Plankton Benthos Res 17(4): 406–429, 2022

Plankton & Benthos Research

Ernst Haeckel's mysterious species, Part II: African Chirodropida (Cnidaria, Cubomedusae)

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Received 3 April 2020; Accepted 17 October 2022 Responsible Editor: Dhugal Lindsay

doi: 10.3800/pbr.17.406

Abstract: Ernst Haeckel described four new chirodropid species in 1880. *Chirodropus gorilla* was seen only on a few occasions along the Western coasts of Africa, while *Chirodropus palmatus* (from St. Helena Island) was never recorded again. Type specimens of both species are lost, leading some scientists to doubt the validity of *C. palmatus*. New specimens assignable to *C. gorilla* from European and South African Museum collections shed light on the identification of both species. Among the *C. gorilla* samples, small mature individuals with more pedalial branches than in the larger specimens were discovered. Further observations on living specimens of the smaller chirodropid from Cameroon suggested that they must be *C. palmatus* because there were only two chirodropid species described from West African waters; comparison with Haeckel's descriptions and drawings confirmed the identification. Additionally, our data showed that *Chirodropus palmatus* must be classified into the family Chiropsalmidae and accommodated in its own genus, *Chimaerus* gen. nov. We also revised definitions of the families Chirodropidae and Chiropsalmidae and re-described both species.

Key words: box jellyfish, *Chirodropus gorilla*, *Chirodropus palmatus*, *Chimaerus*, Cameroon

Introduction

The German scientist Ernst Haeckel (16 Feb 1834*, 09 Aug 1919†) was an "eminent evolutionist, zoologist, medusa specialist, philosopher and painting artist, flamboyant protagonist of Darwinism on the continent, author of "Kunstformen der Natur," "Die Welträtsel" and "Monographie der Medusen," with many artistic pictures of medusae" (Straehler-Pohl 2019: 742). Due to such attributes and also being accused of falsification, he was one of the most disputed scientists of the 19th century (Rütimeyer 1868, Haeckel 1891, Haeckel 1899, Teudt 1909, Haeckel 1910, Blechschmidt 1977, Kraußе 1987, Bowler 1989, Milner 1990, Richards 2008, Straehler-Pohl 2019) which might also cast doubts on his descriptions of new species. For example, he described four new chirodropid species in his "System der Acraspeden" (Haeckel 1880) (see Table 1).

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Supplementary materials may be found in the online version of this article.

Table 1. List of chirodropid species identified and described by Haeckel (1880), including sampling locations and collectors–species observed for the present study are marked in bold.

No.	Original species name (according to Haeckel 1880)	Reference for synonyms	Synonyms/Status	Maximal Size given in literature: BHxBW (mm)	Sampling location/Collector	Actual Suborder	Actual Family
1	***Chirodropus gorilla***	Mayer (1910), Thiel (1928), Uchida (1929):	*Chirodropus gorilla*/ valid	150 × 120	Coast of Lower Guinea (Equatorial Guinea), Chinchozo, Loango/ Falkenstein	Chirodropida	Chirodropidae
		Thiel (1936):	*Chiropsalmus quadrumanus*/ not valid				
		Kramp (1959, 1961), Pagès et al. (1992), Mianzan & Cornelius (1999), Gershwin (2006), Straehler-Pohl (2019):	*Chirodropus gorilla*/valid				
2	***Chirodropus palmatus***	Mayer (1910), Uchida (1929), Mianzan & Cornelius (1999):	Maybe conspecific with *Chirodropus gorilla*/uncertain status	100 × 70	South Atlantic Ocean, Not far from the Island of St. Helena/ Levasseuk	Chirodropida	Chirodropidae
		Thiel (1936):	*Chiropsalmus quadrumanus*/ not valid				
		Gershwin (2005):	*Chirodropus palmatus*/provisionally valid				
		Straehler-Pohl (2019):	*Chirodropus palmatus*/valid				
3	*Chiropsalmus quadrigatus**	Gershwin (2006a), Straehler-Pohl (2019):	*Chiropsoides quadrigatus*/valid	50 × 45	Indian Ocean, Rangoon/Thallitzer	Chirodropida	Chiropsalmidae
4	*Chiropsalmus zygonema*	Thiel (1928)	*Chiropsalmus quadrigatus* (=*Chiropsoides quadrigatus*)/ not valid	60 × 40	South Atlantic Ocean, at the Argentinean coast/Smith	Chirodropida	Chiropsalmidae
		Uchida (1929):	*Chiropsalmus zygonema*/uncertain species				
		Thiel (1936):	*Chiropsalmus quadrumanus*/not valid				
		Southcott (1956):	*Chiropsalmus zygonema*/probably immature form, status unsure				
		Gershwin (2006a):	*Chiropsalmus zygonema*/valid				
		Straehler-Pohl (2019):	*Chiropsalmus zygonema*/valid				

*Confused with other chirodropid species from Asian waters that belonged to other families and genera by Mayer (1910), Southcott (1956), Kramp (1961)

Three of those species were doubted or declared invalid because of never being recorded again (*Chirodropus palmatus* Haeckel, 1880, *Chiropsalmus zygonema* Haeckel, 1880); or were based on juvenile and/or partly destroyed material (*Chiropsalmus quadrigatus* = *Chiropsoides quadrigatus* (Haeckel, 1880)) (e.g. Mayer 1910, Kramp 1961, Gershwin 2005, 2006a, Collins et al. 2011, Straehler-Pohl 2019, 2020); and additionally they were considered as synonyms of other species (Mayer 1910).

The animosities went so far that Mayer (1910) ignored completely Haeckel's classification. Haeckel (1880) defined the new family Chirodropidae for cubomedusae with many-tentacled pedalia and Mayer (1910) did not even mention it. He (Mayer 1910, 1917, 1928) defined the Carybdeidae as an order of Scyphozoa, replacing Haeckel's (1880) order Cubomedusae and all its families with it, and the only genera and species diagnosed by Mayer followed proposals of Agassiz (1881), Maas (1907) and Bigelow (1909).

The only chirodropid species described by Haeckel (1880) that was never doubted, not even by Mayer (1910, 1917, 1928), except by Thiel (1936) who doubted nearly all chirodropid families and genera and wanted to unite all chirodropid species within two genera, was *Chirodropus gorilla* Haeckel, 1880. Although rare, it has been sighted along the western and south-western coasts of Africa or identified in collections several times during the last 140 years (Mayer 1910, Vanhöffen 1920, Thiel 1928, Stiasny 1931, Kramp 1955, 1959, 1961, 1968, Pagès et al. 1992, Mianzan & Cornelius 1999, Straehler-Pohl 2019).

While observing Museum specimens labelled *C. gorilla*, we noticed differences in size and tentacle number per pedalium at maturity. One of them, a small, mature specimen, with higher numbers of tentacles per pedalium than in the large specimens, was the basis of Kramp's (1955) re-description of *C. gorilla*. Therefore, we examined this specimen very carefully as well as small but mature chirodropid specimens from West Africa labelled as *Chiropsalmus quadrumanus* by Kramp (1959) that resembled the afore mentioned specimen. Furthermore, recently collected (2017–2019) chirodropids from Cameroon resembled all of these small-sized Museum animals. Such specimens had features similar to what has been described for *C. palmatus.*

Thus, the goal of this study is to add more information on the anatomy, morphology and taxonomy of the chirodropid species of Western Africa described by Haeckel (1880) and re-described by Kramp (1955, 1959), namely *C. gorilla, C. palmatus* and/or *C. quadrumanus,* combining data from museum collections and newly collected individuals.

Materials & Methods

All information about the specimens observed and the referring collections are listed in Table 2.

All museum specimens labelled as "*Chirodropus gorilla*" (mature, having ≥11 branches per pedalium, bell size of ≤113 mm) and from West and South West Africa were examined. The specimens were either registered museum material, material sampled by Dr. Francesc Pagès and Dr. Josep-Maria Gili (Institut de Ciències del Mar, Barcelona, Spain) during their Benguela XVI Expedition in 1990 or material sampled during an R.V.G.O. Sars Expedition in 2008 along the Namibian coast, provided by Prof. Mark Gibbons (Western Cape University, Cape Town, South Africa).

All medusae were preserved in 5%–10% formalin sea-water; therefore, no molecular analysis could be performed. Anatomical structures were excellently preserved in most specimens, allowing a direct comparison with the structures of chirodropid specimens recently collected from Western Africa.

Between 2017 and 2019, a general assessment of jellyfish diversity along the coastal zone of Kribi, Cameroon, was conducted. Kribi (02°56′06″N, 09°54′36″E) has a rocky coast, and the sea floor is sandy with rocky outcrops (Fig. S7); the environmental parameters during sampling were as follows: temperature (27.80–31.74°C); salinity (14.40–25.77); pH (8.18–10.12); turbidity (4.18–87.50 NTU); and dissolved oxygen (8.94–36.30 mg/L). Hundreds of specimens of box jellyfish were collected as by-catch of a beach seine using a trawl net (10–20 mm mesh size). Samples were transported to the Specialized Research Centre for Marine Ecosystems—Fisheries Research Laboratory, IRAD-Kribi, Cameroon/University of Douala. Morphological identification was done on fresh (Fig. 4) and 4% buffered formalin-seawater-preserved specimens (Fig. 5B). Additional samples were stored in 70% ethanol and kept for future molecular characterization. Collected specimens were tentatively identified as *C. palmatus* based on morphology, the palm-leaf-shaped pedalia being one of the most distinguishing characters as described by Haeckel (1880). Nematocysts were extracted using a modified protocol from Yanagihara et al. (2002). Fresh tentacles were excised and kept in cold seawater (4°C) and nematocysts were harvested at 24-h intervals for up to seven days using a 0.5 mm mesh sieve. The filtrate was then observed using a Carl Zeiss Axiostar transmitted light microscope; undischarged and discharged nematocysts were observed and identified according to Gershwin (2006b).

Additionally, we compared all collected data with the detailed descriptions of both species (Haeckel 1880, 1904, Figs. S1, S5B, S6A, B), with original pencil line drawings (Figs. S2, S3, S5A, from the collections of the Ernst-Haeckel-Haus, Friedrich-Schiller-Universität Jena Institut für Geschichte der Medizin, Naturwissenschaft und Technik), and with Kramp's (1955, 1959) re-descriptions of *C. gorilla* and *C. quadrumanus* from West Africa.

Standard measurements were used (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

Table 2. Specimens from museum collections and unregistered specimens examined for this study.

Collection	Code No.	No. of specimens	Maturity status	Species identification	Original identification	Sampling location#	Collector	Sampling date
SAM	H 4870 (neotype)	1	mature (male)	*Chirodropus gorilla* Haeckel, 1880	Dr F Pagès, 1989: *Chirodropus gorilla*Haeckel, 1880	SFRI-R.S. Africana Cruise#074, St. A8893-074, Namibia, Conception Bay: 23°53S, 14°26.8E	SFRI-R.S. Africana Cruise#074, Dr F Pagès	23 Jun 1989
NHMD	642550	1	mature (male)	*Chirodropus gorilla* Haeckel, 1880	Dr PL Kramp, 1959: *Chirodropus gorilla* Haeckel, 1880	West Africa, Democratic Republic of Congo, 12 Miles West of Muanda, (5°56′S, 12°08′E), 15–18 m	Mission Mbizi 1948–1949, Atlantique Sud Belge	04 Oct 1948
NHMD	642556	1	immature	*Chirodropus gorilla* Haeckel, 1880	Dr PL Kramp, 1959: *Chiropsalmus quadrumanus* Müller, 1859	West Africa, Democratic Republic of Congo, 11 M West South West of Pointe Noire, -5.833333°, 12.050000° (4°52′S, 11°39′30″E), surface	Mission Mbizi 1948–1949, Atlantique Sud Belge, St. 25	05 Sep 1948
MCNB	unregistered	2	immature	*Chirodropus gorilla* Haeckel, 1880	F Pagès, JM Gili, J Bouillon, 1992: *Chirodropus gorilla*Haeckel, 1880	South West Africa, Namibia, Northern Benguela current, Station P-1, 23°03′1″S, 13°38′1″E, 150–152 m, 19.9°C; Station P-5, 23°51′S, 13°57′E, 198 m19.4°C (see also Pagès et al. 1992, Pagès & Gili 1992)	Benguela XVI 1990, F. Pagès	14 Feb 1990
Mark Gibbons Collection	unregistered	2	mature (male)	*Chirodropus gorilla* Haeckel, 1880	Prof MJ Gibbons, 2019: *Chirodropus gorilla* Haeckel, 1880	Namibia, off central Namibia (west of Walvis Bay)	R.V. G. O. Sars Expedition, Prof. Dr. Mark Gibbons	Apr 2008
NHM	1962.1.13.1 (neotype)	1	post-mature (male, spawned)	*Chirodropus palmatus* (Haeckel, 1880)***	JT Swarbrick, Esq, 1962:	West Africa, South West Cameroon, Port of Limbe (former Victoria), (approximately 4°00′16.4″N 9°12′34.8″E)	J. T. Swarbrick, Esq.	1962 (?)
NHM	1962.1.13.2-7	6	post-mature (spawned)	*Chirodropus palmatus* (Haeckel, 1880)***	*Chirodropus gorilla* Haeckel, 1880	West Africa, South West Cameroon, Port of Limbe (former Victoria) (approximately 4°00′16.4″N 9°12′34.8″E)	J. T. Swarbrick, Esq.	1962 (?)
NHM	1962.1.13.8-10	3	female, male, male	*Chirodropus palmatus* (Haeckel, 1880)***	JT Swarbrick, Esq., 1962: *Chirodropus gorilla Haeckel, 1880*	West Africa, South West Cameroon, Port of Limbe (former Victoria) (approximately 4°00′16.4″N 9°12′34.8″E)	J. T. Swarbrick, Esq.	1962 (?)
NHMD	642551	1	female	*Chirodropus palmatus* (Haeckel, 1880)***	Dr PL Kramp, 1952: *Chirodropus gorilla Haeckel, 1880*	West Africa, Liberia, Monrovia harbour, surface, "Galathea" Station 18 (Original: 6°19′N, 10°49′W, corrected to: approximately 6°19′00.4″N 10°49′03.8″W) (see also Kramp 1955)	Galathea Expedition	11 Nov 1950
RBINS	I.G. 16808 St. 136	1	not recorded	*Chirodropus palmatus* (Haeckel, 1880)***	Dr PL Kramp, 1950: *Chiropsalmus quadrumanus* Müller, 1859	West Africa, Angola, St. 136, 45 M South West of Moita Seca, −6.5°, 11.667° (6°30′S, 11°40′E, see also Kramp 1959)	Mission Mbizi 1948–1949, Atlantique Sud	22 Feb 1949
RBINS	I.G. 16808 St. 207	1	not recorded	*Chirodropus palmatus* (Haeckel, 1880)***	Dr PL Kramp, 1950: *Chiropsalmus quadrumanus* Müller, 1859	West Africa, Democratic West Africa, Republic of Congo, St. 207, 25 M West South West of Banana, −5.95°, 12.00° (5°57′S, 12°00′E, see also Kramp 1959)	Mission Mbizi 1948–1949, Atlantique Sud Belge	21 May 1949
RBINS	I.G. 16808 St. 25	2	not recorded	*Chirodropus palmatus* (Haeckel, 1880)***	Dr PL Kramp, 1950: *Chiropsalmus quadrumanus* Müller, 1859	West Africa, Democratic Republic of Congo, St. 25, 11 M West South West of Pointe Noire, -5.833°, 12.05° (4°52′S, 11°39′30″E), dredge, 35 m depth (see also Kramp 1959)	Mission Mbizi 1948–1949, Atlantique Sud Belge	05 Sep 1948
GFG Youbouni	unregistered	428	not recorded	*Chirodropus palmatus (Haeckel, 1880)***	—	West Africa, South Cameroon, Coastal zone of Kribi - Ngoye-Wamie beach (2°57′33.2″N, 9°54′11.9″E) and Nziou-Mahalet beach (2°58′49.8″N, 9°54′42.2″E)	Gisele Flodore Ghepdeu Youbouni, Specialized Research Center for Marine Ecosystems Kribi and Doctorate School University of Douala-Choosen sampling site	Data considered for this paper were collected between June 2017 and January 2018

