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Characterizations of juvenile stages of some semaeostome Scyphozoa (Cnidaria), with recognition of a new family (Phacellophoridae)

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Table of contents

Abstract

Phacellophora camtschatica has long been assigned to the semaeostome scyphozoan family Ulmaridae. Early stages (scyphistomae, strobilae, ephyrae, postephyrae, and young medusae) of the species were compared with those of several other semaeostomes currently assigned to Ulmaridae, Pelagiidae, and Cyaneidae. Juveniles of *P. camtschatica* did not strictly conform with characters of those of any of these families, and appeared intermediate between Cyaneidae and Ulmaridae. A new family, Phacellophoridae, is proposed to accommodate *P. camtschatica*.

Key words: *Chrysaora*, *Cyanea*, *Aurelia*, *Phacellophora camtschatica*, scyphistoma, ephyra, strobila, development, gastric system

Introduction

Semaeostomeae L. Agassiz, 1862 comprises an order of scyphozoan cnidarians traditionally grouped together based on the following medusoid characters: mouth arms four, large, surrounding a single central mouth opening; tentacles if present hollow, occurring on periphery of umbrella or subumbrella (Mianzan & Cornelius 1999). Recent molecular studies reveal that the group is polyphyletic (Collins 2002, Collins *et al.* 2006).

Within the order, family Ulmaridae Haeckel, 1880 comprises an assemblage of several subgroups having uncertain affinities and few common features. The only characters unifying Ulmaridae are: (1) presence of

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simple and/or branched radial canals, (2) a ring canal, and (3) presence or absence of a subgenital cavity (Mayer 1910; Kramp 1961; Russell 1970; Mianzan & Cornelius 1999).

Among ulmarids, the subfamily Sthenoniinae L. Agassiz, 1862 embraces medusae with subumbrellar tentacles. It was established to accommodate *Sthenonia albida* Eschscholtz, 1829, a species described from eastern Russia (coast of Kamtschatka). *Phacellophora camtschatica* Brandt, 1835, described from the same area, was originally assigned to the same subfamily.

Phacellophora camtschatica has been of interest since its discovery because of its peculiar anatomy – having some characters in common with both species of *Aurelia* Lamarck, 1816 and *Cyanea* Péron & Lesueur, 1810 (Brandt 1835; Verrill 1869; Haeckel 1882; Vanhöffen 1906; Kishinouye 1910; Mayer 1910; Bigelow 1913). Four nominal species have been assigned over the years to *Phacellophora*, but only *P. camtschatica*, reportedly with a worldwide distribution, is now considered valid (Bigelow 1913; Fedele 1937a, b).

Referral of *P. camtschatica* to Ulmaridae has been based on morphology of the gastric system of the medusa stage. However, scyphistomae and ephyrae of the species described by Widmer (2006) and Straehler-Pohl and Jarms (2010) share few characters with those of species of *Aurelia*, the only ulmarid genus with known life cycles. Moreover, *P. camtschatica* formed a clade within order Rhizostomeae Cuvier, 1799 in a phylogeny presented by Collins (2002) and Collins *et al.* (2006), whose hypothesis was based on molecular studies.

Our study was undertaken to clarify taxonomic affinities of *P. camtschatica* from observations on morphology of different developmental stages, and on molecular data.

Material and methods

Species studied. We compared morphology and development of the early stages of *Phacellophora camtschatica* with representatives of all other semaeostome families: Cyaneidae [*Cyanea capillata* (Linnaeus, 1758) and *Cyanea lamarckii* Péron & Lesueur, 1810], Pelagiidae [*Chrysaora fuscescens* Brandt, 1835, *Chrysaora lactea* Eschscholtz, 1829, *Sanderia malayensis* Goette, 1886], and Ulmaridae [*Aurelia aurita* (Linnaeus, 1758), *Aurelia limbata* Brandt, 1835] (Table 1). These were bred and cultured in our laboratories at the Zoological Institute in Hamburg (Germany), the Monterey Bay Aquarium in California (USA), and the Department of Zoology, São Paulo (Brazil).

Cultivation. Different developmental stages (scyphistomae, strobilae, ephyrae, post-ephyrae, medusae) were maintained, following procedures described by Jarms *et al.* (2002), Morandini *et al.* (2004) and Widmer (2006, 2008a, b), in 250 mL glass dishes containing natural seawater or in aerated aquaria. Cultivation details and origin of cultures are summarized in Table 2.

Measurements. Morphology and measurements of all scyphistomae (Fig. 1a, b), strobilae (Fig. 3), and ephyrae (Fig. 2a, b) used in the study were compared from photographs taken under the same conditions with a digital camera (ColorView, Soft Imaging System, GmbH). Mature scyphistomae of equal sizes, and strobilae at different stages of strobilation, were oriented laterally in a glass Petri dish (Ø = 5 cm). Ephyrae, with the manubria facing the objective lens of the camera, were placed in depression slides and covered with cover slips. Petri dishes and depression slides were filled with the same water as the culturing dishes. Adaptation time was about 2–5 minutes. Photographs were taken as soon as scyphistomae, strobilae, and ephyrae were fully expanded to avoid extreme variations in temperature, and promptly returned to their culture dishes. Measurements were made, and pictures edited and evaluated, using the program analySIS® (Soft Imaging System GmbH).

Standard measurements for scyphistomae were used (see also Fig. 1b): Total Body Length (TBL) = length from hypostome tip to basal disc; Calyx Length (CL) = length from gastric cavity base to tentacle crown rim; Hypostome Length (HL) = length from tentacle crown base to hypostome tip; Mouth Disc Diameter (MDD) = widest diameter of mouth disc; Stalk Length (StL) = length from basal disc to gastric cavity base. Measuring points and measurements in ephyrae are as described by Straehler-Pohl and Jarms (2010) (see also Fig. 2b): Total Body Diameter (TBD), Central Disc Diameter (CDD), Total Marginal Lappet Length (TMLL), Lappet Stem Length (LStL), Rhopalial Lappet Length (RLL).

TABLE 1. Recent classification of the studied semaeostome species (following Mayer 1910; Kramp 1961; Mianzan & Cornelius 1999). Note that the genus *Phacellophora* was formerly assigned to the family Ulmaridae and the subfamily Sthenoniinae L. Agassiz, 1862.

- Phylum Cnidaria Verrill, 1865
  - Subphylum Medusozoa Petersen, 1979
    - Class Scyphozoa Goette, 1887
      - Subclass Discomedusae Haeckel, 1880
        - Order Semaeostomeae L. Agassiz, 1862
          - Family Cyaneidae L. Agassiz, 1862
            - Genus *Cyanea* Péron & Lesueur, 1810
              - *Cyanea capillata* (Linnaeus, 1758)
              - *Cyanea lamarckii* Péron & Lesueur, 1810
          - Family Pelagiidae Gegenbaur, 1856
            - Genus *Chrysaora* Péron & Lesueur, 1810
              - *Chrysaora fuscescens* Brandt, 1835
              - *Chrysaora lactea* Eschscholtz, 1829
            - Genus *Sanderia* Goette, 1886
              - *Sanderia malayensis* Goette, 1886
          - Family Phacellophoridae fam. nov.
            - Genus *Phacellophora* Brandt, 1835
              - *Phacellophora camtschatica* Brandt, 1835
          - Family Ulmaridae Haeckel, 1880
            - Subfamily Aureliinae L. Agassiz, 1862
              - Genus *Aurelia* Lamarck, 1816
                - *Aurelia aurita* (Linnaeus, 1758)
                - *Aurelia limbata* Brandt, 1835

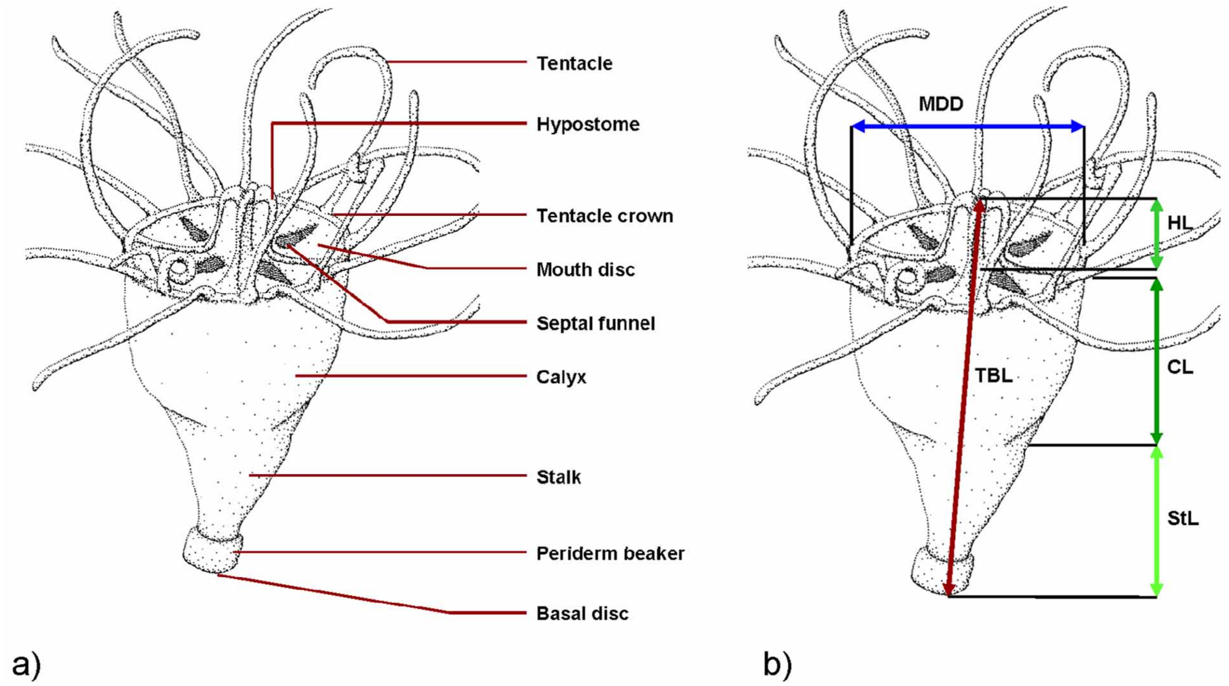


FIGURE 1a+b. Anatomy, measuring points and measurements defined for scyphistomae; CL: calyx length; HL: hypostome length; MDD: mouth disc diameter; StL: stalk length; TBL: total body length.

To compare body dimensions and proportions, the following proportion quotients (%) were used: six scyphistomae and six ephyrae of 2–3 strobilae per species were measured.

Scyphistomae: measurements compared to body length (CL / TBL x 100; HL / TBL x 100; StL / TBL x 100; MDD / TBL x 100); measurements compared to calyx length (MDD / CL x 100).

Ephyrae: measurements compared to body diameter (CDD / TBD x 100; TMLL / TBD x 100); measurements compared to lappet length (RLL / TMLL x 100; LStL / TMLL x 100).

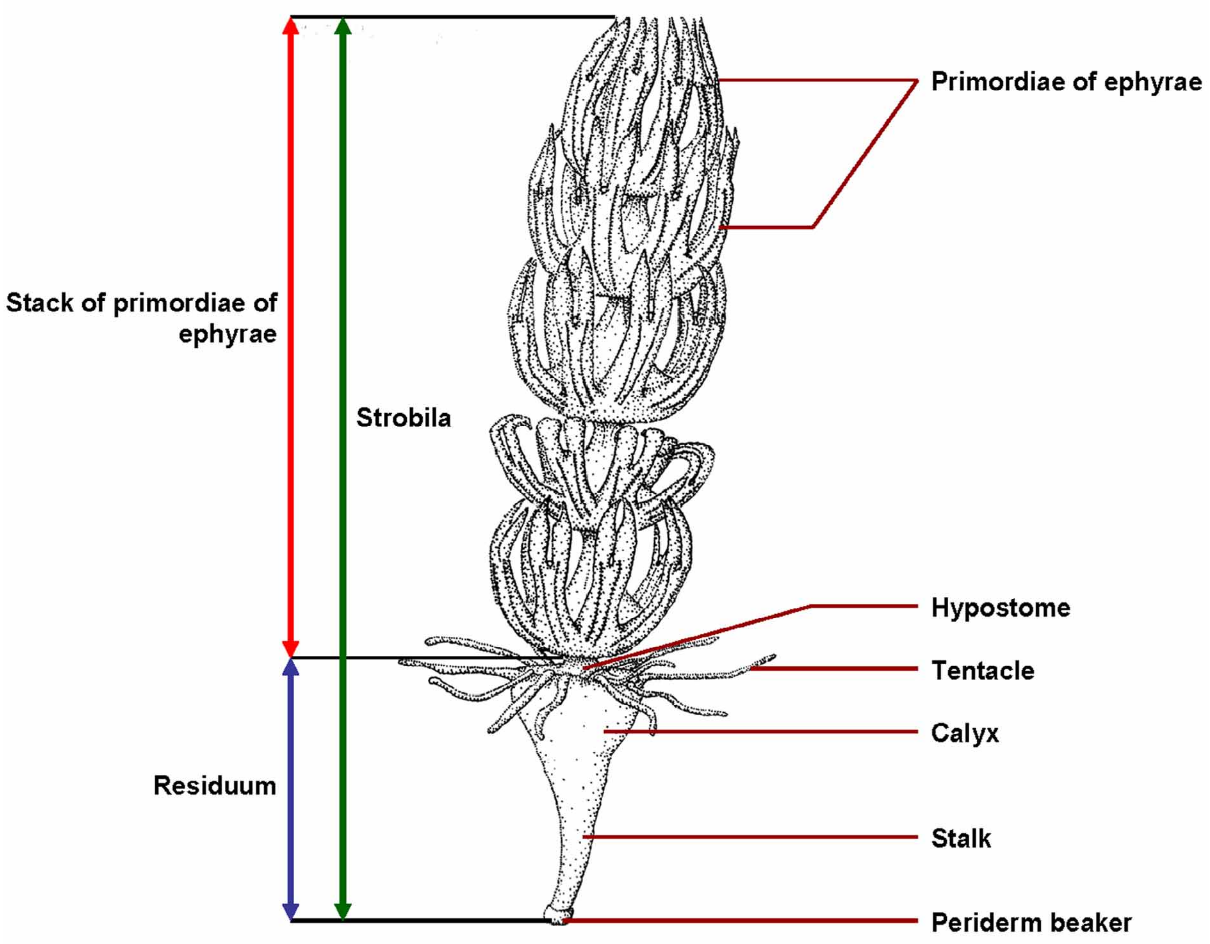


FIGURE 2. Sketch of the end phase of a strobila of *Cyanea capillata*.

