adradial lobes due to 8 shallow incisions. A short way up the 4 perradial incisions, 4 sense clubs are set into flat, heart-shaped niches; each seems to possess next to the small,
Validity of *Carybdea murrayana* Haeckel, 1880

Species-diagnosis: Bell nearly cubic-shaped, truncate at the top, equally high as wide. Stomach square, completely terminal, spherical otolith sack only 1 simple eye (with lense and vitreous body). The four tentacles are simple, cylindrical, without pedalia inserted into the 4 interradial incisions, about as long as the bell height.

Size: bell width 8 mm, bell height 8 mm—ontogeny unknown.

Sampling locality: Chinese Sea; Weber (Comment by ISP: collector).

*Procharybdis cuboides* Haeckel, 1880: (Fig. 8)

Translation of original description (Haeckel 1880, p. 439; Fig. 8A) from German to English:

"430. Species: *Procharybdis cuboides*, Haeckel; nova species.

Species-diagnosis: Bell nearly cubic-shaped, truncate at the top, equally high as wide. Stomach square, completely flat, with 4 short mouth arms. 4 phacellae bipartite, brush-shaped, with very short and numerous gastric filaments, twice as wide as their spaces (Comment by ISP: spaces between phacellae). Bell margin barely lobed, distance of sense niches to bell margin about half as long as the distance between the pedalial bases. Velarium quite broad, very simple, wrinkled. Pedalia nearly lancet-shaped, broadest in the middle, with 2 narrow wings, half as long as the bell height. Tentacles about half as long as the bell height, at the distal end swollen into a roundish knob. Special description and figures will follow in the "Spicilegium-Medusarum". Externally this species is very similar to *Procharagma prototypus* but differs by possessing a broad velarium, which hangs down wrinkled and limp. Also the cubic shape of the bell is less distinct as the bell widens from top to bottom a little.

---

**Fig. 8.** A: Original German text of the description of *Procharybdis cuboides* by Haeckel (1880); B: Mature medusa of *Carybdea arborifera* Maas, 1897 (interradial view); C: gastric phacellum, bar = 1 mm; D: velarium, bar = 2 mm; E: Mature medusa of *Carybdea rastonii* Haacke, 1887 (perradial view); F: apical view on linear gastric phacellae (arrows). go: gonads, gp: gastric phacellum; pd: pedalium; Translation from German to English: see main text.
I. Straehler-Pohl

The genital leaves (Comment by ISP: gonads) are narrow, from top to base narrowing, in the upper fourth sterile (Comment by ISP: barren). The wings of the pedalia very narrow, axial and abaxial of same width. Size: bell width 35 mm, bell height 35 mm—ontogeny unknown.

Sample location: Tropic belt of Pacific Ocean; Sandwich Islands, Balfour (Comment by ISP: collector).7

Discussion

Carybdea murrayana

Fourteen out of the 18 of "Haeckel's cubozoan species" have been doubted or declared as invalid (see Table 1) by many authors in the past and also recently (e.g. Mayer 1910, Kramp 1961, Gershwin 2005a+b, Bentlage & Lewis 2012) because nearly all of his described species never turned up again or were based on doubtful material (e.g. juvenile specimens, destroyed specimens) and also because of his artist's approach to idealise the creatures in his drawings into Art Nouveau style (Haeckel 1904).

Carybdea murrayana is another example, named by Haeckel in 1880 and described and drawn in detail by him in 1882 from two specimens sampled by the naturalist John Murray during the H.M.S. Challenger Expedition in 1877. This species was doubted by Mayer (1910, p. 508) and considered by him to be a probable variety of C. marsupialis, even though Mayer, nevertheless, gave a short description of the species and a hint on how to distinguish this species "from C. marsupialis by its large number of velar canals" in the same publication (Mayer 1910, p. 512).

Bigelow (1938, p. 137) stated that half-grown specimens of C. murrayana or C. marsupialis are not distinguishable, that he would call C. murrayana a "subspecies" of C. marsupialis as was customary in other taxa, and that he would support the introduction of "trinominals into the classification of pelagic coelenterates...".

Ranson (1949, p. 137) and Kramp (1959, p. 15) reported Tamoya haplonema Müller, 1859 from French Guinea, Senegambia region, and Luderitz Bay in South West Africa, sampled by the "Mercator Expedition" in 1937 and the Atlantique Sud Expedition in 1950. Kramp (1959, p. 15) described them as having "12–14 velar canals in each quadrant of the velarium."

The two Tamoya haplonema specimens from Luderitz Bay, S.W. Africa, are described by Ranson (1949) as being in bad condition and that therefore their determination remains "douteuse" (= dubious). Gershwin & Gibbons (2009, p. 49) state that "it is currently unclear if these reports may refer to C. murrayana, or even possibly to C. branchi. Although the range limits of these two species are not yet known, it seems plausible that the northern hemisphere/tropical reports of C. marsupialis and T. haplonema are not referable to the subtropical/cold temperate southern hemisphere C. branchi."

Recent investigations on a Tamoya population in West Africa (Straehler-Pohl, in revision) and the rediscovery and morphological analysis of the mentioned specimens (one Luderitz Bay specimen missing) in the collection of the Royal Belgian Institute of Natural History lead to the agreement with Ranson (1949) that the specimens from West Africa (RBINS I.G. 10910) belong to a Tamoya population but not Tamoya haplonema, which has at present time only been found along the coasts of the Americas. The present author agrees with Gershwin & Gibbons (2009) that the specimen(s) from Luderitz Bay, South West Africa (RBINS I.G. 11204) are C. murrayana and not a Tamoya species.

Kramp (1961) finally synonymised C. murrayana with C. marsupialis.

Nearly 50 years later, Gershwin & Gibbons (2009) described a species from South Africa as C. branchi, though it was conspicuously similar to C. murrayana. In their opinion (Gershwin & Gibbons 2009) C. murrayana is not a synonym of C. marsupialis but they (Gershwin & Gibbons 2009, p. 49) also stated that "... C. murrayana from West Africa could be superficially confused with C. branchi, because both are relatively large carybdeids from Africa, but the velarional canals quickly separate them: in C. branchi the side walls of the canals bear many lateral digitations, whereas these are lacking in C. murrayana. Moreover, C. murrayana has many more canals at the velarional turnover (6 per octant, versus 2) but fewer branches after (about 10 tips reaching velarial margin in C. murrayana; but less than 10 reaching margin in C. branchi)." They declared both species, C. branchi and C. murrayana, as valid.

Gershwin & Gibbons (2009, p. 48) listed also the (1) bell sizes, the (2) presence or absence of conspicuous nematocyst warts on the bell, (3) coloured pigmentation of defined spots on bell and pedalia, (4) number of gastric filaments per gastric phacellum, (5) number and shape of velarional canals as diagnostic characters that should distinguish Carybdea brachii from Carybdea murrayana and (6) the different distribution areas.

These characters are discussed as follows:

(1) As the sizes of the adult medusae of Carybdea brachii are variable (Gershwin & Gibbons 2009, present study: BH: up to 82 mm, mean: 45.58, SD: 10.498, n=35) this is not rated as a distinguishing character for C. murrayana.