*Identifications were done 2015 **Identifications were done in 2016 ***Identifications were done in 2017, ****Identifications were done in 2019 # longitudes and latitudes taken from http://latitude.to or http://google.de/maps NBCN: Naturalis Biodiversity Center Nertherlands, Leiden, MCNB: Museu de Ciències Naturals de Barcelona NHM: British Museum of Natural History, London, RBINS: Royal Belgium Institute of Natural Science, Brussels NHMD: Natural History Museum of Denmark, Copenhagen, SAM: Iziko South African Museum

level of the bell turn-over; interrhopalial diameter (IRD) was measured as the distance between two opposite rhopalia, with the specimen laying flat, one pedalium on another, taking the measurement where the top of the pedalia meet the bell across rhopalia; 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 of the last branch, as a proportion in relation to bell height.

Photographs of museum specimens were taken under the same conditions with a digital camera (Canon Eos 550D), and newly sampled specimens were photographed with a Samsung phone (Tecno Camon 11 phone Camera), and a digital camera (Nikon 5300).

We followed Acevedo et al. (2019) in using the term gonads to refer to areas where gametes are formed. Lateral gonads = interradial, leaf-like gonadal tissues growing along the interradial septa that separate the gastric pouches from each other.

Results

The species *Chirodropus gorilla*

The type material was lost during World War II, therefore, registered material from museum collections and additional unregistered specimens were examined in order to provide an updated description of the species. The original description of *Chirodropus gorilla* by Haeckel (1880) was the base for comparison and inspection of all museum specimens listed in Table 2, therefore, we provide a translation of the original text (Haeckel 1880, pp. 448–449, Plate XXVI; Fig. S1) from German to English as Supplementary Material (Text S1).

There were also mature chirodropid specimens in the collections, which were either labelled as *Chirodropus gorilla* or *Chiropsalmus quadrumanus* from West Africa (Table 2). These specimens were similar at first sight to *C. gorilla* but differed distinctly in bell size and tentacle numbers per pedalium from other mature *C. gorilla* medusae. From a direct comparison of these doubtful mature, small specimens with *C. gorilla* specimens (Table 3) we conclude that they belonged to a different species. The original description of *Chirodropus palmatus* (Figs. S5B, S6, translations: Texts S2, S3), which is the only other chirodropid species described from Western Africa, was checked.

Designation of a neotype for *Chirodropus gorilla*

We designate a neotype for *Chirodropus gorilla* according to Article 75, ICZN (1999) because the holotype was lost (Article 75, Chapter 75.3.4) and Haeckel's description led to some confusion concerning the gonadal structures; e.g. Kramp (1955) misidentified a specimen of *C. palmatus* as *C. gorilla* due to Haeckel's (1880) partly incorrect descriptions of gonadal structures in *C. gorilla*. Kramp (1959) erred again when he misinterpreted 4 pinnate glands of a true *C. gorilla* specimen as (lateral) gonads. This mistake was due to a misinterpretation of Haeckel's (1880) description combined with the line drawing of *C. gorilla*'s (lateral) gonads (Fig. S3). A neotype would help to clarify the internal structures and, therefore, the taxonomic status (Article 75, Chapter 75.3.1) of the species and of the family Chirodropidae.

The definition of the family Chirodropidae was based on

Table 3. Comparison of morphological structures in supposed *Chirodropus* species.

Morphological characters	*C. gorilla*	*C. palmatus*
BH	up to 220 mm	up to 134 mm
IPD	up to 270 mm	up to 150 mm
Mesoglea	thick, thickness nearly equal in all bell parts (apex, side walls)	very thick; thicker in dome-shaped appendix than in side walls
Bell surface	shagreened	smooth
Pedalial structure	Between 9–11 branches/tentacles per pedalium, single proximal pedalial finger distinctly longer than pedalial palm	Between 12–21 branches/tentacles per pedalium; single proximal pedalial finger equal to shorter than pedalial palm
Pedalial canal knee bend	with massive, upward-pointing thorn-shaped appendage	with massive, upward-pointing spike to thorn-shaped appendage
Lateral gonads	none	present
Gastric saccules	cock's-comb shaped with ≥20 grape to digitate-shaped appendages on the interradially pointing rim	conical with ≤10 drop to digitate-shaped appendages on interradially ponting rim
Gastric phacellae	4, vertical, triangular fields of filaments	4, horizontal, U-shaped
in-live colour	bell highly transparent with colorful pattern: reddish brown stripes on adradi, interradi and pedalia; gastric saccules pinkish to mauve coloured; tentacles yellowish to rust coloured	bell highly transparent, colourless; tentacles white

BH: bell height, IPD: Intrapedalial diameter

the species *C. gorilla* emphasizing the lack of lateral gonads as the main feature (Southcott 1956, Gershwin 2006a, Straehler-Pohl 2019); although Haeckel described lateral gonads for this species. We observed as many mature specimens as are available of this rare species and found no trace of lateral gonads but could show where Haeckel (1880) erred.

For reliable reference to the species *C. gorilla* and to support the definition of the family Chirodropidae, we designated a mature intact male specimen from the collection of the Iziko South African Museum in Cape Town as the neotype (SAM-H 4870) according to Article 75, ICZN (1999: chapters 75.3.2, 75.3.3, 75.3.5, 75.3.6, 75.3.7).

Redescription of *Chirodropus gorilla*

As the results of our study show that some features of the species *Chirodropus gorilla* are not congruent with the anatomical diagnosis given by Haeckel (1880), a redescription is presented.

***Chirodropus gorilla* Haeckel, 1880**
(Figs. 1–7)

Chirodropus gorilla: Haeckel 1880: 447–449, Pl. 26, Figs. 1–8; Mayer 1910: 518, 519; Uchida 1929: 182; Stiasny 1931: 139; Thiel 1936: 191, 277, 283, 286, 293, 302; Kramp 1955: 288–29; Kramp 1959: 17–21; Kramp 1961: 308; Kramp 1968: 70; Pagès et al. 1992: 58; Williamson et al. 1996: 261–262, 268–269, 301, 302, 305; Mianzan & Cornelius 1999: 520, 523, 531–533; Fenner 2005: 133; Gershwin 2006a: 37; Straehler-Pohl 2019: 768–771; Straehler-Pohl 2020: 2, 15, 21; Gibbons et al. 2021: 379; Gibbons et al. 2022: 9, 22, 42–45.

Haeckel (1880) indicated the holotype from the Zoological Museum of Berlin, Germany (=Museum für Naturkunde Berlin): Lower Guinea (*authors' comments*: not Lower Guinea but Angola), Loango coast, Chinchozo Station (*authors' comments*: village at the coast, ca. 4.3 km North of Chiloango River mouth), 1 male medusa (No. 1790), before 1880, collected by Falkenstein. However, as mentioned earlier, this specimen is lost.

Examined material:

NEOTYPE (SAM-H 4870: Fig. 3B): Iziko South African Museum, Cape Town: SFRI-R.S. Africana, 38 m sounding vessel, Anchovy Recruitment (South West Africa) survey, Cruise#074, St. A8893-074 (Namibia, Conception Bay: 23°53 S, 14°26.8 E), 1 mature male (BH: 153 mm, IPD: 204 mm, IRW: 90 mm; 11 fingers/pedalium, PL: ca. 84 mm, pedalial palm length: 50 mm, single finger length: 94 mm, VB: 40 mm, ML: 120 mm), Grid 06-01A, 10% formalin sea water, sounding 38 m, 20 m depth, collected by F. Pagès, 23 Jun 1989, time (GMT) 15:14.

Natural History Museum of Denmark: West Africa, Gabon, 12 miles West of Moanda Expedition Atlantique Sud Belge Station 36 (5°56′S, 12°08′E), 1 male specimen (BH 150 mm, 165 mm bell width) (NHMD-642550), badly damaged, no pedalia present, all inner structures still available), 15–18 m, 4 Oct 1948;
Labelled as "*Chiropsalmus quadrumanus*":
West Africa, Republic of Congo, 11M West South West of Pointe Noire, Atlantique Sud Station 25 (4°52′S, 11°39′30″E), 1 immature specimen (BH 70 mm, IPD 88 mm, IPD/BH 1.26, 9 tentacles per pedalium) (NHMD-642556), surface, 5 Sep 1948.

Natural History Museum, London (NHM): West Africa, Ghana, Cape Coast (5°06′14.9″N 1°14′21.8″W), 1 medusa (NHM 27.1.17.1), collected by T. Atkinson (Stiasny 1931)

Unregistered material:

Museu de Ciències Naturals de Barcelona, (MCNB): Namibia, below Walvis Bay, (BENGUELA XVI Expedition: P-I (4): 23°03′1″S, 13°38′1″E; P-3 (5): 23°31′6″S, 13°45′8″E; P-5 (7): 23°51′5″S, 13°57′5″E), numerous unregistered mature and juvenile specimens, Bongo-type nets 40 cm in diameter equipped with 300 and 500-μm meshes, hauls were carried out from 200 m to the surface, 150–198 m, 19.4–19.9°C, 14 Feb 1990, collected by F. Pagès, J.-M. Gili and J. Boullion (Pagès et al. 1992, Pagès & Gili 1992)

University of the Western Cape, Bellville (Mark Gibbons Collection): Namibia, off central Namibia (west of Walvis Bay, 22°48′27.9″S, 14°27′48.7″E) R.V. G.O. Sars Expedition, 1 mature male (BH: 210 mm, IPD: 270 mm, IRW: 130 mm, ML: 153 mm), damaged (no pedalia present), bucket 12, 130 m bottom trawl, sampled by Prof. Mark Gibbons, April 2008.

All museum specimens examined (Table 2) were in good to very good condition concerning the internal structures; immature to mature developmental stages (Table 2) were observed. Some adult specimens (e.g. NHMD-642550 (Fig. 2I), unregistered specimen from Mark Gibbons' collection (Fig. 2J)) lacked the pedalia but were identified without doubt as *C. gorilla* due to distinct features: bell with 8 adradial meridian furrows; characteristic gastric saccules; and sampling location. Those pedalia were not found in the sample jars; perhaps having been broken off during sampling or were cut off to fit the huge specimens into the jars.

