

Taxonomic review of three Japanese species of edible jellyfish (Scyphozoa: Rhizostomeae)

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Abstract: Specimens of three edible jellyfish from Japan, i.e. “Bizen kurage”, “Hizen kurage”, and “Echizen kurage”, are re-examined and re-described so that their nomenclature is stabilized. The “Bizen kurage” is *Rhopilema esculentum* Kishinouye 1891, and the “Hizen kurage” is *Rhopilema hispidum* (Vanhöffen 1888). The “Echizen kurage” is a distinct species of the genus *Nemopilema*. We propose to revive the original name *Nemopilema nomurai* Kishinouye 1922 from the more commonly used *Stomolophus nomurai*. The taxonomic position of *N. nomurai* within the Scapulatae is discussed.

Key words: edible jellyfish, taxonomy, Bizen kurage, Hizen kurage, Echizen kurage, Rhizostomeae.

Introduction

Some jellyfish in the order Rhizostomeae are exploited for human consumption in Japan, China, Korea, and South-east Asian countries. The commercial value of the semi-dried products imported from abroad to Japan is more than 5 billion JPN Yen annually (Omori & Nakano 2001). In spite of their importance as a commodity, only a little is known about the taxonomy of these jellyfish. Their extremely large size, often extending more than 50 cm in diameter of the umbrella, heavy weight, and difficulty of preservation for taxonomic study hinder studies by specialists, and therefore the taxonomy is considerably confused.

It has been said that there are three species that have traditionally been exploited in Japan, namely the “Bizen kurage”, “Hizen kurage”, and “Echizen kurage” (Omori 1981). “Kurage” means jellyfish in Japanese, whereas “Bizen”, “Hizen” and “Echizen” are the old names of the provinces, respectively, where occurrence of the jellyfish was first reported. The “Bizen kurage” was originally described in Japanese by Kishinouye (1890) and later given the species name, *Rhopilema esculenta*, in a brief note (Kishinouye 1891). Kishinouye (1899) re-described *R. esculenta* in English, and western specialists cited this in their studies but not the original description. However, there is a

certain disagreement in color and morphology between the original description of the specimens and re-description such as: in the former, they are deep blue specimens without appendages at the bottom of the fused part of the mouth-arms, whereas the latter include reddish-brown specimens with whip-shaped appendages. Such similarities and differences between the original description and re-description have not been fully discussed as yet.

The “Hizen kurage” was reported by Kishinouye (1897) as a new species, *Rhopilema verrucosa*. As the original description written in Japanese was brief, he re-described the species in English later but again without sufficient drawings (Kishinouye, 1899). Prior to this, Vanhöffen (1888) established a new species *Rhizostoma hispidum* based on specimens collected near Hong Kong. Maas (1903) transferred this species to the genus *Rhopilema*, and suggested that *Rhopilema verrucosa* was a synonym of *Rho. hispidum*. Kishinouye (1922) agreed with him later. According to Vanhöffen (1888), *Rhi. hispidum* carries 4 whip-shaped appendages at the bottom of the fused part of the mouth-arms, however, both Kishinouye (1899) and Maas (1903) did not mention these appendages.

The “Echizen kurage” was also described only in Japanese by Kishinouye (1922) as a new genus and new species, *Nemopilema nomurai*. Uchida (1954) later referred to this species as *Stomolophus nomurai* without sufficient reason for transferring the genus, and Japanese researchers have so

far followed suit (e.g. Shimomura 1959; Yamaji 1966; Yamada 1997). Furthermore, Kramp (1961) and Hon et al. (1978) regarded this species as a synonym of *Stomolophus meleagris*. One of the present authors has previously commented, however, that they are not the same species and proposed to refer to *Stomolophus nomurai* by its original name *Nemopilema nomurai* (Omori & Nakano 2001).

Unfortunately, Mayer (1910), Kramp (1961) and Cornelius (1997) who revised the Rhizostomeae of the world neither examined these Japanese species nor read the original descriptions. As translation difficulties have prevented them from giving an accurate appraisal of these species, taxonomic confusion has not been resolved.

In order to stabilize the nomenclature of these edible jellyfish, in the present study, we collected specimens at various localities in Japan, re-examined morphological features in detail, and re-described the three species.

Materials and Methods

The “Bizen kurage” and “Hizen kurage” occur concurrently and are commercially exploited from June to September at the head of the Ariake Sea, a small bay in Kyushu (Fig. 1), using mainly set-nets on the bottom perpendicular

to the tidal current. They are called “Aka (red) kurage” and “Shiro (white) kurage”, respectively, at the local fishing market. We collected both species on June 15 and August 4, 2000, and again on August 22 and 23, 2002. In addition, we collected a blue medusa, morphologically resembling “Aka kurage”, at Kaseda on the East China Sea side of Kagoshima Prefecture, Kyushu (Fig. 1), on August 3, 2001. The “Echizen kurage” specimens were collected on October 2, 2000, when a dense aggregation of the species was trapped in a large set-net for the yellowtail fishery off Udagou, Yamaguchi Prefecture, Honshu on the Sea of Japan side (Fig. 1).

All specimens were examined immediately at the place of collection. Then, they were fixed in formalin-seawater for detailed morphological study in the laboratory.

Re-description

Rhophilema esculentum Kishinouye, 1891

“Bizen kurage” (Figs. 2, 3, 4)

Rhophilema sp. Kishinouye 1890, p. 47, pl. 2.

Rhophilema esculenta Kishinouye 1891, p. 53; 1899, p. 205, taf. 13, figs. 1–5; Mayer 1910, p. 704, fig. 423; Uchida

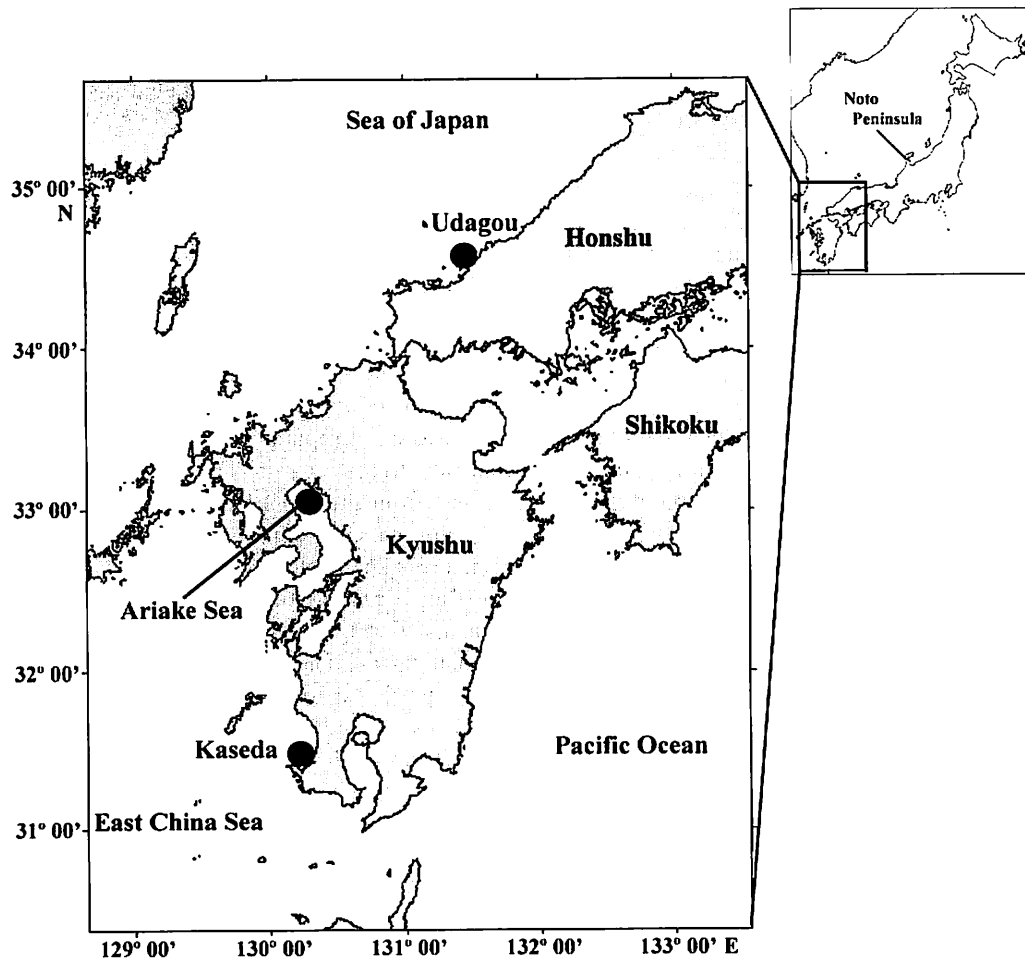


Fig. 1. Map of sampling sites.