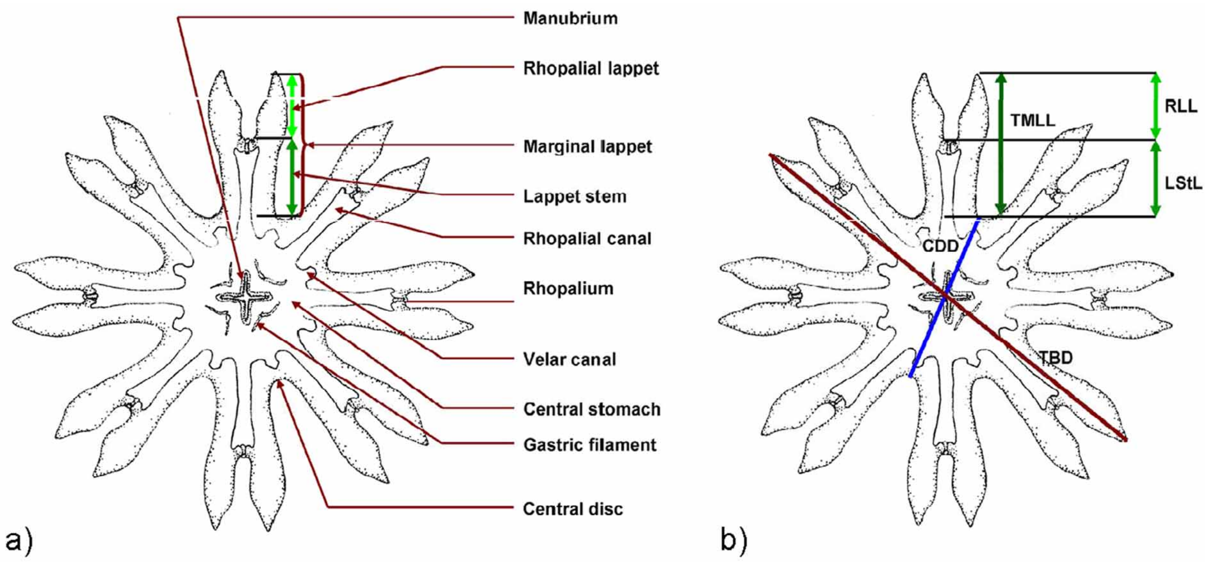


FIGURE 3a+b. Anatomy, measuring points and measurements defined for ephyrae; CDD: central disc diameter; LStL: lappet stem length; RLL: rhopalar lappet length; TBD: total body diameter; TMLL: total marginal lappet length.

Observations on gastric system development. Comparisons of gastric system development were based on photographs of randomly selected ephyrae taken 4 h after feeding, when opacity of their gastrovascular cavities was increased by digested food particles. Photos were taken every second day.

TABLE 2. Temperature and cultivation conditions of the studied species.

Species	Origin of cultures	Temperature [°C] (polyp)	Temperature [°C] (strobila)	Temperature [°C] (ephyra)	Temperature [°C] (medusa)
Sanderia malayensis	?[#]	15–25, a+b	20–25, a+b	20–25b	20–25b
Chrysaora fuscescens	Monterey Bay, California, USA	14c	14c	8–14c+d	14d+e
Chrysaora lactea	Cananéia, southeastern Brazil	22, a	22, a	20–25, b	20–25, b
Cyanea lamarckii	Helgoland, German Bight	15, a	10 a	10–15 a	10–15 a
Cyanea capillata	Helgoland, German Bight	10, a	5 a	5–10 a	10–15 a
Phacellophora camtschatica	Monterey Bay, California, USA	15, a	15 a	15 a, 14 b	14 b
Aurelia aurita	Helgoland, German Bight	10, a	5–10, a	15–25, a+b	23–25, b
Aurelia limbata	Japan	15, a	5–10, a	15–25, a+b	23–25, b

\# the origin of these *Sanderia* cultures from the wild is uncertain as the laboratory in Hamburg received the cultures from the Monterey Bay Aquarium which received the culture from the "Sea Life Center" in England and they could give no further information (Adler 2008)

a glass dishes (250–400 mL) in incubator without daylight
b aerated aquarium with daylight
c glass dishes (petri dishes) kept inside an aquarium with water flowing through
d pseudokreisel (two-foot diameter; Widmer 2008a)
e kreisel (four to five-foot diameter round kreisel or stretch kreisel; Widmer 2008a)

Results

Phacellophora camtschatica

Scyphistoma. Mature scyphistomae (Plate 1, Fig. B) had a mean height of 7.62 mm and a mean oral disc width of 2.45 mm (Table 4c). Tentacles were arranged in a single whorl (ranging from 30–44, mean = 38) around a slightly sunken mouth disc and a cylindrical, four-lipped hypostome. Scyphistomae were yellowish-white to pale orange in colour. The calyx, perched on a stalk of medium length (44% of TBL), was slender and funnel-shaped. The widest body diameter was the mouth disc (70% of the calyx length). The basal disc and ca. 50% of the stalk were enclosed by a narrow, funnel-shaped periderm tube (Fig. 4) left behind when the scyphistoma changed locations (see below).

Asexual reproduction. This involved typical lateral scyphistoma budding (at calyx and stalk junction, typically one bud per scyphistoma at a time), stolonal budding, and polydisc strobilation (Plate 2, Fig. B; strobilation rates: Table 5).

Two stolonal budding types were observed. In Type 1, thin stolons were produced at the junction of calyx and stalk. One or two new scyphistomae, formed in the middle of the stolon, detached from the stolon after forming a basal disc. In stolonal budding Type 2, a new periderm tube was formed at the tip of the stolon. The old scyphistoma was dragged by the stolon from the old periderm tube, and a tiny tissue residuum remaining in the old tube died after a few days. The stolon was resorbed by the newly located parental scyphistoma.

FIGURE 4. *Phacellophora camtschatica*: stalk with funnel-shaped periderm tube.

Ephyra. Newly liberated ephyrae (Plate 3, Fig. B) had a total mean body diameter (TBD), from lappet tip to lappet tip, of 7.77 mm (range: 3.5–10.8 mm, Table 6c) and a mean central disc diameter (CDD) of 5.85 mm, which comprised about 57% of the TBD. Ephyrae had 13–18 marginal arms, flame-shaped and pointed rhopalial lappets, and a single rhopalium per lappet stem, situated between the two rhopalial lappets (Table 6c). Rhopalial lappets measured 53% of the total marginal lappet length (TMLL). The manubrium was of moderate length (≈28% of CDD). There were 1–2 gastric filaments per quadrant in the central stomach. There were 0–2 single tentacle buds above the velar canals. Ephyrae were yellowish in colour with a yellowish-orange gastric system; white nematocyst clusters were scattered over the exumbrella.

During subsequent development, velar lappets were not formed but the umbrella rim between the rhopalial lappets extended and grew outwards, forming sinus-like outward curves (pseudo-velar lappets) when the medusa matured.

Development of ephyral gastric system. The gastric system of newly-released ephyrae (Table 3e, Fig. “Stage 1”; Plates 4 and 5, Figs. A) consisted of a central stomach, 13–18 non-forked, arrow-shaped rhopalial canals, and 13–18 very short, non-forked, arrow tip-shaped velar canals. The tips of the rhopalial canals ended at the base of the rhopalium. The tips of the velar canals ended a short distance above the stomach. One or two single tentacle buds were present on the subumbrella above velar canal tips (Plate 4, Figs. B and F).

In the second stage (Table 3e, Fig. “Stage 2”; Plate 4, Figs. D and H) rhopalial canals developed *3–4 pairs of short side branches*. The velar canals grew in *centrifugal direction*. The sides of each velar canal tip developed branches just below its tip (Plate 4, Fig. G; Plate 5, Fig. B) which fused with the first side branches of the rhopalial canals (Plate 4, Fig. G) forming a *primary ring canal*.

The velar canals and the attached rhopalial side branches grew centrifugally towards the umbrella rim. The primary ring canal morphed into sinus curves (Plate 5, Fig. C). The *second pair of rhopalial canal side branches* fused with the sinus curves when the velar canal tips reached their level (Table 3e, Fig. “Stage 3”) forming a *secondary ring canal*.

In the 4th stage (Table 3e, Fig. “Stage 4”; Plate 5, Fig. D–F) the steps of stage 3 were repeated once or twice until a *final ring canal* was formed below the rhopalia level (Plate 5, Fig. D). The final ring canal produced single tentacles above the velar canal tips (Plate 5, Figs. D and E), and next to the first tentacle buds in a chronological order to form a single row along the ring canal. Additionally, unbranched *blind ending canals* were produced by the ring canal (Plate 5, Fig. F), and grew in centrifugal direction into the outer region of the marginal lappets. New canal connections formed by "Ausstülpungen" (= diverticula from gastric canals, defined by Stiasny 1921; Uchida 1926), others were disconnected by “Inselbildung” (= island formation, meaning the fusion of the roof and bottom of the gastric cavities, defined by Stiasny 1921; Uchida 1926).

Morphology and developmental stages of Pelagiidae, Cyaneidae, and Ulmaridae

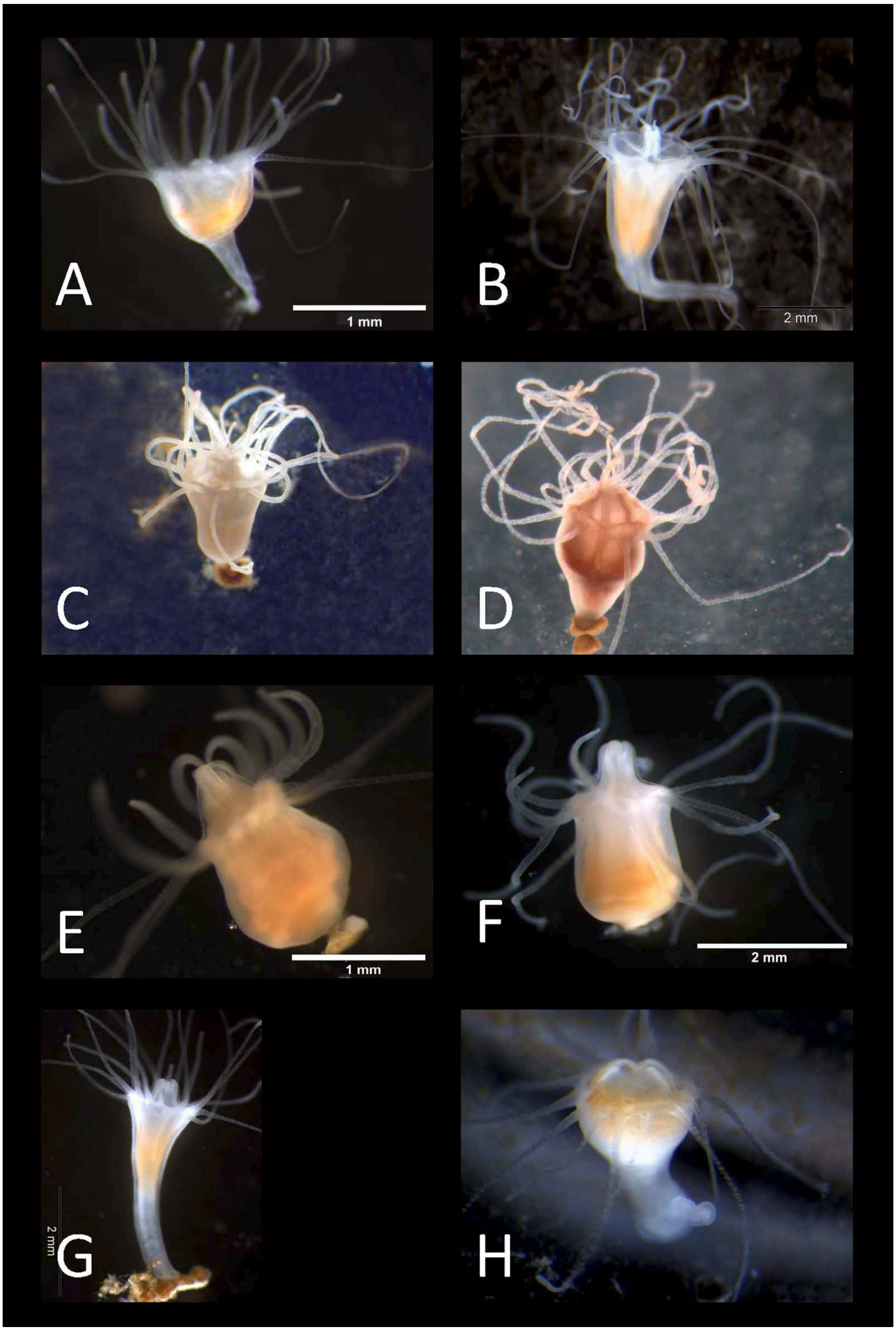


PLATE 1. Polyps of observed species; A= *Sanderia malayensis*, B = *Phacellophora camtschatica*, C = *Chrysaora fuscescens*, D= *Chrysaora lactea*, E = *Cyanea lamarckii*, F = *Cyanea capillata*, G = *Aurelia aurita* (Helgoland), H= *Aurelia limbata*

Scyphistomae (Plate 1):

Pelagiidae (*Sanderia malayensis, Chrysaora fuscescens, and Chrysaora lactea*). Sizes of scyphistomae of the three pelagiid species (Plate 1, Figs. A, C and D) ranged from an average total body length (TBL) of 1.2 mm in *Chrysaora lactea*, to over 1.59 mm in *Sanderia malayensis*, to 2.96 mm in *Chrysaora fuscescens* (Table 4a). The mouth disc diameter (MDD) in all three species equalled the widest body diameter (up to 0.7 fold of the TBL in *Chrysaora lactea*), giving the calyx a cone (*C. fuscescens*, *C. lactea*) to broad funnel-like (*S. malayensis*) shape. Numbers of tentacles ranged from 12–21 (mean = 16) in *C. fuscescens* and *C. lactea* and 22–29 (mean = 25) in *S. malayensis*. In all three species the single whorl of tentacles surrounded a slightly sunken peristome and the short, four-lipped, cone-shaped hypostome (12% of TBL in *Sanderia*). All three species possessed a stalk, which was rather short in the species of *Chrysaora* (≈38% of TBL in *C. lactea*) compared with the long stalk of *S. malayensis* (≈50% of TBL). The basal disc and foot region in polyps of *Chrysaora* were enclosed by a solid periderm collar, while in *Sanderia* the lower part of the stalk and the basal disc were enclosed by a thin, transparent peridermal cuticle.

