**Abstract:** A new hydromedusa belonging to the order Anthoathecata is reported from Sagami Bay, eastern Japan. *Tiaricodon orientalis* sp. nov. can be distinguished from other *Tiaricodon* species by the umbrella size of the medusa, manubrium length, interradial peaks in the subumbrella, and a red band on the upper part of the manubrium. A comparative table of the primary diagnostic characters of the genus is provided. Our morphological and molecular phylogenetic analyses suggest that *Tiaricodon* from China is not *Tiaricodon coeruleus* but *Tiaricodon orientalis*.

**Key words:** distribution, *Halimedusa typus*, medusa, *Tiaricodon coeruleus*, *Urashimea globosa*

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**Introduction**

The family Halimedusidae currently comprises three species in three monotypic genera, *Halimedusa*, *Tiaricodon*, and *Urashimea* (Mills 2000, Bouillon et al. 2006). The Halimedusidae are characterized as follows: medusa usually with a low gastric peduncle and with distinct subumbrellar pockets in jelly above the manubrium base; manubrium cruciform with basal perradial lobes; mouth quadratic to cruciform with lips lined by nematocysts; four radial canals; either with four perradial marginal tentacles or four perradial marginal tentacles and four interradial groups of tentacles, all hollow; gonads either on manubrium or on manubrium and perradial lobes; no mesenteries; marginal bulbs cylindrical with abaxial ocelli (after Bouillon et al. 2006).

The monotypic genus *Tiaricodon* comprises *Tiaricodon coeruleus* Browne, 1902 (Mills 2000). The species was described by Browne (1902) from the Falkland Islands. Browne (1902) classified *Tiaricodon* in the family Tiariidae, however, Mayer (1910) moved it to the family Codonidae Haeckel, 1879, a synonym of Corynidae Johnston, 1836. Browne and Kramp (1939) then removed *Tiaricodon* to the family Moerisiidae in the order Limnomedusae. Petersen (1990) replaced *Tiaricodon* into the Anthomedusae but reclassified the genus into the family Polyorchidae. However, recent morphological comparisons have suggested that *Tiaricodon* is a genus in the family Halimedusidae (Mills 2000).

To date, only one described Halimedusidae species, *Urashimea globosa* Kishinouye, 1910, has been reported from Japanese waters (Kubota & Gravili 2007). In this study, 31 specimens of an unidentified Halimedusidae species were collected from Sagami Bay, eastern Japan. Our morphological and molecular phylogenetic analyses suggest that this Halimedusidae species should be regarded as a new species within the genus *Tiaricodon*.

**Materials and Methods**

**Collection and fixing**

Thirty one medusae of Halimedusidae specimens were collected from near the water surface (within about 1 m) at Chigoga-fuchi and Shonan Fishing Port, Enoshima, Kanagawa Prefecture, eastern Japan (Fig. 1) between 1 May 2018 and 6 April 2020. The medusae were captured with a dip net (mesh size about 0.5 mm). Additionally, specimens of *Urashimea globosa* collected from Tokoro Fishing Port, Tokoro, Hokkaido were used in the molecular phylogenetic analyses (Table 1). Three specimens
were fixed in 3% formalin seawater and deposited in the National Museum of Nature and Science, Tsukuba Japan (NSMT). Two specimens were preserved in 99.5% ethanol for molecular analysis.

**Morphological investigation**

Taxonomic observations and measurements were conducted on both live and preserved specimens. Measurements were made with ImageJ software (NIH, USA) to the nearest 0.01 mm. For nematocyst identification in the medusae, squashes prepared from fresh tissues were examined under a compound microscope (ECLIPSE Ci, Nikon, Japan). Nematocysts were identified according to Mills (2000) and Östman (2000). For determination of the abundance of nematocyst types in the medusae, 50 nematocysts were identified, measured, and counted from the specimens. Measurements were made using Image J (NIH, USA) to the nearest 0.1 \( \mu \)m.

**Molecular phylogenetic analysis**

Near-complete sequences of the nuclear 16S rDNA gene (approximately 600 bp) were used for molecular phylogenetic analyses. Genomic DNA was extracted from the ethanol-preserved tissue of cultured specimens using the DNeasy Blood and Tissue Kit (QIAGEN, Germany) according to the manufacturer’s instructions. 16S rDNA was PCR amplified and sequenced using the primers and protocols outlined in Cunningham and Buss (1993) and Collins et al. (2008). The new sequences were aligned using MEGA 6.06 software with built-in ClustalW (Tamura et al. 2013). Phylogenetic analysis and pairwise distance measurements were determined using the maximum likelihood method with 1000 bootstrap replications in MEGA6. All sequences have been deposited in DDBJ under accession numbers LC605990-LC605993 (Table 1).