1936, p. 77, fig. 46; 1965, p. 239, fig. 250; Wu 1955, p. 36, figs. 1–3.

Rhopilema esculentum—Kramp 1961, p. 380; Hsu & Chin 1962, p. 214, figs. 22, 23; Hon et al. 1978, pp. 2, 13, 1 plate, figs. 1–5; Huang & Wang 1985, p. 1, figs. 1–5; Gao et al. 2002, p. 222, fig. 134.

Rhopilema esculenta var. *asamushi* Uchida, 1927, pp. 216, 233.

Rhopilema asamushi Uchida, 1936, p. 78, figs. 47, 48; 1938a, p. 45; 1938b, p. 149; 1954, pp. 211, 214, 216, fig. 2; 1965, p. 239, fig. 251; Yasuda & Suzuki 1992, p. 147.

The original name of species *esculenta* has been changed to *esculentum* as it must agree in gender with the generic name.

Material

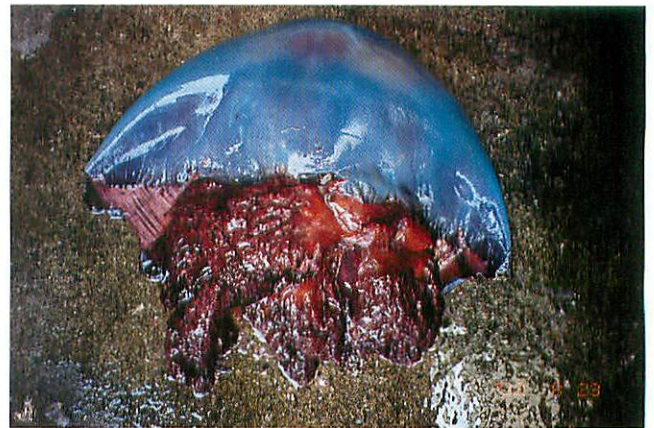
From Ariake Sea: 2 specimens (diameter of umbrella 8.3 and 12.5 cm) collected on June 15, 2000, 1 specimen (44 cm) on August 4, 2000, and 3 specimens (40–58 cm) on August 23, 2002. From Kaseda, Kagoshima Prefecture: 14 specimens (8–13 cm) collected on August 3, 2001.

Type specimens

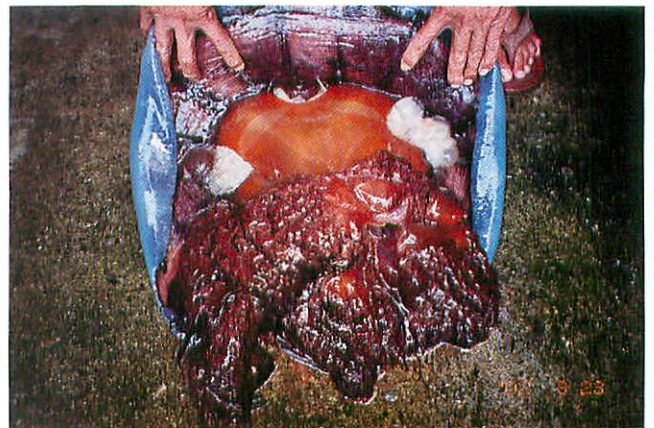
None of the early papers by Kishinouye (1890, 1891, 1899) mention if type specimens were located somewhere. In spite of our survey at museums and universities where the specimens might be lodged, they were not found. Therefore, we selected a specimen collected from the Ariake Sea on June 15, 2000, to serve as the neotype (NSMT-Co1378). It is lodged with two other specimens from the Ariake Sea (NSMT-Co1379, 1380) and 14 specimens from Kaseda (NSMT-Co1386 to 1391) in the National Science Museum, Tokyo.

Description

Umbrella about half as high as broad when swimming; rigid; thick in central part while thin in margin; diameter up to 70 cm when flattened (Fig. 2). Exumbrella smooth, long and short marginal grooves occurring alternately but sometimes with no regular arrangement in small specimens. Eight rhopalia located in umbrella margin, tip of each rhopalium slightly swollen. Marginal lappets rounded; their number in each octant varied from 16 to 18 in the specimens larger than 40 cm in umbrella diameter from the Ariake Sea, while it varied from 7 to 11 in smaller specimens (<13 cm) including those from Kaseda. Surface on exumbrella side of the lappets in the specimens from Kaseda has vertical stripes like narcomedusan otoporpa while no stripes exist in specimens from the Ariake Sea. Eight rhopalia located in umbrella margin, tip of each rhopalium slightly swollen. Rhopalar lappets pointed and laterally narrow (Fig. 3). Sensory pits located on exumbrella just above the rhopalia, narrow, with three points in the lower margin.



A



B

Fig. 2. *Rhopilema esculentum*. Whole body of the largest specimen from Ariake Sea (umbrella diameter 58 cm and pale-blue in color, whereas mouth-arms reddish-brown) collected on August 23, 2002. A. Exumbrellar view. B. Subumbrellar view.

Circular muscle interrupted on rhopalar canals but not interrupted on inter-rhopalar canals, so that the muscles formed eight separate groups. Inner margin of the circular muscle traces a circle. The muscle of the four larger specimens from the Ariake Sea well developed so that anastomosing canal systems invisible, while that of other specimens not so developed.

Radial canals 16; eight rhopalar and eight inter-rhopalar canals. A ring canal runs to connect the mid points of the radial canals. The rhopalar canals reach the umbrella margin; distal ends divide into two and enter into the rhopalar lappets. The inter-rhopalar canals recognized between base of fused mouth-arms and ring canal; distal parts not recognized because they join into anastomosing canal system. The net like anastomosis peripherally decreases in size. The anastomosing canal system on the proximal side of the ring canal communicates with the rhopalar and ring canals but not with the inter-rhopalar canals.

Gonads belt-shaped and folded complexly on lower stomach wall. Four subgenital cavities distinct and are sepa-

