A new species found in the Collection of the Discovery Expedition from 1925–27: Tamoya ancamori sp. nov. (Cnidaria, Cubozoa, Carybdeida, Tamoyidae) from West African waters

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Received 23 August 2019; Accepted 6 March 2020  Responsible Editor: Dhugal Lindsay
doi: 10.3800/pbr.15.189

Abstract: In 1934, Stiasny described cubomedusan specimens from Station 279 of the Discovery Expedition 1925–27 in the Gulf of Guinea, West Africa as Tamoya haplonema. He also presented line drawings of the habitus that raised some doubts on the identification of the species. In the collections of the Natural History Museum of London, the described specimens were still available and in good condition due to their storage in formalin. More specimens could be found in other European museums. The formalin made a genetic analysis impossible but as all anatomical structures were excellently preserved, a direct comparison was possible with the structures in Tamoya haplonema and Tamoya ohboya from the Americas. Due to the morphological comparison with the American Tamoya species it could be confirmed that the African Tamoya specimens are an up-to-now undescribed new Tamoya species, Tamoya anacamori sp. nov., described herein.

Key words: morphology, systematics, museum collections, Tamoya haplonema, Tamoya ohboya

Introduction

There are regions in the world where it is hard to get an overview on the biodiversity, as these regions have either insufficient infrastructure and/or these regions are in conflict areas, like the West African coast (Ellis 2007, Kaldor & Vincent 2006, Kieh 2008) or the Arabian Sea (Pecasting 2011, Brandt 2017, Monks 2018). However, about 100 years or more ago, there were times when specimens were collected in these areas during the “big” oceanic surveys (Haeckel 1882, Discovery Committee 1929, Stiasny 1934). These collections still exist but are largely unaccessed due to a lack of funding and expertise in classical taxonomy in modern times (Grant 2009).

Up to now there are 5 described Tamoya species, Tamoya haplonema Müller, 1859, Tamoya prisomatica Haeckel, 1880, Tamoya bursaria Haeckel, 1880, Tamoya haeckeli Southcott, 1967 and Tamoya ohboya Collins, Bentlage, Gillian, Lynn, Morandini & Marques, 2011, of which only T. haplonema and T. ohboya are considered as valid species while the other three are considered as doubtful (Collins et al. 2011, Bentlage & Lewis 2012, Straehler-Pohl 2019).

Tamoya haplonema was described by Müller (1859) from Brazil but it is known to roam the coasts of the Americas from Argentina to North Carolina (Calder 2009). The second species from the Americas, Tamoya ohboya, described by Collins et al. (2011) roams the Caribbean Sea, as does Tamoya prisomatica according to Haeckel (1880), but T. prisomatica has been considered identical to T. haplonema (Mayer 1910, Kramp 1961, Collins et al. 2011, Bentlage & Lewis 2012, Straehler-Pohl 2019).

There is one more Tamoya species, Tamoya haeckeli Southcott, 1967 that is supposed to be distributed in Asia. It was described first by Haeckel (1880) as Tamoya gargantua Haeckel, 1880 based on a specimen from Samoa (Pacific). Haeckel referred the name to a description by Lesson (1830) based on a completely destroyed carybdeid specimen without any characteristic structure remaining.

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that could distinguish this specimen from other carybdeid species. Therefore, Southcott (1967) followed the discussion and suggestion of Kramp (1956, 1961) and Bigelow (1938) and renamed *T. gargantua* to *T. haeckeli* (Straehler-Pohl 2019). However, this species from Asian waters was never sighted again and might even be a member of

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**Fig. 1.** Similar structures of preserved material (paratype NHM 339) of the Western African *Tamoya* population in the collection of the Natural History Museum of London and the line drawings of Stiasny (1934): A: habitus; B: line drawing of habitus of "*Tamoya haplonema*" from Western Africa (Stiasny 1934, p. 340: Fig. 1a); C: Rhopalial niche; D: line drawing of rhopalial niche of "*Tamoya haplonema*" from Western Africa (Stiasny 1934, p. 340: Fig. 1b); E: line drawing of quadrant of velarium (f: frenulum) of "*Tamoya haplonema*" from Western Africa (Stiasny 1934, p. 340: Fig. 1c); F: quadrant of velarium (f: frenulum).
a different taxonomic group (Bentlage & Lewis 2012, Straehler-Pohl 2019), and its validity is considered doubtful (Collins et al. 2011, Straehler-Pohl 2019).

In 1934, Stiasny referred 6 cubomedusan specimens from the Discovery Expedition 1925–27, Station 279, on the West African coast to Tamoya haplonema. In addition to Stiasny (1934), Ranson (1949) and Kramp (1955, 1959, 1961) identified cubozaans sampled during different surveys from the West African coast as T. haplonema.

During collaboration with André C. Morandini and Sérgio Stampar on Tamoya haplonema at the University of São Paulo in Brazil in 2012, investigations on the validity of Tamoya ohboya, and reference to the line drawings and descriptions of Stiasny (1934; present study: Figs. 1B, D, E), doubt was cast on whether the African specimens are really referable to the species T. haplonema, considering also that the two "populations" are separated by a whole ocean. Therefore, the specimens that Stiasny had described (1955, 1959) including those described by Ranson (1949) and Krampsels (RBINS), Leiden (NBCN) and Copenhagen (NHMD), were searched for in the collections of the Natural History Museum of London (NHM). The described specimens were still available and in excellent condition due to their preservation in formalin (Figs. 1A, 2N, 4A). More specimens were found in the Natural History Museums of Brussels (RBINS), Leiden (NBCN) and Copenhagen (NHMD), including those described by Ranson (1949) and Kramp (1955, 1959)—all in all 12 specimens could be observed.

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Table 1a. Unregistered American Tamoya specimens, and specimens from museum collections examined for this study.

| Collection | Code No. | No. of specimens | Species identification | Sampling location/ additional information | Collector | Sampling date |
|------------|----------|------------------|------------------------|------------------------------------------|-----------|--------------|
| IB-USP     | Unregistered* 6 | 16 | Tamoya haplonema* Müller, 1859 | Itagua, Ubatuba, Sao Paulo, Brazil (23°26′39.1″S 45°02′47.8″W); 22°C, 33.1 PSU, O2 7.78 mg/L; 5–10 m trawl, mud bottom | Sérgio N. Stampar, Ilka Straehler-Pohl | 25 Jul 2012 |
| IB-USP     | Unregistered* 6 | 15 | Tamoya haplonema* Müller, 1859 | Itagua, Ubatuba, Sao Paulo, Brazil (23°26′39.2″S 45°02′24.5″W); 22°C, 32.5 PSU, O2 7.80 mg/L; 5–10 m trawl, mud bottom | Sérgio N. Stampar, Ilka Straehler-Pohl | 26 Jul 2012 |
| IB-USP     | Unregistered* 6 | 5  | Tamoya haplonema* Müller, 1859 | Itagua, Ubatuba, Sao Paulo, Brazil (23°26′37″S 45°02′40″W); 21.9°C, 32.8 PSU, O2 7.32 mg/L; 5–10 m trawl, mud bottom | Sérgio N. Stampar, Ilka Straehler-Pohl | 31 Jul 2012 |
| MZUSP      | 494      | 1  | Tamoya ohboya Collins et al. 2011 | São Sebastião, southeastern Brazil; relaxed in MgCl2, preserved in 4% formalin-seawater | J.C. Freitag | 07 Aug 1999 |
| NMNH       | USNM 1146080 (holotype: T. ohboya) | 1  | Tamoya ohboya Collins et al. 2011 | Divi Flamingo, Bonaire, The Netherlands (~12°8.61′N, 68°16.60′W); preserved in 10% buffered formalin | W. Gillan, M. Wilhemus | 30 Jun 2010 |

* stored in the Zoological Department of São Paulo, working group of AC Morandini. * Identifications were done in 2012. IB-USP: Instituto de Biociências da Universidade de São Paulo. MZUSP: Museum of Zoology of the University of São Paulo. NMNH: Smithsonian’s National Museum of Natural History.