Cyaneidae (*Cyanea lamarckii* and *Cyanea capillata*). Mature scyphistomae of the cyaneids *C. lamarckii* and *C. capillata* were much alike (Table 4b). Those of *C. capillata* were slightly larger (mean height: 2.71; mean peristome diameter: 1.59) than ones of *C. lamarckii* (mean height: 2.21; mean peristome diameter: 1.13). In both species, mean tentacle number was 16 and a large, four lipped, cone-shaped hypostome (up to 28% of TBL in *C. capillata*) was present. However, differences were noted in the shape of the calyx. That of *C. lamarckii* was amphora-shaped (Plate 1, Fig. E), the widest body diameter located in mid-calyx; that of *C. capillata* was vase-shaped (Plate 1, Fig. F), the widest body diameter located near the calyx base (calyx length: 65% of TBL in both species). In both species, the widest body diameter equalled the calyx height. The stalk was very short in both species (7 or 10% of the TBL), and the basal disc was enclosed by a periderm collar as in species of *Chrysaora*.

Ulmaridae, subfamily Aureliinae (*Aurelia aurita* and *Aurelia limbata*). Scyphistomae of the two species of *Aurelia* were distinctly different (Plate 1, Figs. G and H). Those of *A. aurita* were much larger (3.18 mm TBL; 1.19 mm MDD) than ones of *A. limbata* (1.27 mm TBL; 0.83 mm MDD). Tentacle numbers ranged from 18–28 (mean = 23) in *A. aurita* but were constant in number (16) in *A. limbata* (Table 4d). In both species, as in the pelagiids, the MDD was the widest body diameter. The calyx of *A. aurita* was slim and funnel-shaped (66% of the TBL), the MDD was only 0.6 times the calyx length while the MDD in *A. limbata* was 1.5 times the length of the cup to bowl-shaped calyx (45% of the TBL). As in the pelagiid and cyaneid species described above, the hypostome in scyphistomae of Aureliinae studied here were four-lipped, cone-shaped and rather short (17–19% of the TBL). Their stalks were short (17% of TBL in *A. aurita* and 36% of TBL in *A. limbata*) and, as in most described species, the base was enclosed by a periderm collar.

Asexual reproduction and strobilation (Plate 2):

Asexual reproduction (Table 4a–c) in observed species of Pelagiidae (except *Sanderia malayensis*), Cyaneidae, and Aureliinae occurred by typical lateral scyphistoma budding (buds arising at junction of calyx and stalk, with typically one bud per scyphistoma at a given time), and the production of podocysts and pedalocysts. Pedalocyst production was more frequent than scyphistoma budding, with the cysts being produced by thin stolons arising at the junction of calyx and stalk. The stolons attached to the substrate, and a periderm-enclosed pedalocyst formed around the distal, attached portion. Once the pedalocyst was closed off, the stolon detached and retracted and was absorbed by the scyphistoma. Podocysts were formed beneath the basal disc and had the same external appearance as pedalocysts. Scyphistomae of Aureliinae were observed to proliferate also by lateral stolonal budding. Stolonal budding initially resembled pedalocyst production, but a tiny scyphistoma was formed at the tip of the stolon rather than a cyst. The budded scyphistoma attached to the substrate, and the stolon detached and was resorbed by the parent.

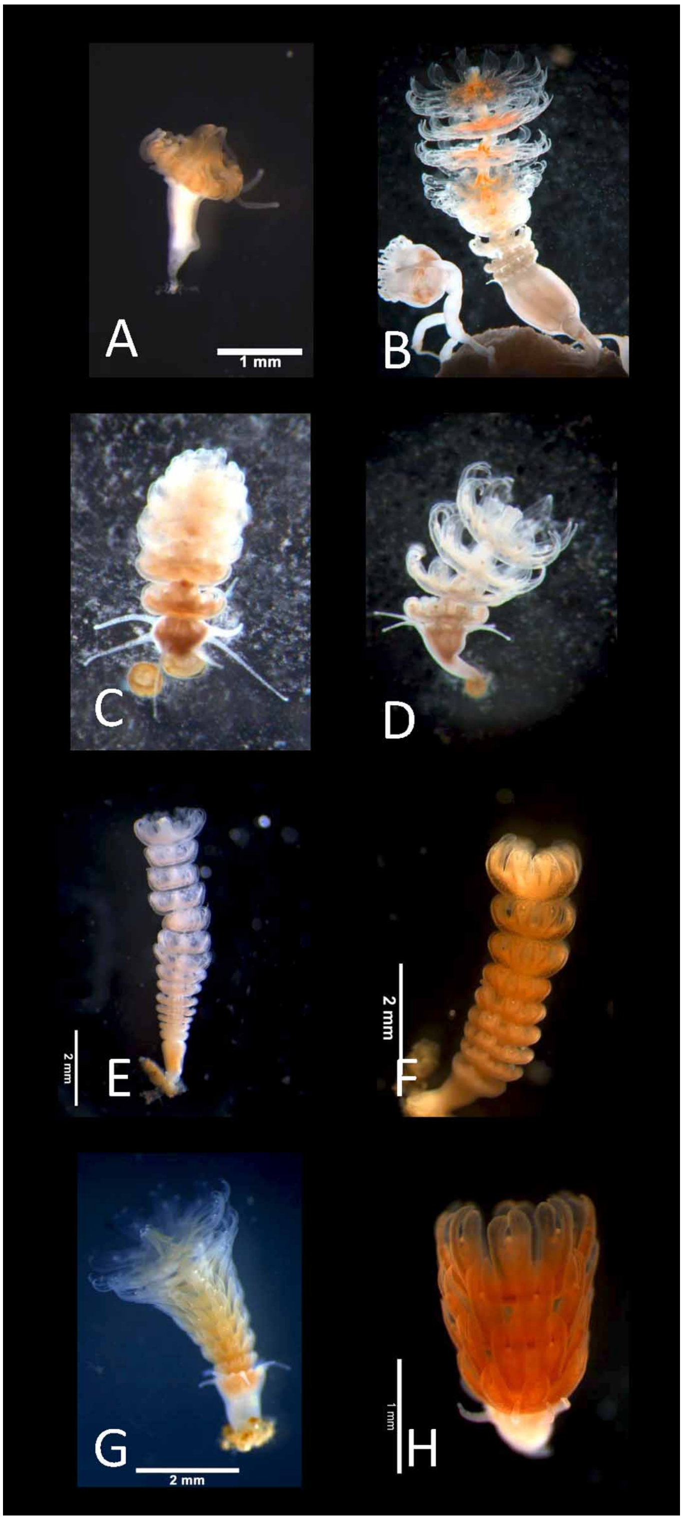


PLATE 2. Strobilae of observed species; A = *Sanderia malayensis*, B = *Phacellophora camtschatica*, C = *Chrysaora fuscescens*, D = *Chrysaora lactea*, E = *Cyanea lamarckii*, F = *Cyanea capillata*, G = *Aurelia aurita* (Helgoland), H = *Aurelia limbata*.

In *Sanderia malayensis*, combined scyphistoma and stolon budding was observed. At the junction of calyx and stalk, a scyphistoma bud with distal oral pole was formed. During development of hypostome and tentacles on the bud, another bud was formed on the opposite side of the scyphistoma, which grew rapidly into a long stolon. The stolon was very supple, and studded at the free end. As soon as this studded free end finally settled on the substrate, the parent scyphistoma began to form a constriction between scyphistoma bud and stolon. The former stalk of the original scyphistoma developed into the stalk of the bud, while the stolon developed into the new stalk of the parent. This form of asexual reproduction was noticed only in *S. malayensis*, which produced no resting stages such as podocysts or pedalocysts.

Strobilation in all observed species was polydiscous (strobilation rates: Table 5) except in *Sanderia malayensis*, which produced one ephyra at a time (monodisc strobilation).

Ephyra (Plate 3):

Although ephyra morphology of observed semaeostomes was quite similar, both *Sanderia malayensis* and *Phacellophora camtschatica* had more than the eight rays characteristic of the others (Table 6a–c).

Sanderia malayensis. Ephyrae had more than eight rays (Plate 3, Fig. A), with very short lappet stems (40% of total marginal lappet length = TMLL) and long, bread-knife-shaped rhopalial lappets (60% of TMLL). Radial canals were club-shaped and forked (Table 6a). Newly detached ephyrae of *S. malayensis* often showed the so called "typical *Chrysaora*-nematocyst pattern" on the exumbrella: two parallel ovoid clusters below the rhopalia on each lappet stem and a circle of round nematocyst clusters above the central stomach (Fig. 5). No marginal tentacle buds were observed.

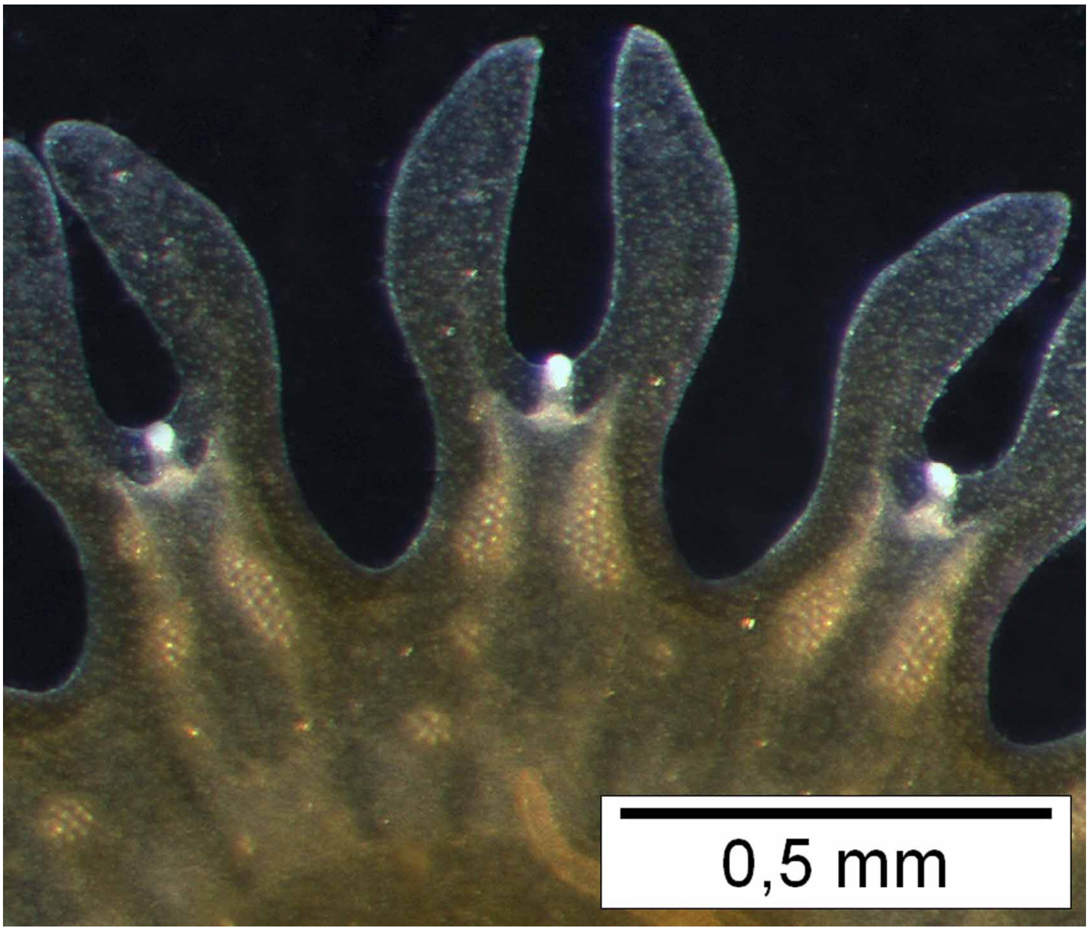


FIGURE 5. *Sanderia malayensis* (dorsal view), typical *Chrysaora*-nematocyst pattern on the exumbrella (photo: Laetitia Adler).

***Chrysaora fuscescens* and *Chrysaora lactea*.** Ephyrae of these species (Plate 3, Figs. C and D) had very short lappet stems (40–42% of TMLL) with long, lancet-like rhopalial lappets (58–60% of TMLL). Rhopalial and velar canals were all slightly forked. The fork tips of the velar canals were level with the base of the lappet stems. The exumbrella bore patterns of nematocyst clusters typical of *Chrysaora* and *S. malayensis*.

***Cyanea lamarckii* and *Cyanea capillata*.** Cyaneid ephyrae (Plate 3, Figs. E and F) also had short lappet stems (43–44% of TMLL) with long lancet-like rhopalial lappets (56–57% of TMLL) and forked radial canals. However, the fork-tips of the velar canals reached well into the stem lappets, being even with the base of the rhopalia in *C. lamarckii* and reaching to the tips of the rhopalia into the rhopalial lappets in *C. capillata*. Typical nematocyst clusters were absent, but all newly detached ephyrae of *C. capillata* had single marginal tentacle buds.

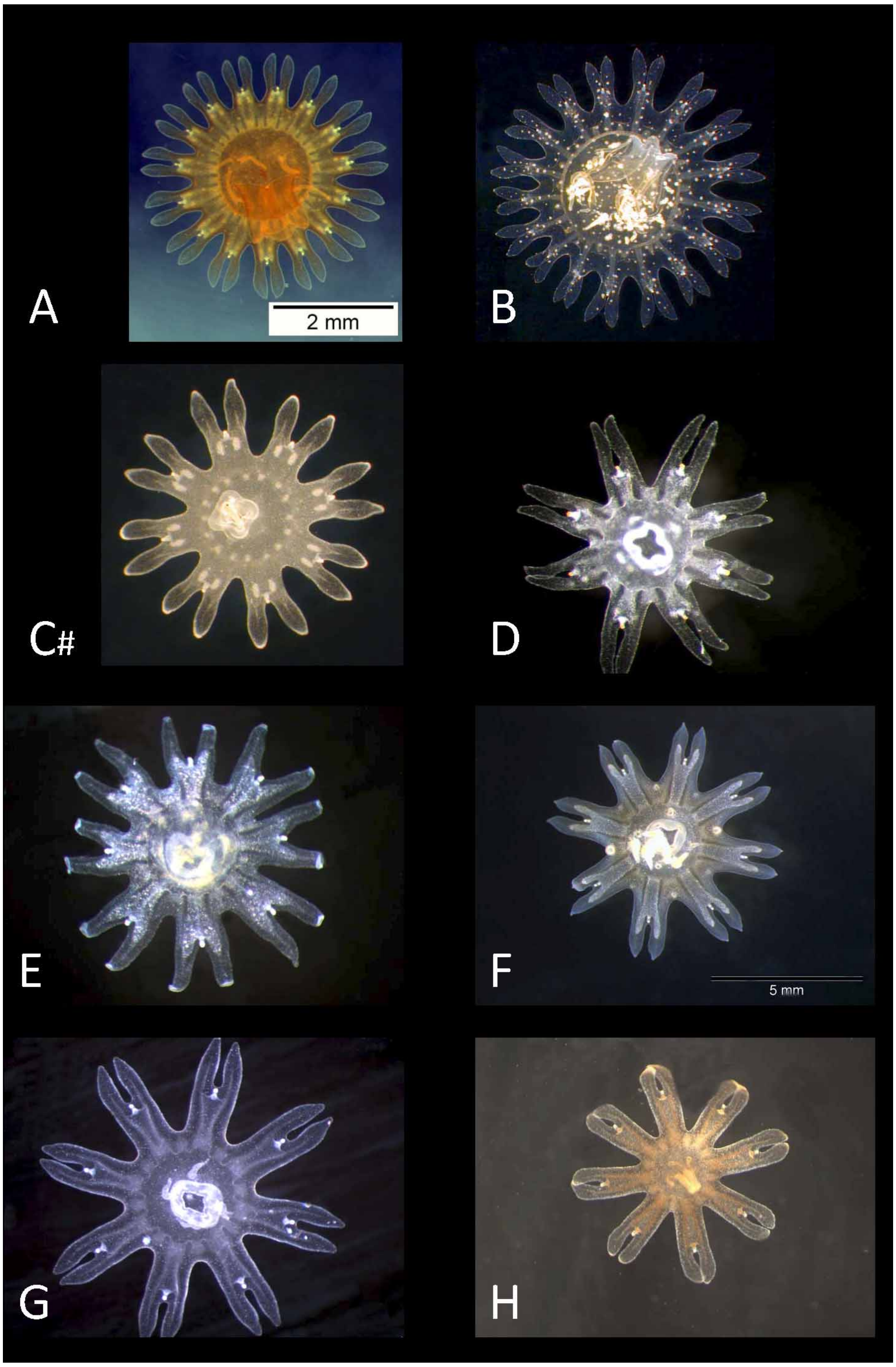


PLATE 3. Ephyrae of observed species; A = *Sanderia malayensis*, B = *Phacellophora camtschatica*, C = *Chrysaora fuscescens*, D = *Chrysaora lactea*, E = *Cyanea lamarckii*, F = *Cyanea capillata*, G = *Aurelia aurita* (Helgoland), H = *Aurelia limbata*.