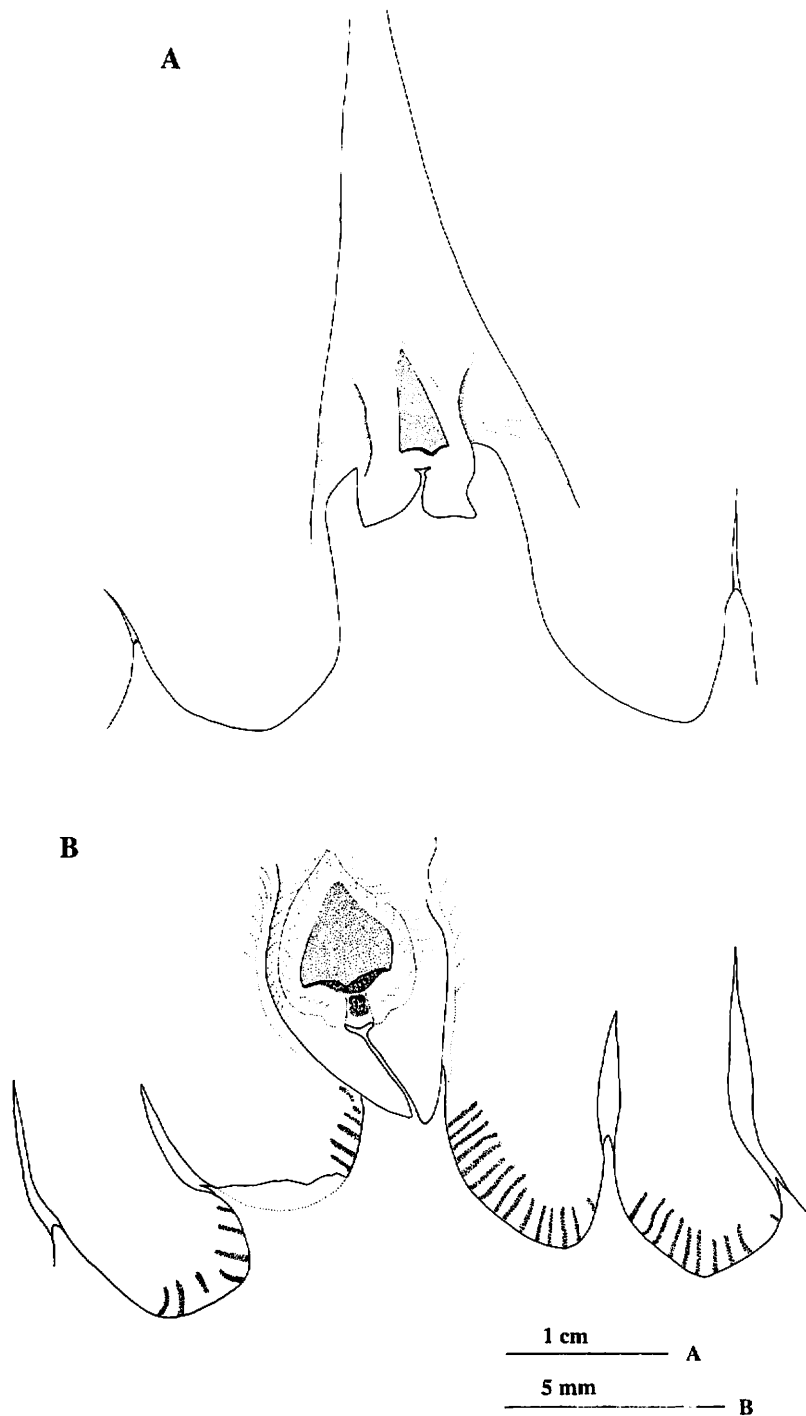


Fig. 3. *Rhopilema esculentum*. Rhopalar lappets and a sensory pit, exumbrellar view. Rhopalar lappets of specimen collected from Kaseda (B) have otoporpa-like stripes in exumbrellar surface although those from Ariake Sea (A), the umbrella diameter of which is 44 cm, have not.

rated from one another by partitions. An opening of subgenital cavity located between neighboring 2 inter-rhopalar canals. A rigid projection exists at front of each opening; its surface rough excepting for the areas close to the rhopalar canals.

Mouth-arms fused with each other for the proximal one-fourth of their length (from the base, where they connect

with the subumbrella, to the distal level of the scapulets) only and divided into eight arms distally. Each arm has three wings, two of them face away from the central axis (outer wings) and the other faces the central axis (inner wing). No window in either inner or outer wings. Each wing divided several times with numerous mouthlets. Margins of the wings form thin membranes, folded complexly

as frills and carrying numerous cirri, each having a small terminal knob. Numerous tentacles exist between the frills. Many fusiform appendages arising from the outer wings and distal part of the inner wing, vary in length, and easily torn off. The appendage at the end of each mouth-arm is the largest and longest. Bottom of the fused part of mouth-arms and the inner wings not connected to each other; five groups of frills exist; central mouth not opened but covered by the central frill. In the specimens from Kaseda, long whip-shaped appendages occur from the above-mentioned frills; total number of the appendages varies from zero to six. In those from the Ariake Sea, however, some tiny tentacle-like (not whip-shaped) appendage occurs in some specimens, but no tentacle in other specimens including the largest one with the pale-blue umbrella.

Scapulets, 16; distal one third of them divided into two wings. Upper side branched many times and folded like frills, but lower side smooth. Numerous mouthlets open. Numerous tentacles occur between the frills, particularly dense in the distal part.

The umbrella faintly reddish or colorless, but sometimes pale-blue in the larger specimen from the Ariake Sea. The circular muscle, mouth-arms and scapulets reddish brown. However, whole body bluish in the Kaseda specimens.

Remarks

This species was first described by Kishinouye (1890) as *Rhopilema* sp. based on 2 preserved specimens collected from Kojima Bay in the Seto Inland Sea, Okayama Prefecture, and many live specimens obtained in Suruga Bay at Okitsu, Shizuoka Prefecture. The original drawings are shown in Fig. 4 in the present paper. Kishinouye (1891) then established the new species *R. esculenta* for the specimens. A complete English translation by the present authors of the original descriptions in 1890 and 1891 will be provided on request.

Materials collected from the Ariake Sea and from Kaseda have the same morphological characters except for the appendages at the bottom of the fused part of the mouth-arms, body color, and vertical stripes on the marginal lappets. Number and shape of the appendages at the bottom of the fused part of the mouth-arms are not a stable character enabling distinction of the species. Various colors of *R. esculentum* have been reported: deep blue and reddish brown (Hattori 1893; Kishinouye 1899), milky white, rarely yellowish brown, and gold (Hon et al. 1978). In the present study we examined specimens that occurred concurrently in the Ariake Sea having colorless umbrellas, faintly reddish and bluish umbrellas. According to local fishermen, all specimens that are collected before mid summer have faintly reddish or colorless umbrella, but large specimens with bluish umbrellas sometimes occur in August and September (Fig. 2). Most of the jellyfish lose the fusiform appendages on the mouth-arms at around that time. Occurrence of specimens having body color intermediate between

the typical reddish brown from the Ariake Sea and the blue from Kaseda indicate that color also seems not to be a useful criterion for distinction of the species. Whether the species from Kaseda should be separated from that from the Ariake Sea only according to the character of the vertical stripes on the marginal lappets is questionable, and we conclude that both specimens from the Ariake Sea and Kaseda belong to the species *R. esculentum*.

Uchida (1927, 1938a, b) described *Rhopilema esculenta* var. *asamushi* and *Rhopilema asamushi* based on specimens collected from Mutsu Bay and Amakusa (Ariake Sea). He considered *R. asamushi* to be a new species because of the presence of stout and spindle-shaped (sensu Uchida 1927) appendages on the mouth-arms, but, that is one of the characters of *R. esculentum*. We could not find the specimen of *R. asamushi* that was examined and deposited by Uchida (1938a, b) at the Amakusa Marine Biological Station. As the type specimen has been lost and his descriptions of *R. esculenta* var. *asamushi* and *R. asamushi*, as well as their distribution, do not show clear differences from *R. esculentum*, we deem them synonyms of *R. esculentum*.

Rhopilema rhopalophora, described by Haeckel (1880) based on a specimen (10 cm in diameter of umbrella) collected from the Indian Ocean east of Madagascar, is closely allied to *R. esculentum* (Mayer 1910). Although Haeckel's original description is too brief to satisfactorily compare with other species, Kishinouye (1891, 1899) noted that *R. rhopalophora* is distinguishable from *R. esculenta* by the presence of triangular prismatic appendages on the mouth-arm rather than fusiform ones. *Rhopilema rhopalophora* was described once again by Stiasny (1933a), based on a small specimen (4.2 cm in diameter of umbrella) from Amoy, China. He argued that *R. rhopalophora* differs from *R. esculenta* in (1) the large number of marginal lappets, 16 per octant, (2) different shape of sensory pits, covered by numerous fine folds, located on a heart-shaped elevation, which extends upward in a tip-like formation, (3) absence of subgenital papillae, (4) different branch systems of canals in mouth-arms, i.e. *R. rhopalophora* had several branches, whereas *R. esculenta* var. *asamushi* had singular branches, (5) different form of appendages, i.e. triangular in transversal section, and (6) color. However, we were unable to observe differences between the two species concerning (2). For character (3), there is a possibility that the difference was merely ontogenetic, as Stiasny's material was not fully developed. The characters (4) and (5) are not suitable characters for identification because Kishinouye's (1899) material had several branches and Stiasny described morphological variation of the appendages himself. Only character (1) seems to differ with certainty between the small *R. rhopalophora* specimens and the present smaller specimens (<13 mm) of *R. esculentum* that have 7 to 11 marginal lappets. Although we cannot conclude as to whether *R. rhopalophora* is indeed different from *R. esculentum*, Gao et al. (2002) have apparently not seen *R. rhopalophora* in Chinese waters since Stiasny's work (1933a).