**Results**

**Phylum Cnidaria Verrill, 1865**  
**Subphylum Medusozoa Petersen, 1979**  
**Class Hydrozoa Owen, 1843**  
**Subclass Hydroidolina Collins, 2000**  
**Order Anthothecata Cornelius, 1992**  
**Suborder Capitata Kühn, 1913**  
**Family Halimedusidae Arai & Brinckmann-Voss, 1980**  
**Genus Tiaricodon Browne, 1902**  
**Tiaricodon orientalis sp. n.**  
Figs. 2–5  
New Japanese name. Wataboshi-kurage

Material examined. Holotype: NSMT-Co 1739 Enoshima, Fujisawa, Kanagawa Prefecture, eastern Japan; 35°17′52.4″N 139°28′32.2″E; May 1, 2018; collector: Gaku

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**Table 1.** Taxa included in the phylogenetic analyses and GenBank accession numbers for the sequences. a) He et al. (unpublished); b) Nawrocki et al. (2010); c) Collins et al. (2008); d) Schuchert (unpublished); and e) Zheng et al. (2014).

| Species                  | Accession No. | Locality (Origin)       | Reference |
|--------------------------|---------------|-------------------------|-----------|
| *Moerisia inkermanica*   | KF962500      | China                   | a         |
| *Moerisia inkermanica*   | KF962501      | China                   | a         |
| *Odessia maeotica*       | GQ395324      | France: Portiragnes     | b         |
| *Polyorchis haplus*      | AY512549      | USA: San Francisco Bay  | c         |
| *Polyorchis penicillatus*| KX355411      | USA: Friday Harbour     | d         |
| *Sphaerocoryne agassizii*| MF538730      | USA: Friday Harbour     | d         |
| *Sphaerocoryne bedoti*   | GQ395322      | Panama                  | b         |
| *Tiaricodon coerules*    | JQ715981      | China: Xiamen Bay       | e         |
| *Tiaricodon coerules*    | JQ715982      | China: Xiamen Bay       | e         |
| *Tiaricodon coerules*    | JQ715983      | China: Xiamen Bay       | e         |
| *Tiaricodon coerules*    | JQ715984      | China: Xiamen Bay       | e         |
| *Tiaricodon coerules*    | JQ715985      | China: Xiamen Bay       | e         |
| *Tiaricodon coerules*    | JQ715986      | China: Xiamen Bay       | e         |
| *Tiaricodon coerules*    | JQ715987      | China: Xiamen Bay       | e         |
| *Tiaricodon orientalis*  | LC605990      | Japan: Enoshima, Fujisawa, Kanagawa | This study |
| *Tiaricodon orientalis*  | LC605991      | Japan: Enoshima, Fujisawa, Kanagawa | This study |
| *Urashimea globosa*      | LC605992      | Japan: Tokoro Fishing Port, Kitami, Hokkaido | This study |
| *Urashimea globosa*      | LC605993      | Japan: Tokoro Fishing Port, Kitami, Hokkaido | This study |
Yamamoto. Paratypes: MSMT-Co 1740 and MSMT-Co 1741. Locality as for holotype, May 1, 2018 and March 13, 2020; collector: Gaku Yamamoto.

**Description.** Mature medusae umbrella bell-shaped (Fig. 2A–C), 9.8 mm high and 8.2 mm in diameter (Table 2). Umbrella apex rounded and mesoglea thickened (Fig. 2A). Exumbrella smooth and nematocysts sparsely scattered (Fig. 2A, B). Stomach with short, basal, sac-like per-radial lobes (Fig. 3A). Peduncle very short and indistinct (Fig. 3A, B). Gonads surrounding the base of the stomach and extending over peduncle along the four per-radial lobes (Fig. 3A). Red to dark red band present on the proximal part of manubrium (Fig. 3A). Manubrium hanging in the umbrella cavity, rectangular bottom, light brown or translucent (Fig. 3A). Gonad-free portion of manubrium length about 0.9 mm, same length as gonad, not extended beyond umbrella margin (Fig. 2A). Mouth cruciform, with four frilled lips (Fig. 3D). Four triangular interradial subumbrellar pockets bulging upward into the mesoglea between radial canals, rising up above the level of the radial canals (Fig. 2A, 3A). Four radial canals and a circular canal (Fig. 3B, E). Velum narrow (Fig. 3E). Tentacular bulbs swollen, each with a dark brown abaxial ocellus (Fig. 3C). Tentacles four, moniliform, tapering to a point, length about twice umbrella height (Fig. 3F).