***Aurelia aurita* and *Aurelia limbata*.** In ephyrae of Aureliinae (Plate 3, Figs. G and H), lappet stems were rather long (52% or 58% of TMLL) compared to those of *Chrysaora* or *Cyanea*. Rhopalial lappets were less pointed, and only the rhopalial canals of *A. aurita* were slightly forked. Rhopalial canals of *A. limbata* were spade-shaped, and the velar canals of both species were unforked and rhombus/diamond-shaped. Ephyrae of both species lacked typical nematocyst cluster patterns and marginal tentacle buds when newly detached.

Development of gastric system of ephyrae (Table 3):

***Sanderia malayensis*, *Chrysaora fuscescens* and *Chrysaora lactea*.** The gastric system of newly-released pelagiid ephyrae (Table 3a-c, Figs. “Ephyra, stage 0”, “Stage 1”) consisted of a central stomach, eight or 16 slightly forked rhopalial canals, and eight or 16 slightly forked velar canals.

In the second stage (Table 3a–c, Fig. “Stage 2”) the velar canals grew in a *centrifugal direction*, following the outgrowing rim of the umbrella. Single primary tentacles (interradial) budded from the margin of the subumbrella at the base of the cleft between the marginal arms as extensions of the velar canals. Rhopalial canals enlarged in this stage by size growth.

In the 3rd stage (Table 3a–c, Fig. “Stage 3”), gastric pouches grew further in a centrifugal direction into the marginal lappets. The side edges of the pouches in the young medusae of *Sanderia malayensis* became frayed. This was noted as the final stage of *Sanderia malayensis*.

In *Chrysaora fuscescens* and *C. lactea*, the terminal ends of the velar canals extended laterally, with the outer edges pushing into the rhopalial canal region. At the marginal corners of the velar canals secondary tentacles began to arise, and rhopalial lappets developed slight embayments at their margins opposite the position of the developing tentacles. When the secondary tentacles were fully developed, the embayments in the rhopalial lappets turned into slits that formed parts of the outer rhopalial lappet region into new tentacular lappets. This was noted as the final stage of *Chrysaora fuscescens* (Table 3b, Fig. “Stage 4”).

Some observed specimens of *Chrysaora lactea* developed another set of tertiary tentacles between the primary and the secondary tentacles, as with the secondary tentacles. Tentacular lappets split in two above the tertiary tentacles (Table 3c, Fig. “Stage 5”).

***Cyanea lamarckii* and *Cyanea capillata*.** The gastric system of newly-released cyaneid ephyrae (Table 3d, Figs. “Ephyra, stage 0”, “Stage 1”) consisted of a central stomach, eight deeply forked rhopalial canals, and eight deeply forked velar canals. One single, or two opposite-situated primary tentacle bulbs were visible below the cleft between the marginal lappets above the velar canals in *C. capillata*.

In the second stage, as in pelagiids, velar canals grew in a *centrifugal direction*, following the outgrowing rim of the umbrella (Table 3d, Fig. “Stage 2”). The single primary tentacles (interradial) budded from the subumbrella at the base of the cleft between the marginal arms as extensions of the velar canals. The rhopalial canals enlarged at this stage by size growth.

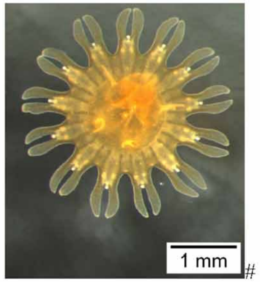
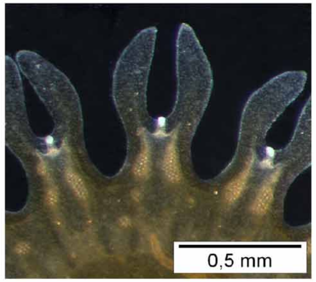
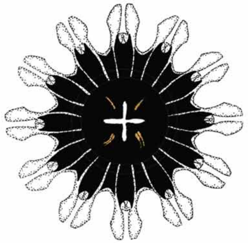
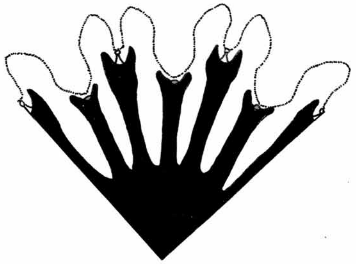
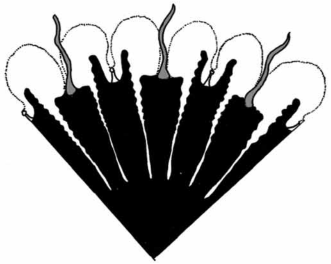
In the last stage (Table 3d, Fig. “Stage 3”), additional tentacles developed next to the primary tentacles and formed U-shaped clusters. Blind ending and sometimes branched canals developed. These canals grew from the margins of the gastric pouches in a centrifugal direction into the marginal lappets. In *C. capillata* these canals grew also into the muscles, forming a distinctive pattern. The side edges of the pouches frayed. Rhopalial lappets remained entire, without forming additional tentacular lappets.

***Aurelia aurita* and *Aurelia limbata*.** The gastric system of newly-released ephyrae (Table 3f-g, Fig. “Stage 1”) consisted of a central stomach, eight slightly forked to non-forked rhopalial canals, and eight non-forked, spade to diamond-shaped velar canals. The tips of the velar canals ended midway between stomach and umbrella rim.

In the second stage (Table 3f–g, Fig. “Stage 2”) the rhopalial canals of both species developed midway a *pair of side branches*. Ephyrae of *A. limbata* formed single velar lappets between the marginal lappets.

Velar canals of both species grew in a *centrifugal direction*. The sides of the velar canal tips also developed side branches which fused with the side branches of the rhopalial canals to form a *primary ring canal*. In *A. limbata* this was also the *final ring canal* (Table 3g, Fig. “Stage 3”).

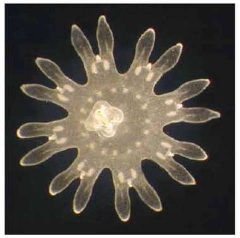
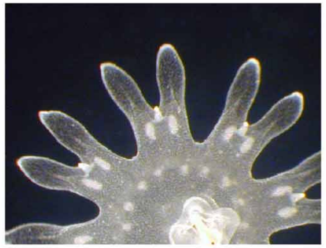
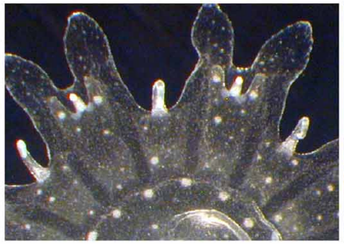
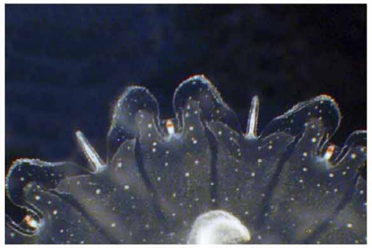
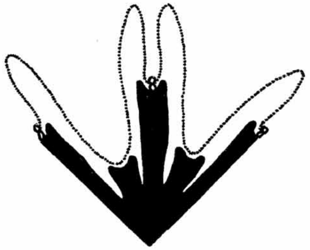
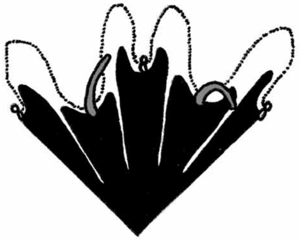
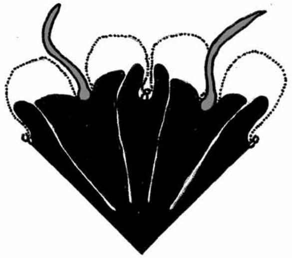
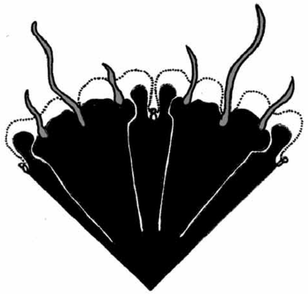
TABLE 3a. Developmental stages of gastric systems of the ephyrae of ***Sanderia malayensis***

Group	Species (Ephyra, stage 0[#1])	Development of Gastric systems[#2]		
		Stage 1	**Stage 2**	**Stage 3**
Pelagiidae	 #	 #		
	 *Sanderia malayensis*			
		• Rhopalial canals are club shaped and slightly forked, fork tips are sharp. • Velar canals are slightly forked: Fork arms level with the lower third of the lappet stems, fork tips are sharp	• The velar canals grow in **centrifugal** direction following the shape of the completing umbrella. • Single tentacle buds appear at the margin of the subumbrella at the base of the cleft between the marginal arms as extentions of the velar canals • Rhopalial canals enlarge by size growth	• the fork tips of the rhopalial canals grow further into the marginal lappets • the tentacles grow out to full length • the side edges of the gastric pouches fray

#: photo taken by Dipl. Biol. Laetitia Adler, PhD candidate

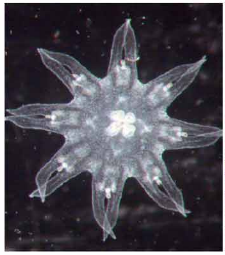
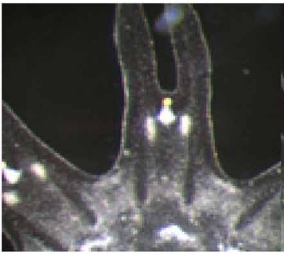
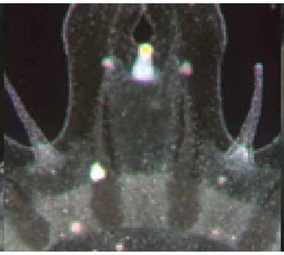
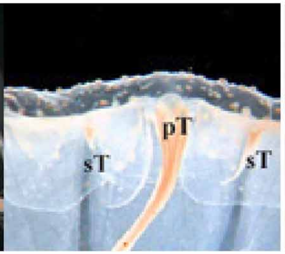
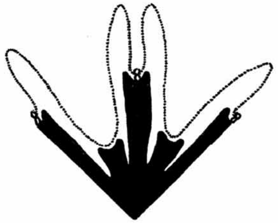
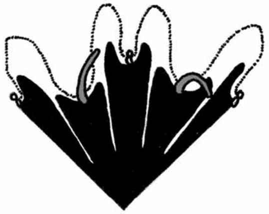
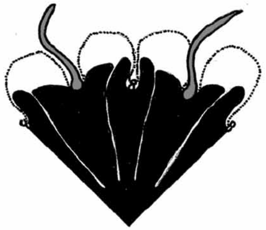
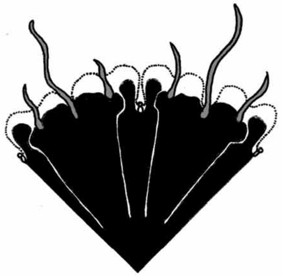
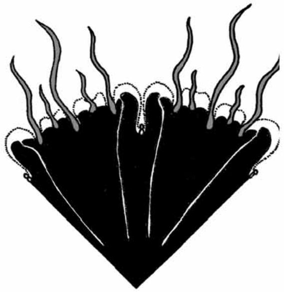
#1: newly detached #2: white = umbrella, black = gastric system without tentacles, grey = gastric canals inside tentacles, brown = gastric filaments

TABLE 3b. Developmental stages of gastric systems of the ephyrae of ***Chrysaora fuscescens***[#]

Group	**Species (Ephyra, stage 0[#1])**	**Development of Gastric systems[#2]**			
		Stage 1	**Stage 2**	**Stage 3**	**Stage 4**
Pelagiidae					
	Chrysaora fuscescens				
		• Rhopalial canals are slightly forked: Fork arms level statolith tip, fork tips are rounded • Velar canals are slightly forked, fork tips are rounded	• The velar canals grow in **centrifugal** direction following the shape of the completing umbrella. • Single tentacle buds appear at the margin of the subumbrella at the base of the cleft between the marginal arms as extentions of the velar canals • Rhopalial and velar canals enlarge by size growth	• the fork tips of the rhopalial canals grow further into the marginal lappets • the terminal ends of the velar canals grow in lateral direction into the marginal lappets	• secondary tentacles sprout at the marginal corners of the velar lappets • rhopalial lappets develop embayments at their margins, in opposite position of the developing tentacles • embayments in the rhopalial lappets turned into slits forming the outer regions into new tentacular lappets

#: after Widmer 2008 #1: newly detached #2: drawings: white = umbrella, black = gastric system without tentacles, grey = gastric canals inside tentacles

TABLE 3c. **Developmental stages of gastric systems of the ephyrae of *Chrysaora lactea***