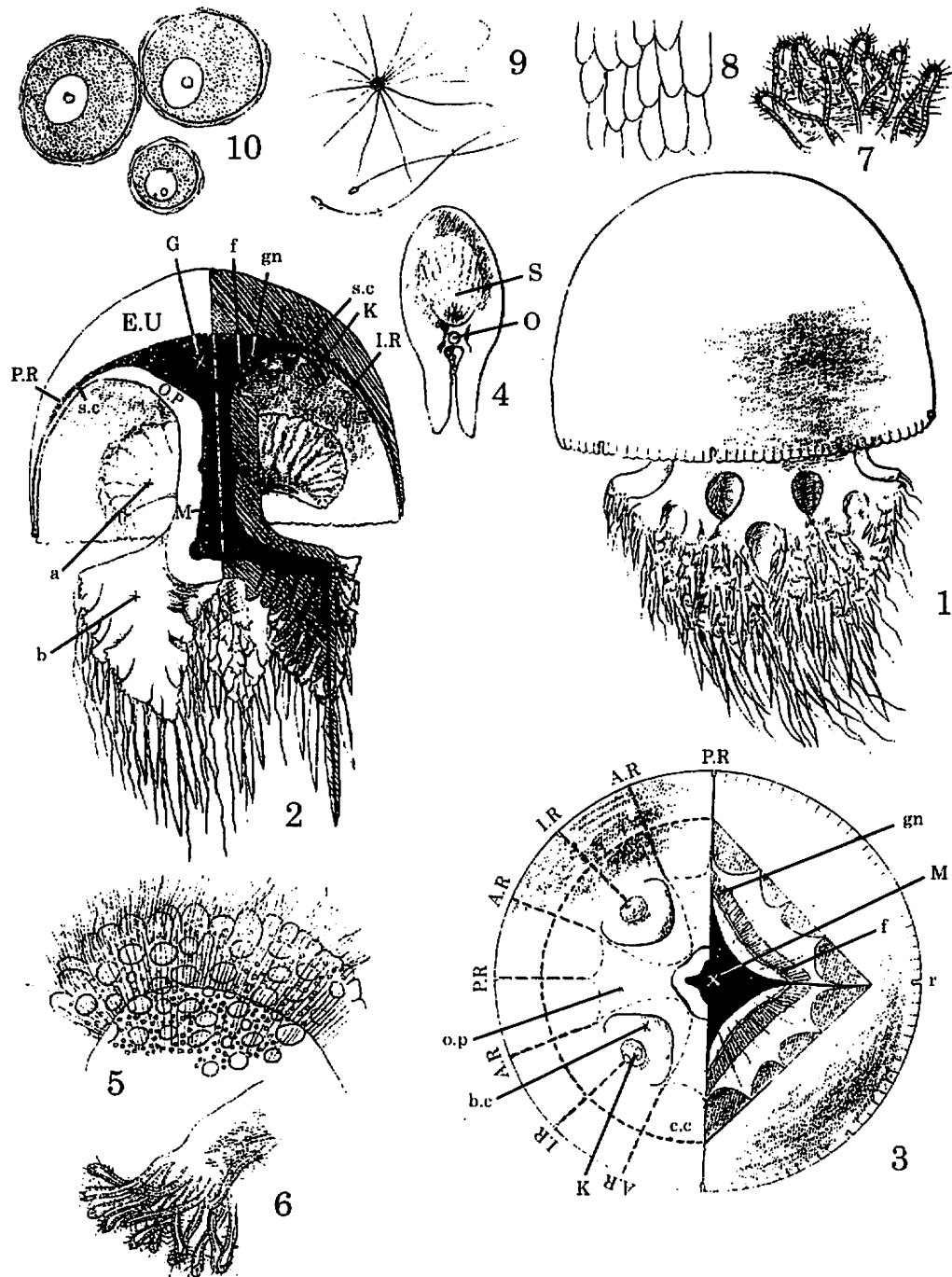


Fig. 4. *Rhopilema esculentum*. After original drawings by Kishinouye (1890).

A.R. Adradius, a. Scapulet, b. Lower mouth-arm, c.c. Circular canal, E.U. Exumbrella, f. Gastric cirri, G. Stomach, gn. Gonad, I.R. Interradius, K. Gelatinous projection, M. Mouth cavity, O. "Hearing organ", O.P. Oral pillar, P.R. Perradius, r. Sense organ, S. "Smell organ", s.c. Subgenital cavity.

1, Whole body, 2. Vertical section, left—section of adradial line, right—section of perradial line, 3. Umbrella, left half—lower view, right half—upper view, 4. Sense organ, 5. A fold of "smell organ", 6. Small tentacle around mouth opening, 7. Gastric cirri, 8. Male sexual organ, 9. Sperm with two mature ones, 10. Ovum.

The life cycle of *R. esculentum* has been revealed. In the sea the medusae need 2–3 months of growth to develop from ephyra to maturity with an umbrella of 25–45 cm in diameter in Liaodong Bay, China (Ding & Chen 1981). In the Minjiang estuary, China, the growth after the ephyra is

divided into three phases, i.e. slower first phase before early May, faster second phase to end of July, and body contraction final phase after August (Lu et al. 1999a, b). Under laboratory conditions a few individuals of the scyphistomae lived more than one year and strobilated repeatedly up to 18

times in one year and 32 times in two years. Each scyphistoma could produce 7–8 ephyrae on average (Chen & Ding 1983). Resource enhancement experiments through releasing ephyrae were successfully done off Liaoning Province, northern Yellow Sea (Chen et al. 1994).

Distribution

Rhopilema esculentum has been recorded in the Seto Inland Sea (Kishinouye 1890), Suruga Bay (Kishinouye 1890), Karatsu Bay (Hattori 1893), Ariake Sea (Hattori 1893, Kishinouye 1899, Uchida 1938b, present study), Wakasa Bay (Yasuda & Suzuki 1992), and East China Sea off Kagoshima Pref. (present study). Also from the Chinese coast from Liaotung Bay to Kwangtung Province and Moppo, Korea (Hon et al. 1978; Gao et al. 2002). In the Ariake Sea very large blooms of this species occurred from 1977 to 1979. There is however no record of occurrence in the Seto Inland Sea or Suruga Bay in recent decades.

Rhopilema hispidum (Vanhöffen, 1888)

“Hizen kurage” (Figs. 5, 6, 7)

Rhizostoma hispidum Vanhöffen 1888, pp. 32, 43, pl. 5, figs. 1, 2.

Rhopilema verrucosa Kishinouye 1897, p. 485; 1899, p. 208, 1 fig.

Rhopilema hispidum (Vanhöffen).—Maas 1903, p. 73, pl. 9, figs. 78–81; Mayer 1910, p. 706; Stiasny 1933b, p. 162, figs. 1–8; Stiasny 1939, p. 17; Uchida 1954, p. 211; Kramp 1961, p. 380; Hsu & Chin 1962, figs. 24, 25; Hon et al. 1978, p. 13, fig. 8; Gao et al. 2002, p. 224, fig. 135.

Rhopilema visayana Light 1914, p. 227, figs. 14–16.

Rhopilema hispidum (Vanhöffen).—Rao 1931, p. 62.

Material

Four young specimens (diameter of umbrella when flattened 4.3, 4.4, 6.4, 6.4 cm) collected on June 15, 2000, 1 specimen (61 cm) on August 4, 2000, and 1 specimen (50 cm) in August, 2000 (date unknown), and 3 specimens (62–70 cm) on August 22, 2002. All were collected from the Ariake Sea. We lodged 6 specimens from the Ariake Sea in the National Science Museum, Tokyo (NSMT-Co 1381–1385).

Description

Umbrella shallow in young specimens while it is about 0.6 times as high as broad in larger specimens when swimming (Fig. 5); diameter up to 70 cm when flattened. Numerous small colorless warts with round tips and comparatively larger yellow or brown warts with pointed tips scattered on exumbrella; all tips directed to umbrella margin. The colored warts occur more densely at the top of the umbrella in the larger specimens, whereas only colorless warts occur in young ones. Eight rhopalia are located on the umbrella

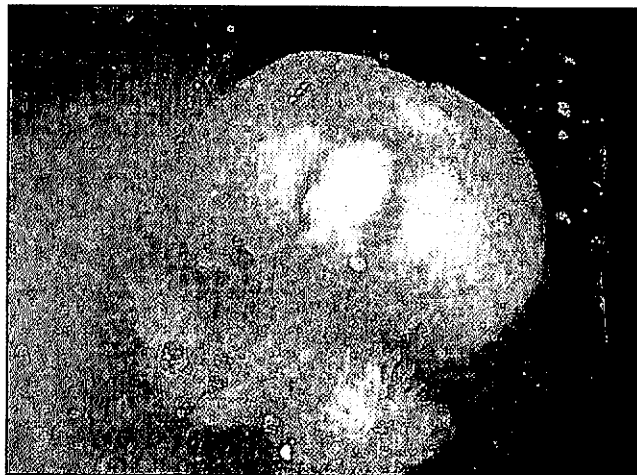


Fig. 5. *Rhopilema hispidum*. Whole body of a specimen from the Ariake Sea (umbrella diameter 62 cm) collected on August 22, 2002.

margin; the tips of them being slightly red or brown in color. Shallow pocket-shaped pit situated on exumbrella just above each rhopalium. Rhopalar lappets laterally narrow, tip of them pointed (Fig. 6D, 6E). Marginal lappets up to eight in number in each octant; the pointed tips of which are skewed slightly anticlockwise in the larger specimens (>60 cm in diameter) although in the others the tips are rounded margin. A short marginal groove runs between each of the marginal lappets. Canal system is distinct in smaller specimens (Fig. 6F); muscle fields triangular, total 16 in number.