Most of the characters listed by Haeckel (1880) could be confirmed except for (1) the heart-shape of the sense niche (Fig. S2C), (2) the ability to lock the pharynx by valves (Fig. 1.4), (3) the exclusive location of the gastric saccules (= pocket arms) inside the gastric pouches (Fig. 1.2), and (4) the presence of 8 pair-wise arranged gonads that are attached over their entire length to the interradial septa and show grape-like appendages at the free rim (Figs. 1.2, S3)—in all specimens examined and identified as *C. go-*

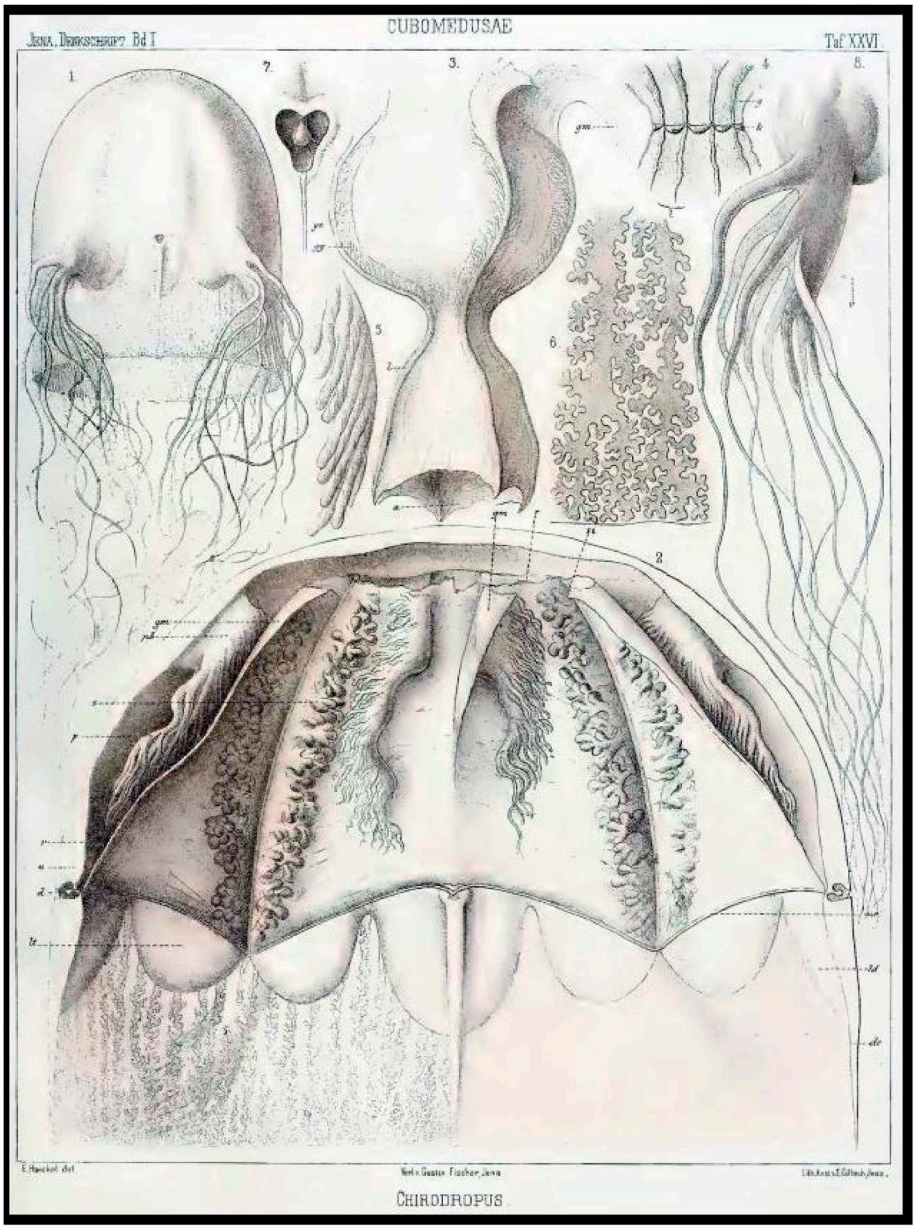

Fig. 1. Published plate with line drawings of medusa structures of *Chirodropus gorilla* by Haeckel (1880): 1: Habitus; 2: Dissected medusa (subumbrellar); 3: Stomach with manubrium and vertical pinnate glands in mesenteries; 4: pylorus flaps that shall close the stomach entrance—note that these structures were not found in any actually dissected medusae (see also main text and Fig. 2G); 5: Pinnate gland; 6: Velarial canal structure; 7: Rhopalial niche cavity; 8: Pedalium with nine fingers with tentacles.

rilla in this study no matter which developmental stage, no additional lateral gonads next to the gonadal tissue of the gastric saccules could be found (Figs 2H–I).

Type locality (original description): West Africa, Angola, Loango coast, Chinchozo (=Chinchoxo, Shinxoxo) Station (village at the coast, ca. 4.3 km North of Chiloango River mouth: approximately 5°10′07.3″S, 12°06′25.2″E)

Type locality (neotype): SFRI-R.S. Africana, Cruise#074, St. A8893-074 (Namibia, Conception Bay: 23°53S, 14°26.8E).

Diagnosis: *Chirodropus* species with pedalia bearing up to 11 bilateral branches, single proximal branch longer than pedalial palm; gastric saccules cock's-comb shaped with long, grape to digitate-shaped appendages, without lateral gonads; vertical, triangular fields of gastric phacellae lining stomach walls.

Re-description: (after Haeckel 1880, Kramp 1959, Straehler-Pohl 2019, Gibbons et al. 2022, and with new data)

Mature medusa:

Bell, in life (Fig. 3A), highly transparent, colourless to brownish with reddish brown stripes lining the meridian bell furrows; pale brown linings marking the pedalia insertions, the midline of the pedalial branches and the sense niche opening; gastric saccules pink to mauve coloured;

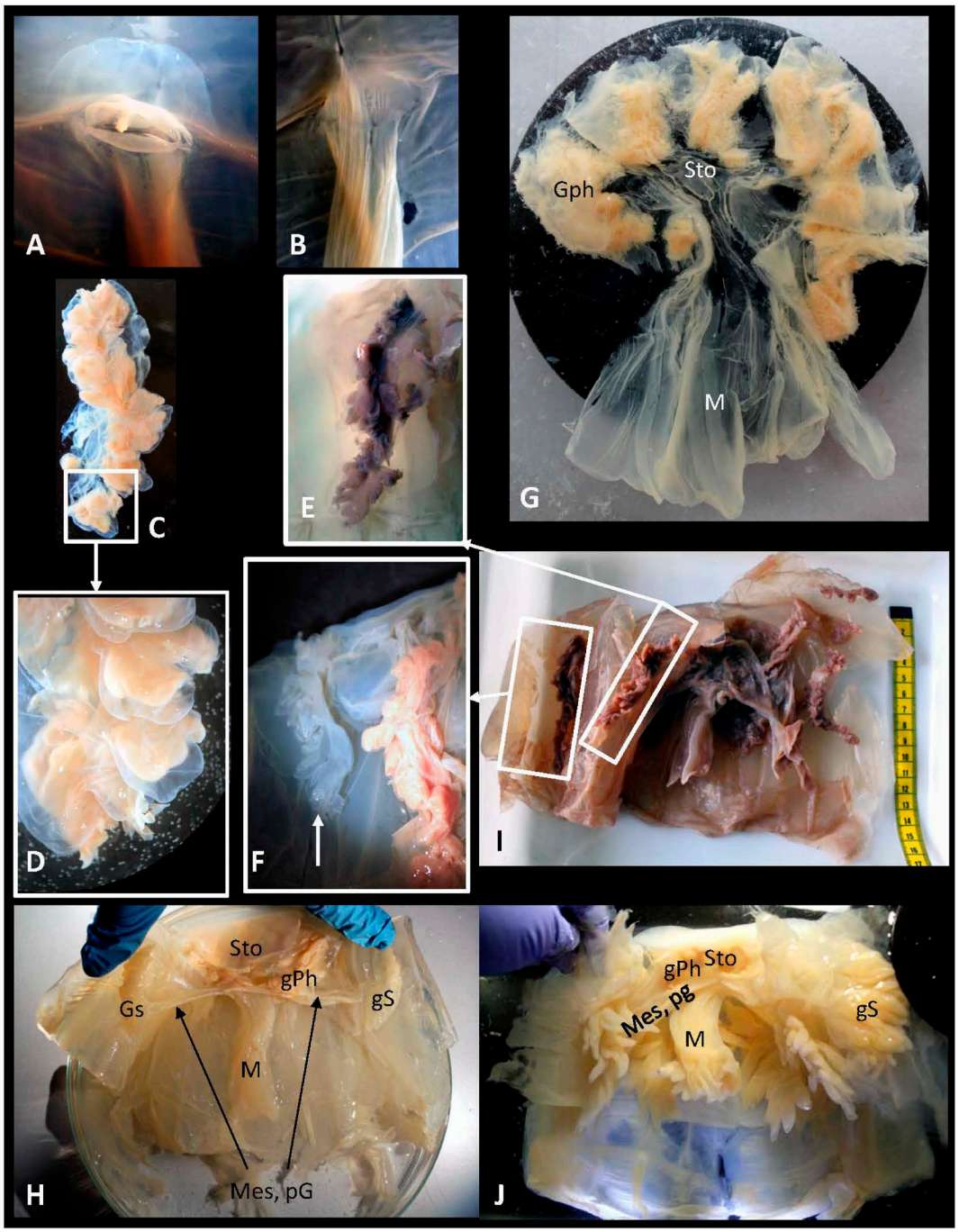

Fig. 2. Structures in medusae of *Chirodropus gorilla*: A: Frown-shaped rhopalial niche opening; B: elipsoid-shaped rhopalial window with attached cord-like frenulum; C+D: Gastric saccule with rounded "grape-like" appendages—note, the gastric saccule consists nearly only of appendages, the original saccule is only a thin sheet; E: Gastric saccule with finger-like appendages; F: "Naked" de sleeved gastric saccule (right) with empty sleeve to the left (white arrow), note "grape-like" appendages on gastric saccule and finger to thread-like shape of appendages in empty sleeve; G: Stomach with broad fields of vertical gastric phacellae and attached manubrium without any pylorus flaps; H: Dissected juvenile medusa of 125 mm bell height, sampled in 1990 by Africana Expedition (Pagès et al. 1992), note gastric saccules are cock's-comb-shaped; I: Dissected adult medusa with 150 mm bell height (NHMD 642550), sampled in 1948 by Sud Belge Expedition; J: Dissected mature medusa of 210 mm bell height (collection of Dr. M. Gibbons), sampled by SARS Expedition in 2008, note gastric saccules take major space of subumbrella cavity, appendices are finger-shaped, saccules are flat, sheet-like. gPh: Gastric phacellum; gS: gastric saccules; M: manubrium; Mes: Mesenterium; pG: Pinnate gland; Sto: stomach; V: velarium.

velarial canals purple; tentacles pale yellow to "rusty" yellowish-brown. Bell hemispherical (Figs. S2D, 1.1, S4A, 3A, B), wider than high (IPD) with rounded edges and 8 adradial, meridian furrows; mesoglea thick, sturdy, slightly thicker at apex; apex slightly arched, no horizontal constriction near the top; structure of bell surface shagreened

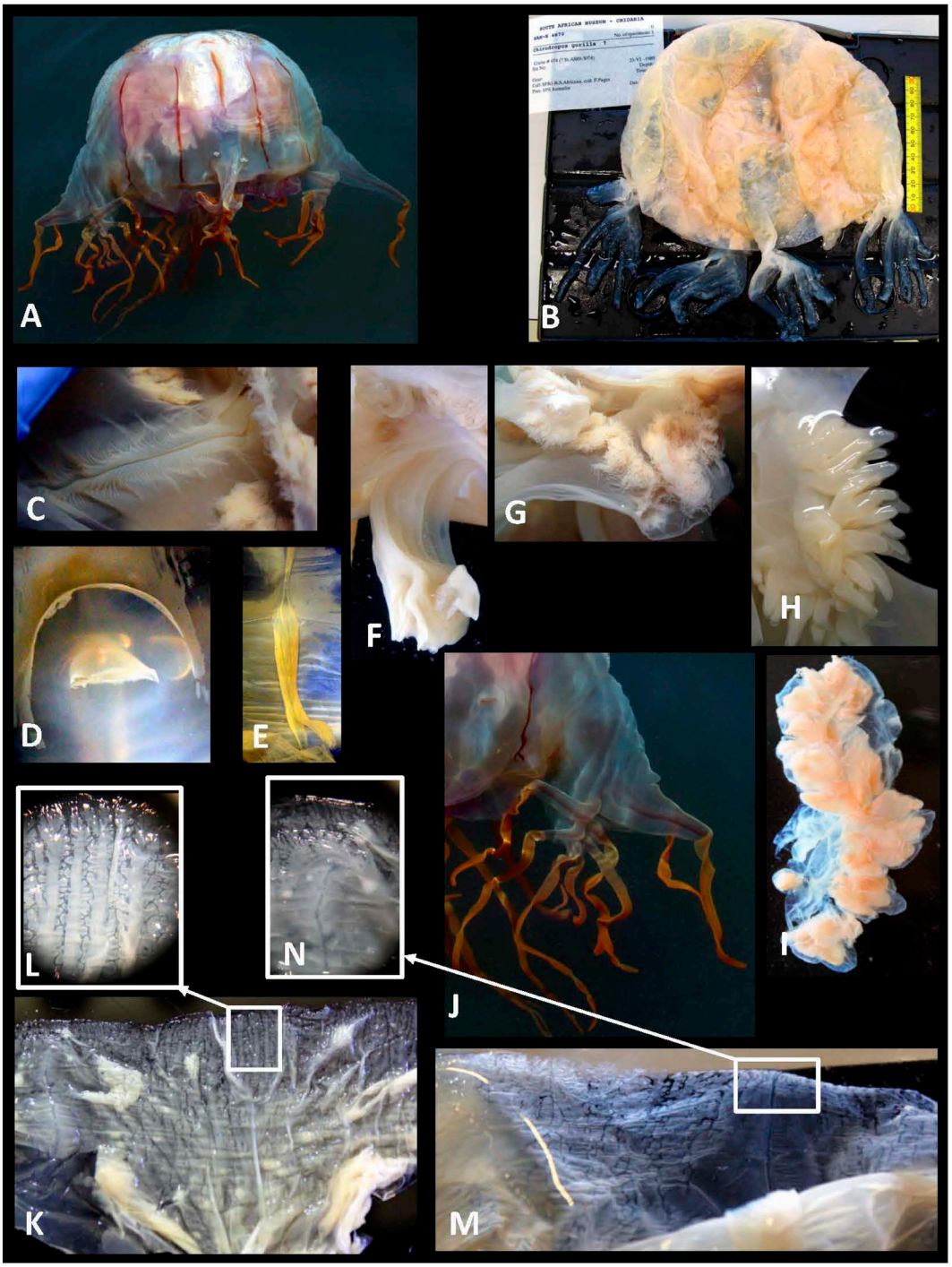

Fig. 3. Structures of mature medusae of *Chirodropus gorilla*: A: Living mature medusa in Lüderitz Bay, southern Namibia (after Straehler-Pohl (2019), p. 771, photo: Simon Elwen, Namibian Dolphin Project, 2011), note brownish coloured stripes on bell and pedalia, rust coloured tentacles and mauve coloured gastric saccules; B: Neotype (SAM-H 4870), mature male medusa (153 mm bell height); C: Pinnate gland; D: Frown-shaped rhopalial niche opening; E: Rhopalial niche window with cord-like frenulum attached; F: Manubrium; G: Fields of gastric filaments of vertical gastric phacellae; H: Gastric saccule with finger-like to branched appendages; I: Gastric saccule with rounded appendages; J: Pedalium of living medusa with reddish brown stripes; K: Octant of velarium; L: Velarial canal structure; M: perradial lappets in velarium; N: Tips of perradial lappets with attached branched canals.