(2) In the opinion of Gershwin & Gibbons (2009, p. 48) "Carybdea murrayana appears to lack exumbrella nematocysts". But Haeckel (1882, pp. 93–94) stated that "the exumbrella appears finely granulated, numerous urticating warts or round groups of thread cells are scattered freely over it". The present author noted that exumbrella nematocyst warts are easily rubbed off in most cubozoan specimens when handled roughly during sampling and after preservation (Straheler-Pohl 2014). Two Brazilian colleagues (AC Morandini, SN Stamper, pers. communication), who sampled C. brachii specimens for this study, and the present author observed that also in C. brachii the nematocyst warts rub off easily when handled in a rough
way (Figs. 4E, 5A), therefore, this is not a reliable character for preserved specimens and obviously Haeckel (1882) had noted nematocyst warts on the exumbrella.

(3) The distinct coloured spots on the pedalia and above the gastric phacellae found in *Carybdea branchi* are not found in the type material of *C. murrayana* (Figs. 1, 5H, K, L) but that is due to the preservation as can be seen by the lack of pigmentation in any of the preserved museum specimens of *C. branchi* (Figs. 4A–C, F, G, N–P). Those same Brazilian colleagues (AC Morandini, SN Stampar) observed additionally that the pigmentation of the colour markings of *C. branchi* fade very quickly when preserved (pers. communication, Figs. 4E, 5A). Therefore, those markings are not reliable distinguishing characters in preserved specimens of *C. branchi* or *C. murrayana*.

(4) The shape and structure of the gastric phacellae of *C. branchi* and *C. murrayana* are equally bushy (Gershwin & Gibbons 2009, p. 47; Haeckel 1882, p. 98; Figs. 5B, I) consisting of several, multi-branched brush-shaped filaments (2B, 5C, 1) the stems of which are tightly bundled and appear fused together, ending in a single root (Gershwin & Gibbons 2009, p. 47; Haeckel 1882, p. 98; Figs. 5C, I). The number of filaments were not counted by Haeckel as 10 to 12 but, rather, he (Haeckel 1882, p. 98) stated that the phacellae are “composed of ten to twelve larger and several smaller branches” which might also be “about 20 closely pressed stalks” as stated by Gershwin & Gibbons (2009) for *C. branchi*. No statistics were able to be applied concerning the number of filaments per phacellum because there was just 1 gastric phacellum cut out of the umbrella of the lectotype that the present author could closely observe, but the present author counted the 12 larger and about 5 smaller gastric filaments. The smaller filaments showed only few branches or none at all—those seemed to be developing filaments (before being preserved). Therefore, I conclude that the final number of filaments in *C. murrayana* cannot be defined because the number increases, like in other cubomedusan species, with age (Acevedo et al. 2019).

(5) During this study the holotype (SAM H4863), some paratypes and other type material (SAM-H 4864, NHM 2000. 1800–1803, 1.G. 11204; RBINS IG 11204, MZB 2015-4807) and also several specimens of *C. branchi* newly sampled at Hout Bay (South Africa) were observed. When comparing the anatomical features of the animals with the data and description by Gershwin & Gibbons (2009) and the description, especially the drawings of Haeckel (1882), and the type material of *C. murrayana*, all animals of both species showed the characters described by Gershwin and Gibbons (2009) for umbrella shape, gastric phacellae and pedalial knee canal bend (Figs. 1–5). However, contrary to the description of Gershwin & Gibbons (2009), the velarial canal patterns of *C. branchi* (Figs. 4S–U, 5G) reflected the patterns drawn by Haeckel (Figs. 2C, 3A, B) and the features observed anew in the type material of *C. murrayana* (Figs. 1H, N–Q, 2F, 5M). There are 2 velarial canal roots per octant in both species, as described by Gershwin & Gibbons (2009), which give rise to 2 to 4 velarial canals each (Figs. 1H, N–Q, 5M, 4S–U, 5G). When counting those canals the number matches 5 to 6 canals per octant, equal to 10 to 12 per each quadrant as described by Haeckel (1882). Therefore, I am convinced that Haeckel (1880, 1882) did not look for canal roots but counted all the canals growing into the velarium and this was misunderstood by Gershwin & Gibbons (2009).

(6) In addition to the morphological features, Gershwin & Gibbons (2009, p. 49) referred also to the sampling sites of Ranson (1949) and Kramp (1955) as mentioned above. This second argument of Gershwin & Gibbons (2009) for having two *Carybdea* species along the southern and western coast of the African continent seems plausible at first but if you look into the distribution of e.g. *Chirodorus gorilla* Haeckel, 1880, you will find that it matches the distribution of *Carybdea branchi* in South Africa (Pagès et al. 1992, Kramp 1961), in the South West, i.e. Namibia (Simon Elwen, Namibian Dolphin Project, pers. comm., 2013; Fig. 4V) and Ch. gorilla also matches the distribution of *Carybdea murrayana* in West Africa (Haeckel 1880, Thié 1928, Stiasny 1931, p. 139, Kramp 1955, 1959, 1961). *Ch. gorilla* travels with the Benguela current from the cold temperate waters of South Africa along the western shores to the tropical waters of West Africa (Pagès et al. 1992). It is quite possible, that *C. branchi* takes the same route as *Ch. gorilla* along the western coast to the shores of Liberia and Guinea, because both species are often found alongside each other (Fig. 4V).

I consider *C. branchi* and *C. murrayana* to be the same species because the morphological characters (as described above and in Table 3), as well as the likely distribution range of both species matches each other. Based on the principle of priority (Article 23, ICZN 1999) *Carybdea murrayana* Haeckel, 1880 is the older name and is, therefore, adopted as the binomen for the *Carybdea branchi* populations along the southern and western African coast; *Carybdea branchi* is to be considered its junior synonym.

All of the above results in the following diagnosis:

**Taxonomy** (based on Straehl-Pohl (2017) and Jarms & Morandini (2019))

- Phylum Cnidaria Verrill, 1865
- Class Scyphozoa Werner, 1973
- Order Cubomedusae Haeckel, 1880
- Suborder Carybdeida Lesson, 1843
- Family Carybdeidae Gegenbaur, 1857
- Genus *Carybdea* Péron & Lesueur, 1810

**Carybdea murrayana** Haeckel, 1880

(Figs. 1–4, 5A–M, 9)

**Original description (Fig. 9A):**

Translation of original description (Haeckel 1880, pp.
Fig. 9. Original German text of the description of Carybdea murrayana by Haeckel (1880, p. 442). Translation from German to English: see main text.

442; Fig. 9A) from German to English: "436. Species: Charbydea murrayana, Haeckel; nova species.

Charbydusa murrayana, Haeckel, 1877; Prodrom. System. Medus. Nr. 408.

Species diagnosis: umbralla bell-shaped, nearly cubic, slightly higher than wide, above low sloped dome, towards oral end slightly widened; side planes nearly square. Stomach completely flat, with 4 short mouth lappets. 4 phacellae bush-shaped, composed of big, brush-shaped, stalked filament clusters. Distance of heart-shaped sense niche to bell rim is half as long as the distance between pedalial bases. Velarium broad, in every quadrant with 12 niche to bell rim is half as long as the distance between pedalial bases. Velarium longish egg-shaped, as long as bell height. Tentacles cylindric, longer than bell height.