Sixteen radial canals run along the subumbrella, eight rhopalar canals and eight inter-rhopalar ones; all canals distinct up to umbrella margin. Distal end of the rhopalar canals divided into two and reaching the base of the rhopalar lappets. Ring canal does not exist. Subumbrellar canal system forms net like anastomoses that peripherally decrease in size. The inner one third of the system connected only to rhopalar canals but not to inter-rhopalar canals. Connections between the anastomosing canal system and the radial canals exist more densely on the distal part of the subumbrella.

Four gonads form a folded belt-shape on the lower stomach wall in young specimens. However, gonads of the adult specimens were too badly damaged to observe due to difficulties in preservation. Four subgenital cavities exist separated from one another. Genital ostia are semicircular in shape, opening between neighboring inter-rhopalar canals. A large and laterally compressed projection is located at the center of each ostium while small projections are located on both sides of the ostium; the surface of both projections are rough although the basal part of the central large projection is smooth.

Mouth-arms are fused with each other for the proximal half of their length (from the base, where they connect with the subumbrella, to some distance below the distal most

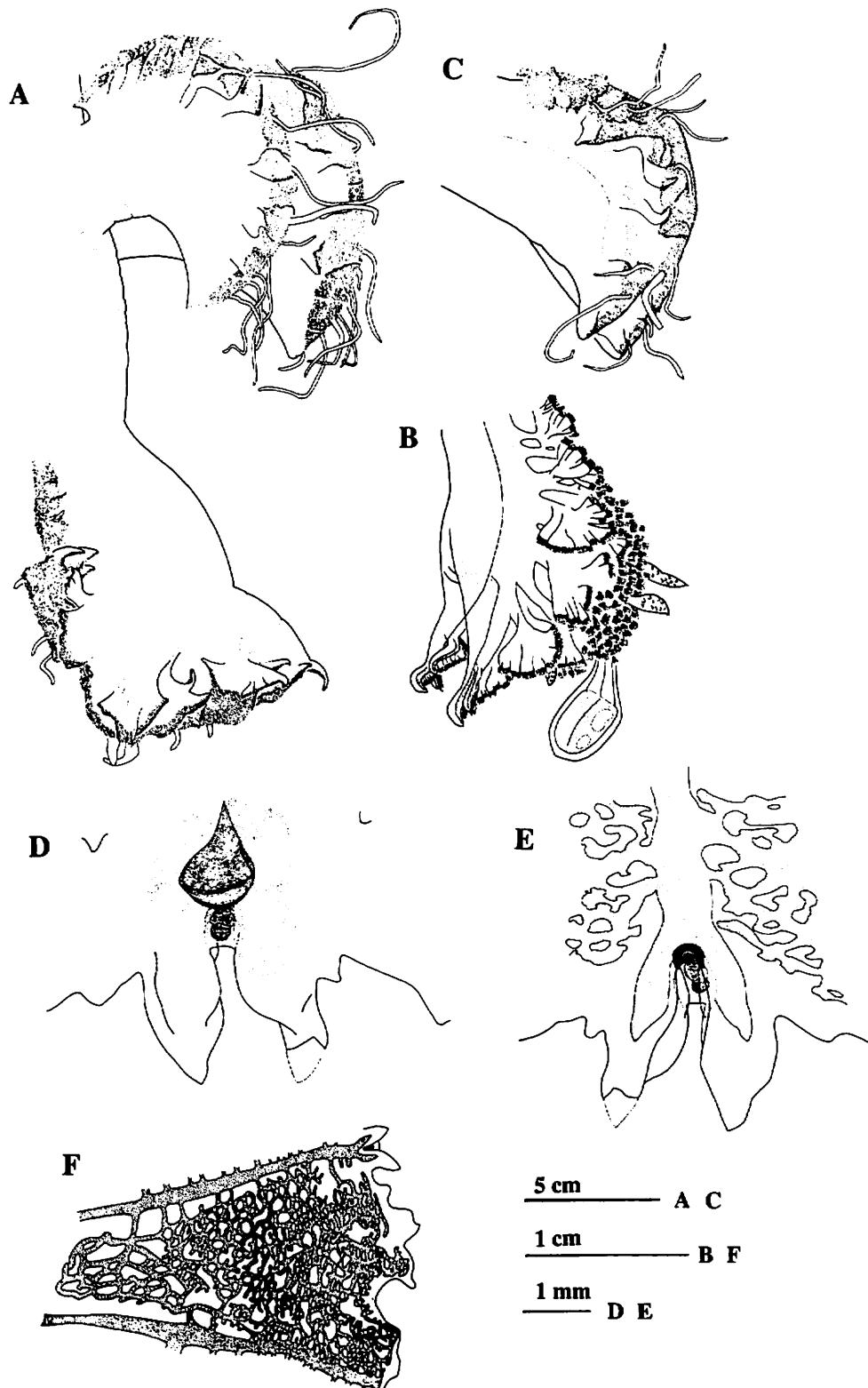


Fig. 6. *Rhopilema hispidum*. A. Mouth-arm and a pair of scapulets, lateral view. Hatched area of the lower distal margin is the lower wing and that of the left margin is the inner wing. No large club-shaped appendages are present on the mouth-arms of this specimen. Large appendages are probably torn off during collection or lost ontogenetically. B. Mouth-arm, lateral view. A large club-shaped appendage exists at the point of contact of the three wings. C. Scapulet, lateral view. D and E. Rhopalar lappets and a sensory pit, exumbrellar view (D) and subumbrellar view (E). One of the two lappets is broken at its tip. F. Anastomosing canal system of subumbrella. A and C are sketched based on a large specimen collected on August 4, 2000, whereas B, D and E are based on a small specimen collected on June 15, 2000.

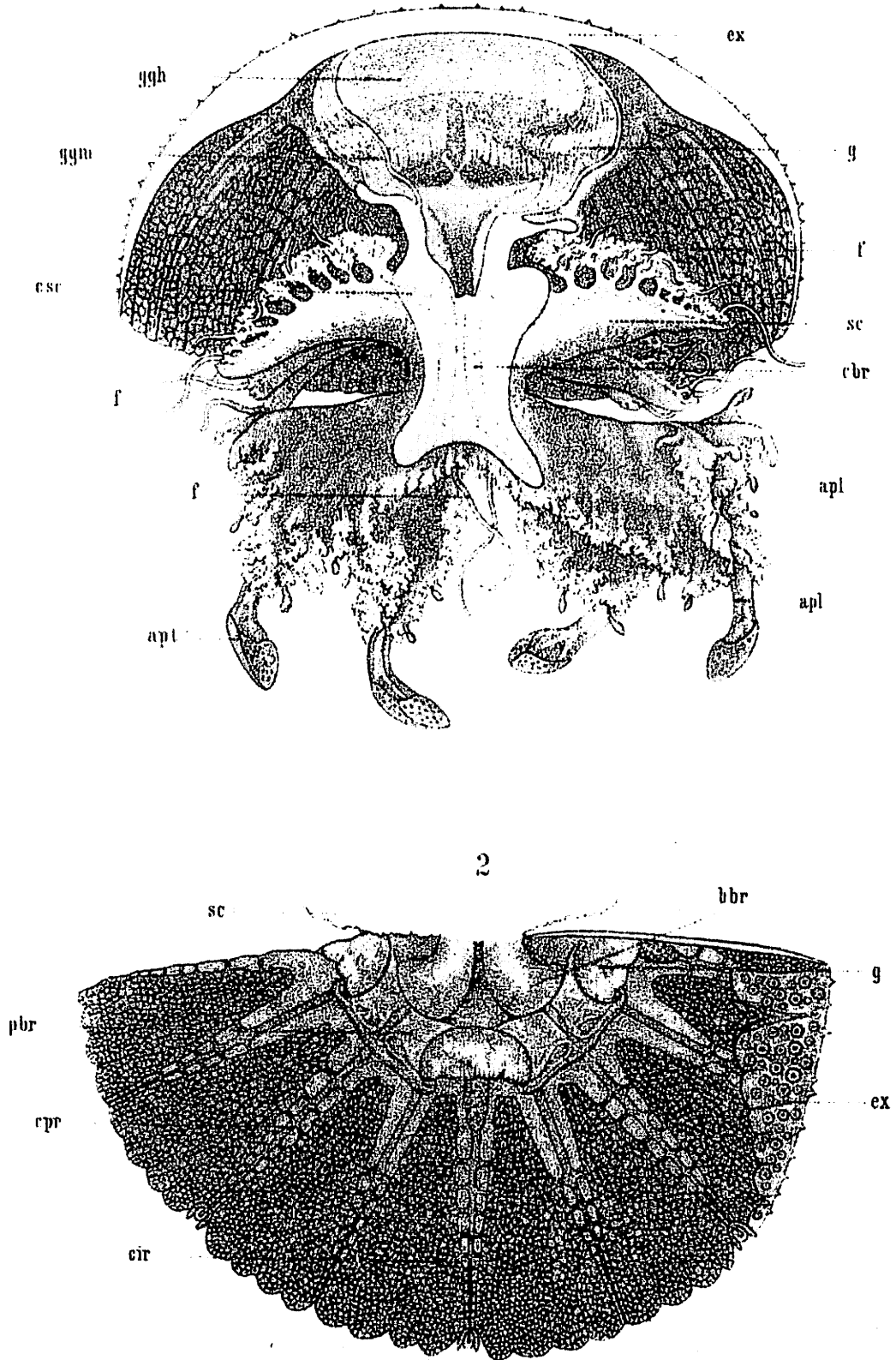


Fig. 7. *Rhopilema hispidum*. After original drawings by Vanhöffen (1888). (Permission for reprinting was given by the source "Senckenbergische Bibliothek, Frankfurt am Main".)