(with leather-like pattern, Fig. 3B); up to 210 mm high, up to 270 mm wide (IPD); bell, manubrium and pedalia free of nematocyst warts. Rhopalial niches (Figs. S2C, 1.7, 2A, S4D, 3D), 4, broad, elipsoid cavity located inside the exumbrella, mounted on and framed by conspicuous, gelatinous, triangular thickenings; orifice very narrow, horizontally slit-like to dumbbell-shaped, upper covering scale, hood-like concave without additional extension, lower

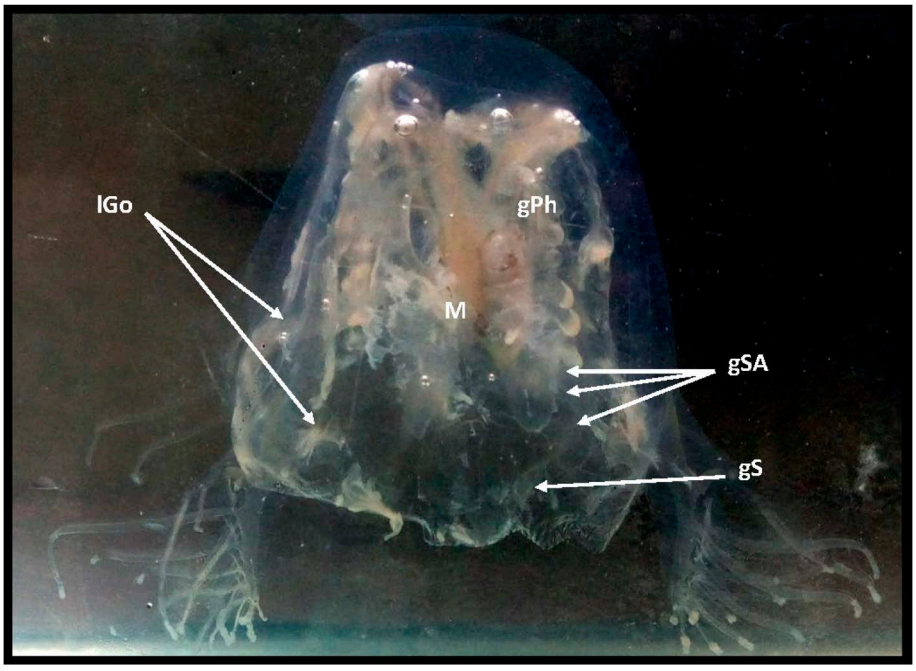

Fig. 4. Living mature medusa of *C. palmatus* sampled at Kribi coast in Cameroon. gPh: gastric phacellae; gS: gastric saccule; gSA: gastric saccule appendage; lGo: lateral gonads; M: manubrium.

covering scale, convex; rhopalial window (Figs. 2B, 3E), elipsoid, very broad, massive, cord-like frenulum attached; 1/6–1/9 of bell height up from the margin; no rhopalial horns; rhopalium with 6 eyes (2 major with lenses + 2 lateral slit eyes + 2 lateral pit eyes). Pedalia, 4, branched (Figs. 1.8, S4G, 3J), 1/3 as long as bell height, with up to 11 finger-like branches: 1 very long, single proximal branch (distinctly longer than pedalial palm) followed by four to five opposite pairs of progressively shorter branches which bear a single tentacle each. Pedalial canals, flattened in cross section, very narrow at base, then flaring, knee-bend volcano-shaped with massive, upward-pointing thorn-shaped appendage (Fig. S4F); lateral canal branches emanate from both sides of undivided main canal, right and left side branches arranged opposite to one another. Tentacles flat in cross section, ribbon-like (Fig. 3A), bearing series of dense nematocyst bands. Manubrium (Figs. 1.3, 2G, 3F), four-lobed, very long (70–75% of BH), reaches nearly bell opening; stomach balloon-like (Fig. 1.3), attached to the bell with well-developed, perradial mesenteries (Figs. 1.3, 2H, J, S4C), mesenteries contain pinnate glands (Figs. S2E, 1.5, 2H, J, S4B, 3C); vertical fields of gastric filaments lining the interradi of stomach (Figs. 2G, 3G), filaments, hundreds, closely spaced (Fig. S4E), multiple rooted, multiple stemmed; four gastric pockets leading from the stomach into the velarial canals. Gastric saccules (Figs. S2A, S3, 1.2, 2C–J, S4C, 3H, I), 8 (4 pairs), situated in the adradia of upper part of subumbrella (pairs: perradial) below the stomach, sheet-like as being very narrow but cock's comb-shaped, partly hollow and pendant, gelatinous inlay enveloped by gonadal tissue (Fig. 2F), covered by glove-like subumbrella tissue (Fig. 2F); ≥20 grape-like to long digitate appendages (up to 45 per sheet according to Kramp (1959)) along interradially pointing rim in at least 2 rows, filling nearly whole subumbrella in mature specimens (Figs. 2J, 3A). No lateral gonads present. Velarium (Figs. S2A, S3, 1.2, S4H, 3K, M), very broad, free of nematocyst warts; velarial canal roots, 1 per octant; velarial canals (Figs. S2F, 1.6, S4I, 3L), 6 main canals per root, main canals branch off uncountable numbers of side canals which are lined by lobed diverticula and forked at the tips; perradial lappets (Figs. S2A, 1.2, S4H, 3M, N), 4 pairs, broad triangular; interradial lappets (Figs. S2B, S3, 1.2), 4 pairs, broad, rounded, all grow complexly branched and lobed side canals which align with the velarial canals, completing the pattern.

Further data: Unknown cnidome. The specimen inspected for nematocysts by Kingston & Southcott (1960) was not *Chirodropus gorilla* (Gershwin 2006b, this study). "No deaths are documented, but they have probably occurred. The geographical distribution of *Chirodropus* is along a coastline where records of envenomation may be difficult to access." (Williamson et al. 1996: 262); "There are neither reported deaths nor serious stings from *Chirodropus gorilla* described from the west coast of Africa, to the author's knowledge, nor from the east coast or Madagascar, although theoretically they should be present." (Fenner 2005: 133). No data on mating and brooding behaviour. Polyp, asexual reproduction, and newly detached medusa unknown. Suggested to be a deeper water species travelling with the currents along the Western African coast

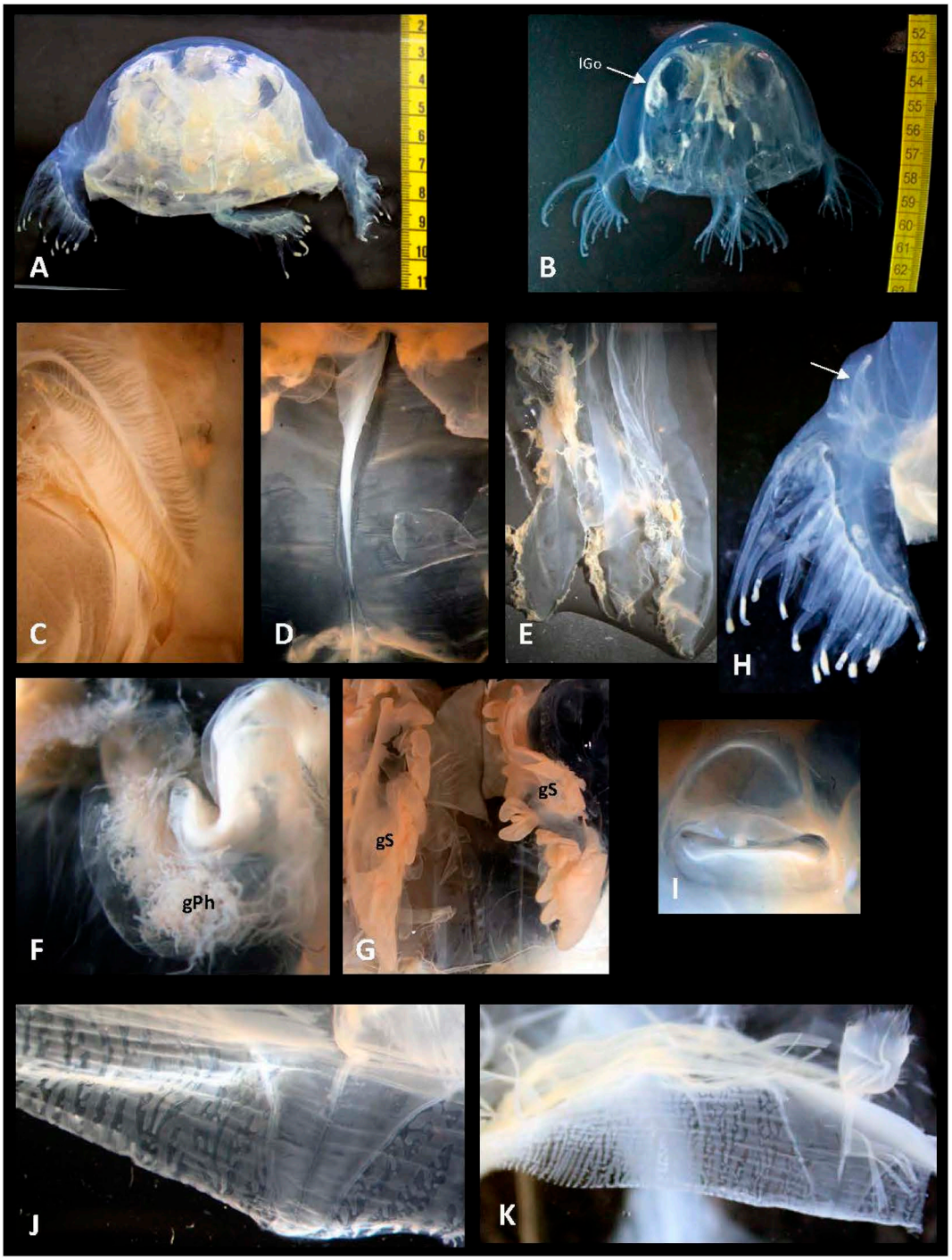

Fig. 5. Characters of *Chimaerus palmatus* comb. nov.: A: Neotype (NMH 1962.1.13.1), post-mature male medusa; B: Newly sampled mature medusa from Kribi coast of Cameroon, note lateral gonads; C: Pinnate gland; D: Mesentery with rhopalial niche window at its tip; E: Manubrium; F: Horizontal, U-shaped gastric phacellum with hundreds of gastric filaments; G: Pair of perradial, cone-shaped gastric saccules with one row of finger-shaped appendages at outer rim; H: Pedalium, note thorn- shaped pedalial knee appendage (white arrow); I: Frown-shaped rhopalial niche opening; J + K: Velarium with perradial lappets. gPh: gastric phacellum; gS: gastric saccule; lGo: lateral gonad.

(Haeckel 1880, Straehler-Pohl 2019, Gibbons et al. 2022). Kramp (1955) thought it to be a coastal species.

Distribution

West Africa: Liberia, Monrovia harbour (6°19′N, 10°49′W) (Kramp 1955); Ghana, Cape Coast (5°6′N, 1°15′W) (Stiasny 1931, Kramp 1959); Angola, Loango coast, near Chinchozo Station (=Chinchoxo Village ca. 2.75 miles (=4426 m) from Chiloango River mouth, approximately 5°10′07.3″S, 12°06′25.2″E) (Haeckel 1880, Hydrographic

