Zoological Studies **59**:35 (2020)
doi:10.6620/ZS.2020.59-35

Zoological Studies

Special Issue: Fossil and Modern Clam Shrimp (Branchiopoda: Spinicaudata, Laevicaudata) **Open Access**

Developmental and Functional Morphology of *Eulimnadia braueriana* Ishikawa, 1895 (Branchiopoda: Spinicaudata) Feeding Structures: Combination of Filtering and Scraping Feeding Mechanisms

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Received 7 August 2019 / Accepted 20 February 2020 / Published 5 August 2020

Special issue (articles 32-46) communicated by Thomas A. Hegna and D. Christopher Rogers

Large branchiopods inhabit diverse continental habitats worldwide. Their feeding ecology, nevertheless, remains largely unknown. The few functional morphology studies that have been conducted have mostly focused on adults or larvae, seldom have the two been compared collectively. In this study, we examined the feeding structures in *Eulimnadia braueriana* Ishikawa, 1895 from nauplius to adult to clarify their feeding mechanisms and then compared them with the other two sympatric branchiopods (*Branchinella kugenumaensis* and *Lynceus biformis*) in Siangtian Pond, Taiwan. Naupliar second antennae and mandibles are similar to those of other species, suggesting filter-feeding. The naupliar feeding structures, including the mandibular palp and naupliar process, gradually degenerate during the juvenile stage. Simultaneously, the molar surface, maxillae, and second antennae continue developing, reaching their adult form in later juvenile substages. The molar surface and thoracopod setal morphology are similar to those of other filter-feeding branchiopods, but adults also have scraping setae on the first several thoracopod pairs. Nearly all naupliar primary feeding structures change through development, particularly during the early juvenile substages, whereas late juvenile substages and adult morphology are similar. *Eulimnadia braueriana* transforms from pelagic filtering nauplii to adults that combine benthic filtering and scraping. Comparisons of molar and thoracopod morphology between coexisting branchiopod species show some similarities and differences in filtering and scraping feeding structures, implying potential foraging resource differentiation among species.

Key words: *Branchinella kugenumaensis*, *Lynceus biformis*, Mandible, Second antenna, Thoracopod.

BACKGROUND

Dynamic and heterogeneous habitats impose selective pressures on the inhabiting organisms. As one of the taxonomic groups that live in a great variety of environments from terrestrial freshwater and saline water habitats to marine ecosystems, crustaceans have evolved diverse morphologies and life history strategies. Crustacean morphological studies have elucidated taxonomic evolutionary histories (Fryer 1985; Lindholm

Citation: Liu JY, Wang CC, Rogers DC. 2020. Developmental and functional morphology of *Eulimnadia braueriana* Ishikawa, 1895 (Branchiopoda: Spinicaudata) feeding structures: combination of filtering and scraping feeding mechanisms. Zool Stud **59**:35. doi:10.6620/ZS.2020.59-35.

2014) and diversification (Watling 1989; Mura 1996; Olesen 2007). Furthermore, the linkage of morphology and function also reveals behavioral strategies, such as feeding (Storch 1925; Ghauri 1983) and reproduction (Plodsomboon et al. 2012; Sigvardt and Olesen 2014). Crustacean morphology studies may contribute to knowledge of their evolution and adaptation.

In continental crustaceans, large branchiopods (Crustacea: Branchiopoda: Anostraca, Notostraca, Laevicaudata, and Spinicaudata) are widely distributed, particularly in harsh aquatic environments such as salt lakes and seasonally temporary wetlands (Brendonck et al. 2008; Rogers 2009). In habitats with significant fluctuations in physiochemical conditions, large branchiopod feeding ecology has been an attractive issue since early 20th century (*e.g.*, Cannon and Leak 1932). Generally, large branchiopod feeding modes have been categorized as four major types: filter-feeding, predatory, scraping and scavenging. Filter-feeding is probably the most primary and common feeding mode in branchiopods (Cannon and Leak 1932). Filter-feeding branchiopods are characterized by dense, plumose setae on the thoracopods, which create a feeding current as the thoracopods move in metachronal synchronicity (Cannon 1932; Fryer 1983). Such dense setation forms a tight mesh that captures and transfers particles along the food groove (Cannon 1932; Fryer 1983).