**Materials and Methods**

**Morphological comparison**

All medusae observed from the West African coast were preserved in 5%–7% formalin, with all anatomical structures being excellently preserved, allowing a direct comparison with the structures of the Tamoya species of the Americas.

**Species observed**

"Tamoya haplonema" from West Africa

All information about the specimens observed and the museum collections are listed in Tables 1a+b.

As the identification of the West African population of "Tamoya haplonema" Müllner 1859" by Stiasny, (1934) was based on descriptions by Müller (1859) of the Brazilian type specimens, these, as well as other specimens from Brazil, were examined:

**Tamoya haplonema from Brazil**

Zoological Museum of São Paulo University (MZUSP): Pontal do Paraná (25°20′–25°57′S, 48°10′–48°35′W), 1 male/female (MZUSP 494), 8 m depth; thirty-six (36) unregistered specimens: Brazil, Itagua, Bay of Ubatuba, (23°26′39.1″S, 45°02′47.8″W) 5–10 m, 22°C, 33.1 PSU, trawl, mud bottom, 25 July 2012, 6 female, 4 male medusae, 6 immature medusae, (23°26′39.2″S, 45°02′24.5″W) 5–10 m, 21.9°C, 32.8 PSU, trawl, mud bottom, 26 July 2012, 7 male medusae, 8 immature medusae, (23°26′37″S,
### Table 1b. Tamoya ancamori sp. nov. specimens from museum collections examined for this study.

| Collection  | Code No. | No. specimens | Species identification* | Original identification | Sampling location | Collector | Sampling date |
|-------------|----------|---------------|--------------------------|-------------------------|-------------------|-----------|---------------|
| NHM         | 338-342  | 5             | Tamoya ancamori n. sp.   | Tamoya haplonema Müller, 1859 | Discovery Expedition Sta. 279, East Atlantic, West Africa, Gulf of Guinea, Off Cape Lopez, Gabun (French Congo), from 8–5 miles N71°E to 15 miles N24°E of Cape Lopez (between approx. 0°27′27.1″S, 9°04′43.4″E and approx. 0°27′03.1″S, 8°28′49.9″E, according to map in Discovery Reports), large otter trawl, head rope 40 ft long (12.2 m): mesh at cod-end 1 1/4 inch (3.2 cm), 58–67 m, 24.6°, 33.08̅ R.R.S. 'Discovery' | R.R.S. 'Discovery' | 10 Aug 1927 |
| NBDC        | 7066     | 1             | Tamoya ancamori n. sp.   | Tamoya haplonema Müller, 1859 | Discovery Expedition Sta. 279, East Atlantic, West Africa, Gulf of Guinea, Off Cape Lopez, Gabun (French Congo), from 8–5 miles N71°E to 15 miles N24°E of Cape Lopez (between approx. 0°27′27.1″S, 9°04′43.4″E and approx. 0°27′03.1″S, 8°28′49.9″E, according to map in Discovery Reports), large otter trawl, head rope 40 ft long (12.2 m): mesh at cod-end 1 1/4 inch (3.2 cm), 58–67 m, 24.6°, 33.08̅ R.R.S. 'Discovery' | R.R.S. 'Discovery' | 10 Aug 1927 |
| RBINS       | I.G. 16808 | 1             | Tamoya ancamori n. sp.   | P.L. Kramp, 1950: Tamoya haplonema Müller, 1859 | St. 153, West Africa, 11 miles North of Port Gentil (00°33′S, 08°50′E) | Atlantique Sud | 15 Mar 1949 |
| RBINS       | I.G. 16808 | 1             | Tamoya ancamori n. sp.   | P.L. Kramp, 1950: Tamoya haplonema Müller, 1859 | St. 142, West Africa, 29 miles South of Cape Lopez, 11 miles North of Port Gentil (01°07′S, 08°38′E) | Atlantique Sud | 09 Mar 1949 |
| RBINS       | I.G. 11.553 | 1             | Tamoya ancamori n. sp.   | P.L. Kramp, 1950: Tamoya haplonema Müller, 1859 | 14th Cruise of "Mercator", West Africa, 8–10 miles of the coast of Sierra Leone (07°05′N, 12°W) | School ship Mercator | 15 Jan 1935 |
| RBINS       | I.G. 10910 | 1             | Tamoya ancamori n. sp.   | Dr. G. Ranson, 1945: Tamoya haplonema Müller, 1859 | Cruise of "Mercator" 1935–1936, West Africa, Senegambia, in front of Gambia, (13°25′N, 16°50′W) | School ship Mercator | 15 Nov 1935 |
| RBINS       | I.G. 10910 | 1             | Tamoya ancamori n. sp.   | Dr. G. Ranson, 1945: Tamoya haplonema Müller, 1859 | Cruise of "Mercator" 1935–1936, West Africa, French Guinea, South of Kassa (Iles of Los) | School ship Mercator | 23 Nov 1935 |
| NHMD        | 642567   | 1             | Tamoya ancamori n. sp.   | P.L. Kramp, 1950: Tamoya haplonema Müller, 1859 | St. 141, West Africa, Sierra Leone, off Freetown | Atlandide | 09 Apr 1946 |

*Identifications were performed between 28 Apr 2015 and 30 Sep 2015 for this study. NBDC: Naturalis Biodiversity Center, Leiden. NHM: Natural History Museum, London. NHMD: Natural History Museum of Denmark, Copenhagen. RBINS: Royal Belgian Institute of Natural Science, Brussels
Table 2. Comparison of characters based on atlantic specimens of *Tamoya* from the Americas and West Africa. (differences marked in **bold** + *Italic*):

| **Tamoya haplonema,** East Atlantic and adjacent seas | **Tamoya sp. West Africa** | **Tamoya ohbaya** |
|----------------------------------|-------------------------|------------------|
| MZUSP 494, registered and unregistered specimens from the Americas (see Table 1a) (Müller 1859, Mayer 1910, Collins et al. 2011, present study) | 12 registered specimens from West Africa (see Table 1b) (Stiasny 1934, present study) | USNM 1146080 (Holotype); data of specimens listed in Collins et al. 2011 as additional material (Collins et al. (2011), present study) |