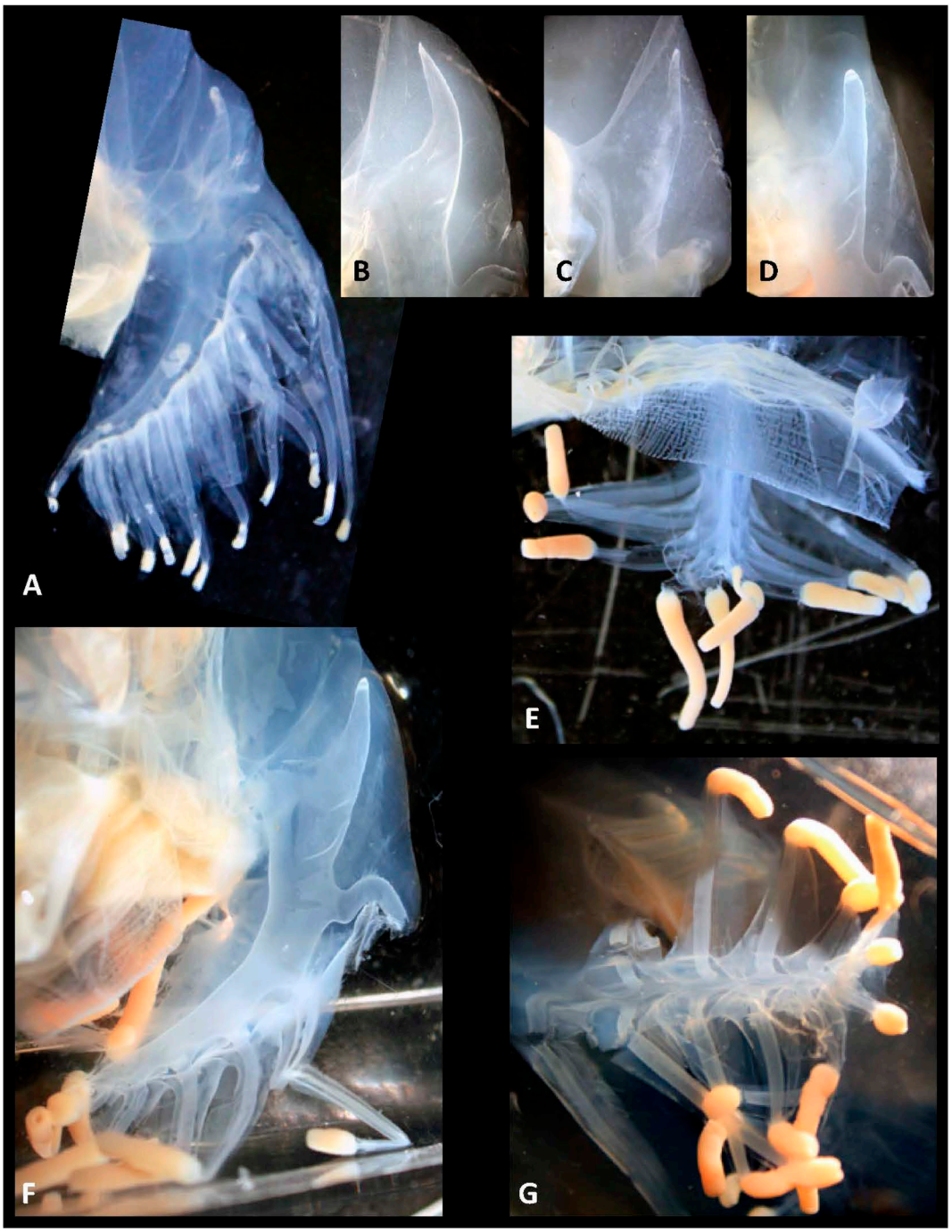

Fig. 6. Pedalial structures of *Chimaerus palmatus* comb. nov.: A: Lateral view of pedalium with 13 fingers; B–D: Different shapes of pedalial canal knee bend appendage; E: Dorsal view of pedalium, note non-separated pedalial canal with bilateral branching; F: lateral view of pedalial canal with huge thorn-shaped canal knee bend appendage; G: Ventral view of pedalium.

Office US Navy 1932, Kramp 1959).

Namibia: Below Walvis Bay (23°03′1″S, 13°38′1″E; 23°31′6″S, 13°45′8″E; 23°51′5″S, 13°57′5″E) (Pagès et al. 1992, Pagès & Gili 1992); Lüderitz (SA Jellywatch, Western Cape University; Simon Elwen—Namibian Dolphin Project, pers. communication 2013), Walvis Bay (22°57′12.2″S, 14°28′51.5″E) (Simon Elwen—Namibian Dolphin Project, pers. communication 2013); off central Namibia (west of Walvis Bay, 22°48′27.9″S, 14°27′48.7″E) (Prof. Mark Gibbons, pers. communication 2019).

The species *Chirodropus palmatus*

The afore mentioned mature but small chirodropid specimens from West Africa were either labelled as *Chirodropus gorilla* or *Chiropsalmus quadrumanus* (Table 2). They

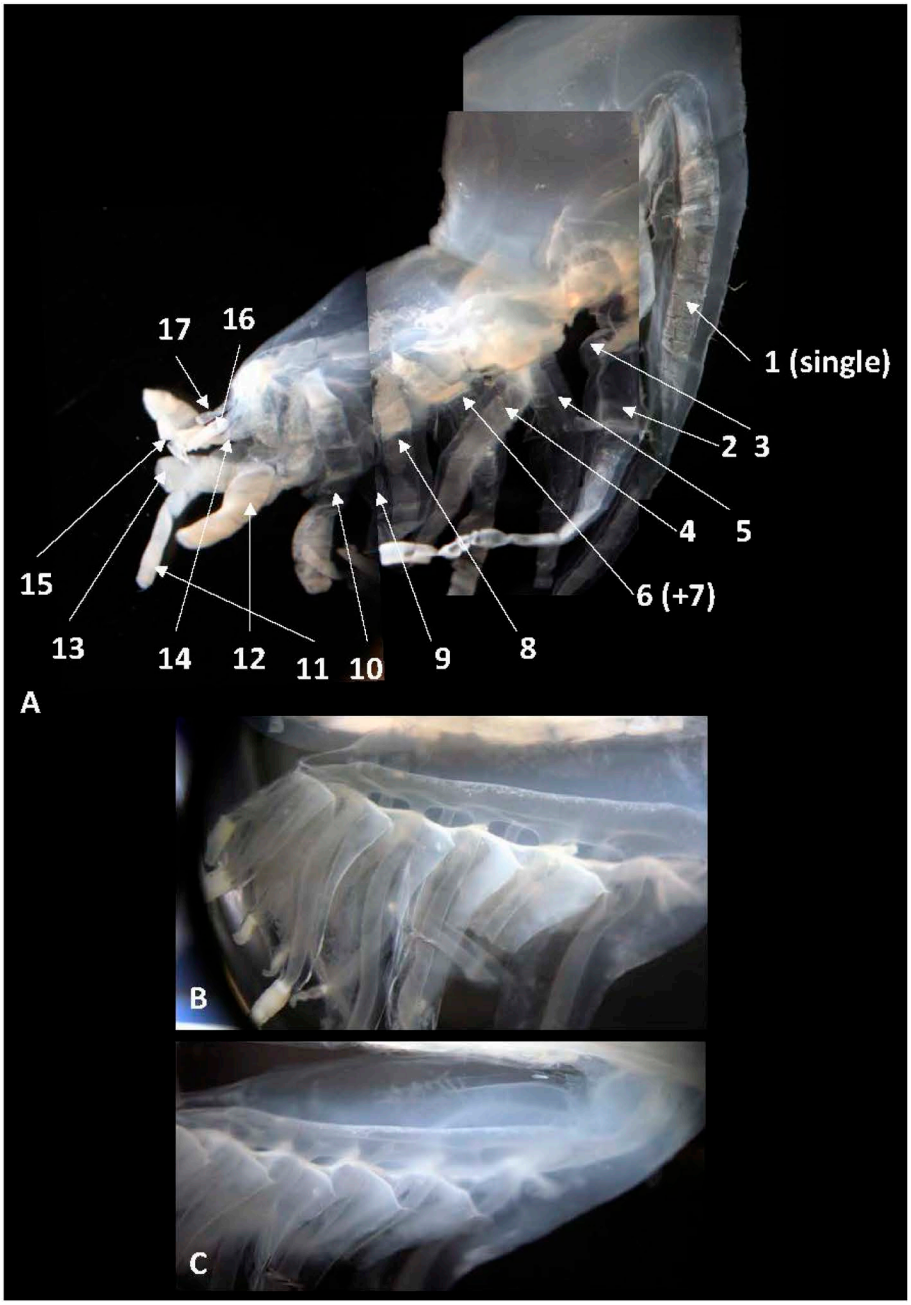

Fig. 7. Structure of 17-fingered pedalium of *Chimaerus palmatus* comb. nov.: A: Detailed lateral view of pedalium with 17 fingers composed from three images; B+C: Overlapping structure of pedalial fingers resembling roof-shingles.

are similar on first sight to *C. gorilla* but differed distinctly in bell size and tentacle numbers per pedalium from mature specimens (Table 3). Because of these differences, we concluded that the small doubtful specimens do not belong to the species *C. gorilla*, due to the peculiar structure of the gastric saccules and the pedalial canal structure, *C. quadrumanus* was also excluded, but perhaps *Chirodropus palmatus* could be considered. As in the case of *C. gorilla*, the type material was lost due to World War II, so registered material from museum collections were examined and those specimens were compared with Haeckel's description and drawings. Therefore we provide a translation (Text S2) of the original text (Haeckel 1880, pp. 448; Fig. S5B), and an additional translation (Text S3) of the detailed figure description (Haeckel 1904, Plate 78 (no page numbers, only plate numbers); Fig. S6B) from German to English in the Supplementary Material.

Accommodating *Chirodropus palmatus* into the family Chiropsalmidae (Tables 4, 5)

Our observations confirmed the statement that next to gastric saccules there are sheet/leaf-like lateral gonads in

Chirodropus palmatus (Haeckel 1904). As suggested by Straehler-Pohl (2019) we conclude that the species should be assigned to a different family and genus other than Chirodropidae and *Chirodropus*. The description and the specimens identified as *Chirodropus palmatus* do possess the pendant perradial gastric saccules in combination with the leaf-like, interradial lateral gonads (which are features of the family Chiropsalmidae) (Table 4). Thus, we propose an amendment in the family diagnosis to accommodate those specimens until future molecular analysis can help clarify the taxonomic status of the family.

There are two valid genera in the family Chiropsalmidae: *Chiropsalmus* and *Chiropsoides*. Both differed from our specimens. The genus *Chiropsalmus* is defined by bilaterally branching pedalia, conspicuous nematocyst warts on the exumbrella and outer pedalial wings, pedalial canals with rounded to angular knee bend without appendages, simple, finger-shaped, pendant gastric saccules and well developed lateral gonads (Table 5). The genus *Chiropsoides* is defined by unilaterally branching pedalia, a smooth exumbrella lacking nematocyst warts, pedalial canals with a volcano-shaped knee bend with a long, narrow spike-shaped appendage, simple conical gastric saccules and well-developed lateral gonads (Table 5). However, *Chirodropus palmatus* lacks nematocyst warts on the exumbrella and outer pedalial wings and its pendant gastric saccules are more cone-shaped than finger-shaped, while the pedalial knee bend bears a massive thorn (Tables 4, 5), all attributes that are found in *Chiropsoides* species. But *Chirodropus palmatus* possesses bilaterally branching pedalia (Tables 4, 5), which is a feature of the genus *Chiropsalmus*. On the other hand, the gastric saccules in both genera are smooth, without the lateral appendages that are present in *Chirodropus palmatus* (Tables 4, 5). Due to differences in the defining features of the two genera of Chiropsalmidae we propose a new genus to accommodate the species *Chirodropus palmatus*, herein named *Chimaerus* gen. nov.

Genus *Chimaerus* gen. nov

Etymology: *Chimæra* (latinized form of the Greek *Χίμαιρα—Chímaira* = "she-goat", masculine suffix–*us*), according to Greek mythology, was a monstrous, fire-breathing hybrid creature of Lycia in Asia Minor, composed of the parts of more than one animal. The term "chimera" has come to describe any mythical or fictional creature with parts taken from various animals, to describe anything composed of very disparate parts. The name-giving chirodropid species *Chimaerus palmatus*

Table 4. Comparison of morphological structures in chirodropid families (after Gershwin 2006, Toshino et al. 2015, present study).

Morphological characters	Family		
	Chirodropidae	Chiropsalmidae	Chiropsellidae
Lateral gonads	no	yes	yes
Gastric saccules	pendant, separated, cock's comb-shaped with ≥20 grape to digitate appendages in 2 or more rows	pendant, separated, smooth, unbranched, finger to cone-shaped	sessile, separated to coalescent, smooth, unbranched mounts

Table 5. Comparison of morphological structures in Chiropsalmidae genera (after Gershwin 2006, Toshino et al. 2015, Straehler-Pohl 2019, present study).

Morphological characters	Genus		
	Chimaerus, gen. nov.	*Chiropsalmus* Thiel, 1936	*Chiropsoides* Southcott, 1956
Bell surface	smooth, no nematocyst warts	with nematocyst warts	smooth, no nematocyst warts
Pedalial structure	bilaterally branching	bilaterally branching	unilaterally branching
Pedalial canal	main canal undivided, bilaterally, alternate branching	main canal undivided, bilaterally, opposite branching	main canal undivided, unilaterally branching with additional lobes between branches
Pedalial canal knee bend	volcano-shaped with massive, upward-pointing thorn-shaped appendage	rounded to angular, no appendage	volcano-shaped with long, narrow spike-like appendage
Tentacle structure	round in cross section	round in cross section	flat in cross section, ribbon-like
Number of tentacles	12–21	2–9	4–11
Lateral gonads	yes	yes	yes
Gastric saccules	with ≤10 drop to digitate-shaped appendages on interradially pointing rims, cone-shaped	smooth, unbranched, finger-shaped	smooth, unbranched, cone-shaped

comb. nov. of this genus displays characters that are also found in species of other chirodropid groups—characters such as high or higher numbers of tentacles per pedalium as in the genus *Chironex* (Chirodropidae), pedalial canal knee bend spikes as in *Chirodropus* (Chirodropidae), lateral gonads and long, pendant, cone-shaped gastric saccules as in *Chirodectes* (Chiropsalmidae) with additional lobes on the saccules as in juvenile *Chironex* (Chirodropidae).

Chirodropus: Haeckel 1880: 447–448; Mayer 1910: 518; Krumbach 1925: 575; Uchida 1929: 182; Thiel 1936: 272, 275, 301, 302, 306; Kramp 1955: 291–292; Kingston & Southcott 1960: 378–380; Kramp 1961: 308; Williamson et al. 1996: 237, 262, 268, 301; Mianzan & Cornelius 1999: 531; Gershwin 2006a: 5, 37; Straehler-Pohl 2019: 768; Gibbons et al. 2022: 42–43.

Chiropsalmus: Kramp 1959: 16; Kramp 1961: 308–309; Williamson et al. 1996: 237, 261.

Type and valid species: *Chimaerus palmatus* (Haeckel, 1880), comb. nov.

Diagnosis: Chiropsalmidae lacking nematocyst warts on the exumbrella; with separated pairs of cone-shaped gastric saccules with drop-shaped appendages on interradially pointing rim; with well-developed lateral gonads; with bilaterally branched, claw-shaped pedalia; pedalial canal entire with thorn to spike-like appendage at pedalial canal knee bend.