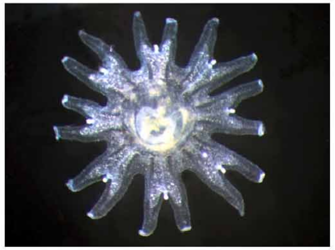
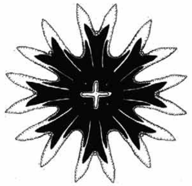
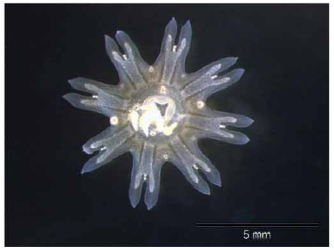
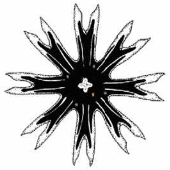
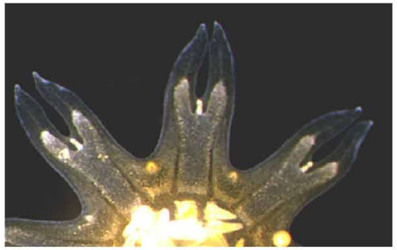
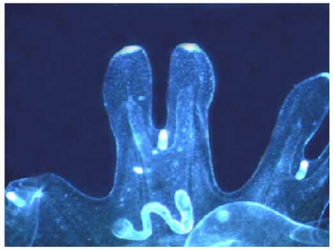
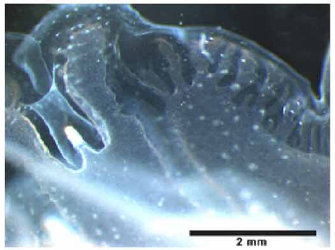
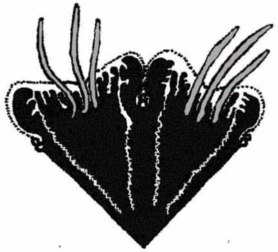
Group	Species (Ephyra, stage 0[#1])	Development of Gastric systems[#2]				
		Stage 1	Stage 2	Stage 3	Stage 4	Stage 5
Pelagiidae	 *Chrysaora lactea*					
						 #
		• Rhopalial canals are slightly forked: Fork arms level with the bases of the the rhopalium, fork tips are rounded • Velar canals are slightly forked, fork tips are rounded	• The velar canals grow in **centrifugal** direction following the shape of the completing umbrella. • Single tentacle buds appear at the margin of the subumbrella at the base of the cleft between the marginal arms as extentions of the velar canals • Rhopalial and velar canals enlarge by size growth	• the fork tips of the rhopalial canals grow further into the marginal lappets • the terminal ends of the velar canals grow in lateral direction into the marginal lappets	• secondary tentacles sprout at the marginal corners of the velar lappets • rhopalial lappets develop embayments at their margins, in opposite position of the developing tentacles • embayments in the rhopalial lappets turned into slits forming the outer regions into new tentacular lappets	• a set of tertiary tentacles sprout between primary and secondary tentacles • the tentacular lappets split in two above the tertiary tentacles.

#: Stage 5 was noted only in few specimen: Some individuals remain in the three-tentacled stage for the entire adult life span. The majority of the specimens collected in estuarine areas of São Paulo state had three tentacles per octant (from the 175 specimens from estuarine areas, only 7 had more than 3 tentacles per octant)

#1: newly detached

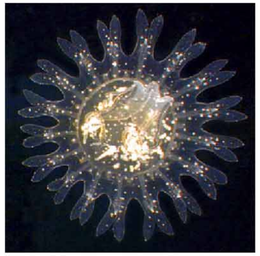
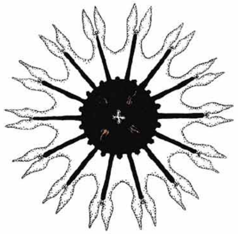
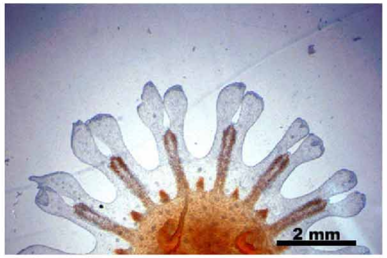
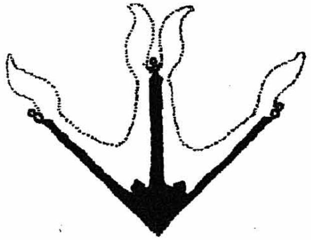
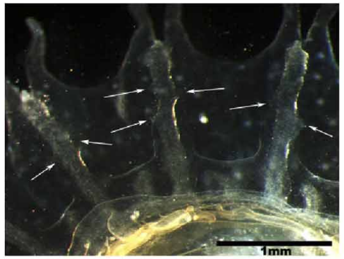
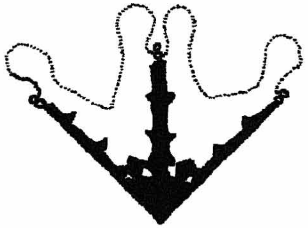
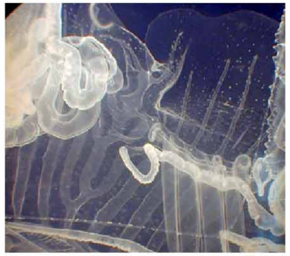
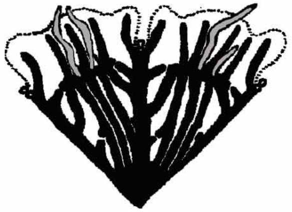
#2: drawings: white = umbrella, black = gastric system without tentacles, grey = gastric canals inside tentacles

TABLE 3d. **Developmental stages of gastric systems of the ephyrae of *Cyanea lamarckii* and *Cyanea capillata***

Group	Species (Ephyra, stage 0[#1])	Development of Gastric systems[#2]		
		Stage 1	Stage 2	Stage 3
Cyaneidae	  *Cyanea lamarckii*   *Cyanea capillata*	  • Forked rhopalial canals, fork spikes well overtop rhopalium and level midway between rhopalium and rhopalial lappet tips • Forked velar canals, fork spikes level with the base of the Rhopalium in the upper third of the lappet stems • *C. capillata* bears already single tentacle buds between marginal lappets	  • The velar canals grow in **centrifugal** direction following the shape of the completing umbrella • Gastric system enlarges mainly by size growth and by growing inside the developing tentacles	  • In the last phase, blind ending, sometimes branched canals are **cetrifugally** developed protruding from the upper edges of the gastric systems into the marginal lappets and in *C. capillata* also into the muscles • the side edges of the gastric pouches fray

#1: newly detached #2: drawings: white = umbrella, black = gastric system without tentacles, grey = gastric canals inside tentacles

TABLE 3e Developmental stages of gastric systems of the ephyrae of ***Phacellophora camtschatica***

Group	**Species (Ephyra, stage 0[#1])**	**Development of Gastric systems[#2]**			
		Stage 1	**Stage 2**	**Stage 3**	**Stage 4**
Phacello-phoridae fam. nov.	  *Phacellophora camtschatica*	  • unforked, narrow rhopalial canals end at the base of the rhopalia • very short, unforked velar canals just overtop the central stomach	  • the rhopalial canals form 3-4 short pairs of side branches (white arrows) • the velar canals grow **centrifugally** and form one pair of side branches each just below their tips which fuse with the first side-branch pair of the rhopalial canals to form a **primary ring canal**	  • the velar canals and the attached rhopaliar canal branches grow further towards the umbrella rim so that the primary ring canal shapes into sinus curves • the second pairs of rhopalial canal side branches fuse with the velar canal tips when they reach their level and form a **secondary ring canal**	  • the steps of stage 3 are repeated till a **final ring canal** below the rhopalia is formed • the final ring canal produces tentacles and unbranched, blind ending canals which grow **centrifugally** into the marginal lappets • some new canal links form, others disconnect again

#1: newly detached

#2: drawings: white = umbrella, black = gastric system without tentacles, grey = gastric canals inside tentacles, brown = gastric filaments

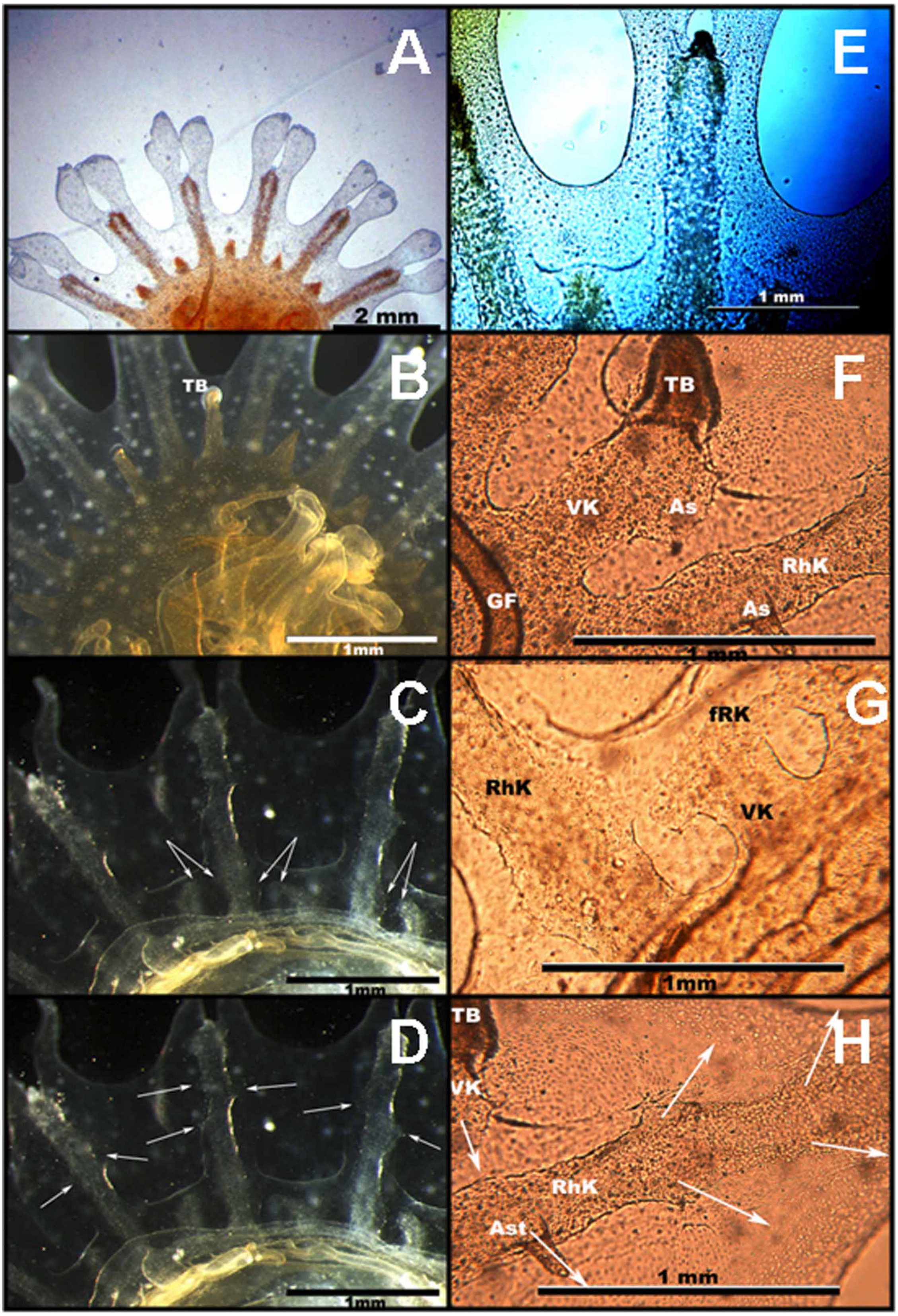


PLATE 4. Early development of gastric system in the ephyra of *P. camtschatica*; binocular- and microscopical views: A+E) Gastric system of a newly detached ephyra, B+F) 3-week-old ephyra with first tentacle buds, C+G) 4-week-old ephyra developing a ring canal (white arrows point to side branches which will form the ring canal, D+G) 4-week-old ephyra developing additional side branches (white arrows) along the rhopalial canals; As: side branches; fRK: forming ring canal; GF: gastric filament; RhK: rhopalial canal; TB: tentacle bud.

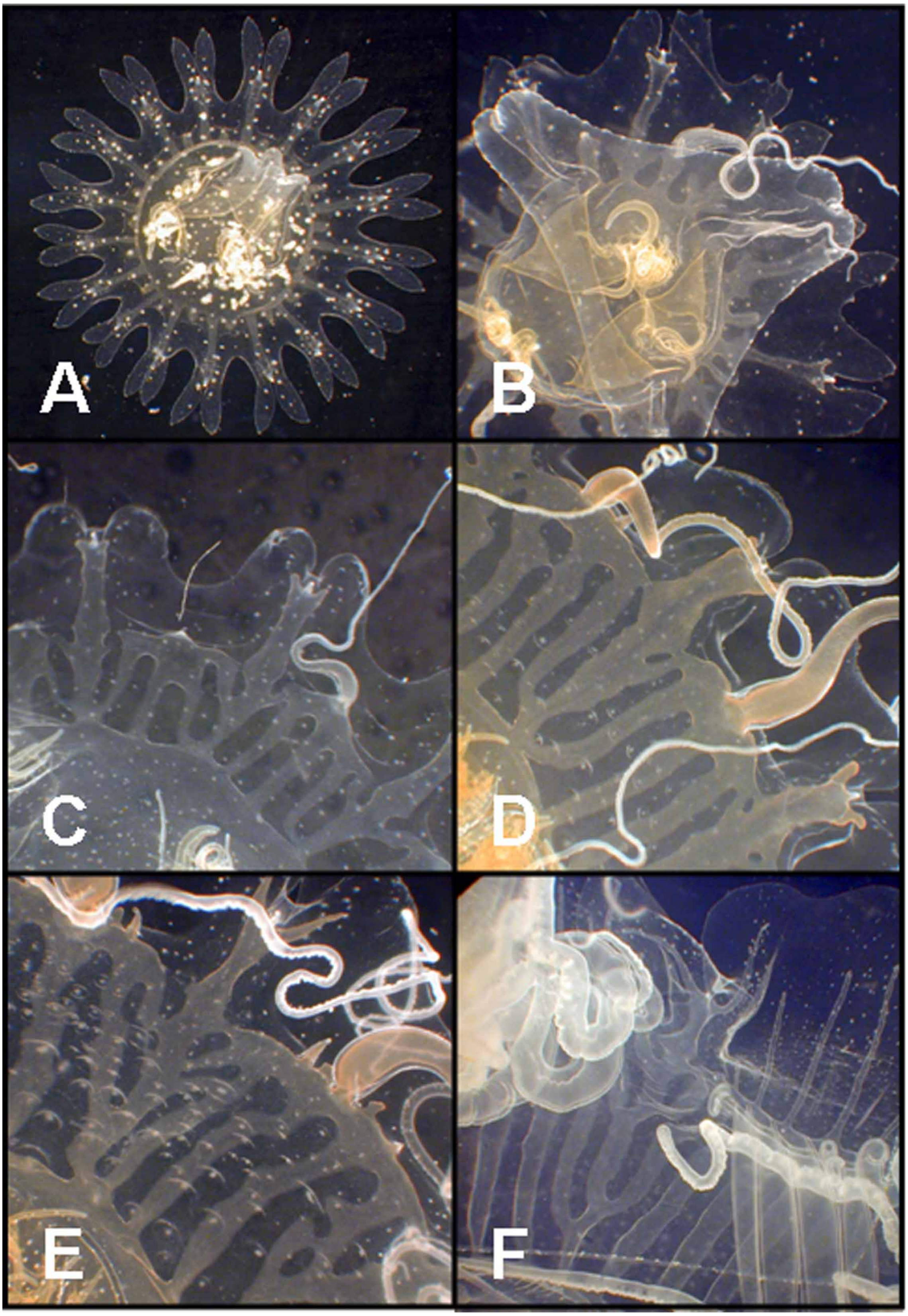
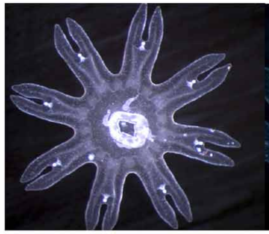
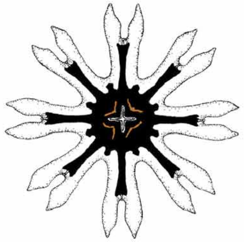
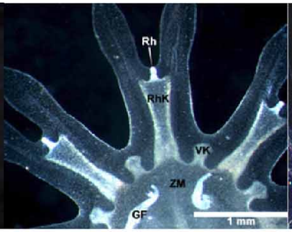
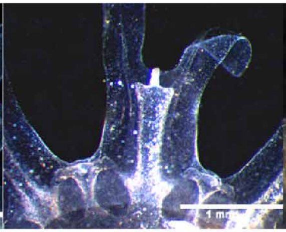
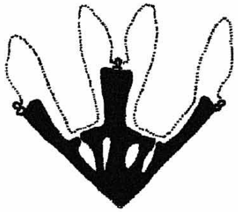
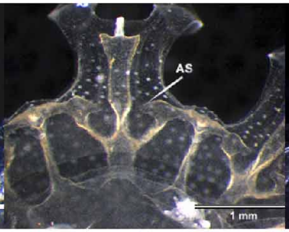
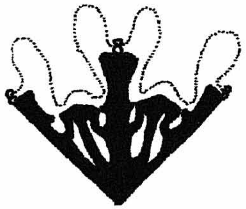
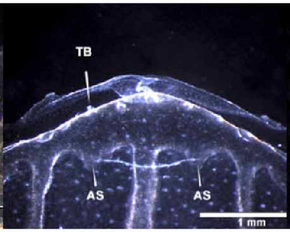
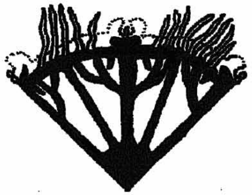