**Bell**
- transparent, colourless to brownish or bluish (in-life: Fig. 4); translucent whitish (preserved: Fig. 2A)
- sturdy, thick mesogloea
- cylindrical to pyramidal with rounded edges (Fig. 2A)
- apex, **very thick mesogloea, slightly arched,** without horizontal constriction (Figs. 2A, B)
- nematocyst warts, large, densely scattered, prominent, round, colourless, **from apex to velarium** (Fig. 4) (Mayer 1910, p. 513: "Bell ..., with vertical sides, and relatively flat top. Exumbrella surface thickly covered with white, wart-like clusters of nematocysts[...]. Gelatinous substance of bell transparent.")
- transparent, colourless to whitish (preserved) (Figs. 1A, 2N, O, 3A)
- sturdy, thick mesogloea
- pyramidal with rounded edges (Figs. 1A, 2N, 3A)
- apex, **mesogloea slightly thicker than bell walls,** slightly arched, without horizontal constriction (Fig. 1A)
- nematocyst warts, large, densely scattered, prominent, round to oval, colourless, **from apex to bell margin** (Figs. 1A, B, 3B, F) (Stiasny 1934, p. 340–341: "... more or less cylindrical form, the mesogloea not thickened at the apex, [...] The FORM OF THE BELL is cylindrical with a widening in the middle part (Fig. 1 a). The EXUMBRELLA of the medusa is, in the upper parts, thickly covered with small or larger, oval or round, wart-like, colourless clusters of nematocysts. Towards the proximal part of the umbrella they diminish in size. [...] The COLOUR is greyish white, [...] The clusters of nematocysts on the exumbrella are nearly transparent, without pigmentation.")
- transparent, colourless (in-life: Fig. 3B); translucent whitish (preserved: Fig. 3A)
- sturdy, thick mesogloea
- cylindrical to pyramidal with rounded edges (Figs. 3A, B)
- apex, **very thick mesogloea, slightly arched,** without horizontal constriction
- nematocyst warts, large, densely scattered, prominent, round, white, **from apex to velarium** (Fig. 3A, B, L) (Collins et al., 2011, p. 59: "Bell translucent, densely covered in conspicuously raised nematocyst warts.")

**Size (mature)**
- BH: up to 165 mm
- IRD: no data
- IPD: up to 120 mm
- **IPD/BH: ca. 0.70** (mean: 0.72, SD: 0.059, n=39)
- PL: up to 60 mm
- PW: up to 36 mm
- BH: up to 100 mm
- IRD: no data
- IPD: up to 89 mm
- **IPD/BH: ca. 0.90** (mean: 0.89, SD: 0.014, n=12)
- PL: up to 48 mm
- PW: up to 17 mm
- **IPD/BH: ca. 0.70** (Collins et al. 2011: Figs. 1A, D)
- PL: No data available
- PW: no data available
- Collins et al., 2011, p. 58: "Material examined: [...]61 mm BH (bell height; measured from velarial turn-over to top of bell), 29 mm IRW (interradial bell width), [...] 67 mm BH, 32 mm IRW, [...]63 mm BH, 30 IRW, ... ", p. 59: "Stomach extending to about1/3 of bell height into subumbrellar cavity")

**Gonads**
- interradial (Fig. 2B)
- paired, 4
- size, covering entire area of gastric pouch from stomach to bell margin (Figs. 2A, B)
- interradial (Figs. 2O, 3A)
- paired, 4
- size, length from stomach to bell margin, covering entire area of gastric pouch in upper half tapering in lower half towards rhopalial niche level, flaring again below rhopalial niche level (Fig. 1A, 2N, O, 3A, B)
- interradial (perradial according to Collins et al. 2011, p. 59)
- paired, 4
- size, covering entire area of gastric pouch from stomach to bell margin
Table 2. continued

| Tamoya haplonema, East Atlantic and adjacent seas | Tamoya sp. West Africa | Tamoya ohboya |
|-----------------------------------------------|------------------------|---------------|
| MZUSP 494, registered and unregistered specimens from the Americas (see Table 1a) (Müller 1859, Mayer 1910, Collins et al. 2011, present study) | 12 registered specimens from West Africa (see Table 1b) (Stiasny 1934, present study) | USNM 1146080 (Holotype); data of specimens listed in Collins et al. 2011 as additional material (Collins et al. 2011, present study) |

- leaf-shaped, very thin tissue, many folded, separated by perforated interradial septum, attached at entire length of septum (Fig. 2B)
- sexes unimorph until immediately before spawning, when female gonads turn brownish to ochre in colour, male gonads turn blue to bluish green in colour (Stracheler-Pohl 2019); opaque white in preserved specimens (7% formalin) (Fig. 2A)

(Mayer 1910, p. 513: "The 8 genital organs are curtain-like sheets with frilled edges, which project from the 4 interradial septa into the perradial gastrovascular pouches of bell on either side. In old specimens the gonads are so large that their free edges overlap beyond the central line of each perradial stomach-pouch.")

Pedalia

- 4, single, simple
- non-stalked
- slightly keeled at midline in upper half
- irregular broad leaf-shaped
- PL ca. 40% of BH
- PW ca. 60% of PL

Inner wing

- flattened, nearly semicircular shaped (Fig. 2E)
- incision above tentacle insertion, not overhanging tentacle insertion
- nematocyst warts, none (Fig. 2E)
- 4, single, simple
- slightly stalked (Fig. 2R)
- slightly keeled at midline in upper 2/3 (Fig. 3I)
- narrow leaf-shaped (Figs. 2R, 3I)
- PL ca. 40–50% of BH
- PW ca. 40% of PL

- no incision above tentacle insertion, not overhanging tentacle insertion (Figs. 2R, 3I)
- nematocyst warts, none (Figs. 2R, 3I)

- flattened after 1/3, narrow semi-oval (Figs. 2R, 3I)

- no incision above tentacle insertion, not overhanging tentacle insertion (Figs. 2R, 3I)
- nematocyst warts, none (Figs. 2R, 3I)

- flattened, semi-oval shaped

- flattenned, semi-oval shaped

- no incision above tentacle insertion, not overhanging tentacle insertion
- nematocyst warts, densely scattered on pedialial canal level, numbers decrease to zero towards midline of inner wing (Fig. 3D)

(Collins et al., 2011, p. 59: "[...]
- nematocyst warts, both on outer keel and inner wing; pedialial wing scalpel-shaped as in Tamoya haplonema.")