Specific description and illustration will follow in the "Deep-sea medusa of the Challenger-Expedition." The species is closer to C. marsupialis than to other species, but differs from C. marsupialis by the broad velum (Comment ISP: velarium), which contains twice as many velar canals; also these are richer dendritic ramified. Furthermore, the sculpture of the exumbrella is different. Very conspicuous are the phacellae, which are composed of many delicate, stalked brush-like or tiny, palmate tree-like filaments.

Size: bell width 50 mm, bell height 60 mm—ontogeny unknown.

Sample location: West coast of Africa, near Sierra Leone, in 200 fathoms (= 1200 feet) depth.

Latitude: 3° 10’ N, Longitude: 14° 51’ W. Challenger Station 348. John Murray (Comment ISP: collector)."

Diagnosis

Carybdea species with single rooted, multiple stemmed, epaulette-shaped gastric phacellae, pedalial canal knee bend with volcano-shaped appendage and 2 velar canal roots/ocitant with 1-5 complexly-branched and lobed canals with rounded tips; in-life, brownish coloured spots located above gastric phacellae, pedalia bases and tentacle insertion are characteristic for this species (but this pigmentation fades fast following preservation).

Etymology: This species was named in honour of Haeckel's friend John Murray F.R.S.E., one of the naturalists of the expedition and first assistant in the Challenger Commission (Haeckel 1882).

Synonyms:

Alatina alata; Gershwin & Gibbons 2009: 41 (=Carybdea alata, mentioned as misidentification, synonym for C. branchi);

Carybdea alata: Uchida 1970: 289 (specimen sampled off Cape Town used for comparison with Japanese medusa), 291–293 (detailed morphological description and line drawing of Cape Town specimen); Branch et al. 1994: 32 (pl. 13.1; South West Africa); Gershwin & Gibbons 2009: 41, 42 (mentioned as misidentification, synonym of C. branchi);

Carybdea branchi: Gershwin & Gibbons 2009: 41–50 (throughout, species description, comparison with other species), 49 (distinguishing C. murrayana from C. branchi, distribution ranges); Bentlage et al. 2010: 495 (Fig. 1: Maximum likelyhood topology tree of life for Cubomedusa); Bentlage & Lewis 2012: 2598 (Fig. 2D: medusa), 2605 (species list of genus Carybdea), Gueroun et al. 2015: 1 (mentioned); Acevedo 2016: 15 (Abstract: geographical restriction of Carybdea species), 17 (list of observed species and sample locations), 19 (systematic account), 29–32 (Figs. 5F–J, redescription of species), 34–35 (Table 1: Sampling area, GENBANK accession, Fig. 7: Phylogenetic reconstruction, Table 2: Estimates of evolutionary divergence), 40 (discussion on distribution of carybdeids from African coasts), 41 (comparison of C. branchi with "Carybdea from California"), 42 (Table 4: character comparison between Carybdea species), 43–44 (Identification key, phylogeny, biogeography); Straehler-Pohl et al. 2010: 130 (Table 1, species list of examined unregistered specimens), 131 (key to Carybdea species based on morphology of observed species), 134 (Fig. 2E: images of characteristic structures: gastric phacellae, pedalia, velarial canal pattern), 136 (discussion, comparison to C. confusa, C. branchi ≠ C. confusa); Acevedo et al. 2019: 515 (Abstract: confirmation of validity of names of distinct species), 517 (list of observed species and sample locations), 519–520 (Table 1: Sampling area, GENBANK accession; systematic account), 526–528 (redescription of species, Figs. 2F–J), 534–536 (Table 2: Estimates of evolutionary divergence, Fig. 8: Phylogenetic reconstruction, Fig. 9: Revised distribution of Carybdea species), 538–539 (discussion on distribution of carybdeids from African coasts), 539–541 (comparison of Carybdea populations worldwide, identification key, Table 4: Character comparison between Carybdea species, phylogeny, biogeography);

Carybdea sp. B: Gershwin 2006b: 9 (Table 1: Comparison of medusa cnidomes of cubozoan species), 30 (Plate 11: images of nematocysts);

Carybdea sp., South Africa: Gershwin 2005a: 75 (Table 2.13. Comparison of medusa cnidomes of cubozoan species), 103 (3.4.11 Proposed revised classification of the
Validity of Carybdea murrayana Haeckel, 1880

Carybdea marsupialis: Kramp 1955: 315 (Table III: Geographical distribution of neritic medusae: IV. W. African coasts), 541 (phylogeny and distribution of carybdeids from African coasts), 541 (mentioned in synonymy list: comparison with C. confusa and distribution of Carybdea from African coasts), 541 (phylogeny and distribution of Carybdea from African coasts), 541 (mentioned in synonymy list: comparison with C. confusa and distribution of Carybdea from African coasts), 541 (comparison of Carybdea with Carybdea from California); Straehler-Pohl et al. 2017: 131 (comparison with C. confusa by literature data as holotype seems to be lost), 136 (comparison with C. confusa, difference is the higher number of velarial canals, C. murrayana ≠ C. confusa); Acevedo et al. 2019: 516 (keywords), 520 (systematic account, synonymy list: comparison with C. marsupialis by Haeckel (1882)), 524 (mentioned in remarks for C. xaymacana as being listed with C. murrayana as synonyms for C. marsupialis by Kramp (1961) and Studebaker (1972)), 40 (discussion of similarities of structures and distribution of Carybdeidae from African coasts), 41 (comparison of Carybdea murrayana with Carybdea from California); Straehler-Pohl et al. 2017: 131 (comparison with C. confusa by literature data as holotype seems to be lost), 136 (comparison with C. confusa, difference is the higher number of velarial canals, C. murrayana ≠ C. confusa); Acevedo et al. 2019: 516 (keywords), 520 (systematic account, synonymy list: comparison with C. marsupialis by Haeckel (1882)), 524 (mentioned in remarks for C. xaymacana as being listed with C. murrayana as synonyms for C. marsupialis by Kramp (1961) and Studebaker (1972)), 353 (discussion of similarities of structures and distribution of Carybdeidae from African coasts), 541 (phylogeny and biogeography: no specimens for morphological or genetic comparison, therefore no statement on this species).