PLATE 5. Development of gastric system of *P. camtschatica* from ephyra to medusa stage; binocular- and microscopical views: A) Newly detached ephyra, B) 2nd developmental stage: velar canals develop pair of side branches, C) 3rd developmental stage: primary ring canal is shaped into sinus curves by centrifugal directed growth of velar canals, D) 4th developmental stage: final ring canal is formed below the rhopalia level, E) the final ring canal produces single tentacles above the velar canal tips in chronological order, F) unbranched, blind ending canals are produced by the final ring canal which grow into the marginal lappets.

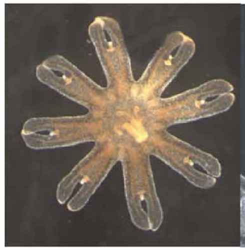
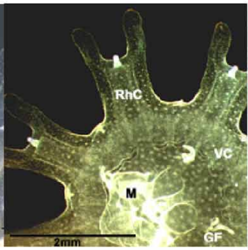
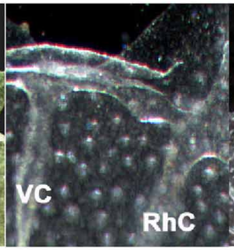
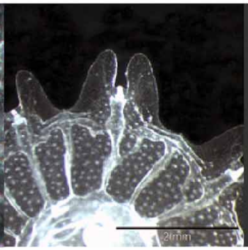
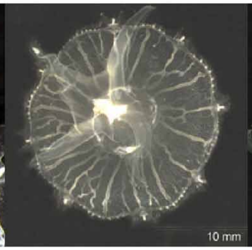
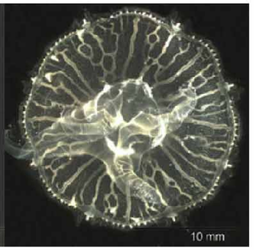
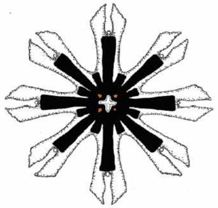
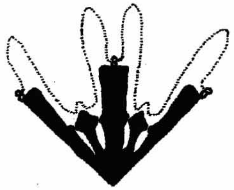
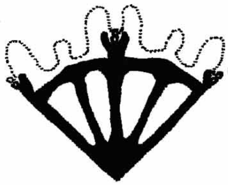
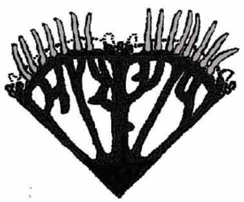
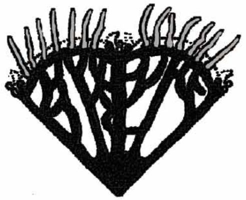
TABLE 3f. Developmental stages of gastric systems of the ephyrae of ***Aurelia aurita***

Group	Species (Ephyra, stage 0#1)	Development of Gastric systems#2				
		Stage 1	Stage 2	Stage 3	Stage 4	Stage 5
Ulmaridae	  *Aurelia aurita*	  • rhopalial canals with slightly forked tips end at the base of the rhopalia • short, spade to diamond shaped, unforked velar canals end midway between stomach and umbrella rim	  • the rhopalial canals form midway 1 short pair of side branches • the velar canals grow **centrifugally** and form one pair of side branches each just below their tips which fuse with the pair of side branches of the rhopalial canals to form a **primary ring canal**	  • velar canals and attached rhopalial canal branches grow towards the umbrella rim, the primary ring canal shapes into sinus curves • **single velar lappets** are formed between rhopalial lappets • a second pair of rhopalial canal side branches fuse with the velar canal tips below the rhopalia and form a **final ring canal**	  • the final ring canal produces tentacle buds and unbranched, secondary canals#3 which grow **centripetally** and fuse with the canals formed by the primary ring canal	  • tentacles grow out • more secondary canals are produced and grow **centripetally** to fuse with secondary canals or the rhopalial canals • the velar canals are connected with the rest of the gastric system exclusively by the final ring canal

#1: newly detached #2: drawings: white = umbrella, black = gastric system without tentacles, grey = gastric canals inside tentacles, brown = gastric filaments,

#3: secondary canals: connect the ring canal with rhopalial, velar and secondary canals, always direct connection with ring canal

TABLE 3g. Developmental stages of gastric systems of the ephyrae of ***Aurelia limbata***

Group	**Species (Ephyra, stage 0[#1])**	**Development of Gastric systems[#2]**					
		Stage 1	**Stage 2**	**Stage 3**	**Stage 4**	**Stage 5**	**Stage 6**
Ulmaridae							
	 *Aurelia limbata*						
		• rhopalial canals with unforked tips end at the base of the rhopalia • spade-like shaped, unforked velar canals end right below umbrella rim	• the rhopalial canals form midway 1 short pair of side branches • the velar canals grow tips which grow **centrifugally** and form one pair of side branches each just below their tips • **single velar lappets** grow between the marginal lappets	• the side branches of the velar canals fuse with the pair of side branches of the rhopalial canals to form a **final ring canal**	• the final ring canal produces tentacle buds and unbranched, secondary canals[#3] which grow **centripetally** and fuse with the rhopalial canals or with other secondary canals	• tentacles grow out • more secondary canals are produced by the ring canal which grow **centripetally** to fuse with secondary canals, the rhopalial and velar canals	• the secondary canals produce tertiary canals[#4] which connect the secondary canals to each other • a complex net pattern of gastric canals is formed • the velar canals are connected with the rest of the gastric system by the final ring canal and a few secondary or tertiary canals

#1: newly detached #2: drawings: white = umbrella, black = gastric system without tentacles, grey = gastric canals inside tentacles, brown = gastric filaments

#3: secondary canals: connect the ring canal with rhopalial, velar and secondary canals, always direct connection with ring canal

#4: tertiary canals: connect secondary canals with each other or with rhopalial or velar canals, no direct connection to ring canal

In *A. aurita* the velar canals and the attached rhopalial side branches grew further on centrifugally towards the umbrella rim, shaping the primary ring canal into sinus curves. Then *single velar lappets* formed between the rhopalial lappets as outgrowths of the umbrella margin. A *second pair of rhopalial canal side branches* arose in the upper third of the rhopalial canal (Table 3f, Fig. “Stage 3”). These rhopalial canal side branches fused with the sinus-curved primary ring canal to form the *final ring canal* in *A. aurita*.

In the fourth stage (Table 3f-g, Fig. “Stage 4”) the final ring canal of both species produced synchronically a single row of tentacle buds above the velar canal tips, and unbranched *secondary canals* (secondary canals connect the ring canal directly to the rhopalial, the velar or the secondary canals). In *A. aurita* the secondary canals grew in a *centripetal direction* and fused with the canals of the former primary ring canal. In the case of *Aurelia limbata*, the secondary canals fused with the rhopalial or with other secondary canals.

In the fifth stage (Table 3f–g, Fig. “Stage 5”), tentacles began to grow. The ring canal produced additional secondary canals which grew centripetally to fuse with other secondary canals, or with the rhopalial canals and additionally, in *A. limbata*, with the velar canals.

This stage was the final stage in development of the medusa of *A. aurita*. Velar canals were connected to the rest of the gastric system exclusively by the final ring canal, and *no secondary canals fused with the velar canals*.

A sixth stage was noted in *A. limbata*. In this last stage (Table 3g, Fig. “Stage 6”) the secondary canals produced *tertiary canals* (tertiary canals connect secondary canals with each other or with rhopalial or velar canals; they have no direct connection to the ring canal) which grew in a centripetal direction and fused with secondary, rhopalial or velar canals. A complex net pattern of gastric canals was formed.

Velar canals were connected to the rest of the gastric system by the final ring canal, *and by a few secondary or tertiary canals.*

Discussion

Development. As noted by Mayer (1910), Kramp (1961), Russell (1970), and Mianzan and Cornelius (1999), the family Ulmaridae comprises “all species which show simple and/or branched radial canals and a ring canal, a subgenital cavity which may or may not be present”. The group consists of eight subfamilies: Aureliinae, Deepstariinae, Ulmarinae, Sthenoniinae, Poraliinae, Stygiomedusinae (Mianzan & Cornelius 1999), Tiburoniinae (Matsumoto, Raskoff & Lindsay 2003) and Stellamedusinae (Raskoff & Matsumoto 2004).

Among Ulmaridae, details of development and life cycle are known only for Aureliinae (genus *Aurelia*) and Sthenoniinae (genus *Phacellophora*), so comparisons are possible only between members of these subfamilies and with other semaeostomes having known life cycles. Several authors have suggested that some deep water ulmarid species may undergo a holopelagic life cycle (Larson 1986), as observed in the coronate species *Periphylla periphylla* (Jarms *et al.* 1999). There are also data suggesting that the ulmarid *Poralia* sp. (Poraliinae) from deep waters of Monterey Bay Canyon is probably a holopelagic, brooding jellyfish, lacking scyphistoma stages in its life cycle (Chad Widmer, unpublished results).

Anatomical differences in scyphistomae of most observed species were minimal (references in Table 5a–c). Most distinct were *S. malayensis* and *P. camtschatica* in the length of the stalk (44% of TBL in *P. camtschatica* and 51% of TBL in *S. malayensis*), in the inflexible, funnel-shaped periderm tube of *P. camtschatica*, and in the thin transparent periderm cuticle that encloses the basal disc and about one-half of the stalk of *S. malayensis* (Widmer 2006; Adler 2008; Adler & Jarms 2009). Mean numbers of tentacles in *S. malayensis* and *P. camtschatica* were also much higher than in those of the other species, but the difference may be an artefact of laboratory conditions. Scyphistomae of *Aurelia aurita* collected in the field for this study had as many as 28 tentacles, but the number declined to 16 in most specimens over several months as reported in studies by Delap (1906) and Östman (1997) and for cyaneid species by Delap (1905), Hargitt & Hargitt (1910), and Russell (1970). *Phacellophora camtschatica*, like *Sanderia malayensis*, seems to have a “double symmetry” in their ephyrae (see below) and numbers of tentacles may also be higher.