Outer wing

- semi-oval shaped, narrower than inner wing (Fig. 2E)
- broadly edged at base
- nematocyst warts, round to irregular shaped warts/bands, scattered (Fig. 2E; easily rubbed off in preserved specimens)
- narrow semi-oval shaped, narrower than inner wing (Figs. 2R, 3I)
- sharply edged
- nematocyst warts, presently none (likely rubbed off as they were noted in 1934 by Stiasny) (Figs. 2R, 3I)

- semi-oval shaped, narrower than inner wing
- broadly edged at base
- nematocyst warts, mostly round to irregular shaped warts/bands, scattered (Fig. 3D)

(Collins et al., 2011, p. 59: "[...] nematocyst warts, both on outer keel and inner wing")

Pedial canal

- cross section, triangular at base, diamond-shaped at midsection, flattened oval/ellipsoid towards distal end (Figs. 2E)
- cross section, triangular at base, diamond-shaped at midsection, flattened oval/ellipsoid towards distal end (Figs. 2R, 3I)

- cross section, triangular at base, diamond-shaped at midsection, flattened oval/ellipsoid towards distal end
Table 2. continued

| Tamoya haplonema, East Atlantic and adjacent seas | Tamoya sp. West Africa | Tamoya ohboya |
|-------------------------------------------------|------------------------|--------------|
| MZUSP 494, registered and unregistered specimens from the Americas (see Table 1a) (Müller 1859, Mayer 1910, Collins et al. 2011, present study) | 12 registered specimens from West Africa (see Table 1b) (Stiasny 1934, present study) | USNM 1146080 (Holotype); data of specimens listed in Collins et al. 2011 as additional material (Collins et al. 2011, present study) |

- 'flaring after 2/3 distance towards tentacle insertion, distal end broadly flared (Fig. 2E)'
- mostly straight
- 'knee bend sharply edged rectangular (90°-angle), without any appendages' (Figs. 2F, G)

(Mayer 1910, p. 513: '4 pedalia, 30 mm. long, flat, spatula-shaped, and sharp-edged. [...] There are large, white, wart-like clusters of nematocysts over the pedalia [...]')

Tentacles
- 4, single
- flesh coloured to brownish, sometimes with light brown stripes (live: Figs. 2H, I); light pink (preserved: Fig. 2A)
- width, broadly flared at base, nearly same from below base to distal end (Figs. 2A, H, I, 4)
- 'broad, cross-section, flattened (in-life, preserved)' (Figs. 2H, I)
- 'ribbon-like, bearing series of dense nematocyst bands' (Figs. 2H, I)
- up to 165 cm in length (in-life)

(Mayer 1910, p. 513: 'Tentacles 90 mm. long, hollow, very flexible and bearing regularly spaced rings of nematocysts that are capable of inflicting a severe sting to the hand. [...] The long, flexible tentacles are milky-yellow, often with a faint purple hue.')

Rhopalial niches
- cavity, irregularly heart shaped, with two upwards turned bays (can be mistaken for rhopalial horns) (Fig. 2D)
- orifice, slit-like to brown-shaped (Fig. 2C)
- covering scales: upper, 1, rounded convex, lower, 1, sharply edged triangular convex (Fig. 2C)
- 1/7 up from margin
- number of eyes per rhopalium, 6

- cavity, irregularly heart-shaped, with two upwards turned bays (can be mistaken for rhopalial horns) (Figs. 2Q, 3H)
- orifice, slit-like to brown-shaped (Figs. 1C, D, 2P, 3G)
- covering scales: upper, 1, rounded convex, lower, 1, rounded convex (Figs. 1C, D, 2P, 3G)
- 1/8 up from margin
- number of eyes per rhopalium, 6

- cavity, irregularly shaped, with two upwards turned bays (can be mistaken as rhopalial horns: Fig. 3C)
- orifice, slit-like to brown-shaped
- covering scales: upper, 1, rounded convex, lower, 1, soft triangular convex
- 1/7 up from margin
- number of eyes per rhopalium, 6

- 'tapering slightly after knee bend, flaring towards tentacle insertion, distal end broadly flared (Fig. 3D)'
- mostly straight (Fig. 3D)
- 'knee bend triangular to sharply edged rectangular (90°-angle), without any appendages' (Figs. 3E, F)

(Collins et al. 2011, p. 59: "Pedalial canal bend with prominent spike.")
Table 2. continued

| Tamoya haplonema, East Atlantic and adjacent seas | Tamoya sp. West Africa | Tamoya ohboya |
|-----------------------------------------------|------------------------|---------------|
| MZUSP 494, registered and unregistered specimens from the Americas (see Table 1a) (Müller 1859, Mayer 1910, Collins et al. 2011, present study) | 12 registered specimens from West Africa (see Table 1b) (Stiasny 1934, present study) | USNM 1146080 (Holotype); data of specimens listed in Collins et al. 2011 as additional material (Collins et al. (2011), present study) |
| (Mayer 1910, p. 513: "The sensory-clubs have 2 large median and 4 small lateral eyes, all being upon the inner side of the bulb. The large eyes are provided with prominent convex lenses and are ectodermal. There is a large terminal mass of concretions of entodermal origin (ISP => ectodermal. There is a large terminal mass of concretions of entodermal origin (ISP => statocyst)."

Rhopalial horns

• none

Velarium

• broad (≥ 1/3 of bell diameter)
• nematocyst warts, numerous, large, loosely scattered (Figs. 2L, M)
• canal roots, 3 per octant (Fig. 2L)
• canals, broad, next to frenulum, 2–3, middle, 2, next to pedalium, 1 (Fig. 2L)
• very complexly patterned, deeply forked, dendritic branching, not anastomosing (Stiasny 1934, p. 341: "The SENSORY PIT, which lies in a broad flask-shaped thickening of the exumbrella, is a broad deep groove and opens with a single large orifice (Fig. 1 b). The upper and under squamae rhopalares (ISP => covering scales) here run parallel and do not form two round orifices as has been described by Uchida in T. alata (1929, fig. 87 B). The SENSORY ORGAN bears six eyes, two larger medians and two pairs of smaller ones of a feeble brownish yellow colour.")

• narrow (ca. 1/5 of bell diameter)
• nematocyst warts, none (Fig. 2X)
• canal roots, 3 per octant (Fig. 2X, 3N)
• canals, broad, next to frenulum, 1, middle, 2–3, next to pedalium, 3–4 (Fig. 2X, 3N)
• very complexly patterned, strongly branched, delicately dendritic ends with rounded, "capi
tate" tips, not anastomosing (Figs. 1E, F, 2X, 3N)

• broad (≥ 1/3 of bell diameter)
• nematocyst warts, many, same sizes and as densely scattered as on exumbrella (Figs. 3K, L, white arrows, 3K)
• canal roots, 3 per octant (Fig. 3K, brackets)
• canals, broad, next to frenulum, 2–3, middle, 2, next to pedalium, 1 (Fig. 3K, red Romanic numbers)
• very complexly patterned, deeply forked, growing close to each other with diverticula mainly at distal ends of canals, not anastomosing (Fig. 3K)

• none (Collins et al., 2011, p. 59: "Velarium broad; numerous canals per octant, growing close to each other with diverticula mainly at distal ends of canals (Fig. 3F). Velarium sprinkled on exumbrellar side with many white nematocyst warts (Fig. 3F)."