The smallest young medusa had a UH of 0.8 mm, UD of 0.9 mm (Fig. 4A). Mesoglea on apex of the exumbrella was thinner than that of adults. With few exumbrellar nematocysts. Manubrium short and thin, translucent to whitish, length about half of umbrella height. Red spots or bands absent on the proximal part of manubrium. Mouth simple and circular. Four radial canals and a circular canal. Subumbrellar pockets absent. Velum narrow. Tentacular bulbs swollen, each with a dark brown abaxial ocellus. Tentacles four, cateniform, with about thirty annulate, white nematocyst batteries.

The second-smallest medusa had UH 2.2 mm, UD 2.1 mm (Fig. 4B). Mesoglea thickened and umbrella ovoid

| Specimen No. | UH (mm) | UD (mm) | Sex  | Sampling site            | Date      | Lat. Long.       |
|--------------|---------|---------|------|--------------------------|-----------|------------------|
| NSMT-Co 1739*| 9.8     | 8.2     | Female | Enoshima, Fujisawa, Kanagawa, Japan | 2018/5/1  | 35°17′52.4″N, 139°28′32.2″E |
| NSMT-Co 1740 | 5.7     | 5.3     | Male  | Enoshima, Fujisawa, Kanagawa, Japan | 2018/5/1  |                  |
| NSMT-Co 1741 | 3.2     | 3.0     | Female | Enoshima, Fujisawa, Kanagawa, Japan | 2020/3/13 | 139°28′32.2″E |

**Fig. 2.** Preserved mature medusae of *Tiaricodon orientalis* sp.: A) lateral, B) apical, and C) oral views. Scale bar represents 2 mm.
in shape (Fig. 4B). Manubrium short and thin gonad surrounding base of stomach. Red band present on proximal part of manubrium. Four interradial peaks present in mesoglea between radial canals.

The third-smallest medusa had UH 3.2 mm, UD 3.0 mm (Fig. 4C). Mesoglea more thickened. Red band clearer and four interradial peaks became blade-shaped.

**Cnidome.** Two different nematocyst types were identified and measured in the adult medusae (Table 3, Fig. 5A, B). Stenoteles were found on all parts. Desmonemes were found on both tentacular bulbs and tentacles.

**Molecular phylogenetics.** In the resulting maximum likelihood tree (Fig. 6), four major monophyletic clades were formed in the suborder Capitata: 1) *Tiaricodon* spp.;
Table 3. Cnidomes of *Tiaricodon orientalis* sp. nov.. D, L represent capsule diameter and length, respectively, in µm.

| Part       | Type     | Min | Max   | Mean  | SD    | N  |
|------------|----------|-----|-------|-------|-------|----|
| Tentacle bulb | Desmoneme | 1.39| 2.97  | 2.29  | 0.53  | 10 |
|            |          | 7.26| 10.41 | 8.93  | 1.18  | 10 |
| Stenotele  |          | 6.66| 9.17  | 7.72  | 0.79  | 10 |
|            |          | 8.36| 11.60 | 10.19 | 1.14  | 10 |
| Tentacle   | Desmoneme | 6.92| 7.53  | 7.23  | 0.22  | 10 |
|            |          | 16.26| 17.50 | 16.90 | 0.57  | 10 |
| Stenotele  |          | 10.60| 11.25 | 10.86 | 0.32  | 10 |
|            |          | 14.34| 15.10 | 15.01 | 0.17  | 10 |
| Mouth      | Stenotele | 9.17| 10.83 | 9.96  | 0.49  | 10 |
|            |          | 10.07| 12.50 | 11.27 | 0.71  | 10 |

Fig. 5. Nematocysts of *Tiaricodon orientalis* sp. nov.: A) stenoteles, B) desmonemes. Scale bars represent 10 µm.