TABLE 4a. Polyp morphology and references — Pelagiidae

Species	**Culture conditions (Temperature)**	**Polyp size [mm]**	**MDD**	**Number of tentacles**	**Stalk (Shape/ length [mm]/ proportion)**	**Hypostome (Shape/ length [mm]/ proportion)**	**Periderm shape**	**Asexual reproduction forms**	**Reference**
Chrysaora hysoscella	5.6–18.9°C	-	-	16	short^{z}	-	-	polyp buds	Delap (1901)
	15°C	max. 2.5	1.75	14–16	short/ 0.25 / 10% of TBL	-	-	podocysts	Morandini *et al.* (2004)
	5–15°C	1.03–1.43, mean: 1.26	0.71–0.93, mean: 0.84	16	short / 0.23–0.36 / 17–25% of TBL	short, cone to cylindrical / 0.25–0.29 / 20–24% of TBL	beaker	latereral polyp buds, podocysts	Straehler-Pohl (2009)
Chrysaora fuscescens	14°C	2.96	1.47	15–19, mean: 16	short	distinct clavate / 0.5 / 17% of TBL	thin peridem-cover	stolonial podocysts	Widmer (2008b) present study
Chrysaora colorata	-	2.0–5.0	1.5–2.0	16	short^{z}	amorph to square	-	podocysts	Gershwin & Collins (2002)
Chrysaora lactea	22°C	1.15–3.0, mean: 1.76	0.75–1.7, mean: 0.97	12–21, mean: 16	short / 0.56/ ≈30% of TBL	medium length, cone-shaped / 0.2 / ≈11% of TBL	beaker	podocysts	Morandini *et al.* (2004) present study
Chrysaora quinquecirrha	22°C	1.0–4.0, mean: 3.75	0.6–1.5	13–20	short / 1.5 / 37% of TBL	-	-	podocysts	Morandini *et al.* (2004)

Continued next page

TABLE 4a. (continued)

Species	Culture conditions (Temperature)	Polyp size [mm]	MDD	Number of tentacles	Stalk (Shape/ length [mm]/ proportion)	Hypostome (Shape/ length [mm]/ proportion)	Periderm shape	Asexual reproduction forms	Reference
Chrysaora melanaster	20–25°C	2.0–3.0	-	16	short	medium length, cone-shaped^{p}	-	podocysts	Kakinuma (1967)
	22°C	2.0–3.2	1.8	16–18	short / 0.2 / 6% of TBL	-	-	podocysts	Morandini *et al.* (2004)
Chrysaora achylos	15°C	-	-	16^{p}	short	short, cone-shaped^{p}	-	podocysts	Schaadt *et al.* (2001)
Sanderia malayensis	20°C	6	0.8–1.2	22–40	long^{p}	short / cone-shped^{p}	-	polyp buds, stolonial buds	Uchida & Sugiura (1978)
	15–28°C	2.38–3.14, mean: 2.76	0.81–1.39, mean: 1.1	22–32	long^{p}	short	thin, transparent periderm layer	conservative buds, stolons, swimming buds, shedding of tentacle tips, longitudinal fission, shedding of gastric tissue balls	Adler (2008) Adler & Jarms (2009)
	15–25°C	1.41–1.91, mean: 1.59	0.60–1.25, mean: 0.78	22–29, mean: 25	long / 0.81 / 51% of TBL	short, cone-shaped / 0.18 / 12% of TBL	thin transparent periderm cuticle	simultane polyp and stolon buds	present study

TBL = total body length MDD = mouth disc diameter p = data taken from photos z = data taken from sketches - = no statement

TABLE 4b. Polyp morphology and references — Cyaneidae

Species	**Culture conditions (Temperature)**	**Polyp size [mm]**	**MDD**	**Number of tentacles**	**Stalk (Shape/ length [mm]/ proportion)**	**Hypostome (Shape/ length [mm]/ proportion)**	**Periderm shape**	**Asexual reproduction forms**	**Reference**
Cyanea lamarckii	6.6–20°C (44–68°F)	4.0	2.0	24–28, max. 33	-	-	-	podocysts	Delap (1905) Russell (1970)
	10–15°C	1.71–2.71, mean: 2.21	0.78–1.46, mean: 1.13	16	short/ 0.23 / 10% of TBL	medium length/ 0.53/ 24% of TBL	beaker	polyp buds, podocysts	present study
Cyanea capillata	5–7°C	-	-	16^z	long and slender	-	-	podocysts	Gröndahl & Henroth (1987)
	-	smaller than *Aurelia*	-	> 20, mean: 16	short to medium length^z	medium length, cone shaped^z	beaker^z	stolonial polyp buds	Hargitt & Hargitt (1910)
	5–10°C	2.51–3.02, mean: 2.71	1.40–1.84, mean: 1.59	16–17, mean: 16	short/ 0.19 / 7% of TBL	medium length / 0.76 / 28% of TBL	beaker	polyp buds, podocysts	present study
Cyanea nozakii	21°C, 22–26°C	0.4–2.0	-	≥16	short and thick	flexible and of moderate length	-	podocysts, pedalcytes	Dong *et al.* (2006, 2008)

TBL = total body length MDD = mouth disc diameter p = data taken from photos z = data taken from sketches - = no statement

TABLE 4c. Polyp morphology and references — Aureliinae and Phacellophoridae fam. nov.

Species	Culture conditions (Temperature)	Polyp size [mm]	MDD	Number of tentacles	Stalk (Shape/ mean length [mm]/ proportion)	Hypostome (Shape/ mean length [mm]/ proportion)	Periderm shape	Asexuel reproduction forms	Reference
Aurelia aurita (Samples taken in harbour of Helgoland)	-	-	-	up to 27	-	-	-	-	Östmann (1997)
	10–15°C	1.5–2.5	-	16–24	short	-	-	lateral and stolonial polyp buds, longitudinally fission, transverse fission, podocysts, Pedalcytes	Holst (2008)
	44–68°F	smaller than polyp of *Chrysaora*	-	25	short to long	-	-	lateral and stolonial polyp buds, longitudinally fission, fragmentation$^{\#}$	Delap (1906)
	5–15°C	3.03–3.80, mean: 3.18	0.90–1.57, mean: 1.19	18–28, mean: 23	short / 0.55/ 17% of TBL	medium length/ 0.54 / 17% of TBL	beaker	lateral and stolonial polyp buds, podocysts, pedalcytes	present study
Aurelia labiata	-	2–3	1–2	16–20	-	short, cruciform	-	lateral and stolonial polyp buds, podocysts	Gershwin (2001)
	-	1.7–2.9, mean: 2.2	0.9–2.2, mean: 1.4	16–21, mean: 18.7	-	-	-	podocysts	Widmer (2006)
Aurelia limbata	3–1°C, 0–15°C	0.4	0.6	16	short	dome shaped^{z}	-	lateral and stolonial polyp buds	Uchida & Nagao (1963)
	5–15°C	0.94–1.41, mean: 1.27	0.61–0.94, mean: 0.83	16	short/ 0.46/ 36% of TBL	short / 0.24 / 19% of TBL	beaker	lateral and stolonial polyp buds, podocysts	present study
Phacellophora camtschatica	14°C	7–11, mean: 7.95	2.2–3.5, mean: 2.65	30–44, mean: 37.5	medium length, two distinct regions with either thin or thick diameters	short, cone shaped^{p}	transparent, funnel shaped periderm	lateral and stolonial polyp buds, less frequently by fission	Widmer (2006)
	14–15°C	4.85–11.0, mean: 7.62	1.25–3.5, mean: 2.45	30–44, mean: 38	long / 3.49 / 52% of TBL	very short/ 0.59 / ≈8% of TBL	slim, solid periderm tube	lateral and stolonial polyp buds	present study

TBL = total body length MDD = mouth disc diameter p = data taken from photos z = data taken from sketches - = no statement
# = Parts of the manubrium were actively left behind on the glass screen of the aquarium and developed into a polyp

Methods of asexual reproduction in *S. malayensis* and *P. camtschatica* differ from the other species. No podocysts are produced (Uchida & Sugiura 1978; Widmer 2006; Adler 2008; Adler & Jarms 2009), stolon budding in *P. camtachatica* is more often used for changing location than for lateral scyphistoma budding (Type 3 of asexual reproduction, Adler & Jarms 2008), and scyphistomae budded only at the midpoint of the stolon and not at the tip of the stolon as in Aureliinae and Cyaneidae (Hargitt & Hargitt 1910, Uchida & Nagao 1963, Yasuda 1979, Arai 1997, Holst 2008). Asexual reproduction in *S. malayensis* was described and defined in detail by Adler (2008) and Adler and Jarms (2009). As in *P. camtschatica*, there was no production of podocysts and pedalocysts. Only simultaneous scyphistoma and stolon bud production, as described earlier by Uchida & Sugiura (1978), was observed in *S. malayensis*. It is a very different process from the stolonial budding of *P. camtschatica*. Only the typical lateral scyphistoma budding (Type 1 of asexual reproduction, Adler & Jarms 2008) in both species is the same as in Pelagiidae, Cyaneidae, and Aureliinae (Hargitt & Hargitt 1910; Uchida & Nagao 1963; Yasuda 1979; Arai 1997, 2009; Holst 2008; Straehler-Pohl 2009).

Polydisc strobilation occurred in all observed groups (see references in Table 9) with one exception, *S. malayensis*, which undergoes monodisc strobilation (Uchida & Sugiura 1978; Adler 2008; Straehler-Pohl 2009). Otherwise, the type of strobilation is not a useful character in distinguishing the species.

Major differences are apparent in the anatomy (references in Table 10) and development of ephyrae considered here (e.g. developmental direction of gastric systems, development of the final ring canal – if a ring canal is present –, development of the primary medusa tentacles, and development of velar or tentacular lappets) (Table 6). Unlike ephyrae of Aureliinae and Cyaneidae (Delap 1905, 1906; Uchida & Nagao 1963; Russell 1970; Gröndahl & Hernroth 1987; Higgins *et al.*, 2008), ephyrae of *P. camtschatica* and *S. malayensis* usually bear considerably more than eight rhopalia (Uchida & Sugiura 1975; Larson 1986; Widmer 2006; Adler 2008; Straehler-Pohl & Jarms 2010) as in ephyrae of *Cassiopea andromeda* Bigelow, 1900 (Bigelow 1900; Gohar & Eisawy 1960a, b; Straehler-Pohl & Jarms 2010). A close relationship between *P. camtschatica*, *S. malayensis*, and *C. andromeda* is discounted based on morphology of their medusae and scyphistomae, asexual reproduction methods (Gohar & Eisawy 1960b; Uchida & Sugiura 1978; Hofmann *et al.* 1978; Adler 2008; Adler & Jarms 2009; Straehler-Pohl 2009), and development of ephyrae (Gohar & Eisawy 1960b; Uchida & Sugiura 1975; Adler 2008; Straehler-Pohl 2009). In light of this we suggest that the “doubled marginal symmetry” observed in certain scyphozoans evolved independently in different lineages.

The rhopalial lappet length (= RLL) of *P. camtschatica* was up to 53% of the total marginal lappet length (= TMLL), closer to values in Pelagiidae (RLL: 58–60% of TMLL) and Cyaneidae (RLL: 56–57% of TMLL) than in Aureliinae (RLL: 42–48% of TMLL).

Development of the gastric system and tentacles in medusae of all observed taxa best reveals distinctions between the groups (Table 6). Enlargement of the surface of the gastric system in Pelagiidae and Cyaneidae is mainly achieved by volume growth of the gastric pouches (Thiel 1970; Morandini *et al.* 2004, 2006; Widmer 2008; Adler 2008). It is also achieved in the last stage in cyaneids by the development of short, branched, blind-ending canals at the edges of the gastric system that take on a frayed look (Russell 1970). Some of the blind-ending canals also grow centrifugally into the muscles and/or marginal lappets (Stiasny & van der Maaden 1943; Thiel 1970).

The surface of the gastric system of Aureliinae is enlarged by development of a complex network of secondary and tertiary canals instead of mere expansion in volume of the radial canals (Uchida 1934; Uchida & Nagao 1963). The radial canals initially grow in a centrifugal direction, and form a primary and/or final ring canal which connects velar and rhopalial canals (Uchida & Nagao 1963, Thiel 1970). This is different than observed in Cyaneidae, in which radial canals remain completely separated (Stiasny & van der Maaden 1943; Thiel 1970; Russell 1970). Ring canals of Aureliinae develop secondary and tertiary canals which change the direction of development by growing in a centripetal direction (Uchida & Nagao 1963; Thiel 1970). Secondary and tertiary canals connect radial canals with the ring canal.

In Aureliinae, velar lappets are formed as additional single diverticula above the velar canal tips (Russell 1970). No gastric canals grow into the velar or rhopalial lappets. Cyaneids form no velar lappets but grow blind-ending, branched canals into the rhopalial lappets. Like cyaneids, pelagiids form no velar lappets, but the original rhopalial lappets are split into several tentacular lappets in *Chrysaora hysoscella* (Linnaeus, 1767), *C. fuscescens*, and *C. lactea* (Russell 1970; Morandini *et al.* 2004, 2006; Widmer 2008).

TABLE 5. Strobilation rates and references.

	Strobilation rate / type		
Species	Number of Ephyrae/ Strobila	Reference	Number of Ephyrae/ Strobila; Strobilation type (Present study)
Chrysaora hysoscella	5z	Delap (1901)	-
	13	Chuin (1930)	
	1–3	Lambert (1936)	
	4–6	Morandini *et al.* (2004)	
	12	Straehler-Pohl (2009)	
Chrysaora fuscescens	up to 60	Widmer (2008b)	up to 60, polydisc
Chrysaora lactea	2–10	Morandini *et al.* (2004)	up to 10, polydisc
Chrysaora quinquecirrha	5–6	Littleford (1939)	-
	3–9	Cargo & Schultz (1966)	
	1–16 (mean: 5; mode: 4)	Calder (1974)	
	15	Morandini *et al.* (2004)	
Chrysaora colorata	up to 56	Gershwin & Collins (2002)	-
Chrysaora melanaster	20–30	Morandini *et al.* (2004)	-
	20–30	Kakinuma (1967)	
Chrysaora achylos	>18p	Schaadt *et al.* (2001)	-
Sanderia malayensis	1	Uchida & Sugiura (1978)	1, monodisc
		Adler & Jarms (2009)	
		Straehler-Pohl (2009)	
Cyanea capillata	8–12	Delap (1901),	10–17, mean: 12; polydis
	11	Russell (1970),	
	4–12	Lambert (1936)	
Cyanea capillata	1, 3–5	Hargitt & Hargitt (1910),	5–12, mean: 8; polydisc
		Gröndahl (1988)	
	4–8	Lambert (1935)	
Cyanea nozakii	1–2	Dong *et al.* (2006, 2008)	-
Aurelia aurita	9–15	Delap (1906),	12–22, mean: 15; polydisc
	up to 30	Spangenberg (1968),	
	25–30	Lambert (1935),	
	20–30	Berrill (1949),	
	up to 6	Yasuda (1979)	
Aurelia labiata	1, >20	Gershwin (2001)	-
Aurelia limbata	3–22, mean: 10–16	Uchida & Nagao (1963)	8–10, mean: 9; polydisc
Phacellophora camtschatica	8–15	Widmer (2006)	8–15, mean: 12; polydisc

TABLE 6a. Ephyra morphology and references — Pelagiidae

Species	Culture conditions (Temperature)	TBD [mm]	CDD [mm] and/or Proportions	No. of Marginal Lappets	Lappet Proportions: LStL / RLL compared to TMLL	Shape of Rhopalial Lappet/ Distinctions	Gastric System	Colour	Reference
Chrysaora hysoscella	5.6–18.9°C	2.0	- / 37% of TBD^{z}	8	60% / 40% of TMLL^{z}	rounded tips / *Chrysaora*-typical nematocyst clusters	forked radial canals	pink	Delap (1901)
	15°C	1.62–2.0	-	-	-	- / *Chrysaora*-typical nematocyst batteries	-	pale orange	Morandini *et al.* (2004)
	15–22°C	1.7–3.3, mean: 2.4	- / 44% of TBD^{p}	8	45% / 55% of TMLL^{p}	- / *Chrysaora*-typical nematocyst clusters, sometimes present sometimes not	slightly forked radial canals with rounded tips^{p}	pink	Holst (2008)
	10–15°C	2.84–3.40, mean: 3.18	1.18–1.42, mean: 1.32 / 42% of TBD	8	45% / 55% of TMLL	round spatula-like / -	slightly forked radial canals with rounded tips		Straehler-Pohl (2009) Straehler-Pohl & Jarms (2010)
Chrysaora fuscescens	14°C	2.0–4.0, mean: 3.13	- / 47% of TBD	6–10, meam: 8	40% / 60% of TMLL	lancet-like / *Chrysaora*-typical nematocyst clusters	forked radial canals, rhopalial canals with short, rounded fork tips, velar canals with pointed fork tips	light brown	Widmer (2008b) present study
Chrysaora colorata	-	2.0–3.0	- / 55% of TBD^{p}	8	44% / 56% of TMLL^{p}	lancet-like / *Chrysaora*-typical nematocyst clusters	-	deep violet	Gershwin & Collins (2002)
	20°C	2.0–4.1, mean: 3.05	-	8	-	-	-	red	Widmer (2008b)
Chrysaora lactea	22°C	1.0–2.0	0.5–1.0	8	-	lancet-like / rhopalia yellowish, *Chrysaora*-typical nematocyst clusters	forked radial canals with short, rounded fork tips, very short velar canals	transparent	Morandini *et al.* (2004)

continued next page

TABLE 6a. (continud)