Chimaerus palmatus (Haeckel, 1880) comb. nov

Chirodropus palmatus: Haeckel 1880: 448; Mayer 1910: 519; Uchida 1929: 182; Thiel 1936: 286, 293, 302; Kramp 1961: 308; Williamson et al. 1996: 262, 268, 301; Mianzan & Cornelius 1999: 533, 534; Gershwin 2006a: 37; Gershwin 2006b: 15; Straehler-Pohl 2019: 772–773; Straehler-Pohl 2020: 3; Gibbons et al. 2022: 43, 46–47.

Chirodropus gorilla: Vanhöffen 1920: 17; Thiel 1928: 2, 16–17; Kramp 1955: 288; Kramp 1959: 18, 20; Kramp 1968: 70.

Chirodropus palmata: Thiel 1936: 277, 283.

Chiropsalmus quadrumanus: Kramp 1959: 16–17; Williamson et al. 1996: 261, 305.

Chirodropus (specimen(s), A303 from Ghana): Kingston & Southcott 1960: 378–380.

Designation of a neotype for *Chimaerus palmatus* comb. nov

The type material of the species (from South Atlantic Ocean, not far from the Island of St. Helena, before 1880, collected by Levasseur) housed in the Berlin Museum was lost due to World War II. All specimens examined (Table 2) were in good to very good condition concerning the internal structures, fully mature to post-mature (specimens had already spawned) developmental stages (Table 2). Thus, because the holotype was lost (ICZN 1999, Article 75, Chapter 75.3.4), and due to Haeckel's description having led to a lot of confusion concerning the gonadal structures, we designate a neotype for the species in order to provide stability and precise identification of morphological features. For a reliable reference for the species, and to support the definition of the new genus *Chimaerus*, we designated a post-mature male (preserved during spawning with gonadal tissue residues inside the gastric system and gastric saccules), of an anatomically intact specimen in the collection of the Natural History Museum in London as the neotype (NMH 1962.1.13.1) according to Article 75, ICZN (1999: chapters 75.3.2, 75.3.3, 75.3.5, 75.3.6, 75.3.7).

Examined material:

NEOTYPE (NMH 1962.1.13.1: Fig. 10A): Natural History Museum, London: Southern Cameroon, Port Victoria (*comment*: =Limbe, approximately 4°00′16.4″N, 9°12′34.8″E), 1 post-mature, male specimen, BH 77 mm, IPD 96 mm, IRD 57 mm, IRD/BH 0.74 mm, IPD/BH 1.25, 17 pedalial fingers per pedalium; 13 Jan 1962, collector J.T. Swarbrick, Esquire.

Further specimens labelled as "*Chirodropus gorilla*":

Natural History Museum, London: Southern Cameroon, Port Victoria (*comment*: =Limbe, approximately 4°00′16.4″N, 9°12′34.8″E), 9 specimens (NMH 1962.1.13.2–10: BH 49–83 mm (mean: 70 mm, SD: 11.24, n: 9), IPD 70–103 mm (mean: 88 mm, SD: 11.28, n: 7), IRD 45–61 mm (mean: 52 mm, SD: 7.27, n: 7), IRD/BH 0.6–0.74 mm (mean: 0.71 mm, SD: 0.05, n: 7), IPD/BH 1.04–1.25 (1.20,SD: 0.08, n: 7), 13–17 pedalial fingers per pedalium (mean: 15, SD: 1.63, n: 9)) from mature (nos. 8–10, female, male, male) to post mature (nos. 2–7), 13 Jan 1962, collector J.T. Swarbrick, Esquire.

Natural History Museum of Denmark, Copenhagen: Liberia, Monrovia harbour, "Galathea" Station 18 (Original: 6°19′N, 10°49′W, corrected to: approximately 6°19′00.4″N, 10°49′03.8″W), 1 female medusa (NHMD-642551: BH 79 mm, IPD 98 mm, IRD 57 mm, IRD/BH 0.72, IPD/BH 1.24, 13 pedalial fingers per pedalium), surface, 11 Nov 1950 (Kramp 1955).

Further specimens labelled as "*Chiropsalmus quadrumanus*":

Royal Belgium Institute of Natural Science, Brussels: Angola, South West of Moita Seca, Atlantique Sud Expedition Station 136 (6°30′S, 11°40′E), 1 specimen (RBINS I.G. 16808_1: BH 70 mm, IPD 95 mm, IRD 55 mm, IRD/BH 0.79, IPD/BH 1.36, 13 pedalial fingers per pedalium), 22 Feb 1949 (Kramp 1959); Democratic Republic of Congo, 25 miles West North West of Banana, Atlantique Sud Station 207 (5°57′S, 12°00′E), 1 specimen (RBINS I.G. 16808_2: BH 88 mm, IPD 110 mm, IRD 64 mm, IRD/BH 0.73, IPD/BH 1.25, 13 pedalial fingers per pedalium), 21 May 1949 (Kramp 1959); Republic of Congo, 11M

West South West of Pointe Noire, Atlantique Sud Station 25 (4°52′S, 11°39′30″E), 2 specimens (RBINS I. G. 16808_3a: BH 113 mm, IPD 150 mm, IRD 82 mm, IRD/BH 0.73, IPD/BH 1.33, 17 pedalial fingers per pedalium; RBINS I. G. 16808_3b: BH 104 mm, IPD 130 mm, IRD 75 mm, IRD/BH 0.72, IPD/BH 1.25, 13 pedalial fingers per pedalium) (Kramp 1959).

Unregistered material from Specialized Research Centre for Marine Ecosystems—Fisheries Research Laboratory, IRAD-Kribi, Cameroon/University of Douala:

Kribi coastal zone, South East/Central Atlantic, the Nziou-Mahalet and Ngoye-Wamie beaches. A total of 428 samples were collected between June 2017 and January 2018. Morphometrics and measurements were taken, but male and female differentiation was not done due to limited capacity for sexual differentiation.

Nziou-Mahalet (2°58′49.8″N, 9°54′42.2″E), 26 specimens (BH 58–120 mm, IRD 60–110 mm, NT 13–15), 14 Jun 2017; 35 specimens (BH 46–122 mm, IRD 42–118 mm, NT (not counted)) 14 Jun 2017; 28 specimens (BH 64–134 mm, IRD 68–124 mm, NT (not counted)), 16 Jun 2017; 6 specimens (BH 60–128 mm, IRD 60–136 mm, NT not counted), 21 Jun 2017; 26 specimens (BH 55–125 mm, IRD 54–120 mm, NT not counted), 23 Jun 2017; 14 specimens (BH 56–109 mm, IRD 76–125 mm, NT not counted), 7 Jul 2017; 31 specimens (BH 43–118 mm, IRD 50–117 mm, NT 7–16), 18 Jul 2017; 1 specimen (BH 92 mm, IRD 100 mm, NT 13), 19 Sep 2017; 17 specimens (BH 54–90 mm, IRD 66–108 mm, NT 11–14), 1 Jan 2018.

Ngoye-wamie (2°57′33.2″N, 9°54′11.9″E), 26 specimens (BH 27–100 mm, IRD 26–109 mm, NT 9–14), 20 Jul 2017; 61 specimens (BH 29–107 mm, IRD 35–115 mm, NT 8–16), 21 July 2017; 18 specimens (BH 60–108 mm, IRD 74–128 mm, NT 10–14), 25 Jul 2017; 22 specimens (BH 53–109 mm, IRD 79–12 mm, NT 9–16), 7 Aug 2017; 9 specimens (BH 72–96 mm, IRD 90–105 mm, NT not counted), 8 Aug 2017; 40 specimens (BH 62–102 mm, IRD 78–119 mm, NT 11–16), 9 Aug 2017; 1 specimen (BH 85 mm, IRD 98 mm, NT 13), 17 Aug 2017; 14 specimens (BH 65–99 mm, IRD 84–115 mm, NT 11–15), 18 Aug 2017; 6 specimens (BH 70–90 mm, IRD 84–109 mm, NT 13–14), 21 Aug 2017; 6 specimens (BH 76–100 mm, IRD 90–121 mm, NT 12–14), 29 Aug 2017; 14 specimens (BH 53–83 mm, IRD 45–72 mm, NT 8–16), 23 Sep 2017; 2 specimens (BH 83–90 mm, IRD 70–70 mm, NT 12–16), 7 Nov 2017; 1 specimen (BH 65 mm, IRD 55 mm, NT not counted), 11 Nov 2017.

Type locality (original description): South Atlantic Ocean, not far from the Island of St. Helena

Type locality (neotype): Southern Cameroon, Port Victoria (*comment*: =Limbe, approximately 4°00′16.4″N, 9°12′34.8″E)

Diagnosis (emended after Haeckel 1880): *Chimaerus* species with pedalia with up to 21 bilateral branches, single proximal branch equal or shorter in length than pedalial palm; gastric saccules cone-shaped with drop to digitate-shaped appendages, with lateral gonads; gastric phacellae horizontal and U-shaped.

Redescription: (after Haeckel 1880, Straehler-Pohl 2019, Gibbons et al. 2022, and new data)

Mature medusa:

Bell, in-life (Fig. 4), colourless transparent, with slightly opaque, yellowish to brownish gastric saccules, gastric filaments and lateral gonads, tentacles whitish. Bell, hemispherical, wider than high in most cases, with rounded edges, apex domed, with horizontal constriction near the top present in some specimens; mesoglea thick, sturdy, distinctly thicker at apex (Figs. S5A, S6A, 5A, B); structure of bell surface smooth; in-life bell height up to 122 mm, bell width (IPD) up to 150 mm (IRD) up to 136 mm (preserved specimens up to 113 mm high and 150 mm wide (IPD)). Rhopalial niches (Fig. 5I), 4, broad, ellipsoid cavity located inside the exumbrella, mounted and framed by conspicuous, gelatinous, triangular thickenings; orifice very narrow, horizontally slit-like to dumbbell-shaped, upper covering scale, hood-like concave without additional extension (flap), lower covering scale, convex; rhopalial window (Fig. 5D), ellipsoid, small, frenulum attached; 1/6 of bell height up from the margin; no rhopalial horns; rhopalium with 6 eyes (2 major with lenses+2 lateral slit eyes+2 lateral pit eyes). Pedalia, 4, branched (Figs. 5H, 6, 7), ≥3/4 of bell height in length, between 12 and 21 finger-like branches: 1 long, single proximal branch (equal to or shorter than pedalial palm, never longer) followed by six to ten opposite pairs of progressively shorter branches that bear a single tentacle each; broad bases of branches overlap each other like roof shingles (Figs. 7B, C). Pedalial canals, flattened in cross section, very narrow at base, then flaring (Fig. 6F), knee-bend volcano-shaped with massive, upward-pointing spike to thorn-shaped appendage (Fig. 6B–C); lateral canal branches emanate from both sides of undivided main canal (Figs. 6E, G), right and left side branches arranged opposite to one another but alternating (Fig. 6G). Tentacles round (filiform) in cross section (Figs. 6E–G), bearing series of densely aligned p-mastigophores. Manubrium (Figs. S5A, 5E), four-lobed, very long, reaches (in-life) nearly bell opening, shorter in preserved specimens; stomach balloon-like (Fig. S5A), attached to the bell with well-developed, perradial mesenteries (Fig. 5D), mesenteries contain large pinnate glands (Fig. 5C); gastric phacellae (Fig. 5F), 4, horizontal, U-shaped, hundreds filaments closely spaced, multiple rooted, multiple stemmed, simple; four gastric pockets leading from the stomach into the velarial canals. Gastric saccules (Figs. 4, 5G, 8B–E), 8 (4 pairs), situated in the adradia of upper part of subumbrella below the stomach, framing perradia, cone to finger-shaped, partly hollow and pendant,

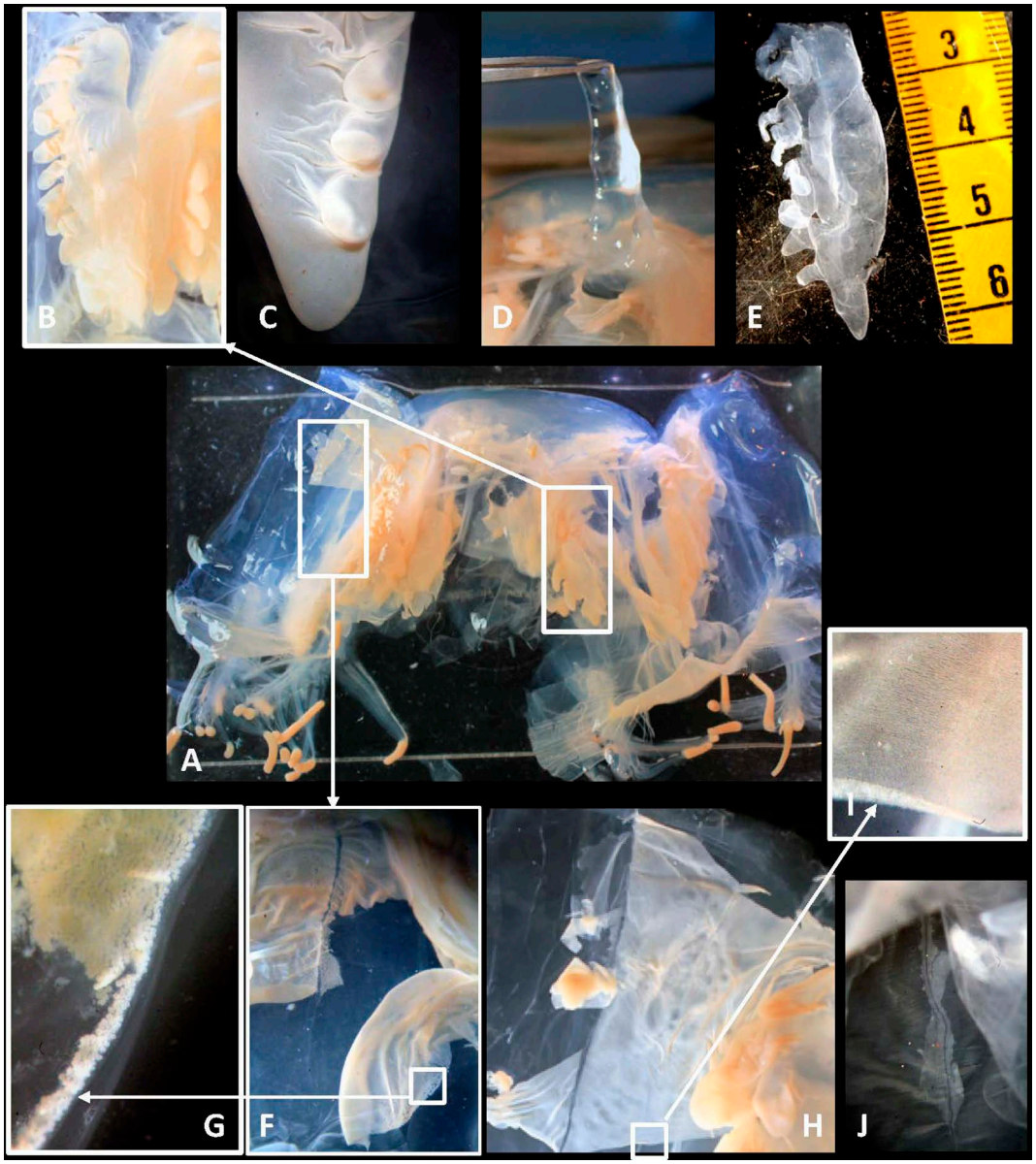

Fig. 8. Structures of gastric saccules and lateral gonads of *Chimaerus palmatus* comb. nov.: A: Dissected medusa; B: Pair of perradial gastric saccules, note finger-shaped appendages; C: Tip of con- shaped gastric saccule with drop-shaped;D: Gelatinous, exumbrellar finger of gastric saccule; E: Empty subumbrellar gastric saccule sleeve; F: Lateral gonads (female); G: Close-up of lateral gonad tissue with eggs; H: Lateral gonads (male); I: Close-up of lateral gonad tissue with fingeprint pattern; J: Regenerating gonadal tissue.