Fig. 6. Maximum likelihood tree for eight anthomedusan taxa based on the nuclear 16S rDNA data set. Scale bar indicates branch length in substitutions per site. Nodal support values are presented as the ML bootstrap value; only values >50% are shown.
Table 4. Pairwise genetic distances (K2P) based on 440 positions of 16S sequences among Anthomedusae. The analysis involved 16 sequences.

| No. | No. 1 | No. 2 | No. 3 | No. 4 | No. 5 | No. 6 | No. 7 | No. 8 | No. 9 | No. 10 | No. 11 | No. 12 | No. 13 | No. 14 | No. 15 | No. 16 | No. 17 |
|-----|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1   | Tiaricodon orientalis sp. nov. LC605990 | 0.000 |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| 2   | Tiaricodon orientalis sp. nov. LC605991 |       | 0.004 | 0.004 |       |       |       |       |       |       |       |       |       |       |       |       |
| 3   | Tiaricodon coeruleus JQ715981           |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| 4   | Tiaricodon coeruleus JQ715982           |       |       |       | 0.004 | 0.004 | 0.000 |       |       |       |       |       |       |       |       |       |       |
| 5   | Tiaricodon coeruleus JQ715983           |       |       |       | 0.006 | 0.006 | 0.002 | 0.002 |       |       |       |       |       |       |       |       |       |
| 6   | Tiaricodon coeruleus JQ715984           |       |       |       | 0.004 | 0.004 | 0.000 | 0.000 | 0.002 |       |       |       |       |       |       |       |       |
| 7   | Tiaricodon coeruleus JQ715985           |       |       |       | 0.006 | 0.006 | 0.002 | 0.002 | 0.002 | 0.000 |       |       |       |       |       |       |       |
| 8   | Tiaricodon coeruleus JQ715986           |       |       |       | 0.004 | 0.004 | 0.000 | 0.000 | 0.002 | 0.000 | 0.002 | 0.000 |       |       |       |       |       |
| 9   | Tiaricodon coeruleus JQ715987           |       |       |       | 0.004 | 0.004 | 0.000 | 0.000 | 0.002 | 0.000 | 0.002 | 0.000 |       |       |       |       |       |
| 10  | Urashimea globosa LC605992              | 0.093 | 0.093 | 0.093 | 0.093 | 0.093 | 0.095 | 0.095 | 0.093 | 0.093 | 0.093 | 0.093 |       |       |       |       |       |
| 11  | Urashimea globosa LC605993              | 0.093 | 0.093 | 0.093 | 0.093 | 0.093 | 0.095 | 0.095 | 0.093 | 0.093 | 0.093 | 0.093 | 0.093 |       |       |       |       |
| 12  | Moerisia inkermanica KF962500           | 0.129 | 0.129 | 0.124 | 0.124 | 0.127 | 0.127 | 0.127 | 0.124 | 0.124 | 0.124 | 0.120 | 0.120 | 0.120 | 0.120 | 0.120 | 0.120 |
| 13  | Moerisia inkermanica KF962501           | 0.129 | 0.129 | 0.124 | 0.124 | 0.127 | 0.127 | 0.127 | 0.124 | 0.124 | 0.124 | 0.120 | 0.120 | 0.120 | 0.120 | 0.120 | 0.120 |
| 14  | Odessia maeotica GQ395324               | 0.148 | 0.148 | 0.153 | 0.153 | 0.156 | 0.156 | 0.156 | 0.153 | 0.153 | 0.153 | 0.169 | 0.169 | 0.168 | 0.168 | 0.168 | 0.168 |
| 15  | Polyorchis haplus AY512549              | 0.234 | 0.234 | 0.232 | 0.232 | 0.234 | 0.234 | 0.234 | 0.232 | 0.232 | 0.232 | 0.220 | 0.220 | 0.250 | 0.250 | 0.250 | 0.270 |
| 16  | Polyorchis penicillatus KX355412        | 0.228 | 0.228 | 0.231 | 0.231 | 0.234 | 0.234 | 0.231 | 0.231 | 0.231 | 0.218 | 0.218 | 0.218 | 0.258 | 0.258 | 0.276 | 0.050 |
| 17  | Sphaerocoryne agassizii MF538730        | 0.215 | 0.215 | 0.218 | 0.218 | 0.221 | 0.221 | 0.218 | 0.218 | 0.218 | 0.218 | 0.218 | 0.218 | 0.221 | 0.221 | 0.250 | 0.217 |
| 18  | Sphaerocoryne bedoti GQ395322           | 0.192 | 0.192 | 0.192 | 0.192 | 0.192 | 0.192 | 0.192 | 0.192 | 0.192 | 0.184 | 0.184 | 0.195 | 0.195 | 0.245 | 0.212 | 0.209 | 0.090 |
2) *Urashimea globosa*; 3) *Moerisia inkermanica*; and 4) *Odessa maeotica*. The monophyly of Halimedusidae, including clades 1 and 2, was evident in the 16S phylogenetic tree with high bootstrap values (99%), supporting the validity of the family. The Kimura 2-parameter distance between *Tiaricodon orientalis* sp. nov. and "*T. coerulesus" (see Discussion) from China was 0.005–0.007, which is considered to represent intraspecific variability (Zheng et al. 2014, Lindsay et al. 2015, Schuchert 2005, 2018, Table 4).