Predatory morphological indicators are sharp, robust and larger thoracopod spines and molar teeth (Fryer 1966; Martin and Cash-Clark 1995; Rogers et al. 2006). These characters can be found in certain Cladocera (Martin and Cash-Clark 1995), Anostraca (Fryer 1983; Rogers et al. 2006), and Notostraca (Fryer 1988). Although morphological traits of scraping or scavenging species are similar to filter-feeders, they generally have stout setae or spines on the thoracopod portions that come in contact with the substrate (Martin 1989; Fryer and Boxshall 2009). Their mouthparts may also vary slightly in that they can ingest harder particles than filter-feeders (Ghauri 1983; Richter 2004; Fryer and Boxshall 2009). There are also species in which the feeding structures have multiple functions, keeping a more complex diet under different circumstances (Mertens et al. 1990; Brendonck 1993).

The smooth clam shrimps (order Laevicaudata) have been described as scrapers (Martin 1989; Fryer and Boxshall 2009). The thoracopods and carapace generate a steady water flow along the food groove, drawing the scraped particles towards the mouth (Cannon 1932; Fryer 1983). In spiny clam shrimps (order Spinicaudata), feeding modes vary greatly. Scraping structures were identified in *Imnadia* (Botnariuc 1947); filter-feeding was suggested in *Limnadia*, *Cyzicus*, and *Leptestheria* (Storch 1925; Cannon 1932; Emberton 1980; Martin and Cash-Clark 1995). Although these few available studies cover all spinicaudatan families, information on feeding mode development is lacking. Studies on branchiopod nauplius morphology mainly aimed at taxonomic and evolutionary issues (Pai 1958; Williams 1994; Fritsch and Richter 2012). Additionally, for species whose nauplius and adult have widely different behavior and utilize different microhabitats such as *Eulimnadia braueriana* Ishikawa, 1895 (Liu et al. 2016), the juvenile stage is an intermediate period with prominent changes. Thus, ontogenic feeding structure morphology studies could bridge the gap between nauplius and adult foraging habits.

Eulimnadia braueriana in Taiwan is found sympatrically with two other large branchiopod species, the anostracan *Branchinella kugenumaensis* (Ishikawa, 1895) and laevicaudatan *Lynceus biformis* (Ishikawa, 1895), in Siangtian Pond at northern Taiwan (Wang et al. 2012). Siangtian Pond has hydroperiods that often last shorter than branchiopod life spans due to porous sediment substrate (Huang et al. 2010; Wang et al. 2014). Crowding of branchiopods in the few available pits is a very common phenomenon near the end of a hydroperiod (Wang et al. 2012 2018). Previous studies showed partial vertical distribution segregation among the sympatric large branchiopod species in Siangtian Pond (Wang et al. 2012). Furthermore, *E. braueriana* displayed a phototactic change from positive to negative during development (Liu et al. 2016). The spatial distribution and phototaxis of *E. braueriana* may relate to its foraging ecology. In this study, we approached *E. braueriana* feeding mechanisms through feeding structure morphology examination across three developmental stages (*i.e.*, nauplius, juvenile and adult) and then compared its primary feeding structures with the coexisting *B. kugenumaensis* and *L. biformis* adults.

Our results suggest a continuous change in feeding mechanisms from planktonic, filtering nauplii to filtering adults with ability to scrape sessile materials through *E. braueriana*'s ontogeny. The comparisons of feeding structure morphologies among coexisting large branchiopods reveal some similarities as well as differences in the filtering and scraping feeding between species.

MATERIALS AND METHODS

Eulimnadia braueriana specimens were cultured in the laboratory with aged tap water under 12/12 hours light/dark cycle at 22–24°C water temperature or sampled from the field during the 2014 hydroperiod (late May to mid-June). Adult specimens of *Lynceus biformis* and *Branchinella kugenumaensis* were obtained during the same hydroperiods. Fresh specimens were placed on ice for 30–120 seconds to cease movement before they were preserved in 5% formalin overnight at 4°C and then were serially dehydrated to 70% ethanol for storage.