gelatinous inlay (Fig. 8D) enveloped by gonadal tissue covered by glove-like subumbrella tissue (Fig. 8E); ≤10 drop-like to digitate appendages along the rim in 1 to 2 rows (Figs. 8B, C), very long, reaching nearly the bell opening in mature specimens (Fig. 4). Lateral gonads, 4 pairs, leaf-like, attached to interradial septa (Figs. S5A, S6A, 4, 5B, 8F–I). Velarium (Figs. 5J, K), broad, free of nematocyst warts, velarial canal roots, 1 per octant; velarial canals, 1 main canal per root, main canal, menorah-shaped, branching off numerous side canals which are lined by lobed diverticula, tips sharp; perradial lappets (Fig. 5J), 4 pairs, broad triangular; interradial lappets, 4 pairs, broad, rounded, all grow complexly branched and lobed side canals which align with the velarial canals, completing the pattern.

Further data

All characters listed by Haeckel (1880, 1904) could be confirmed except for the number of 21 gelatinous fingers per pedalium (Figs S5A, S6A). In the collections there were several specimens that were obviously sampled after spawning (remnants of gonadal tissue left in the gastric pockets, pedalial canals etc.) and there was one specimen that was already in the stage of regenerating its gonadal tissue after spawning (NHM 1962.1.13.2, Fig. 8J). This observation suggests a life span of more than one spawn-

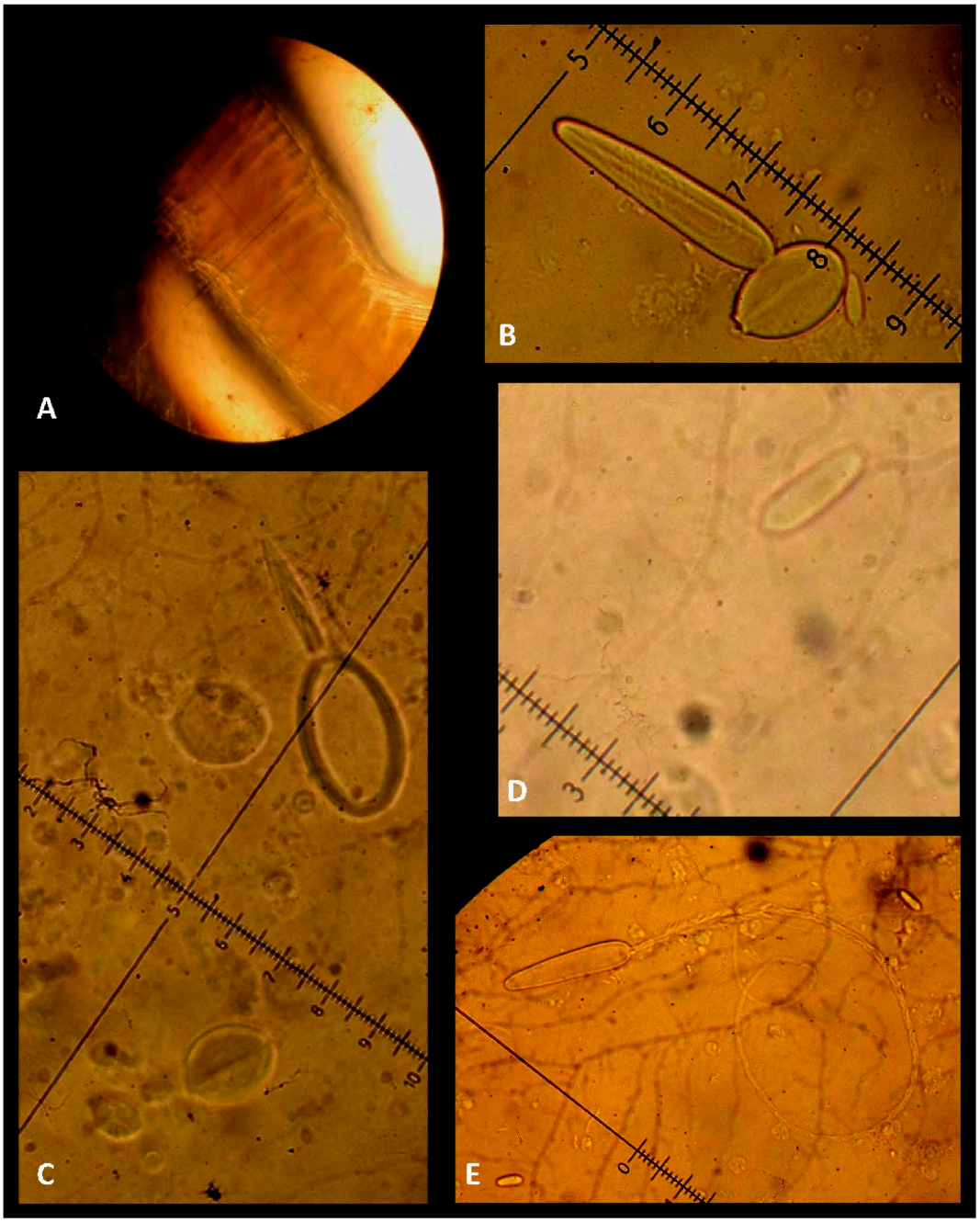

Fig. 9. Nematocysts of *Chimaerus palmatus* comb. nov. A: p-mastigophores aligned on tentacle; B: (From the left to the right) Undischarged banana-shaped p-mastigophore, large oval p-rhopaloid and Small ellipsoidal Isorhiza; C: Discharged and undischarged large oval p-rhopaloid; D: Undischarged small ellipsoidal Isorhiza; E: Discharged p-mastigophores.

ing season, maybe even for several years. We examined specimens with 12 to 17 fingers per pedalium; the smaller specimens had in general less fingers than bigger specimens. If medusae of this species live more than one season and increase not only their bell size but also the number of branches in their pedalia, then a number of 21 fingers per pedalium would be possible as with the growth of tips in an antler of an elk. Another possibility is that Haeckel (1880, 1904) miscounted the number of fingers per pedalium due to their complex structure. Their high transparency, the broad width of their fingers and the overlapping structure add to the difficulty in counting the number of fingers, as experienced by us. The pencil line drawing of Haeckel (Fig. S5A) shows less than 21 fingers per pedalium. Because both explanations for the high number of fingers per pedalium in Haeckel's specimen are possible, we define the number of tentacles in this species as between 12 and 21.

Four different tentacular nematocyst types were identified, based on Kingston & Southcott (1960) and Gershwin

(2006b): banana-shaped microbasic *p*-mastigophores (Figs. 9A, B, E); rod-shaped isorhizae (Figs. 9B, D); large oval *p*-rhopaloids (Figs. 9B, C); and small spherical microbasic *p*-rhopaloids (no figure). There are no data on stinging ability; or on mating and brooding behaviour, polyp stage, asexual reproduction, and newly detached medusa.

The diet of *C. palmatus* is mostly constituted of small shrimps, fish and crab species, as evidenced by an assessment of the gastrovascular cavity content (unpublished data). This species constitutes the most common jellyfish found in beach seine nets in Kribi.

Distribution

British Overseas Territory: Saint Helena Island (*comment*: approximately 16°00′23.5″S, 5°41′22.3″W) (Haeckel 1880);

West Africa: Liberia, Monrovia harbour, "Galathea" Station 18 (Original: 6°19′N, 10°49′W, corrected to: approximately 6°19′00.4″N, 10°49′03.8″W) (Kramp 1955); Ghana, Accra (Kingston & Southcott 1960); Southern Cameroon, Limbe (approximately 4°00′16.4″N, 9°12′34.8″E), Kribi (2°58′49.8″N, 9°54′42.2″E–2°57′33.2″N, 9°54′11.9″E); Angola, South West of Moita Seca (6°30′S, 11°40′E) (Kramp 1959), Muculla (Thiel 1928); Democratic Republic of Congo, 25 miles West North West of Banana, (5°57′S, 12°00′E) (Kramp 1959); Republic of Congo, 11 miles West South West of Pointe Noire, (4°52′S, 11°39′30″E) (Kramp 1959).

General systematics arrangements

Due to the changes proposed (re-descriptions and new genus) we understand that three taxonomic groups have to be emended when removing the species *Chimaerus palmatus* comb. nov. from the family Chirodropidae, and genus *Chirodropus* and newly accommodating it into the family Chiropsalmidae. Table 3 summarizes the morphological differences between supposed *Chirodropus* species. Below we present the classification and reorganized diagnoses of families Chirodropidae and Chiropsalmidae and the genus *Chirodropus* based on Straehler-Pohl (2017), Jarms & Morandini (2019) and Straehler-Pohl & Jarms (2022).

Phylum Cnidaria Verrill, 1865
Subphylum Medusozoa Petersen, 1979
Class Scyphozoa Goette, 1887
Order Metamorphida Straehler-Pohl & Jarms, 2022
Suborder Cubomedusae Haeckel, 1880
Infraorder Chirodropida Haeckel, 1880

Family Chirodropidae Haeckel, 1880 sens. emend

Chirodropidae: Haeckel 1880: 424, 430–434, 445–446; Krumbach 1925: 529, 567, 569, 570, 575; Thiel 1936: 195, 219, 306–307; Bigelow 1938: 135; Southcott 1956: 276–277; Kramp 1961: 307–308;Cleland & Southcott 1965: 79, 125, 126, 129, 131; Mianzan & Cornelius 1999: 529, 531, 532; Carrette et al. 2002: 1548; Collins 2002: 421, 422; Matsumoto 2004: 147, 151;Cornelius et al. 2005: 399, 400; Oba et al. 2004:173; Gershwin 2005: 8, 9, 54, 62, 84, 103, 122, 155, 170; Morandini et al. 2005: 293; Shorten et al. 2005: 267; Gershwin 2006a: 2, 4, 5, 11, 16, 17, 37; Daly et al. 2007: 152; Nogueira & Haddad 2008: 163; Lewis & Bentlage 2009: 60; Bentlage et al. 2010: 495, 497, 498; Sucharitakul et al. 2017: 33, 34, 35, 39–40; Straehler-Pohl 2019: 764; Straehler-Pohl 2020: 2, Gibbons et al. 2022: 42–47.

Carybdeidae: Mayer 1910: 500–519.

Chiropsalmidae: Thiel 1936: 306–308.

Diagnosis: (after Haeckel 1880, revised by Gershwin 2006a, Straehler-Pohl 2019, Gibbons et al. 2022, emended herein)

Chirodropida with branched or cock's-comb-like perradial gastric saccules lacking leaf-like, interradial lateral gonads (or being an insignificant, diminished and possibly functionless structure (Southcott 1956: p. 278)) or lacking gastric saccules but with filamentous gonads (Gershwin 2006a); pedalia branched.

Valid genera: †*Anthracomedusa* Johnson & Richardson, 1968, *Chirodectes* Gershwin, 2006, *Chirodropus* Haeckel, 1880, *Chironex* Southcott, 1956

Genus *Chirodropus* Haeckel, 1880 sens. emend

Chirodropus: Haeckel 1880: 429, 447–448; Mayer 1910: 518; Krumbach 1925: 566, 571, 575; Uchida 1929: 182, 185, 187; Thiel 1936: 194, 272, 275, 283, 293, 300, 302, 306–307; Kramp 1955: 291–292; Kramp 1961: 308; Gershwin 2006a: 5, 17, 25, 37; Straehler-Pohl 2019: 764, 768; Gibbons et al. 2022: 42–45.

Chiropsalmus: Thiel 1936: 300, 302, 307.

Type and valid species: *Chirodropus gorilla* Haeckel, 1880

Diagnosis: (after Haeckel 1880, Kramp 1961, Straehler-Pohl 2019, Gibbons et al. 2022, emended herein)

Chirodropidae with 8 sheet-like gastric saccules with ≥20 grape to digitate appendages arranged in ≥2 rows along interradially pointing rim; pedalial main canals bilaterally branching, non-forked.

Family Chiropsalmidae Thiel, 1936 sens. emend

Carybdeidae: Müller 1859: 11; Mayer 1910: 500–519; Mayer 1917: 184, 230; Mayer 1928: 184, 190.