Adradial lapps

• none (Fig. 2L)

Perradial lappets

• none (Fig. 2L)

• none (Figs. 1E, F, 2X, 3N)

• none (Collins et al., 2011, p. 59: "...; perradial lappets absent")

Structures of digestive systems

• manubrium, intermediate in length (1/5 of BH) reaching into lower bell half, mouth arms, 4, broad, large nematocyst warts lining perradial folds on mouth tube and lips (Figs. 2B, J)
• stomach, large (1/3 of the bell height), balloon-like (Fig. 2B)
• mesenteries, well developed

• manubrium, long (1/4–1/3 of BH) reaching into lower bell half, mouth arms, 4, broad, nematocyst warts, none (Figs. 2O, V)
• stomach, large (1/2 of the bell height), balloon-like (Fig. 2O)
• mesenteries, well developed

• manubrium, intermediate in length (1/5 of BH) reaching into lower bell half (Fig. 3A, B), mouth arms, 4, broad, large nematocyst warts on mouth lips (Fig. 3H, NW+arrows)
• stomach, large (1/3 of the bell height), balloon-like (Fig. 3A)
• mesenteries, well developed
gastric phacellae, 4, interradial, vertical rows, in the upper 2/3 of stomach, gastric filaments, hundreds, tree-like branched, 1 to 3 branched filaments per single stalk, 1 to 3 branches per filament (Figs. 2B, K)

(Müller, 1859, pp. 5, 8: "The dermatosparic stomach takes up the bottom of the bell; blown up it is more or less spherical and is, due to a narrow, closable area, separated from the very mobile, at the end flared, tetragonal and into 4 lappets split mouth funnel (ISP: manubrium). [...] the mouth funnel [...] itself, in general, does not reach half of the bell height. [...] Alternating with the mouth lappets the stomach wall shows 4 opaque stripes which, observed through a loupe, unravel into groups of extremely numerous, worm-like and slowly worm-like moving filaments of 5–6 mm length and 0.15–0.2 mm width which extend into the stomach cavity. In T. haplonema the stripes stretch in straight, upwards lines along the two upper third of the stomach wall; the filaments are mostly one to two times forked into 2 to 3 long branches, in rare cases more ramified. [...] you find in T. haplonema 4 thin, vertical diaphragms which run from the stomach to the midline of the side pouches and separate the cavity between stomach and bell into 4 chambers. Their dimension varies between individuals; occasionally they nearly reach the marginal bodies (ISP: rhopalia) at the side pouches, at the stomach they might reach the origin of the mouth lappets. [...] stomach etc. partly studded with single, partly with roundish groups of nettle cells which causes a lively burning; ...")

Table 2. continued

| Tamoya haplonema, East Atlantic and adjacent seas | Tamoya sp. West Africa | Tamoya ohboya |
|-----------------------------------------------|------------------------|--------------|
| MZUSP 494, registered and unregistered specimens from the Americas (see Table 1a) (Müller 1859, Mayer 1910, Collins et al. 2011, present study) | 12 registered specimens from West Africa (see Table 1b) (Stiasny 1934, present study) | USNM 1146080 (Holotype); data of specimens listed in Collins et al. 2011 as additional material (Collins et al. (2011), present study) |

‘gastric phacellae, 4, interradial, vertical rows, from top to sphincter of stomach, gastric filaments, hundreds, tree-like branched, 2 to 6 branched filaments per single stalk, 3–6 branches each per filament (Figs. 2W, 3C, D, E) (*Stiasny 1934, p. 340: "...the large wide stomach, the transparent, well-developed, crescent-shaped mesenteries, and the gastric filament arranged in vertical interradial rows along the sides of the stomach. [...] The STOMACH is large and broad. The many filiform unbranched gastric cirri run in long vertical rows along the interradial sides of the stomach. The MESENTERIES are very distinct. They are completely transparent, crescent-shaped and strongly protruding.")"

45°02′40″W) 5–10 m, 21.9°C, 32.8‰, trawl, mud bottom, 31 July 2012, 1 female, 4 male medusae.

**Tamoya ohboya from the Caribbean Sea**

Smithsonian National Museum of Natural History (NMNH), Washington D.C.:  
Holotype (USNM 1146080), sex undetermined, 61 mm BH (bell height; measured from velarial turn-over to top of bell), 29 mm IRW (interradial bell width), collected 30 June 2010 at Divi Flamingo, Bonaire, Netherlands (~12°8.61″N, 68°16.60″W) by W. Gillan and M. Wilhemus (Collins et al. 2011: p. 58).

**Measurements**

Standard measurements were used (Straehler-Pohl 2014, Acevedo et al. 2019): bell height (BH)=length between bell turn-over (velarium excluded from measurement) and top of apex; interpedalial diameter (IPD)=distance between opposite pedalia (outer pedalial wing edges) at the level of the bell turn-over; interrhopalial diameter (IRD)=distance between opposite sense niches; interrhopalial width (IRW)=distance between consecutive rhopalia; pedalia width (PW) and length (PL) were also measured.

Photographs were taken with digital cameras Canon Powershot G12 and Canon Eos 550D. Photos from *Tamoya ohboya* were provided by the courtesy of A. G. Collins, A.
Migotto and Ned Deloach, taken during the study of Collins et al. (2011).

“Gonads” in Cubozoa

The study follows Acevedo et al. (2019) in using the
term gonads to refer to areas where gametes are formed.

Results

The characters listed in Table 2 show distinct differences in the morphological structures of the observed West African Tamoya specimens compared to the American Tamoya haplonema and Tamoya ohboya, resulting in the following diagnosis:

Taxonomy
(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 Lesson, 1843
Family Tamoyidae Haeckel, 1880
Genus Tamoya F. Müller, 1859
Tamoya ancamori sp. nov. (Figs. 1, 2N–X, 3)

Tamoya ancamori sp. nov.

Etymology: Name honors Prof. Dr. André Carrara Morandini (an=André, ea=Carrara, mor=Morandini, masculine suffix “i”) who supported the author over many years with valuable advice and material concerning taxonomic rules, old literature and classical systematic methods.

Synonyms:
Tamoya haplonema: Stiasny 1934: 339–342 (systematic, species description; Figs. 1a–c); Ranson 1949: 123 (systematic species list of collection of Belgian Schoolship “Mercator”), 137 (description of sample localities and specimens); Kramp 1955: 287–288 (sampling locations in West Africa, description of 1 specimen in Copenhagen collection from Sierra Leone, West Africa); Kramp 1959: 15 (description of 3 specimens from Belgian West African expedition from Sierra Leone); Kramp 1961: 307 (synonymy list for Tamoya haplonema)

Tamoya ancamori: present study

Type material:
HOLOTYPE: United Kingdom: Natural History Museum, London (NHM): One (1) specimen, male, (BMNH 338), 67 mm BH, IPD 60 mm, IRD 52 mm, 33 mm PL, 13 mm PW, 0.90 IPD/BH ; R.R.S. ‘Discovery’, Sta. 279, East Atlantic, West Africa, Gulf of Guinea, Gabun (French Congo). Off Cape Lopez, from 8.5 miles N71°E to 15 miles N24°E (between approx. 0.27°27.1’S, 9°04’43.4”E and approx. 0°27’03.1’S, 8°28’49.9”E, according to map in Discovery Reports) of Cape Lopez, large otter trawl, head rope 40 ft long (12.2 m): mesh at cod-end 1 1/4 inch (3.2 cm), 58–67 m, 24.6°, 33.08% (Discovery reports Vol. 1 1929; Stiasny 1934; this study: Fig. 4A–N).