Carybdea marsupialis: Kramp 1955: 315 (Table III: Geographical distribution of neritic medusae: IV. W. African sections: in Cape Verde Islands); Kramp 1961: 305 (synonymises Carybdea murrayana with Carybdea marsupialis); Studebaker 1972: 9 (Taxonomy, synonym of C. marsupialis), 10 (discussion: C. murrayana is bigger and has more velar canals than C. marsupialis but Kramp (1961) lists C. murrayana as a synonym of C. marsupialis, therefore, also listed as synonym); Charybdea murrayana: Haeckel 1880: 442 (short description); Haeckel 1882: 92 (etymology); 93–101 (species description), Plate 26; Haecke 1887: 592, 597–598 (comparison with Carybdea rastoni); Haeckel 1904/1998: 190 (short description/figure descriptions), Plate 78, Figs. 5, 6; Kishinouye 1910: 6 (bell structure comparison with C. mora (=C. brevipedalia)); Stiasny 1939: 43 (mentions the 2 specimens sampled by Challenger Expedition not far from Sierra Leone); Gueroun et al. 2015: 1 (mentioned); Tamaya haplonema: Ranson 1949: 137 (species list of medusae, 2 medusae collected 4 miles off Luderitz Bay, Namibia, bad condition, therefore, difficult to determine); Pagès et al. 1992: 57–58 (species description and line drawing of habitus and velarium, sampling location, distribution); Gershwin & Gibbons 2009: 41 (mentioned as misidentification, synonym of C. branchi);

Type material:
LECTOTYPE: Natural History Museum, London (NHM): 1 mature female (1882.10.9.2a: 1 medusa, completely dissected, broken in 3 parts: BH: ca. 56 mm, IPD: ca. 68 mm, IRD: no measurement possible), West Coast of Africa, not far from Sierra Leone (30°10′N, 14°51′W), Challenger Expedition 1872–76 Station 348, from 400 m depth, collected by J. Murray, April 9, 1876. (Haeckel 1882).
PARALECTOTYPE: Natural History Museum, London (NHM): 1 mature female (1882.10.9.2b: 1 medusa, whole but cut open: BH: ca. 44 mm, IPD: ca. 53 mm, IRD: ca. 29 mm), same data as Lectotype. (Haeckel 1882).

Additional Material:
Registered material:
Labelled as Carybdea branchi Gershwin & Gibbons, 2009
“HOLOTYPE” (Carybdea branchi): South African Museum, Cape Town (SAM): South east corner of Alfred Basin, Cape Town, in front of the Two Oceans Aquarium, Victoria & Albert Waterfront (33°54′52.7″S, 018°25′07.4″E), 1 specimen (SAM-H4863; Fig. 4B), hand-dipped from surface, 18 January 2001, collected by L. Gershwin & L. Hoensen (Gershwin & Gibbons 2009)
“PARATYPES” (Carybdea branchi): South Australian Museum, Adelaide: South Africa: Soldhana Bay, SAM-H923 (≡RVS A262), 28 April 1958; SAM-H924 (≡RVS A389F), SAM-H925 (≡RVS A389A), 2 specimens (SAM-H926 (≡RVS A389 H, I)), SAM-H928 (≡RVS A389J), SAM-H929, SAM-H1064, April 1959; Langebaan, SAM-H927 (≡RVS A298), collected by University of Cape Town (Ecol. Survey LB.514), 28 April 1958; SAM-H930 (≡RVS A389M), SAM-H931 (≡RVS A389L), SAM-H932 (≡RVS A389K), immature, collected by ?University of Cape Town, April 1959; SAM-H933 (≡RVS A390), immature, University of Cape Town, SB 112, 14 July 1946; probably Langebaan, 3 specimens (SAM-H934 (≡RVS A376)), University of Cape Town, 20 August 1946 (Gershwin & Gibbons 2009)
Naturalis Biodiversity Center Netherlands (NBCN), Leiden: South Africa: Port Elisabeth, 4 specimens (NNM 5228), 26 May 1936 (Gershwin & Gibbons 2009)
Iziko South African Museum, Cape Town: South Africa:
no location data (SAM-H4860), collected by G. Branch; off Langebaan Jetty (SAM-4861), 29 September 1959, collected by University of Cape Town Research, by hand at surface; no loc. data, 1 male (SAM-H4862), 14 April 1963, collected by University of Cape Town Ecological Survey #CP 696 A; same data as holotype, 2 specimens (SAM-H4864a+b; Fig. 4C); same data as holotype, 4 specimens (SAM-H4865); same loc. as holotype, 6 specimens (SAM-H4866), 17 January 2001, L. Gershwin & G. Branch (Gershwin & Gibbons 2009)

**Labelled as "Carybdea robsonae Gershwin, 2000":**
Natural History Museum, (NHM), London: Four (4) specimens (NHM 2000.1800-1803; Fig. 4D), Simon’s Town Docks, False Bay, South Africa, collected by Gershwin & Gibbons 2009, this study (after Haeckel 1880, com-

**Labelled as "Tamoya haplonema Müller":**
Royal Belgian Institute of Natural Science (RBINS), Brussels: Africa, Namibia, 4 miles off Lüderitz Bay, 1 specimen (RBINS I.G. 11204), Cruise of the "Mercator", 18 January 1937 (Ranson 1949).

Unregistered specimens:
Nature Historical Museum of Denmark, Copenhagen (NHMD): NHMD unnumbered, False Bay, collected by Papenfuss during the "Africana" Expedition. (Gershwin & Gibbons 2009)

“Specimens from the Ronald V. Southcott collection are indicated with his initials (RVS) and correspond to extensive notes archived in the South Australian Museum” (Gershwin & Gibbons 2009, p. 42)

Iziko South African Museum, Cape Town (SAM): Cape Peninsula, Oudekraal (34°10’S, 18°15’E), 1 specimen labelled as "Cubomedusa, presented by Prof. Trueman, 1975. Oudekraal”. (Pagès et al. 1992).

**Examined material:**
Registered material:
Lectotype, paralectotype, SAM-H4863, SAM-H 4864a+b, RBINS I.G. 11204, NHM 2000.1800–1803.

Unregistered material:
South Africa, Hout Bay (34°03’4.8"S, 18°20’53.99"E), morphological structures of 5 preserved adult specimens and photos of detailed structures of 7 living animals collected and provided by A. C. Morandini, May 05, 2013; South Africa, Cape Town, Two Oceans Aquarium 5 living individuals.

1 specimen, NHMD unnumbered ("Africana” Expedition)

**Type location:** West Coast of Africa, not far from Sierra Leone (30°10’N, 14°51’W), Challenger Expedition 1872-76 Station 348, depth=400 m.

**Revised description:** (after Haeckel 1880, 1882, complemented with data by Gershwin & Gibbons 2009, this study)

**Adult medusa:**
Bell, in-life (Figs. 4A, V), highly transparent, densely scattered with white nematocyst warts of different shapes and sizes (Fig. 4A, F, K, M) from apex to bell margin (bigger nematocyst warts at interradial furrows and bell margin, smaller nematocyst warts on bell sides and apex), gastric phacellae, with yellowish to reddish-brown coloured spots (Fig. 4A), pedallum (Figs. 4A, M), outer wing base, light brown coloured, outer wing distal end, reddish brown coloured, tentacles light pink—pigmentation fades very fast to invisibility after preservation (Figs. 4B–G, 5A, E, F), bell then opaque yellowish to white, tentacles pink to flesh coloured; bell, cube-shaped, slightly higher than wide, preserved specimens: up to 82 mm (BH), up to 99 mm (IPD), up to 51 (IRW), sturdy, shallow interradial furrows, apex, thick mesogloea, convex, with horizontal constriction near top.