level of the scapulets), and divided into eight arms distally. Each arm has three wings, two of them face away from the subumbrellar surface (lower wings) and the other faces the central axis (inner wings) (Fig. 6A, 6B). Each wing margin is divided into several subwings; its margin complicated and folded into thin membranes with numerous cirri with a small terminal knob. No tentacles. A large club-shaped appendage with a roughly textured swollen end exists on the junction point of the three wings in the four smaller specimens; its length is variable. No such large appendage observable however in the larger specimens. In addition to this appendage, one or two short club-shaped appendages are located on each wing. The bottom of the fused part of the mouth-arms forms an H-shaped frill; the central mouth is not open at the bottom. However, 2–4 long whip-shaped appendages occur at the junction points of neighboring inner wings; in addition, two short whip-shaped appendages occur on the inner side of the long whip-shaped appendages.

Scapulets, 16; blade-shaped, occurring in pairs on both sides of each mouth-arm ridge (Fig. 6A, 6C). Each scapulet branches into two at the distal end. Upper margin complicatedly folded with numerous mouthlets, while lower margin smooth. Several tentacles, varying in length, occur on the upper margin of the scapulets. A thick tentacle exists at the junction where each scapulet branches.

Remarks

The outline of the present species resembles that of *Rhopilema verrilli* (Fewkes 1887) because the umbrella is shallower than a hemisphere and two of the three mouth-arm wings (outer wing) face away from the central axis. *Rhopilema hispidum*, however, is distinguished from *R. verrilli* by (1) the presence of numerous warts on the exumbrella, (2) the presence of a large club-shaped appendage with a swollen end on the junction point of the three wings. For reference, the original drawings of *R. hispidum* by Vanhöffen (1888) are shown in Fig. 7.

Rhopilema hispidum is easily distinguished from *R. esculentum*, which occurs in the same region by (1) thinner umbrella, (2) tiny projections on exumbrella, (3) triangular muscle fields, (4) absence of ring canal, (5) fused part of mouth-arms longer, (6) frill-shaped areas of margin of the two mouth-arm wings lie along horizontal axis, and (7) a large club-shaped appendage with a swollen end on each mouth-arm (Table 1).

Rhopilema nomadica Galil et al. (1990) is closely allied to *R. hispidum*. Galil et al. (1990) reported that the two species could be distinguished from each other by the blunt tuberculation on the exumbrella and the mouth-arms ending in vermicular filaments in *R. nomadica*. Concerning their former character, if “the blunt tuberculation” correlates to “warts on the exumbrella” as described in the present study, it is not a suitable character for species distinction. This is because *R. hispidum* specimens have two kinds of

warts on the exumbrella, pointed and blunt ones, and in the smallest two specimens from our material have only blunt warts. The latter character seems to differ from *R. hispidum*. Although Galil et al. (1990) did not discuss this point, the characteristic projection on the outer surface of each rhopalar lappet is sketched in their figure of *R. nomadica*. Such a projection has not been observed in *R. hispidum*. Further morphological studies on *R. nomadica* are needed.

There is a dubious species *Pilema clavigera* that was originally described by Haeckel (1880) based on a specimen (9.0 cm in diameter of umbrella) from Hong Kong. Mayer (1910) noted that *R. hispidum* is possibly identical to *P. clavigera*. However, the original description of *P. clavigera* includes a ring canal, although it is only barely discernable. Although Mayer (1910) did not mention this point, it is one character that distinguishes *P. clavigera*. Haeckel’s description is without illustration and again very brief, but we hesitate to conclude that *R. hispidum* is a synonym of *P. clavigera*.

Distribution

Rhopilema hispidum has been recorded from Hong Kong (Vanhöffen 1888), off Fukien and Kwangtung coasts, China (Hsu & Chin 1962; Hon 1978), the Ariake Sea (Kishinouye 1897, 1899; present study), Southern Japan (Uchida 1954), Taytay Bay, Palawan (Light 1914), Malay Archipelago (Maas 1903), Semarang and Jakarta, Java (Stiasny 1933b), Orissa Coast, Bay of Bengal (Rao 1931), and off Kamaran, southern Red Sea (Stiasny 1939). We also found them at Kotabaru and Kualatambangan in Kalimantan and Sittwe in Myanmar recently (Kitamura, 2003).

Nemopilema nomurai Kishinouye 1922

“Echizen kurage” (Figs. 8, 9, 10)

Nemopilema nomurai Kishinouye 1922, p. 343, fig. 9; Uchida 1936, p. 81.

Stomolophus nomurai (Kishinouye)—Uchida 1954, p. 209, fig. 2; Uchida 1965, p. 239, fig. 249.

Stomolophus meleagris—Hon et al. 1978, p. 3, fig. 9; Gao et al. 2002, p. 225, fig. 136 (not *Stomolophus meleagris* L. Agassiz 1862).

Materials

Three adult specimens collected at Udagou, Sea of Japan on October 1 (diameter of umbrella 120 cm) and October 2 (50 and 69 cm), 2000.

Type specimen

Neither Kishinouye (1922) nor Uchida (1936) mentioned the location of the type specimens. As the original type specimens are missing, we selected a specimen collected from Udagou on October 2, 2000 to serve as the neotype

Table 1. Morphological comparison of three species of edible jellyfish in Japan.

	<i>Rhopilema esculentum</i>	<i>Rhopilema hispidum</i>	<i>Nemopilema nomurai</i>
Exumbrella	smooth	with two types of warts, tiny and comparatively larger	with granule-like warts
Projections at front of subgenital cavity	presence	presence	absence
Coalescent part of mouth-arms	basal one-fourth of the length	basal half of the length	basal one-fourth of the length
Windows in mouth-arms and scapulets	absence	absence	presence
Types of appendages on mouth-arm	fusiform	club-shaped	whip-shaped

and lodged it at the National Science Museum, Tokyo (NSMT-Co 1392).

Description

Umbrella rigid and thick, about half as high as broad when swimming; diameter up to 120 cm. Whole of the exumbrella covered by colorless granular warts; marginally located warts of smaller diameter than central ones. Marginal lappets 8 in number in each octant; each lappet divided into two round sub-lappets. Eight rhopalia located on umbrella margin. Rhopalar lappets short and slender (Fig. 9F). A sensory pit narrow groove in shape, located on exumbrella just above each rhopalium. Subumbrellar muscle well developed, divided into 16 sector groups, located between adjacent radial canals. The muscle run across the distal half of the inter-rhopalar canals but not the rhopalar canals.

Radial canals 16; 8 rhopalar and 8 inter-rhopalar canals. Both rhopalar and inter-rhopalar canals easily distinguishable right up to the umbrella margin. Because the well-developed muscles cover almost all area of the subumbrella, anastomosing canal system not visible, and circular canal unknown whether present or not.

Four subgenital cavities separated from each other by partitions. Genital ostia elliptical without projections at the entrance.