Species	Culture conditions (Temperature)	TBD [mm]	CDD [mm] and/or Proportions	No. of Marginal Lappets	Lappet Proportions: LStL / RLL compared to TMLL	Shape of Rhopalial Lappet/ Distinctions	Gastric System	Colour	Reference
	22°C	2.25–2.38, mean: 2.3	1.0 / ≈43% of TBD	8	20% / 80% of TMLL	lancet-like / rhopalia yellowish, *Chrysaora*-typical nematocyst clusters	forked radial canals with short, rounded fork tips, very short velar canals	transparent	present study
Chrysaora quinquecirrha	22°C	2.45–2.75	-	-	-	-	-	pink	Morandini *et al.* (2004)
Chrysaora melanaster	22°C	2.0–3.0	-	-	-	-	-	pink	Morandini *et al.* (2004)
	20–25°C	2.0–3.0	- /43% of TBD^{p}	8^{p}	40% / 60% of TBD	lancet-like, rhopalial lappets parallel to each other / *Chrysaora*-typical nematocyst clusters^{z,p}	forked radial canals with pointed tips, velar canal tips very long (level with rhopalia base)^{z,p}	light pink	Kakinuma (1967)
Chrysaora achylos	-	1.0–2.0	0.5–1.0^{p} / 48% of TBD	8^{p}	-	lancet-like^{p} / *Chrysaora*-typical nematocyst clusters^{p}	forked radial canals with short rounded fork tips^{p}	-	Schaadt *et al.* (2001)
	20°C	1.5–3.1, mean: 2.66	-	8	-	-	-	clear with maroon central ring	Widmer (2008b)
Sanderia malayensis	20°C	2.4–4.3	- / 59% of TBD^{p}	12–24, mean: 16	40% / 60% of TMLL^{p}	lancet-like^{p} / *Chrysaora*-typical nematocyst clusters at thebase of marginal lappets	slightly forked radial canals	brownish	Uchida & Sugiura (1975, 1978)
	20–25°C	≈3.0	- / 62% of TBD	11–16, mean: 14	38% / 62% of TMLL^{p}	lancet-like^{p} / *Chrysaora*-typical nematocyst clusters at thebase of marginal lappets	slightly forked radial canals^{p}	deep orange-brown	Adler (2008)
	20–25°C	3.60–3.79, mean: 3.67	2.12–2.31, mean: 2.19 / 60% of TBD	13–16, mean: 15	40% 60% of TMLL	bread-knife-shaped / 1–2 gastric filaments per quadrant	forked radial canals	orange-brown	Strachler-Pohl & Jarms (2010) present study

CDD = Central Disk Diameter LStL = Lappet Stem Length p = data taken from photos RLL = Rhopalial Lappet Length TBD = Total Body Diameter
TMLL = Total Marginal Lappet Length z = data taken from drawings - = no statement given in the publication

TABLE 6b. Ephyra morphology and references — Cyaneidae

Species	Culture conditions (Temperature)	TBD [mm]	CDD [mm] and/or Proportions	No. of Marginal Lappets	Lappet Proportions: LStL / RLL compared to TMLL	Shape of Rhopalial Lappet/ Distinctions	Gastric System	Colour	Reference
Cyanea lamarckii	44–68°F	4.00	-	8	-	lancet like^z/ 0 gastric filaments per quadrant^z	forked rhopaliar canals, tips reach into rhopalar lappet,; forked velar lappets, tips reach into lappet stem^z	white	Delap (1905)
	-	4.00	-	8	-	lancet like with broad blade^z/ 1 gastric filament per quadrant^z	forked rhopalar and velar canals ^{z}	white	Russell (1970)
	10–15°C	2.15–2.64, mean: 2.33	0.99–1.16, mean: 1.06 / 45% of TBD	8	44% / 56%of TMLL	sword shaped / 0 gastric filament per quadrant	forked rhopalar canals, tips reach far into the rhopalar lappets; forked velar canals, tips reach to level of base of rhopalia in margial lappet	bluish to pale mauve	Straehler-Pohl & Jarms (2010)/ present study
Cyanea capillata	-	-	-/ 46% of TBD^z	8^z	50% / 50% of TMLL^z	pointed/ marginal tentacles are clearly visible by the time of release	(forked) radial canals extend out into marginal lappets	orange	Gröndahl & Henroth (1987)
	19°C	2.0–4.4	-	8^z	-	pointed^z/ newly released ephyrae possess 0–1 tentacles	-	-	Higgins III *et al.* (2008)
	5–10°C	5.97–9.54, mean: 8.55	2.43–3.79, mean: 3.34/ 41% of TBD	8	43% / 57% of TMLL	lancet like/ 2–8 tentacles buds when newly released	forked rhopaliar canals, tips reach far into the rhopaliar lappets, forked velar canals, tips reach to tip level of rhopalia into the marginal lappets	red orange	Straehler-Pohl & Jarms (2010)/ present study

CDD = Central Disk Diameter LStL = Lappet Stem Length p = data taken from photos RLL = Rhopalial Lappet Length TBD = Total Body Diameter
TMLL = Total Marginal Lappet Length z = data taken from drawings - = no statement given in the publication

TABLE 6c. Ephyra morphology and references — Aureliinae and Phacellophoridae fam. nov.

Species	Culture conditions (Temperature)	TBD [mm]	CDD [mm] and/or Proportions	No. of Marginal Lappets	Lappet Proportions: LStL / RLL compared to TMLL	Shape of Rhopalial Lappet/ Distinctions	Gastric System	Colour	Reference
Aurelia aurita	-	-	- / 45% of TBD^{z}	8^{z}	66% / 34% of TMLL^{z}	rounded tips^{z}/ no marginal tentacles visible after release	radial canals extend not into the rhopalar lappets; tips rounded^{z} / -	light blue transparent	Gröndahl & Henroth (1987)
	44–68°F	a bit smaller than 4 mm	- / 44% of TBD^{z}	8–12, mean: 8	53% / 47% of TMLL^{z}	rounded tips/ 0–1 gastric filaments per quadrant	forked rhopalial canals, tips stretch into rhopalial lappets, unforked velar canals	-	Delap (1906)
	15–25°C	3.86–4.5, mean: 4.19	1.44–1.81, mean: 1.66 / 40% of TBD	8	52% / 48% of TMLL	broad lancett shaped / 1–2 gastric filaments per quadrant	spade shaped to slightly forked rhopalial canals, rhombus shaped velar canals	milky to bluish	Straehler-Pohl & Jarms (2010) present study
Aurelia limbata	9–13°C	3.0–4.5	/ 43% of TBD^{z}	8	marginal lappet a bit longer than radius of disc - 52% / 48% of TMLL^{z}	rather narrow tips which overlap inside / statocyst is bright yellowish, 1–2 gastral filaments per quadrant	rather wide radial canals, large adradial out-pockets	pale yellow or greyish yellow	Uchida & Nagao (1963)
	15–25°C	2.62–5.33, mean: 3.66	1.07–1.71, mean: 1.26 / 35% of TBD	8	58% / 42% of TMLL	bread knife shaped/ 1 gastric filament per quadrant	spade like, unforked radial canals	greenish yellow with reddish brown	Straehler-Pohl & Jarms (2010) present study
Phacello-phora camtscha-tica	14°C	3.5–6.2, mean: 5.3	- / 60% of TBD	13–18, mean: 16	45% / 55% of TMLL^{p}	pointed/ 2 gastric filaments per quadrant, rudiments of 4 single primary tentacles budding from the subumbrella at the base of the cleft between the marginal arms	very slim, pointed radial canalsp	yellow to orange	Widmer (2006)
	15°C	3.5–10.8, mean: 7.77	5.64–6.46, mean: 5.85/ 57% of TBD	13–18, mean: 15.5	47% / 53% of TMLL	pointed flame shaped / 1–2 gastric filaments per quadrant	arrow shaped rhopalial canals, arrowhead shaped velar canals	yellowish, gastric system: yellowish orange	Straehler-Pohl & Jarms (2010) present study$^{\#}$

CDD = Central Disk Diameter LStL = Lappet Stem Length p = data taken from photos RLL = Rhopalial Lappet Length TBD = Total Body Diameter
TMLL = Total Marginal Lappet Length z = data taken from drawings - = no statement given in the publication

The gastric system in ephyrae of *Phacellophora camtschatica* is enlarged by development of several side branch pairs from the edges of the rhopalial canals that resemble the first pair of side branches in ephyrae of Aureliinae. These side branch canals grow chronologically in a centrifugal direction and fuse with the single, non-branched velar canals to ring canals. Each ring canal is deformed by further centrifugal growth of the velar canals and by renewed fusing with other rhopalial side branches until a final ring canal is formed just below the rim of the umbrella, resembling that in Aureliinae. During further growth of the stomach, the "innermost branches of the rhopalar canals are cut off from the main canal and are transformed into interrhopalar canals" as surmised by Kramp (1952), or phase out by "Inselbildung" (for definition, see Stiasny 1923; Uchida 1926) when fusion with the developing ring canal and other side branches is completed (Table 6: Fig. "Stage 4"). The ring canal develops blind-ending secondary canals (Mayer 1910; Stiasny 1934; Fedele 1937a, b; Larson 1986; Mianzan & Cornelius 1999) which grow in a centrifugal direction into the marginal lappets (Plate 5, Fig. F), similar to the blind-ending canals observed in Cyaneidae. After the final ring canal is formed, development of the gastric system in *P. camtschatica* is directed centrifugally as in Cyaneidae, and not centripetally as in Aureliinae (Thiel 1970). Development of the net-like gastric system in Aureliinae is much more intricate than in Cyaneidae (Uchida 1960; Thiel 1970; Werner 1973; Straehler-Pohl 2009).

As in Cyaneidae, but unlike in Aureliinae, no velar lappets are formed in ephyrae of *P. camtschatica* by budding of additional diverticula above the velar canal tips (Plate 5). Instead, growth of the marginal rim of the exumbrella is extended until a sinus-curved connection (a pseudo velar lappet) is formed between the rhopalar lappets, somewhat resembling tentacular lappets of species of *Chrysaora* (Russell 1970).

Although tentacles of *P. camtschatica* form a single row (Kishinouye 1910; Mayer 1910; Larson 1986, Plate 5), as in Aureliinae, their ontogeny is more like tentacle development in Pelagiidae and Cyaneidae. The first tentacles in cyaneids and pelagiids are budded from the tips of the velar canals (Russell 1970; Morandini *et al.* 2004, 2006; Widmer 2008; Straehler-Pohl 2009) and all others arise one after another (Thiel 1962, 1970; Russell 1970); tentacles in Aureliinae arise synchronically from the final ring canal (Chapman 2001). But even if tentacles of the Pelagiidae are formed chronologically, their tentacles stand singly at the edge of the subumbrella, each one separated by a tentacular lappet, and not in a single row covered by a marginal lappet. Single rows of tentacles of this kind are also known in the cyaneid genus *Desmonema* (Mayer 1910; Stiasny & van der Maaden 1943; Larson 1986). Comparisons of development undertaken here provide evidence that *P. camtschatica* may be more closely related to Cyaneidae than to Aureliinae or Pelagiidae.

Systematics

Comprehensive taxonomic revisions of the Scyphozoa are generally lacking (excluding older monographs by authors such as Haeckel, Mayer, and Stiasny). A detailed morphological approach, accompanied by careful study of the literature, can provide a foundation for a more stable taxonomy of the Scyphozoa. An example is a recent revision of the genus *Chrysaora* by Morandini & Marques (2010). Moreover, molecular data may provide insights and additional characters in support of a more stable classification of the group.

In the molecular phylogenetic hypothesis of Collins (2002) and Collins *et al.* (2006), *P. camtschatica* formed a clade with Rhizostomeae. This clade was presented as the sister group of all other Semaeostomeae. This configuration was not explained or clarified except for the statement: "Ulmaridae (*Aurelia* and *Phacellophora*) most likely gave rise to Rhizostomeae" (Collins *et al.* 2006: 109, Figs. 3, 6), which was also supported by Bayha *et al.* (2010). The position of *Phacellophora* could not be completely clarified in Collins *et al.* (2006) because the analysis did not include samples of several semaeostome subgroups.

In our opinion, *Phacellophora camtschatica* is not referable to any of the families Pelagiidae, Cyaneidae, or Ulmaridae. Instead, we consider the genus *Phacellophora* to be intermediate between Cyaneidae and Ulmaridae, and maintain that it should be removed from the latter family.

Among Ulmaridae, *Phacellophora* has until now been included with the genus *Sthenonia* in the subfamily Sthenoniinae (Kramp 1961). Unfortunately, the type species of that monotypic genus, *Sthenonia albida* Eschscholtz, 1829, has not been observed since its original description (Haeckel 1880; Vanhöffen 1906, Mayer 1910).

Our attempts to locate specimens of *S. albida* were unsuccessful, and comparisons with present material are currently possible only from the poorly written description and accompanying original figure as no holotype was preserved by Eschscholtz. Nevertheless, the species (and the genus and subfamily based on it) has long been considered valid. Accordingly, we maintain the subfamily Sthenoniinae within Ulmaridae and propose a new family to accommodate *Phacellophora camtschatica*.

Family Phacellophoridae, fam. nov.

Diagnosis. Semaeostome Scyphozoa with gastric cavity and having radial canals (simple and branched) joining marginal ring canal; mouth arms broad, curtain like; subumbrellar tentacles in 16 linear clusters; gonads protrusive, sac-like; subgenital pits absent.

During development, gastric system extending solely in a centrifugal direction, even after formation of final ring canal below marginal lappets of umbrella; forming pseudo-velar lappets that connect rhopalial lappets of two rhopalia; blind ending, straight, normally unbranched canals, growing from ring canal into pseudo-velar lappets; tentacles developing chronologically in linear clusters at subumbrella margin; rhopalar canals branched; single velar canals unbranched.

Type genus: *Phacellophora* Brandt, 1835.

Type species: *Phacellophora camtschatica* Brandt, 1835.

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