Rhopalial niches (Fig. 4K: in-life; Figs. 1D, K, 4J, L, M, 5D: preserved), 4, orifice broadly heart- to “Y”-shaped, upper covering scale, triangular with pointed tip, many very small, round nematocyst warts on scale, bottom open with no lower covering scales (in preserved specimens: lower rim of orifice can have appearance of additional narrow scales (Figs. 1D, 4J, L, M, 5D) but that is a preservation artefact due to water loss), ca. 1/5–1/4 of bell height up from margin; rhopalium with 6 eyes (2 major with lenses +2 lateral slit eyes +2 lateral pit eyes).

Pedalia, 4, single, long (length approx. 1/2 BH), flattened, scalpel-shaped, brownish colour marks on base and distal end of outer wing (Figs. 4A, M: in-life), inner wing, free of nematocyst warts, very narrow at base, flaring towards midsection, tapering again towards distal end (twice as high as broad), very slightly overhanging tentacle insertion (Fig. 4M, O, 5E), outer wing, slightly narrower than inner wing, densely scattered with irregular, white nematocyst warts and bands (Figs. 4A, M, O, P); pedalial canals, square in diameter with lateral keels, distinctly depressed at base, broadening after knee bend, going straight with even width through pedalium, flaring at tentacle insertion, knee bend, volcano shaped, upturned knee bend without appendage (Figs. 1G, L, 4O–Q, 5E, F, L, arrows); tentacles, 4, banded with nematocyst battery rings, round to slightly oval in cross section, starkly flared at base, tapering towards distal end (Figs. 4A–D, M, 5A, H).

Velarium, free of nematocyst warts, velarial canal roots, 2 per octant (Figs. 1H, N–Q, 3B, 4S–U, 5G, M), velarial canals, 2–4 per root, slim in width, canals deeply forked, multiple branched, lobed, some side branches tend to grow in centripetal direction (Figs. 1A, O, 4T, 5G, M), sometimes pointed, mostly rounded tips; canals flanking frenulum same complexity and size as canals flanking pedalia, with 2 to 3 lobed main branches and several lobed side branches, resembling “gnarled” trees (Figs. 2C, F, 4S, T).

Manubrium, intermediate in length (ca. 1/5–1/4 of BH in length; Fig. 4R), four-lobed, conspicuously long and broad mouth arms (2/3 of manubrium length) (Fig. 4R); stomach,
flat, shallow; gastric phacellae, 4, epaulette-shaped (Figs. 2B, E, 3A7, 4H, 5B, I), single rooted, mounted on four stomach corners (Figs. 3A3, 4A, F, G), consisting of ca. 15–20 brush-shaped filaments (Fig. 2B) per quadrant, multiple stalked, stalks of filaments tightly aligned, originating from one root (Fig. 4I (arrow), 5C, I); gastric pockets, 4, leading into velarial canals.

 Gonads, 4 pairs, broad leaf- to egg-shaped (Figs. 1E, J, 4E, I), pleated edges, covering length of the gastric pouches from stomach corner to bell margin, tapering slightly towards stomach rim and bell margin, lateral margins slightly overlapping, separated by imperforated, interradial septum. Sexes, separated but unimorph.

 **Nematocysts:** (after Gershwin 2006b; Gershwin & Gibbons 2009)

 Tentacles: small oval isorhizas (13.39–17.62 \(\mu m \times 6.06–8.20 \mu m\), and heterotrichous microphone euretyles (19.33–31.12 \(\mu m \times 11.98–16.39 \mu m\)).

 Pedalia and Exumbrella (nematocysts grouped in warts): spherical isorhizas (15.53–20.64 \(\mu m\), and oval ?amastigophores (15.42–16.30 \(\mu m \times 9.54–11.05 \mu m\)).

 Sting: fire-like pain lasting about 10 minutes, cessation of heart-beat, followed by abnormally rapid heartbeats for a few minutes (Gershwin & Gibbons 2009).

 **Mating behaviour, brooding behaviour, polyp, asexual reproduction, newly detached medusa:** Unknown

**Distribution**

**Africa:**
- **West Africa:** West Coast of Africa, not far from Sierra Leone. (30°10′N., 14°51′W), Guinea (Haeckel 1880, 1882; Kramp 1955, 1959)
- **South Africa:** from Port Elisabeth along the south coast, to Laangebaan, Soldhana Bay, on the west coast; south east corner of Alfred Basin, in front of the Two Oceans Aquarium, Victoria & Albert Waterfront, Cape Town (33°54′52.7″S, 018°25′07.4″E); Soldhana Bay; Langebaan; Port Elisabeth; Simon’s Town Docks, False Bay; (Gershwin & Gibbons 2009); Hout Bay (34°03′4.8″S, 18°20′53.99″E), swimming at surface near pier (A.C. Morandini, S.N. Stampar, pers. communication); Cape Peninsula, Oudekraal (34°10′S, 18°15′E) (Pagès et al. 1992)
- **Namibia:** 4 miles off Lüderitz Bay (Ranson 1949); Lüderitz Bay (Simon Elwen (Namibian Dolphin Project), photographed March 04, 2011; person. communication, 2013, Fig. 4V).

**Carybdea murrayana** was first found in a deep trawl to 400 m depth on the Western Coast of Africa near Sierra Leone in the Gulf of Guinea (Haeckel 1880, 1882) but it is not clear if *C. murrayana* was sampled that deep or on the way up. It seems to travel along the western shores of the African continent with the Benguela current (Pagès et al. 1992). It is a cold water species found in kelp forests similar to its congener *Carybdea confusa* from California, USA (Straehler-Pohl et al. 2017).

**Revisional remarks on Procharagma prototypus Haeckel, 1880 and Procharagma cuboides Haeckel, 1880**

**Procharagma prototypus** Haeckel, 1880 (Figs. 6B–D, 7A–F, 2A–K, 4A–N)

 Mayer (1910: p. 507) considered that “It is not improbable also that future studies will show that Haeckel’s *Procharagma* is actually *Carybdea.*” as it “appears to be composed of immature or imperfectly known young specimens of *Carybdea*”.

 According to the details in the description of Haeckel (1880) and according to the presently accepted morphological character diagnosis *Procharagma prototypus* Haeckel, 1880 is a member of the Family Carybdeidae (diagnosis: heart-shaped sense niche ostia with 1 upper covering scale without lower covering scale) (Bentlage & Lewis 2012, Acevedo 2016, Acevedo et al. 2019, Straehler-Pohl 2019). There is no distinctive character that validates the maintenance of the genus *Procharagma*, and because Carybdeidae is a monogenic family, the species is accommodated in the genus *Carybdea* (diagnosis: gastric phacellae brush-shaped, epaulette-shaped or linear horizontal rows of filaments) (Bentlage & Lewis 2012, Acevedo 2016, Acevedo et al. 2019, Straehler-Pohl 2019).