Mouth-arms, J-shaped in lateral view, fused with each other for the proximal one-fourth of their length (from the base, where they connect with the subumbrella, to distal end level of the scapulets), and divided into eight arms distally. Each of the eight arms has three wings, two of them face outwards (outer wing) and the other faces central axis (inner wing) (Fig. 9A, 9B). Each wing complexly branched; margin of the wings formed by a thin membrane, with numerous cirri, and is folded complexly into frills (Fig. 9C). Each cirrus has a small terminal knob. Windows open in the outer wings in 2–3 rows. Mouthlets open among the folds. Numerous whip-shaped appendages occur on the wings. The appendages on the lower part of each wing longer and denser than those on the upper part. At the bottom of the fused part of the mouth-arms, the upper ends of the inner wings connect to each other via a thin H-shaped membrane (Fig. 9D); center of the fused part



Fig. 8. *Nemopilema nomurai*. Whole body. (Photo. by K. Fujimura, October 1995, the Sea of Japan off Tsuruga, Fukui Pref.)

slightly depressed, without any appendages or filaments. A central mouth running through the center of the fused mouth-arms and reaching to near the bottom, but not open as the thin membrane covers the opening.

Scapulets, 16, located on fused portion of mouth-arms; distal half branches into two wings (Fig. 9E). Windows open. Upper side with complex branching and folded into frills, while lower side smooth. Numerous mouthlets open and tentacles located on the upper side.

Umbrella slightly reddish brown in color. Complex branches on the mouth-arms deep reddish brown.

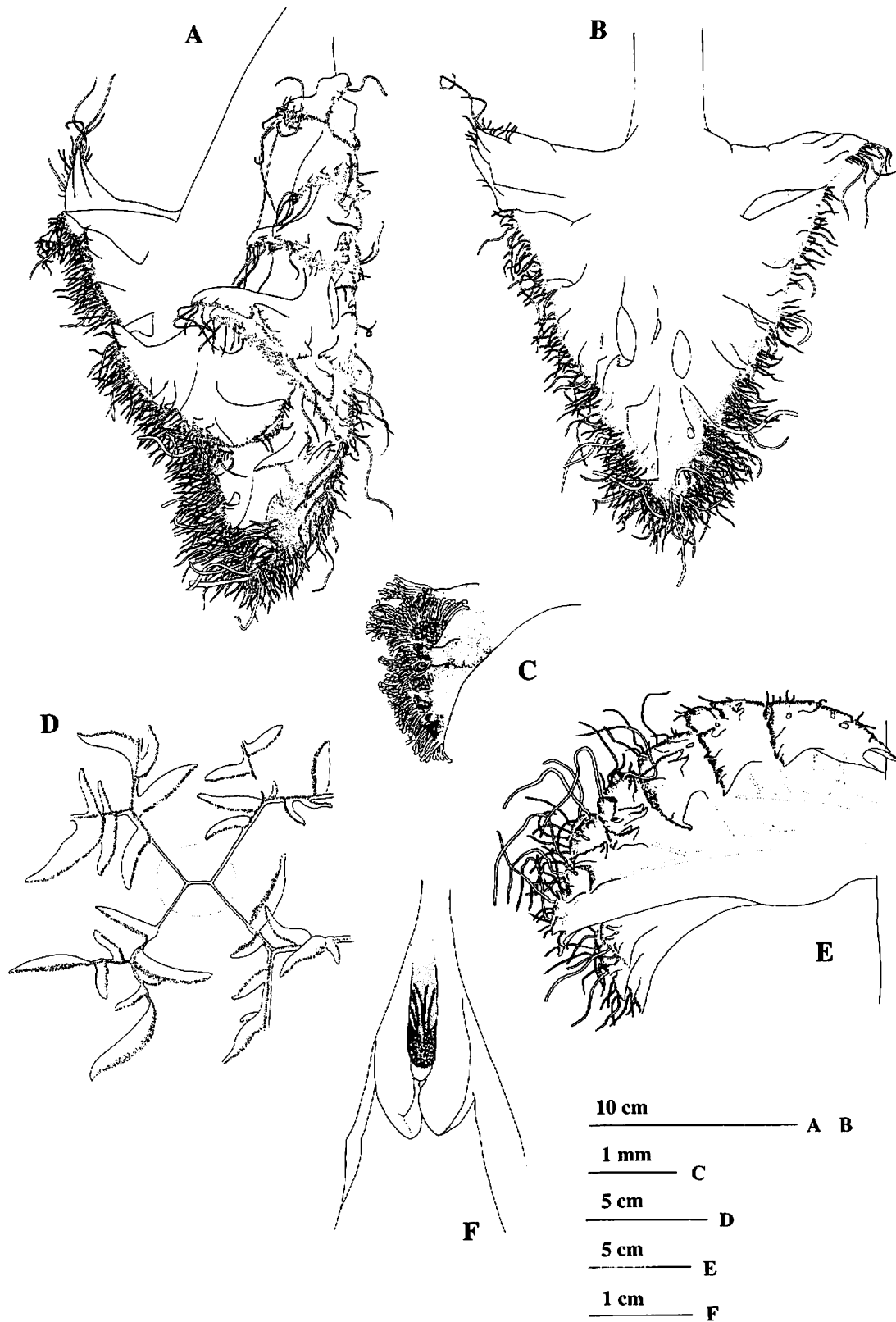


Fig. 9. *Nemopilema nomurai*. A. Mouth-arm, lateral view. The left margin is the outer wing on which tentacles occur densely and the right margin is the inner wing. B. Mouth-arm, outer view. A and B are sketched based on the same mouth-arm. C. Frill-like thin membrane with numerous cirri at the mouth-arm margin. D. Bottom of the coalescent mouth-arms. An H-shaped membrane connects the upper ends of the inner wings. E. Scapulet, lateral view. Distal half is divided into two wings. F. Rhopalar lap-pets and a sensory pit, exumbrellar view. All figures are sketched based on the specimen with an umbrella diameter of 69 cm.

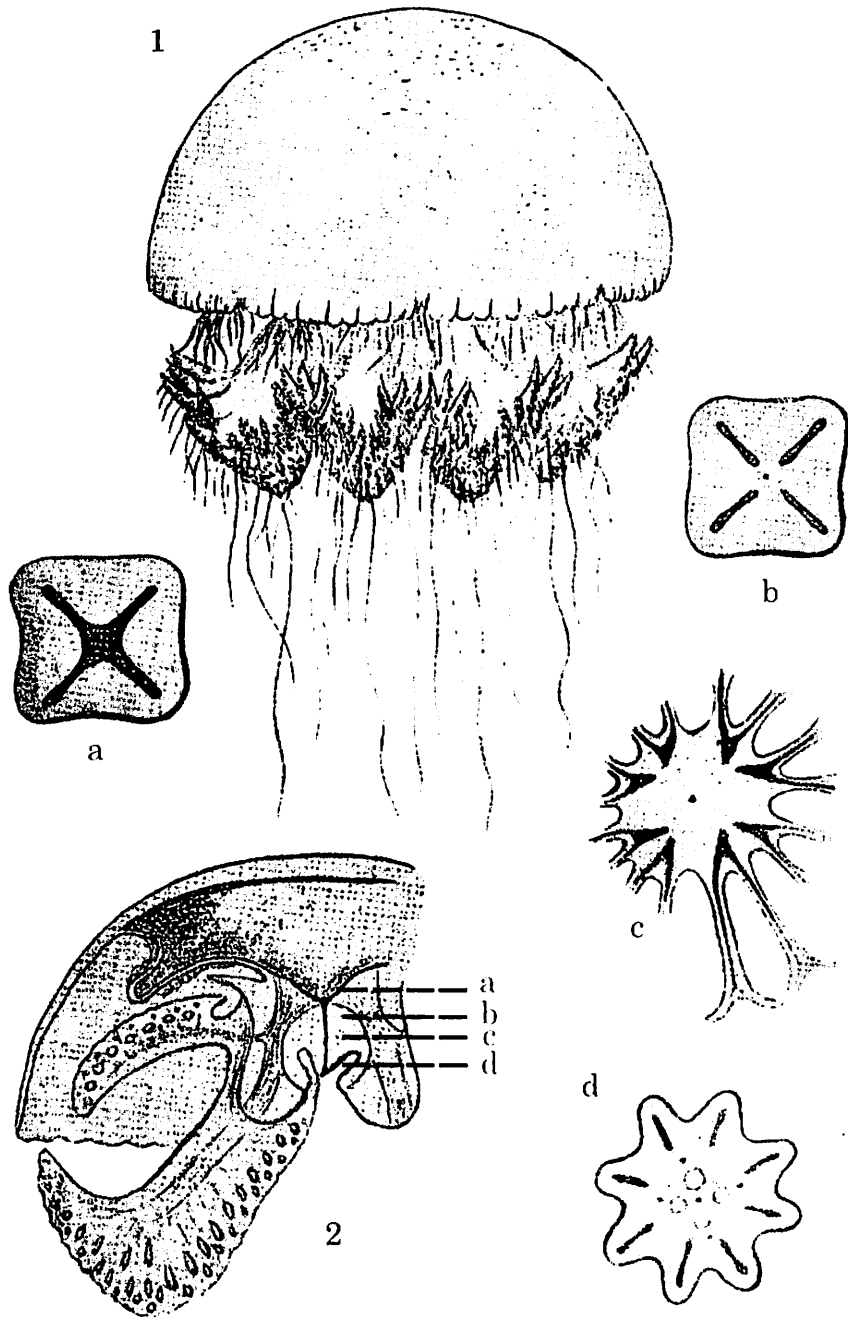


Fig. 10. *Nemopilema nomurai*. After original drawings by Kishinouye (1922).