**Habitat and ecology.** Medusae of *Tiaricodon orientalis* sp. nov. appeared in shallow waters (5 to 10 m depth) during April and May in a range of mild-temperature localities in Sagami Bay, eastern Japan. The medusae swim by contracting their tentacles and relaxed with extended tentacles (Fig. 7). Early life cycle including embryogenesis, polyp and medusa budding are unknown. Stinging events attributed to *T. orientalis* have not been reported.

**Etymology.** The specific name ‘orientalis’ is a Latin adjective, referring to the locality (the Far East) where the new species has been found.

**Differential diagnosis.** A comparison of key features of the species in the genus *Tiaricodon* is presented in Table 5. All species of *Tiaricodon* have a bell-shaped or globular umbrella, four radial canals and four tentacles, and an abaxial ocellus on basal tentacle bulbs (Browne 1902, Schuchert 1996, Nogueira Júnior et al. 2019). *Tiaricodon orientalis* sp. nov. can be distinguished from other *Tiaricodon* species by its umbrella size, the shape of the subumbrellar pockets, and the length of the manubrium (Table 5). The umbrella size of *Tiaricodon orientalis* is 2.5 times smaller than that of *T. coerulesus* (type locality: Falkland Islands) and about 3 times larger than that of *Tiaricodon* sp. from Brazil. The four subumbrellar pockets are triangular in *T. orientalis* and "*T. coerulesus" from China, knee-shaped in *T. coerulesus* and *T. sp. from Brazil, and absent in *T. sp. from New Zealand. The length of the manubrium is short, about half of the subumbrella cavity in *T. orientalis* and *Tiaricodon* spp. from China and Brazil, while reaching almost to the umbrella margin in *T. coerulesus* and *Tiaricodon* sp. from New Zealand. A red band on the proximal part of the manubrium is present in *T. orientalis* and "*T. coerulesus" from China and Brazil, but absent in *T. coerulesus* and *T. sp. from New Zealand.

**Discussion**

Prior to our study, only one *Tiaricodon* species, *Tiaricodon coerulesus*, had been recorded from the South Atlantic in the Falkland Islands and the coast of Argentina, the South Pacific in several locations in South America, China, and the Weddell Sea in the Southern Ocean (Browne 1902, Kramp 1948, Kramp 1968, Zhang 1982, Lin and Zhang 1990, Mills 2000). Schuchert (1996) reported *Tiaricodon* sp. from Wellington Harbor, New Zealand, however, the specimen was not identified to species level because it was not fully grown. The distributions of the two species, *T. coerulesus* and *T. orientalis*, do not appear to overlap.

*Tiaricodon orientalis* can easily be confused with the hydromedusa *Hydrocoryne miurensis* Stechow, 1908 in Japan. This species has been reported from the coastal areas of Honshu and Hokkaido (Minemizu et al. 2015). *Hydrocoryne miurensis* appears during winter and summer around the coast of Enoshima (Yamashita & Sakiyama 1999, Sakiyama & Adachi 2001, Adachi et al. 2003). Both species have bell-shaped umbrellas, four interradial peaks in the subumbrella, four radial canals, four tentacles, tentacular bulbs with an abaxial ocellus and red band or spots present on the middle part of the gonad (Uchida 1927, 1932, 1967). However, the maximum umbrella size of *T. orientalis* is larger than that of *H. miurensis* (9.8 mm vs. 3.0 mm, respectively). Additionally, mesoglea of the umbrella is conspicuously thickened in *T. orientalis* while it is thin in *H. miurensis*, and the nematocysts on the exumbrella of *T. orientalis* are distributed sparsely, rather than in high concentrations as in *H. miurensis*.