 Mayer (1910: p. 508) considered *Procharagma prototypus* as a young medusa of *Carybdea rastonii*. Like *C. rastonii* (Fig. 8E) the gastric phacellae of *P. prototypus* are described as linear bands (Fig. 6A), but *C. rastonii’s* distribution range is up to now restricted to South and West Australia (Matsumoto 1995, 2004, Williamson et al. 1996) while the specimens described by Haeckel (1880; Fig. 6A, B, 7B–C) were sampled in the “Chinese Seas”. “Chinese Seas” is a term used in the 19th century for a series of marginal seas in the West Pacific Ocean expanding from Japan to Borneo, consisting of the Yellow Sea (between Korea and northern China), the East Chinese Sea (between the Japanese Islands and middle China) and the South Chinese Sea (between South China and Myanmar) (Meyers Großes Konversations-Lexikon 1906, p. 59, Sendlinger 2008, pp. 126, 690, Wikipedia: China Sea). The only other carybdeid species with linear bands of gastric phacellae and which lives in the East Chinese Sea is *Carybdea brevipedalia* Kishinouye, 1891 (Chae et al. 2017).

 Therefore, the present author concludes that *Procharagma prototypus* is identical to *Carybdea brevipedalia*, which would therefore be a junior synonym. Referring to the rule of priority (ICZN 1999), the nomenclature to be used is *Carybdea prototypus* (Haeckel, 1880) because there exists a detailed type illustration and description as alternative to a lost preserved specimen as proof.

**Carybdea prototypus** (Haeckel, 1880)

**Synonyms** (species “original” descriptions with different names and first authors)

*Procharagma prototypus* Haeckel, 1880

*Carybdea brevipedalia* Kishinouye, 1891

*Carybdea mora* Kishinouye, 1910
Carybdea brevipadalía Kishinouye, 1891
Carybdea mora Kishinouye, 1910

Procharybdis cuboides Haeckel, 1880

Mayer (1910: p. 505) considered the genus *Procharybdis* as "...probably only a young *Charybdea*" due to the diagnosis of Haeckel (1880) that the velarium does not possess frenulae nor velarial canals.

Following the same reasoning used for *Procharagma prototypus* and based on the description of *Procharybdis cuboides* (translation above), the species is referred to the Family Carybdeidae and to the genus *Carybdea* (Bentlage & Lewis 2012, Straehler-Pohl 2019), agreeing with Mayer's (1910: p. 505) conclusion.

Mayer (1910: p. 506) also concluded that *Procharybdis cuboides* is a young stage of *Carybdea rastonii*. But the gastric phacellae of *C. rastonii* (Fig. 8E) are organised in linear bands (Fig. 8F), the bell is more cylindrical (BH: up to 35 mm, BW: up to 30 mm) and *C. rastonii*’s distribution range is currently thought to be restricted to South and West Australia (Matsumoto 1995, 2004, Williamson et al. 1996). The specimen described by Haeckel (1880; Fig. 8A) has bipartite, brush-shaped gastric phacellae and was sampled in the Sandwich Islands (which are now called the Hawaiian Islands: Sendlinger 2008, p. 303, Wikipedia: Hawaiian Islands)—the only *carybdeid* species located there that fits the descriptions of Haeckel (brush-shaped gastric phacellae (Fig. 8C), narrow pedalia, narrow gonads which taper from top to base, bell nearly cubic but slightly wider at the bell opening than at the apex, BH, BW: about 35 mm) is *Carybdea arborifera* Maas, 1897 with a bell height of up to 35 mm and a bell width of up to 33 mm (Maas 1897, Mayer 1906, Bentlage et al. 2010, Crow et al. 2015, own observations; Fig. 8B).

Therefore, the present author concludes that *Procharybdis cuboides* is identical with *Carybdea arborifera*, which therefore is a junior synonym. Referring to the rule of priority (ICZN 1999) the nomenclature to be used is *Carybdea cuboides* (Haeckel, 1880) as there exists a detailed description as alternative to a preserved specimen as proof.

*Carybdea cuboides* (Haeckel, 1880)

**Synonyms** (species “original” descriptions with different names and/or first authors)

- *Procharybdis cuboides* Haeckel, 1880
- *Charybdea arborifera* Maas, 1897
- *Carybdea arborifera* Maas, 1897

**Acknowledgements**

I would like to thank Miranda Lowe, MSc, curator and collection manager at the British Museum of Natural History in London, United Kingdom, Dr. Yves Samyn (Curator of the echinoderm collections and head-conservator of the Recent Invertebrate Collections of the Royal Belgian Institute of Natural Sciences in Brussels (RBINS)) and Dr. Martin Vinther Sørensen (Associate professor at the University of Copenhagen, and senior curator of Porifera, Cnidaria, Mollusca and microscopic invertebrates) and his Collection Manager Laura Pavesi at the Natural History Museum of Denmark, for hosting me in the museums, allowing me to use their facilities and making the necessary samples in the collections available on short notice in 2015.

Special thanks also to Dr. Wayne Florence (Senior curator for marine invertebrates) and Albe Bosman, MSc (Collections manager) of the Iziko South African Museum and Dr. Mark Gibbons (Professor for Biodiversity and Conservation Biology at the University of the Western Cape, Cape Town) for arranging my visit to the marine invertebrate collection on short notice in 2019 and giving me the opportunity to observe the holotype and other material of *Carybdea branchi*. And thank you, Mark, for not being too disappointed with me when telling you that your *Carybdea branchi* will be a junior synonym of *Carybdea murrayana*.

Many thanks also to Dr. Lars Tschacher and Dr. Marcus Balluff for supporting this project by allowing me to take a day off during a business trip to be able to visit the South African Museum to inspect the holotype of *C. branchi*.

The images of the original line drawings of Haeckel were provided by Dr. Thomas Bach with courtesy of the Ernst-Haeckel-Haus, Friedrich-Schiller-Universität Jena Institut für Geschichte der Medizin, Naturwissenschaft und Technik.

I am also grateful to two anonymous reviewers for their constructive suggestions, especially giving the hint to contact Dale Calder for clarification of ICZN (1999) rules of priority. Many thanks also to Dr. Dhugal Lindsay for editing the orthography and grammar of the manuscript.

My visits to the collections of the Natural History Museum London and Natural History Museum in Denmark in 2016 and 2017 were sponsored by the SYNTHESYS Program of the European Commission (DK-TAF-5580, GB-TAF-6151, GB-TAF-7146), financed by a European Community Research Infrastructure Action under the FP7 Integrating Activities Programme for research in European Museums.

**References**

Acevedo DMJ (2016) Biology, ecology and ecophysiology of the box jellyfish *Carybdea marsupialis* (Cnidaria: Cubozoa). PhD Thesis. Universidad Politécnica de Cataluña. 138 pp.