PARATYPES:
United Kingdom: Natural History Museum, London (NHM): Four (4) specimens: female (NHM 339), 74 mm BH, 66 mm IPD, 53 mm IRD, 30 mm PL, 12 mm PW, 0.89 IPD/BH; female (NHM 340), 97 mm BH, 84 mm IPD, 67 mm IRD, PL 45 mm, 17 mm PW, 0.87 IPD/BH; male (NHM 341), 86 mm BH, 77 mm IPD, 64 mm IRD, 30 mm PL, 11 mm PW, 0.90 IPD/BH; female (NHM 342), 77 mm BH, 70 mm IPD, 54 mm IRD, 29 mm PL, 12 mm PW, 0.91 IPD/BH; same sampling data as holotype.

The Netherlands: Naturalis Biodiversity Center, Leiden (NBN): One (1) specimen, male, (NBCN 7066) 100 mm BH, 89 mm IPD, 70 mm IRD, 48 mm PL, 17 mm PW, 0.89 IPD/BH; same sampling data as holotype.

Additional material:
Belgium: Royal Belgian Institute of Natural History, Brussels (RBINS):
Two (2) specimens (I.G. 16808): 1) Atlantique Sud, St. 153, West Africa, 11 miles North of Port Gentil (00°33’S, 08°50’E), 1 female (BH: 90 mm, IPD: 78 mm, IPD/BH=0.87), 15.03.1949, ident. P.L. Kramp, 1950. 2) Atlan-

Fig. 2. Comparison of morphological structures of Tamoya haplonema (A–M) from the Americas (Western Atlantic) with structures of the Tamoya ancamori population (N–X) from Western Africa (Eastern Atlantic): Tamoya haplonema: A: Habitus with scale; B: Dissected habitus, note stomach (black bracket, st: stomach) and gastric phacellae (white bracket, gp: gastric phacellae); C: Rhopalial niche, note niche cavity bays above upper covering scale which can be mistaken as rhopalial horns; D: Rhopalial window (subumbrella view of rhopalial niche), note high bays of niche cavity and irregularly jagged margin of cavity; E: Pedalium, note nematocyst warts covering outer wing, no nematocyst warts on inner wing (white dotted line marks inner wing margin); F: Pedalial canal knee bend (lateral view), note nearly 90°-angle of knee bend without appendage; G: Pedalial canal knee bend (dorsal view); H: Tentacle structure, brownish variation; I: Tentacle structure, colourfully striped variation; J: Manubrium, note nematocyst warts (NW) lining midline furrow of mouth arms; K: Gastric phacellae, note multi-branched, brush-like structure of gastric filaments; L: Octant of velarium (f: frenulum, pb: pedalial base), note nematocyst warts (NW), velarial canal roots (brackets I–III) and velarial canal numbers per root (I–III); Tamoya ancamori: N: Habitus with scale (paratype NHM 340, male); M: Dissected habitus (paratype NHM 340), note stomach (black bracket, st: stomach) and gastric phacellae (white bracket, gp: gastric phacellae); P: Rhopalial window (paratype NHM 340), note niche cavity bays above upper covering scale which can be mistaken as rhopalial horns; Q: Rhopalial window (subumbrella view of rhopalial niche; holotype NHM 338, male), note high bays of niche cavity and irregularly jagged margin of cavity; R: Pedalium (paratype NHM 340), note lacking warts on outer and inner wing; S: Pedalial canal knee bend (lateral view; paratype RMNH 7066, male), note thorn-like appendage of knee bend; T: Pedalial canal knee bend (dorsal view; paratype NHM 341, female); U: Tentacle structure (paratype NHM 339, female), note filiform (round diameter) structure; V: Manubrium (holotype NHM 338), note that nematocyst warts are lacking; W: Gastric phacellae (paratype RMNH 7066), note multi-branchied structure with short stem and very long filaments of gastric filaments; X: Octant of velarium (paratype RMNH 7066), note lack of nematocyst warts, velarial canal roots (brackets I–III) and velarial canal numbers per root (I–III), (f: frenulum, pb: pedalial base).
tique Sud, St. 142, West Africa, 29 miles South of Cape Lopez, 11 miles North of Port Gentil (01°07′S, 08°38′E), 1 male (BH: 67 mm, IPD: 58 mm, IPD/BH=0.87), 09.03.1949, ident. P.L. Kramp, 1950.

One (1) specimen (I.G. 11.553), 14th Cruise of "Mercator", West Africa, 8–10 miles of the coast of Sierra Leone (07°05′N, 12°W), 1 immature (BH: 40 mm, IPD: 40 mm, IPD/BH=1.00), 15.01.1938, ident. P.L. Kramp, 03.05.1950.

Two (2) specimen (I.G. 10910): 1) Cruise of “Mercator” 1935–1936, West Africa, Senegambia, in front of Gambia, (13°25′N, 16°50′W), 1 immature, gonads beginning to show (BH: 34 mm, IPD: 35, IPD/BH=0.97), 15.11.1935, ident. Dr. G. Ranson, 1944. 2) Cruise of “Mercator” 1935–1936, West Africa, French Guinea, South of Kassa (Iles of Los), 1 immature (BH: 48 mm, IPD: 43 mm, IPD/ BH=0.90), 23.11.1935, ident. Dr. G. Ranson, 1945.

Denmark: Natural History Museum of Denmark, Copenhagen (NHMD):

One (1) specimen, 1 male, (NHMD 642567) (BH: 70 mm, IPD: 63, IPD/BH=0.90), Atlandide, St. 141, West Africa, Sierra Leone, off Freetown, 09.04.1946, ident. P.L. Kramp, 01.12.1946.

Type locality: West Africa, Gulf of Guinea, Gabon (French Congo), Off Cape Lopez (between approx. 0°27′27.1″S, 9°04′43.4″E and approx. 0°27′03.1″S, 8°28′49.9″E, according to map in Discovery Reports) (Stiasny 1934; present study)

Diagnosis:
Tamoyidae species with triangular knee bend with upwards-turned thorn-like appendage, no nematocyst warts on manubrium and velarium and 3 velarial canal roots/oc- tant with increasing number of strongly branched velarial canals from frenulum to pedalium (1/2–3/3–4).

Description:
Mature medusa: (preserved specimen)
Bell, transparent, tentacles, light pink to flesh coloured, gonads, opaque brown-orange to flesh-coloured (Figs. 1A, 2N, 4A).

Bell, pyramidal with rounded edges, higher than wide (Figs. 1A, 2N, 4A), up to 100 mm (BH), up to 89 mm (IPD), sturdy, shallow interradial furrows, densely scat-

Fig. 3. Morphological structures of Tamoya ohboya (A–K) (images A–C, E, H, I after Collins et al. 2011): A: A: Holotype (USNM 1146080); B: adult medusa (photo by N. Deloach); C: sense niche with frown-like opening–note the black structures that resemble rhopalial horns but are not as these structures are parts of the sense niche cavity; D: pedalium (photo by N. Deloach); E: sharply edged knee bend of pedalial canal without any appendage but with a curved edge due to preservation artefact (lateral view); F: pedalial knee bend (dorsal view; photo provided by A. G. Collins); G: tentacle structure, note strongly striped pattern (photo by N. Deloach); H: balloon-like stomach with manubrium, note vertical gastric phacellae (GP) and nematocyst warts (NW) on manubrium; I: gastric phacellae (arrows, bracket) lining vertically the stomach corner; J: Gastric filaments – note the brush-like structure; K: quadrant of velarium with velarial canals, note 3 velarial roots (brackets, I–III) with decreasing number of velarial canals from frenulum (f) to pedalium (pd), note also nematocyst warts on velarial canals (NW) (photo provided by A. G. Collins); L: enhanced nematocyst warts on velarial canals.
tered with large, prominent, colourless nematocyst warts (Fig. 4B, F) from apex to pedial base level or to bell margin, velarium free of nematocyst warts (Figs. 1F, 2X, 4N); apex, mesoglea slightly thicker than bell walls, slightly arched, no horizontal constriction near top.