The seasonal distribution of *Tiaricodon* has been observed in Xiamen Harbor, China (Xu & Chen 1998). The species appears between November and May and is most abundant in winter (January and February). It is found in water temperatures of 13°C to 20°C and salinities of 13.1 to 21.9. Adult and young medusae of *T. orientalis* were collected between April to May in Sagami Bay. The water temperature is 16°C to 21°C during these months (Japan Meteorological Agency 2020). Polyps of *T. orientalis* may produce medusae during winter and spring.

The morphological observations made during this study provide evidence that *Tiaricodon* from Sagami Bay is a new species. However, the *Tiaricodon* species collected from New Zealand and Brazil remain unidentified (Schuchert 1996, Nogueira Júnior et al. 2019). The Brazilian *Tiaricodon* specimens depicted in Nogueira et al. (2019) resemble our new species much more closely than *T. coerulesus*, especially the manubrium-shape and the colored band on the manubrium. Additional investigations are needed to understand the diversity, ecology, and distribution of *Tiaricodon*. 

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**Fig. 7.** Live medusa of *Tiaridocon orientalis* sp. nov.: A) swimming, B) relaxing.
Table 5. Morphology of *Tiaricodon* in previous and the present study. Bars represent a lack of data.

|                     | *Tiaricodon orientalis* sp. nov. | *Tiaricodon coeruleus* | *Tiaricodon* sp. | *Tiaricodon* sp. (identified as *Tiaricodon coeruleus*) | *Tiaricodon* sp. |
|---------------------|----------------------------------|------------------------|------------------|--------------------------------------------------------|-----------------|
| **UH/UD (mm)**      | 9.8/8.2                          | 25/24                  | 2.6/—            | 8/6                                                    | 3–3.3/—         |
| **No. of tentacles**| 4                                | 4                      | 4                | 4                                                      | 4               |
| **No. of radial canals** | 4                                | 4                      | 4                | 4                                                      | 4               |
| **Umbrella**        | Bell-shaped, smooth               | Bell-shaped, smooth    | Bell-shaped with scattered stenoteles, denser towards margin | Bell-shaped     | Bell-shaped                                              |
| **Subumbrellar pocket** | Triangular                       | Knee-shaped            | Absent           | Absent                                                 | Triangular      |
| **Peduncle**        | Indistinct                        | Short, broad           | Very slight      | Shallow                                                | Indistinct      |
| **Manubrium**       | Short, reaching less than half of subumbrella cavity height | Almost as long as bell cavity | Tubular, reaching almost the level of the velum, cylindrical with quadrangular base, lacking stomach pouches | Almost as long as bell cavity | Short, reaching less than half of subumbrella cavity height |
| **Red band**        | Present                           | Present                | —                | —                                                      | Present         |
| **Gonad**           | Surrounding the base of the stomach and extending over the peduncle along the four perradial sac-like lobes | Surrounding the base of the stomach and extending over the peduncle along the four perradial sac-like lobes | Not developed (immature) | Incipient gonad tissue visible on stomach pouches | Present         |
| **Velum**           | Narrow                            | Narrow                 | —                | —                                                      | Present         |
| **Abaxial ocellus on basal bulbs** | Present                         | Present                | Present          | Present                                                | —               |
| **Nematocysts**     | Stenoteles, desmonemes            | —                      | —                | —                                                      | —               |
| **Distribution**    | Sagami Bay, Japan                 | Falkland Islands       | Wellington Harbor, New Zealand | Yellow Sea, Taiwan Strait, South China Sea, Xiamen Harbor Xu and Chen (1998) Xu et al. (2014) | Wellington Harbor, New Zealand |
| **References**      | This study                        | Browne (1902)          | Schuchert (1996) | Schuchert (1996)                                       | Nogueira et al. (2019) |
Our molecular phylogenetic analyses show that *T. orientalis* and "*Tiaricodon coerulesus*" reported in Zhen et al. (2014) clearly belong to the same species. It was interesting to note that the *Tiaricodon* clade showed a well-supported relationship with *Urashimea* and *Odessia* (Fig. 6), suggesting that they could all belong to well-defined clade of Capitata (see Nawrocki et al. 2010). The genera *Moerisia*, *Odessia* and *Urashimea* have solitary polyps, presumably like *Tiaricodon* (see Bouillon et al. 2006, Xu and Chen 1998), and they thus also share a derived morphological trait as most Capitata (sensu stricto) polyps are colonial.

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