Acevedo M, Straehler-Pohl I, Morandini AC, Stampar SN, Bentlage B, Matsumoto GI, Yanagihara A, Toshino S, Fuentes V (2019) Revision of the genus *Carybdea* (Cnidaria: Carybdeidae): clarifying the identity of its type species *Carybdea marsupialis*. Zootaxa. 4543(4): 515–548. https://doi.org/10.11646/zootaxa.4543.4.3

Bentlage B, Cartwright P, Yanagihara AA, Lewis C, Richards GS, Collins AG (2010) Evolution of box jellyfish (Cnidaria: Cubozoa), a group of highly toxic invertebrates. Proc R Soc B 277: 493–501. http://dx.doi.org/10.1098/rspb.2009.1707

Bentlage B, Lewis C (2012) An illustrated key and synopsis of
the families and genera of carybdeid box jellyfishes (Cnidaria: Cubozoa: Carybdeida), with emphasis on the "Irukandji family" (Carukidae). Journal of Natural History 46(41–42): 2595–2620. DOI 10.1080/00222933.2012.717645

Blechschmidt E (1977) The Beginnings of Human Life. Heidelberg Science Library, Springer-Verlag, New York, 128 pp. DOI 10.1007/978-1-4612-6347-0

Bigelow HB (1938) Plankton of the Bermuda Oceanographic Expeditions VIII. 5. Medusae taken during the Years 1929 and 1930. Zoologica, 23(5): 99–180.

Bowler PJ (1989) Evolution: The History of an Idea. University of California Press, Berkeley (California), 496 pp.

Branch GM, Griffiths CL, Branch ML, Beckley LE (1994) Two Oceans: A guide to the Marine Life of Southern Africa. David Philip, Cape Town, 360 pp.

Campbell RD (1974) Cnidaria. In: Giese AC, Pearse, JS (Eds), Reproduction of marine invertebrates. Vol I. Acoelomate and pseudocoelemate metazoans. Academic Press, pp 133–199.

Chae J, Yoon W-D, Kim BH, Ki J-S (2017) First Record of Box Jellyfish, Carybdea brevipedalia (Cnidaria: Cubozoa: Carybdeidae) from Korean Coastal Waters: Morphology and Molecular Descriptions. Animal Systemat, Evol Divers 33(1): 8–16. doi.org/10.10535/ASED.2017.33.1.059

Claus C (1878) Ueber Charybdea marsupialis. Arb zool Inst Univ Wien 1: 6–56+5 plates.

Collins, AG, Bentlage B, Gillan W (B), Lynn TH, Morandini AC, Marques AC (2011) Naming the Bonaire banded box jelly, Tamoya ohboya, n. sp. (Cnidaria: Cuboza: Carybdeida: Tamoyidae). Zootaxa 2753: 53–68. http://dx.doi.org/10.11646/zootaxa.2753.1.3

Crow GL, Chiaverano LM, Crites J, Khramov MA, Holland B (2004) Type Specimens and Scientific Memory. In: Collins AG, Bentlage B, Gillan W (B), Lynn TH, Morandini AC (Eds), The Beginnings of Human Life. Heidelberg Science Library, Springer-Verlag, New York, 128 pp. DOI 10.1007/978-1-4612-6347-0

Daston L (2004) Type Specimens and Scientific Memory. In: Mitchell WJT (Ed) Critical Inquiry. 31(1): 153–182. DOI 10.1086/427306

Gershwin L-A (2005a) Taxonomy and Phylogeny of Australian Cubozoa. PhD Thesis. School of Marine Biology and Aquaculture, James Cook University, 202 pp.

Gershwin L-A (2005b) Carybdea alata auct. and Manokia stiasnyi, reclassification to a new family with description of a new genus and two new species. Mem Queensl Mus 51(2): 501–523.

Gershwin L-A (2006a) Comments on Chirophthalmus (Cnidaria: Cubozoa: Chirodropida): a preliminary revision of the Chirophthalmidae, with descriptions of two new genera and two new species. Zootaxa 1231: 1–42.

Gershwin L-A (2006b) Nematocysts of the Cubozaa. Zootaxa 1232: 1–57.

Gershwin L-A, Gibbons MJ (2009) Carybdea branchi, sp. nov., a new box jellyfish (Cnidaria: Cubozaa) from South Africa. Zootaxa 2088: 41–50.

Gueroun SKM, Acevedo MJ, Kéfi-Daly Yahia O, Deidun A, Fuentes VL, Piraino S, Daly Yahia MN (2015) First records of Carybdea marsupialis proliferation (Cnidaria: Cubozaa) along the eastern Tunisian coast (Central Mediterranean). Ital J Zool 1: 1–6. DOI: 10.1080/11250003.2015.1045945

Haacke, W. (1887) Die Scyphomedusen des St. Vincent Golfoes.

Jenaische Naturwissenschaftliche Zeitschrift 20: 588–638+3 plates.

Haeckel E (1880) System der Acraspeden: Zweite Hälfte des Systems der Medusen. Denkschr Med Natwiss Ges Jena 2: 361–672.

Haeckel E (1882) II. — Report on the deep sea medusae. In: Thomson FT, Murray J (Eds) Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873-76 under the command of Captain George S. Nares, R.N., F.R.S. and Captain Frank Tourelle Thomson, R.N. Zoology, Vol IV, Part II, 154 pp.+32 plates.

Haeckel E (1891) Apologetisches Schlüßwort. In: Anthropogenie oder Entwicklungsgeschichte des Menschen gemeinhinländische wissenschaftliche Vorträge über die Grundzüge der menschlichen Keimes- und Stammesgeschichte 3. Auflage, Wilhelm Engelmann, Leipzig, pp. 857–864.

Haeckel E (1899) Die Welträthsel. Gemeinverständliche Studien über monistische Philosophie [Translation: The Riddle of the Universe at the Close of the Nineteenth Century]. Verlag von Emil Strauß, Bonn, 473 pp. (http://www.deutschtextarchiv.de/book/show/haeckel_weltraethsel_1899)

Haeckel E (1904/1998) Kunstformen der Natur: mit beschreibendem Text, allgemeiner Erläuterung und systematischer Überseicht. Neudruck der Erstausgabe des Bibliographisches Instituts in Leipzig und Wien, 1904, Prestel-Verlag, München, New York, 280 pp.+100 plates.

Haeckel E (1910) Sandalion. Eine offene Antwort auf die Fälschungs-Anklagen der Jesuiten. 1–5. Tausend, Neuer Frankfurter Verlag GmbH, Frankfurt am Main, 55 pp.

ICZN (1999) International Code of Zoological Nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature, London, UK, 306 pp.

Jarms G, Morandini AC (2019) Chapter 5: Phylogeny and systematics. In: Jarms G, Morandini AC (Eds) A World Atlas of Jellyfish. Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg, Special Edition, English Edition, Dölling and Galitz Verlag, pp. 33–37.

Kishinouye K (1891) Zwei neue Medusen von Charybdea (Ch. brevipedalia sp., Ch. latigenitalia n.sp.). The monthly publication of the Zool Soc Japan 3: 36–45.

Kishinouye K (1910) Some Medusae of Japanese Waters. J Coll. Sci Imp Univ Tokyo 27(9): 2–35+5 plates.

Krampl PL (1955) The Medusae of the Tropical West Coast of Africa. Atlantide Report 3: 239–324.

Krampl, PL (1959) Medusae mainly from the west coast of Africa. Mem IERSNB 3(6): 1–33.

Krauß E (1887) Ernst Haeckel. In: Goetz D, Jahn I, Wächtel T. (Ed.), Handbuch der Zoologie. W de Gruyer, Berlin, pp. 323–372.