Marsupialidae: Agassiz 1862: 174.

Chirodropidae: Haeckel 1880: 424, 430–435, 445–446; Ranson 1949: 123; Morandini et al. 2005: 283, 293; Collins et al. 2006: 106, 114; Morandini et al. 2006: 2; Nogueira & Haddad 2008: 157, 158, 163; Rizman-Idid et al.

2016: 6, 13; Sucharitakul et al. 2017: 34; Straehler-Pohl 2019: 756, 764; Gibbons et al. 2022: 43, 47.

Drepanochiridae: Krumbach 1925: 566, 567, 569, 570, 575; Uchida 1929: 181; Thiel 1936: 291; Calder 2009: 9, 15.

Chiropsalmidae: Thiel 1936: 307; Gershwin 2006a: 2–3, 5, 36, 36; Gershwin 2006b: 18; Daly et al. 2007: 152; Bentlage et al. 2010: 495, 497; Straehler-Pohl 2019: 772, 780; Straehler-Pohl 2020: 3.

Diagnosis: (after Thiel 1936, revised by Gershwin 2006b, emended herein)

Chirodropida with non-sessile, finger-like to cone-shaped gastric saccules, with or without lobes on interradially pointing rims; pedalia branched.

Valid genera: *Chiropsalmus* Agassiz, 1862, *Chiropsoides* Southcott, 1956, *Chimaerus* gen. nov.

Genus *inquirendum*: *Chiromedusa* Thiel, 1928

Discussion

Chirodropus gorilla

Most of the characters listed by Haeckel (1880) could be confirmed except for (1) the heart-shape of the sense niche (Fig. S2C), (2) the locking ability of the pharynx by valves (Fig. 1.4), (3) the exclusive location of the gastric saccules (= pocket arms) inside the gastric pouches (Fig. 1.2) and (4) the presence of 8 pairwise-arranged gonads that are attached to the interradial septa along their full-length and have grape-like appendages at the free rim (Figs. S3, 4.2). These characters are discussed as follows:

(1) The rhopalial niches (=sense niche) cavities are ellipsoid in *Chirodropus gorilla*, not heart-shaped and the niche openings are frown-shaped to horizontally slit-like with one upper and one lower covering scale (Figs. 2A, S4D, 3D).

(2) No lockable mechanisms like valves in the manubrium, pharynx and stomach as described by Haeckel (1880) could be observed during the dissection of several specimens (Fig. 2G).

(3) As in all chirodropid species, the gastric saccules of *Chirodropus gorilla* (Figs. 2C–F) are comprised of two main structures, the gelatinous inlay that consists of an outgrowth of the inner exumbrella (Fig. 8D) and the glove-like tissues of the subumbrella (Fig. 2F, left) that follows, in shape and growth direction, the gelatinous outgrowth of the exumbrella. Therefore, the gelatinous part of the gastric saccule starts to grow inside the gastric pouches, but the larger and more complex it becomes, the subumbrella starts to form a glove-like structure that covers the gelatinous outgrowth (Southcott 1956). This "filled glove" hangs, not freely inside the gastric pouch, but also as an outgrowth of the subumbrella outside the gastric pouch cavity but inside the subumbrella cavity (Figs. 2I–J). Between those two parts grows a gonadal tissue layer that takes the shape of the subumbrella glove in mature specimens (Fig. 2F, left). Haeckel (1880) stated that the single specimen that he examined was badly damaged, even if most structures seemed to be well-preserved. When examining the mature but damaged specimen NHMD-642550 (Fig. 2I) from Moanda (=Loanda)/Gabon the structure that was damaged the most was the delicate subumbrella tissue. Most of it was absent or hanging in shreds, some gastric saccule gloves were ripped from the gelatinous inlay covered with gonadal tissue (Fig. 2F), therefore, it might have been hard for Haeckel to see if the gastric saccules were situated exclusively inside the gastric pouches or hanging into the subumbrella cavity.

(4) That might also be the reason as to why Haeckel described additional, thin, leaf-like gonads with grape-like appendages next to the gastric saccules. In all specimens examined for this study, no matter which developmental stage, no additional lateral gonads next to the gonadal tissue of the gastric saccules could be found (Figs. 2H–I). However, when the gonadal tissue of the gastric saccules is separated from the covering subumbrella glove, the empty appendages take finger-like shapes (Fig. 2F, left), while the gonadal appendages take finger to grape-like shapes (Fig. 2F, right). Haeckel had never examined a chirodropid species before examining the *Chirodropus* species (Haeckel 1880). Our own experience is when dissecting mature chirodropid medusae, especially *C. gorilla* when damaged, it is hard to see which structure belongs where (Fig. 2F, I). Haeckel had only studied the article and the drawings of *Chiropsalmus quadrumanus* by Müller (1859, at that time in the genus *Tamoya*), which possesses gastric saccules and lateral gonads. Therefore, if Haeckel found both stages (empty gloves and naked gonadal tissue) next to each other within his damaged specimen, as in Fig. 2F, the most logical thing for him would have been to assume that the "glove" represented the gastric saccule (=pocket arm) while the naked gonadal tissue represented the gonads, as in his line drawing (Haeckel 1880, Plate XXVI, Fig. 2; present study Fig. 1.2), where the gonads are more highly contrasted than the gastric saccules. Haeckel had examined another mature chirodropid species, his *Chirodropus palmatus* (now in the genus *Chimaerus*), before he inspected *C. gorilla*. The specimen of *C. palmatus* seemed to have been less damaged because he did not state that there was any damage (Haeckel 1880). As in *Chiropsalmus quadrumanus*, Haeckel's specimen had both structures: intact gastric saccules and lateral gonads (Haeckel 1904; see also translation Text S3). We assume that Haeckel, therefore, described and drew both structures for *C. gorilla* as common chirodropid structures (Haeckel 1880: 447–448). Kramp (1959: 20) also examined *C. gorilla* specimens and described the gonads as ". . . attached along the interradial septa, and each of them has a feather-like appearance consisting of two lateral leaves densely transversally folded (fig. 3 a, b), but they have no grape-like clusters of swellings as figured by Haeckel.". Referring to the drawings by Kramp (1959, Fig. 3a, b), he was mistaken because he did not refer to gonadal structures at all but to the four pinnate

glands (Figs S4B, 3C) that belong to the gastric system and are situated within the perradial mesenteries not the interradial septa. Pinnate glands are unique structures that are found in every chirodropid species (Straehler-Pohl 2019). Therefore, Kramp (1955) also did not find any lateral gonads next to the gastric saccules in *C. gorilla*.

***Chimaerus palmatus* comb. nov**

The species *Chirodropus palmatus* is one example of a chirodropid species with doubtful identity. This species had only been reported in the original description (Haeckel 1880, 1904). The preserved type material seems to have been lost during World War II. Mayer (1910) considered this species as a juvenile specimen of *Chirodropus gorilla,* but he did not state it as invalid and instead suggested to postpone the decision as to its validity until more variations concerning the number of pedalial appendages/tentacles in *C. gorilla* specimens were known (Straehler-Pohl 2019: 772). Up to now, no medusae of *C. gorilla* with more than 11 tentacles per pedalium have been found (Haeckel 1880, Kramp 1955, 1959, Pagès et al. 1992, Simon Elwen, Namibian Dolphin project (personal communication in 2013), Straehler-Pohl 2019, present study). In addition, a juvenile with only a third of the bell height compared to adults would probably not have developed a pedalial palm with 21 branches, since the branching of the pedalium/increasing of number of tentacles continues during growth (Gershwin 2005: 161), at least until maturity (Straehler-Pohl 2019: 772). According to Gershwin (2005: 122) "due to its distinct morphology," *Chirodropus palmatus* "should be regarded as provisionally valid until a re-description can be made on new material."

We observed mature chirodropid specimens in different collections labelled as "*Chirodropus gorilla*" or "*Chiropsalmus quadrumanus*" from West Africa that looked similar at first sight to *C. gorilla,* but differed distinctly in bell size and tentacle number per pedalium. After observing all those museum specimens and undertaking a comparison with the literature, we identified the specimens and accommodated them into a new genus as *Chimaerus palmatus* comb. nov. A detailed comparison showed that the gastric saccules of *C. gorilla* of all stages were flat to sheet-like with numerous (≥20) digitate to grape-like, sometimes branched and lobed, appendages, arranged in at least 2 rows per saccule (Figs 2C–F, S4C, 3H). While in *Chimaerus palmatus* comb. nov., the saccules were conical to digitate with less numerous (≤10), simple drop- to finger-like appendages, arranged in 1-2 rows per saccule (Figs. 13B, C). This was also confirmed by Kramp (1959: 16–17), who identified the specimens as "*Chiropsalmus quadrumanus*" due to their finger-like, non-flat structure. In some of the specimens that he inspected the gastric saccules were smooth or just slightly wrinkled and not conspicuously "irregularly lobed" (Kramp 1959: 17, Fig. 1), some having a notched margin. He also described that, contrary to *C. quadrumanus* from Brazil where the gastric saccules were attached to the inner exumbrella in the most proximal part, the gastric saccules of the African specimens were attached to the bell wall "by almost half their inner margin" (Kramp 1959: 17), as described by Haeckel (1880) for *C. palmatus*. Kramp compared the African specimens with specimens from Brazil and stated that "in all essential features these specimens agree with *Chiropsalmus quadrumanus*" (Kramp 1959: 16), which would include also the lateral gonads and U-shaped, horizontally-arranged gastric phacellae that we detected. We examined the same specimens as Kramp (1959) and found additionally the conspicuous structure of the pedalia. The first and last authors also observed *C. quadrumanus* in Brazil and can state that it possesses smooth, finger-like gastric saccules that are quite even in diameter throughout their length and bluntly rounded, while the African specimens have a conical shape with a tapering diameter and sharp tips. The pedalial knee bend in *C. quadrumanus* is angular to rounded, without a thorn-like appendage (Gershwin 2006a, Straehler-Pohl 2019), while the African specimens possess a pedalial knee bend with a huge spike to thorn-like appendage (Figs. 6B–D).

Our work emphasizes that detailed morphological studies can still provide insightful characters that are consistent and important for species distinction. Although we focused on old preserved museum specimens, there are also some data on recently collected ones, but from an area that was poorly explored in terms of gelatinous zooplankton. The zoologist Ernst Haeckel has been accused of describing morphological characters that are not present in certain species that he described– and our study is an example of this. However, we should highlight that Haeckel's descriptions are often accurate and, in many cases, based on damaged specimens. Thus, the author combines observable characters with observations of similar and "thought-to-be related" species to provide a more "complete" description of a damaged animal he believed was a new species. Nowadays, we have access to advanced methods and techniques that allow us to provide better and more complete descriptions of the marine fauna; but we should not disregard the old literature entirely and always bear in mind that those researchers were doing their best at the time to describe the biodiversity as they interpreted it (Straehler-Pohl 2020).

Electronic supplementary material

The online version of this article (doi: 10.3800/pbr.17.406) contains supplementary materials:

Text S1: Haeckel (1880) "*444. Species:* Chirodropus gorilla, *Haeckel; nova species. Plate XXVI.*

Text S2: Haeckel (1880) "*443. Species:* Chirodropuspalmatus, *Haeckel; nova species.*

Text S3: "*Fig. 1* Chirodropus palmatus *Family of Chirodropidae*

Fig. S1. Original German text of the species description of

Chirodropus gorilla by Haeckel (1880, pp. 448-449, translation see below).

Fig. S2. Original pencil line drawings of medusa structures of *Chirodropus gorilla* by 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).

Fig. S3. Original pencil line drawing of dissected medusa of *Chirodropus gorilla* by 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).

Fig. S4. Structures of juvenile medusa of *Chirodropus gorilla* sampled in 1990 by Africana Expedition (Pagès et al. 1992).

Fig. S5. Original pencil line drawing (A, between 1877 and 1904, with courtesy of the collections of the Ernst-Haeckel-Haus, Friedrich-Schiller-Universität Jena Institut für Geschichte der Medizin, Naturwissenschaft und Technik) and (B) original description of *Chirodropus palmatus* by Haeckel (1880, p. 448, in German, translation see below).

Fig. S6. Line drawing (after Haeckel 1904, Plate 78, Fig. 1) and and figure caption (B, in German, translation see below) of *Chirodropus palmatus* by Haeckel (1904).

Fig. S7. Sandy (A) and rocky (B) beaches of Kribi in Cameroon, sampling location of *Chimaerus palmatus* comb. nov.

Acknowledgements

ISP is grateful to Dr. Josep-Maria Gili, Dr. Verónica Fuentes and Dr. Melisa Judith Acevedo (Institut de Ciències del Mar-CSIC, Barcelona, Spain) and Dr. Mark Gibbons (University of the Western Cape, Cape Town) for giving her the opportunity to observe immature and mature *C. gorilla* specimens in their collections. We would also like to thank MSc Miranda Lowe (British Museum of Natural History, London), Dr. Yves Samyn (Royal Belgian Institute of Natural Sciences, Brussels), Dr. Martin Vinther Sørensen (University of Copenhagen) and Laura Pavesi (Natural History Museum of Denmark), and Dr. Wayne Florence and Albe Bosman (Iziko Museum of South Africa) for hosting ISP in museums during 2015, 2016, 2017 and 2019. Original line drawings from Haeckel were kindly provided by Dr. Thomas Bach (Ernst-Haeckel-Haus, Friedrich-Schiller-Universität Jena Institut für Geschichte der Medizin, Naturwissenschaft und Technik). GFYG is grateful to the scientific team of the Institute of Agricultural Research for Development for laboratory facilities at the Specialised Research Center for Marine Ecosystems (CERECOMA)– Fisheries Research Laboratory for believing in us and for all their support. We would like to thank two anonymous reviewers for their constructive suggestions. ISP was 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. ACM had financial support from FAPESP (2019/20042-6) and CNPq (309440/2019-0). This is a contribution of NP-BioMar USP.

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