Rhopalial niches (Figs. 1C, 2P, 4G), 4, cavity, heart shaped (Figs. 2Q, 4H), with two upwards turned bays that can be mistaken as rhopalial horns (Figs. 1C, 2P, G, 4G, H), no rhopalial horns, rhopalial window also heart-shaped (Figs. 2Q, 4H) with irregularly frayed lower end, orifice, slit-like to frown-shaped, upper covering scale, 1, rounded convex, lower covering scale, 1, rounded convex, ca. 1/8 of bell height up from margin; rhopalium with 6 eyes (2 major with lenses + 2 lateral slit eyes + 2 lateral pit eyes).

Pedalia (Figs. 2R, 4I), 3 to 6 branches per filament (Fig. 4D); gastric filaments (Figs. 2W, 4D, E), hundreds per row, lining stomach walls from top to sphincter (Figs. 1B, 2O), balloon-like, large (1/2 of BH in length); mesenteries well developed; gastric phacellae, 4, interradial, vertical rows, lining stomach walls from top to sphincter (Figs. 1B, 2O, 4C), gastric filaments (Figs. 2W, 4D, E), hundreds per quadrant, short-stemmed with very long branches, multiple rooted: 2 to 6 branched filaments per single stalk (Figs. 2W, 4E), 3 to 6 branches per filament (Fig. 4D); gastric pockets, 4, leading into velarial canals.

Gonads, 4 pairs, thin tissue, spearhead-shaped, (Figs. 2N, O, 4B), covering entire area of gastric pouches in upper half, tapering in upper third and in lower half towards rhopalial niche level, flaring again below rhopalial niche level, smooth edges, from stomach corner to bell margin, separated by perforated, interradial septum. Sexes, separated but unimorph.

Nematocysts: no data due to lack of availability of an appropriate microscope at the museums.

Stinging: no data.

Mating behaviour, brooding behaviour, polyp, asexual reproduction, newly detached medusa: No data.

Distribution (Fig. 5, green area)

West Africa:

Sierra Leone, Off Freetown (Atlantide Station 141) (Brun 1950, Kramp 1955)

Off Sierra Leone (7°05′N, 12°00′W) (Kramp 1959)

Guinea, South of Kassa Island (Île de Los) (Ranson 1949)

Gulf of Guinea, Gabon (French Congo), Off Cape Lopez ('Discovery', Sta. 279) (Discovery Commitee 1929, Stanney 1934); 29 miles South of Cape Lopez (1°07′S, 8°38′E), 11 miles North of Port Gentil near Cape Lopez (0°33′S, 8°50′E) (Kramp 1959)

The Gambia (13°25′N, 16°50′W) (Ranson 1949)

Southern Africa: Namibia, Bay of Lüderitz (Ranson 1949)

Discussion

The family Tamoyidae represents a monogenic family containing the sole genus Tamoya. At present there are considered two valid species of Tamoya (T. haplonema, T. ohboya), and three doubtful species (T. bursaria, T. prismaticata, T. haeckeli). Tamoya haplonema was the first species of the genus described and is therefore the type species.

Differential diagnosis: Tamoya haplonema and Tamoya ohboya from the Americas vs. “Tamoya haplonema” (Tamoya ancamorii n. sp.) from West Africa (Table 2):

Tamoya haplonema is one of the few cubozoan species that has never been re-named. Its identity was based on the unmistakably horizontally aligned gastric filaments (Müller 1859, Haeckel 1880, Kramp 1961, Southcott 1967; Figs. 2B, K) which also defines the identity of its genus (Haeckel 1880, Kramp 1961, Southcott 1967, Bentlage et al. 2010, Collins et al. 2011, Strachler-Pohl 2019), confirmed since Collins et al. (2011) described a new Tamoya species from Bonaire in the Caribbean Sea, Tamoya ohboya. Combined with the horizontally aligned gastric phacellae, the genus possesses a cylindrical to pyramidal bell densely scattered with large, raised nematocyst warts (Figs. 2A, 3B), and a rhopalial niche with a slit to frown-shaped horizontal opening but without rhopalial horns (Bentlage et al. 2010, Collins et al. 2011, Strachler-Pohl 2019; present study:
Figs. 2C, 3C) which are characteristic for the family Ca-
rukiidae (Bentlage et al. 2010, Bentlage & Lewis 2012). In
T. haplonema and T. ohboya the pedalia are leaf- to scal-
pel-shaped (Müller 1859, Mayer 1910, Collins et al. 2011,
Straehler-Pohl 2019) and possess a pedalial canal that is
characteristically broadly flared at its distal end (Straehler-
Pohl 2019; Figs. 2E, 3D) merging with broad, flat tentacles which resemble horizontally ribbed ribbons (Figs. 2H, I, 3D, G). Its velarium is broad and contains 3 velarial canal roots per octant, which split into 1 to 4 broad, complexly branched canals per root (Straehler-Pohl 2019; Fig. 2L). Most of these main characters were also found in "Tamoya haplonema" from West Africa. Differences can only be found if focusing on the details of these characters.

The bells of the American, or true, T. haplonema and the Caribbean T. ohboya are more cylindrical shaped than pyramidal (Figs 2A, 3A, B) with an IPD/BH ratio of about 0.70 (T. haplonema: mean: 0.72, SD: 0.059, n=39; T. ohboya: mean: 0.71, SD: 0.016, n=2: Collins et al. 2011: Figs. 1A, D) while the African Tamoya specimens show a body shape that is more pyramidal (Figs. 2N, 4A) with an IPD/BH ratio of about 0.90 (mean: 0.89, SD: 0.014, n=12).

The pedialal canals of T. haplonema (Straehler-Pohl 2019; present study: Fig. 2E) and T. ohboya (Collins et al. 2011: Fig. 3B; present study: Fig. 3D) are broad at knee bend level, taper towards midsection and flare again broadly towards the distal end, while the width of the pedialal canal of the mistakenly-identified African specimens is nearly equally broad throughout the pedialum only flaring slightly at the distal end (Figs. 2R, 4I). The pedialal knee bend of T. haplonema is square with an angle of nearly 90° without an appendage (Figs. 2F, G), the one of T. ohboya is sharply edged with an upwards curved keel (Fig. 3E), described as a "prominent spike" by Collins et al. (2011) but which seems not to be a spike but rather a preservation artefact due to the pedialum not being straight, upon close inspection of Fig. 3F. The shape of the pedialal knee bend of the African Tamoya specimens is triangular with an appended peak, resembling an upwards bent horn (Figs. 2S, T, 4J, K). The tentacles of the African specimens are round in cross section (filiform) below the flattened base part (Figs. 2U, 4L) and not flattened throughout the tentacle length like in T. haplonema from Brazil and T. ohboya from the Caribbean. However, the filiform tentacle structure might be a preservation artefact as Collins et al. (2011) states they observed this artefact in preserved T. ohboya medusae (Collins et al. 2011: Fig. 3A; present study: Fig. 3A) because photos of living animals of T. ohboya show a flattened structure in the extended tentacles (Collins et al. 2011: Fig. 1; present study: Figs. 3B, G, 5).