1. Whole body, 2. Body in cross section, a. horizontal section along the line a, b. the same along the line b, c. the same along the line c, the same along the line d.

Remarks

Western scientists, probably due to language difficulties, have not so far seriously assessed the taxonomic status of *Nemopilema nomurai*. English translation and illustration of the original description (Kishinouye 1922) are as follows. We attempted to write just as he had described.

“Nemopilema nomurai Kishinouye: The type specimen was collected in December at Fukui Prefecture facing to

the Sea of Japan. With scapulets; mouth-arms without club-shaped appendages, but with numerous filaments; genital ostia without projections; mouth-arms and scapulets with numerous windows varying in size.

Umbrella, hemispherical and rigid (Fig. 10-1). Bell shallower and jelly thinner than in Rhopilema esculenta. Exumbrella with numerous small warts. The warts, that are located towards the center of the umbrella, longer than the marginal ones. Umbrella margin with total of about 120 lappets, about 12 lappets in each octant. Marginal clefts

deep and shallow alternately. At a glance, each octant seems to have 6 marginal lappets, and each lappet has a shallow depression. Circular muscle well-developed. Central part of subumbrella divided by 16 radial canals (Fig. 10-1).

Mouth-pillars, 4, short and narrow; their outer dimensions widen and the outer margin undulates as three waves. The mouth pillar longer than wide. Mid mouth-pillar is about one-fourth of width of subgenital cavity. Wide groove presents on upper surface. Inner ends fused to each other and form a horizontal shelf; the shelf is thin, and its outer margin pointed. Entrances of genital ostia located on inter-radial line; ellipsoid in shape, flat and with no projection.

Mouth-arm disc, wide and thick. Distal end of the disc divided into 8 mouth-arms. Four interradial sinuses located at depressed bottom of the disc; these sinuses directed to the outer and upper sides. Scapulets, 16, located adradially. They are depressed laterally and branched into two at the distal end; half-moon in shape in lateral view.

Mouth-arms, long, extending vertically; each branches into two at distal end, which is triangular in shape with three margins containing mouth-folds in cross section. Two of the three margins face outwards and the other margin faces inward. Mouth-folds well developed and extend laterally and upward, forming numerous triangular projections.

The mouth-arms contain numerous windows varying in size, as with *Lobonema smithi* described by Mayer (1910) from Manila Harbor, Philippines. Each window is slender and pointed on the upper bell-ward side, but slightly broad on the lower side. The windows are arranged in three rows vertically along the central axis of the mouth-arms, and two rows along the mouth-folds. Usually, the upper windows are larger than the lower ones. Larger specimens have larger windows. In the scapulets rounded windows usually in 2 rows located along the mouth-folds; in this case the lower windows are larger than the upper ones, although both are smaller than those located on the mouth-arms (Fig. 10-2). Both mouth-arms and scapulets with numerous filaments. The filaments on the scapulets are thick and short, whereas those on the lower part of the mouth-arms become gradually longer, and longest at the distal end which is purple in color.

Gastric cavity, slightly depressed vertically. Its outline cross-shaped, 16 straight canals running, perradially, interradially, and adradially, from gastric cavity to bell margin. There is a network of anastomosing canals between the above-mentioned 16 canals. Ring canal unclear. From the bottom of the gastric cavity, four perradial canals and a central mouth develop. In horizontal section the perradial canals laterally depressed, whereas the central mouth very narrow and hard to see (Fig. 10-2a, b, c, d). The four perradial canals slightly curve outwards and dichotomize at the umbrella-wards edge of the mouth-arm disk, then forming the adradial canals. Each adradial canal branches into two narrow canals, which enter the scapulets, branching extensively, and finally open into the mouth-folds of the

scapulets. After producing two branches, the adradial canals continue into the mouth-arms. Before entering the mouth-arms, one of the adradial canals produce thin canal that is directed inward- and downward to open at the cross-shaped mouth-folds on the bottom of the mouth-arm disc. The adradial canals, after entering the mouth-arms, branch several times, and open at the mouth-folds. The adradial canals divided into a main canal and many branches that directed three sides of the mouth-folds.

Umbrella colorless, margins of the lappets brown. Oral pillar, mouth-arm disc, scapulets, and mouth-arms are slightly brown. Mouth-folds chocolate brown or yellowish-brown.

Although the umbrella diameter of the specimens is about 90 cm, many become larger than this. The largest medusa is about 150 kg in weight. At Fukui Prefecture, this species occurs post-August, with highest abundances in October and November. All medusae are swept offshore or die during December. Small specimens have not yet been observed. Perhaps the present species dwells in bottom waters during its early developmental stages.

The present species exhibits many characters found in members of the genus *Rhopilema*. However, it can be distinguished from members of that genus by the absence of club-shaped appendages on the mouth-arms, and its lack of a projection near the genital ostium. I propose the name *Nemopilema nomurai*, n. gen. n. sp. for this species after Mr. Kan-ichi Nomura, Director of the Fukui Prefecture Fisheries Experimental Station."

This original description by Kishinouye falls within the bounds of our redescription based on specimens from Udagou.

Because of the presence of 16 scapulets, the present species is included in the superfamily Scapulatae, which is composed of two families, the Rhizostomatidae and the Stomolophidae. The Rhizostomatidae are characterized by (1) mouth-arms fused along the basal part only, (2) without a central mouth, and (3) the distal part of the mouth-arms forms 3-winged structure (see Cornelius 1997; Mianzan & Cornelius 1999). The present species is included in this family. Kramp (1961) considered that the family Rhizostomatidae includes three genera, i.e. *Eupilema*, *Rhizostoma*, and *Rhopilema*. *Eupilema* species have no appendage. *Rhizostoma* species have a club-shaped terminal appendage on each mouth-arm, precluding the placement of the present species within either of these genera. *Rhopilema* species resemble the present species in the presence of large scapulets and of numerous appendages. However, the present species is distinguished from members of the genus *Rhopilema* by; 1) presence of windows in the outer wings of the mouth-arms and scapulets, (2) absence of a projection in front of the subgenital ostium, and (3) absence of large appendages such as club-shaped or fusiform appendages on the mouth-arms. Apparently, judgments by Uchida (1936) and Kramp (1961) synonymizing

Nemopilema into the genus *Stomolophus* were in error. We suggest that the present species be retained in the genus *Nemopilema*.

Generic diagnosis of *Nemopilema* is as follows: size of exumbrellar warts increases towards the center; with a narrow central mouth covered by a membrane at the bottom of the fused portion of the mouth-arms; no projection at the entrance of the genital ostia; mouth-arms fused along the basal one-fourth of their length, J-shaped, with scapulatae, with windows in 2–3 rows; with whip-shaped appendages on the mouth-arms but lacking fusiform or club-shaped appendages (Table 1).

People in Japan sometimes use parts of this medusa as bait for sea bream fishing.

Distribution

Sea of Japan off Kyushu and Honshu, Japan (Kishinouye 1922; Shimomura 1959, present study). Liao-tung Bay, Pohai, and Yellow Sea coasts to off Shoushan, Zhejiang Province, China (Hon et al. 1978) and northern part of the East China Sea (Gao et al. 2002). Its distribution is perhaps restricted to the marginal seas of the northwestern Pacific around Korea, China and Japan. Its life history is not well known, but we assume that scyphistoma of this species may be produced along the coasts of the Korean Peninsula and northern China in spring. Liberated medusae grow rapidly and drift from the western reaches of the Sea of Japan to arrive along the coast of Japan after summer.

Nemopilema nomurai sometimes occurs so abundantly in the Sea of Japan that set-nets are broken and fish in the nets are damaged due to by-catches of this species. In 1958 the very large occurrence extended from the Sea of Japan even to the Tsugaru Strait and drifted south down along the Pacific coast of Japan (Shimomura 1959). Yasuda (1995) reported a fresh mass occurrence of the present species along the Japanese coast of the Sea of Japan in 1995. In 2000 and 2003, other very large occurrence, which were a serious fisheries nuisance, occurred along the Sea of Japan from end of August to November.

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