Krauß E (1904/1998) Kunstformen der Natur: mit beschreibendem Text, allgemeiner Erläuterung und systematischer Überseicht. Neudruck der Erstausgabe des Bibliographisches Instituts in Leipzig und Wien, 1904, Prestel-Verlag, München, New York, 280 pp.+100 plates.

Krauw E (1983) Ernst Haeckel. In: Goetz D, Jahn I, Wächtel T. (Ed.), Handbuch der Zoologie. W de Gruyer, Berlin, pp. 323–372.

Krauw E (1987) Ernst Haeckel. In: Goetz D, Jahn I, Wächtel E, Wußing H (Eds) Biographien hervorragender Naturwissenschaftler, Techniker und Mediziner, Bd 70, 2nd Edition, Emil Strauß, Bonn, 473 pp. (http://www.deutschtextarchiv.de/book/show/haeckel_weltraethsel_1899)

Krauw E (1910) Sandalion. Eine offene Antwort auf die Fälschungs-Anklagen der Jesuiten. 1–5. Tausend, Neuer Frankfurter Verlag GmbH, Frankfurt am Main, 55 pp.

Kramp PL, Murray J (Eds) Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873-76 under the command of Captain George S. Nares, R.N., F.R.S. and Captain Frank Tourelle Thomson, R.N. Zoology, Vol IV, Part II, 154 pp.+32 plates.

Kramp PL (1955) The Medusae of the Tropical West Coast of Africa. Atlantide Report 3: 239–324.

Krauß E (1887) Ernst Haeckel. In: Goetz D, Jahn I, Wächtel E, Wußing H (Eds) Biographien hervorragender Naturwissenschaftler, Techniker und Mediziner, Bd 70, 2nd Edition, Leipzig: BSB BG Teubner Verlagsgesellschaft 1985, 151 pp.

Krauw E (1925) Scyphozoa. In: Kükenthal, W. & Krumbach, T. (Ed.), Handbuch der Zoologie. W de Gruyer, Berlin, pp. 323–372.

Krauw E (1983) Ernst Haeckel. In: Goetz D, Jahn I, Wächtel T. (Ed.), Handbuch der Zoologie. W de Gruyer, Berlin, pp. 323–372.
off the West Coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross" during 1891, Lieutenant Commander Z. L. Tanner, U.S.N., Commanding. Mem Mus Comp Zoology Harv Coll 23(1): 1–92+15 plates.

Marques AC, Collins AG (2004) Cladistic analysis of Medusozoan and cnidian evolution. Invert Biol 123: 23–42. http://dx.doi.org/10.1111/j.1744-7410.2004.tb00139.x

Matsumoto GI (1995) Observations on the anatomy and behaviour of the cubozoan Carybdea rastioni Haacke. Mar Freshw Behav Physiol 26: 139–148.

Matsumoto GI (2004) Cubozoa. In: Hutchins M, Conway W-Páll-Gergely B (2017) Should we describe genera without molecular phylogenetic support? Zootaxa 4232(4): 593–596.

Meyers Großes Konversations-Lexikon (1906). Definition Chinesisches Meer. Vol 4, Leipzig, p.59. Available at: http://www.zeno.org/Meyers-1905/A/Chinesisches…

Mianzan H, Cornelius P (1999) Cubomedusae and Scyphomedusae. In: Boltsvovskoy D (Ed) South Atlantic Zooplankton, Vol. 1. Backhuys Publishers, Leiden, The Netherlands, pp. 513–559.

Milner R (1990) The Encyclopedia of Evolution: Humanity's Search for Its Origins (A Henry Holt Reference Book). Owl Books, Henry Holt and Company, New York, 483 pp.

Morandini AC, Marques AC (2010) Revision of the genus Alatina. J Mar Freshw Res 7(2): 254–280 + 3 plates.

Stiasny G (1931) Die Rhizostomen des British Museum (Natural History) in London. Zool Medd 14: 137–178.

Stiasny G (1939) Scyphomedusen von der Congomündung. Rev Zool Bot Afr 33(1): 42–43.

Straehler-Pohl I (2014) Critical evaluation of characters for species identification in the cubomedusa genus Malo (Cnidaria, Cubozoa, Carybdeida, Carukiiidae). Plankton Benthos Res 9(2): 83–98. https://doi.org/10.3800/pbr.9.83

Straehler-Pohl, I. (2017) Cubozoa and Scyphozoa: The results of 20 years of scyphozoan life cycle research with new results on cubozoan life cycles to suggest a new nomenclature referring to both classes. In: Frontiers in ecological studies of jellyfish. (eds. Toyokawa M, Miyake H, Nishikawa J), Seibutsu Kenkyu Sha Co. Ltd. (Organisms Research Co. Ltd.), Tokyo, 17–29.

Straehler-Pohl I, Gul S (2017) Rediscovery and description of the cubomedusa Alatina grandis (Agassiz & Mayer, 1902) (Cnidaria: Cubozoa: Alatinidae) from Pakistani waters. Plankton Benthos Res 12(1): 1–14. https://doi.org/10.3800/pbr.12.1

Straehler-Pohl I, Matsumoto G, Acevedo M (2017) Recognition of the Californian cubozoan population as a new species—Carybdea confusa n. sp. (Cnidaria, Cubozoa, Carybdeida). Plankton Benthos Res 12(2): 129–138. https://doi.org/10.3800/pbr.12.129

Straehler-Pohl I, Toshino S (2015) Carybdea morandinii—New investigations on its life cycle reveal its true genus: Carybdea morandinii Straehler-Pohl & Jarms, 2011 becomes Alatina morandinii (Straehler-Pohl & Jarms, 2011). Plankton Benthos Res 10(4): 167–177. DOI: 10.13140/RG.2.1.4928.1049

Studebaker JP (1972) Development of the cubomedusa, Carybdea marsupialis. Masters thesis. Department of Marine Sciences, University of Puerto Rico College of Agriculture and Mechanical Arts Mayaguez, Puerto Rico, 60 pp.

Teudt W (1909) Im Interesse der Wissenschaft. Haeckels Fälschungen und die 46 Zoologen etc. Naturwissenschaftlicher Verlag des Keplerbundes, Godesberg, 104 pp.

Thiel ME (1928) The Scyphomedusen des Zoologischen Staats-Institut und Zoologischen Museums in Hamburg. 1. Cubomedusen, Stauromedusen und Coronatae. Mitt Hamb Zool Mus 43: 1–34.

Thiel ME (1936) Cubomedusae In: Dr. HG Bronns Klassen und Ordnungen des Tierreichs. Zweiter Band: Spongioria, Coelenterata, Echinodermata, 11. Abteilung Coelenterata, 2. Buch Scyphomedusae, 2. Lieferung. Akademische Verlagsgesellschaft mbH, Leipzig, pp. 173–308.

Uchida T (1929) Studies on the Stauromedusae and Cubomedusae, with special reference to their metamorphosis. Jpn J Zool 2: 103–193.

Uchida T (1970) Revision of Japanese Cubomedusae. Plankton Seto Benthos Res 17(5): 289–297.

Wikipedia. Definition Sandwich Islands. Available at: https://en.wikipedia.org/wiki/Hawaiian Islands

Wikipedia. Definition Chinese Sea. Available at: https://