The rhopalial niche opening of all Tamoya species is framed by two covering scales that give the opening a slit to frown-like appearance. The difference between the species from the Americas (T. haplonema) and the specimens from West Africa (Tamoya ancarnori n. sp.) is the shape of the lower covering scale, which is softly rounded in the West African material (Fig. 2P, 4G) while it shows a ridge at the midline in the material from the Americas, giving it a three-dimensional pyramidal form (Collins et al. 2011: Fig. 3E; present study: Figs. 2C, 3C). The cavity is heart-shaped (Fig. 2Q) with irregularly shaped windows in all species (Figs. 2D, Q, 3C, 4H; Collins et al. 2011: Fig. 3E), more pronounced in T. haplonema.

The stomach of all species is balloon-like and large, ca. 1/3 of the bell height in length in T. haplonema from Brazil and the Caribbean T. ohboya (Müller 1859, Collins et al. 2011: Fig. 1D; present study: Figs. 2B, 3H) and slightly larger at ca. 1/2 of the bell height in length in the African Tamoya specimens (Fig. 2O). The stomach is supported by well-developed mesenteries in all species and specimens with no obvious differences. Inside the stomach, vertical gastric phacellae line the interradii, consisting of rows of hundreds of branched gastric filaments per phacella. The filaments consist of single stems that branch either brush-like (T. haplonema: Müller 1859, T. ohboya: Collins et al. 2011: Fig. 3K; present study: Figs. 2K, 3J) or tree-like in the African specimens (Figs. 2W, 4D, E) into different numbers of filaments per species (see Table 2).

The gonads in both the American species are sheet-like pairs that cover the whole area of the gastric pouches from stomach to velarium, the edges are multiply folded (Müller 1859, Collins et al. 2011; Figs. 2A, B) while the gonads in the African specimens are slim, spear-head shaped and with smooth edges (Figs. 2N, O, 4B) that leave open a large space around the rhopalial niche.

The manubrium of all species and specimens is large and the mouth arms square, but in T. haplonema and T. ohboya from the Americas the mouth arms bear large nematocyst warts (Müller 1859, Collins et al. 2011: Fig. 3C, Straehler-Pohl 2019; present study: Figs. 2J, 3H), while the mouth arms in the African population are free of nematocyst warts (Figs. 2V, 4M) — this is not regarded as a preservation artefact or due to them being rubbed-off due to rough handling, as the more exposed warts on the outside of the bells of the African specimens are at least in most parts still present. The same can be noticed on the velarium — the American species show numerous nematocyst warts on the exumbrellar side of the velarium (Müller 2019).
Fig. 5. Distribution of Tamoya populations: Tamoya haplonema roams the Western Atlantic and adjacent Caribbean Sea from Argentina to North Carolina while Tamoya ancamori roams the Eastern Atlantic along the coasts from Sierra Leone to Namibia. Blue spots mark type location.

1859, Mayer 1910, Collins et al. 2011: Fig. 3F, Strachler-Pohl 2019; Figs. 2L, M, 3K, L) while the velarium of the African species is free of nematocyst warts (Figs. 1F, 2X, 4N).

The most obvious difference next to body size, pedalial canal knee bend and lacking nematocyst warts on the manubrium and velarium are the number and arrangement of velarial canals per octant. The velarial canal system of the
American *T. haplonema* and *T. ohboya* consist of 3 velarial canal roots per octant (Figs. 2L, 3K: brackets I–III) and 1 to 3 velarial canals per root. The African specimens also possess 3 velarial canal roots (Figs. 2X, 4N: brackets I–III) but the number of velarial canals per root in the African specimens increases from frenulum towards the base of the pedalium (Figs. 2X, 3N: root I: 1 canal; root II: 2–3 canals; root III: 3–4 canals) while the canals in the American *T. haplonema* and *T. ohboya* decrease in number per root from frenulum towards the base of the pedalium (Figs. 2L, 3K: root I: 3 canals; root II: 2 canals; root III: 1 canal).

**Differences between Tamoya haplonema and Tamoya ohboya:**

The differences between the American *Tamoya* species, *T. haplonema* and *T. ohboya*, are so marginal (Table 2; Collins et al. 2011, Straehler-Pohl 2019) that the validity of the latter is questionable (Straehler-Pohl 2019), without an additional molecular analysis to clarify their relationship.

**Identification of the West African Tamoya population:**

Based on above listed differences in morphological characters, it can be concluded that the African population is a member of the genus *Tamoya* but belongs not to the American species *Tamoya haplonema*, but instead represents a new species, *Tamoya ancamori* n. sp.

**Acknowledgements**

I would like to first thank Prof. Dr. André Carrara Morandini. Without the knowledge that he provided concerning detailed morphological comparisons and his invitation to join a project to observe the Brazilian cubozoan species, including *Tamoya haplonema*, this study would not have been possible and perhaps this species would never have been noted as different from the other *Tamoya* species. I would also like to thank Miranda Lowe (Principal Curator and Collections Manager, The Natural History Museum, London) who made my first visit to the museum possible after short notice, her friendly welcome and her help in all matters concerning the collection during all three visits in 2015, 2016 and 2017. Additionally, I would like to thank Dr. Martin Vinter Sorensen (Curator of the Invertebrate collection of the Zoological Museum of the University of Copenhagen) who gave me access to the collection and his facilities during my visits in 2015, 2016 and 2017 and connected me to the museum in Brussels. Gratitude is also due to his Collection Manager, Laura Pavesi, who was of great help during my research and who gave me the information concerning the SYNTHESYS projects of the European Commission. A also owe a lot of gratitude to Dr. Yves Samin (Curator of the RBINS Museum of Brussels, Belgium), Dr. Leen van Ov Vegen (senior researcher) and Koos van Egmond (Curator of the Naturalis Museum in Leiden, The Netherlands) for giving me access to their collections and help during my stays. Additionally, I am grateful to Prof. Dr. Alvaro Esteves Migotto (Lecturer and zoologist at CEBIMar, University of S o Paulo), Dr. Allen G. Collins (Zoologist at the National Systematics Lab of NOAA’s National Marine Fisheries Service & National Museum of Natural History, Smithsonian Institution) and Ned DeLoach (photographer) for providing me with images of *Tamoya ohboya* (courtesy also to Zootaxa: Collins et al. 2011).

And last but not least, many thanks to two anonymous reviewers for constructive suggestions.

I was supported by the SYNTHESYS Projects (DK-TAF-5580, GB-TAF-6151, GB-TAF-7146) http://www.syntheses.info/ which are financed by a European Community Research Infrastructure Action under the FP7 Integrating Activities Programme.

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