General specimen observation and dissection were made using a Leica mz125 light microscope. Photographs were taken with Canon EOS 550D mounted on the light microscope with an adapter. Samples prepared for scanning electron microscopy (SEM) were serially dehydrated to 100% ethanol and changed to 100% acetone before critical point drying. They were then mounted on carbon tape, coated with gold, and observed with FEI Inspect S SEM or Hitachi Tabletop TM-3000 SEM.

Developmental stages were determined based on morphology. Nauplii are defined as individuals without a complete carapace that covers the whole body. The nauplius stage was further divided into seven substages following Olesen and Grygier (2003). Juveniles are defined as those possessing a fully grown carapace but have not reached sexual maturity. Based on the developed number of setose thoracopods, the juvenile stage was divided into the early (fewer than ten setose thoracopods) and late (more than ten setose thoracopods) juvenile substages. Adults have a fully developed carapace and mature reproductive structures. Males, which are relatively rare in this species (Huang and Chou 2015), can be identified by the first two thoracopod pairs, *i.e.*, the claspers. Hermaphrodites are characterized by the whitish eggs that are visible in the ovaries or on the dorsal side of the body. When describing area definition of adult molar surface morphology, we followed Brendonck's (1994) descriptions of *Streptocephalus coomansi* Brendonck and Belk 1993.

RESULTS

General morphology

Eulimnadia braueriana shows gradual morphological transformation until reaching maturity (Fig. 1). The first nauplius substage has an oval trunk and a large pair of second antennae (Fig. 1A). The trunk elongates through nauplius development (Fig. 1B–D). The telson becomes more pointed and the carapace anlage starts to form in nauplius substage five (Fig. 1E). Different from the nauplius substage six (Fig. 1F), the animal curves ventrally and the carapace reaches to the third thoracopod pair at the dorsal side in substage seven (Fig. 1G). Thoracopod buds are visible in the nauplius substages six and seven (Fig. 1F, G), but they are still underdeveloped and unable to move. Upon reaching the first juvenile substage, the carapace covers the trunk and all thoracopods (Fig. 1H). Growth lines on the carapace are not seen in the juvenile substages and the number of setose thoracopods develops from seven to eleven pairs before maturation (Fig. 1H, I). The spiny telson gradually develops during these juvenile substages (Fig. 1H, I). After maturation, individuals bear ova (Fig. 1J, K) or have two pairs of claspers (Fig. 1L). In large hermaphrodites, the carapace dorsal margin is slightly arcuate (Fig. 1K) compared to males (Fig. 1L).

Naupliar second antenna

The second antenna is the most prominent appendage in the nauplius stage (Fig. 2A). It is mobile upon hatching and can be divided into three antennomeres: the protopod, endopod and exopod (Figs. 2A, 3A).

The protopod is generally smooth (Fig. 3A). The basal protopodal coxa bears the elongated, conical naupliar process (or proximal masticatory spine; Fig. 3B) that becomes bifid at the fourth substage (Fig. 3C). The distal masticatory spine is located on the protopod distoposteriorly to the naupliar process, bearing well-spaced setae in the distal half (Fig. 3A). At the protopod apex projects the anterior endopod and the posterior exopod.

The endopod is slightly shorter than the exopod (Fig. 3A). The exopod bears a subdistal, posteriorventral row of five articulated setae each with a single row of short setulae from approximately mid-length to the distal apex. On the other hand, the endopod setae are concentrated at the distal margin, each with a distal row of short setulae.

The distal masticatory spine and the naupliar process on the protopod are slightly curved medially (Fig. 3A). The naupliar process is apically bifid from the fourth substage on (Fig. 3C). The setulae on the posterior branch are unevenly arranged whereas those of the anterior branch are two parallel, longitudinal rows with apices directed distally (Fig. 3C). During the anterior-posterior strokes of the second antenna, the naupliar process reaches below the labrum on the posterior stroke (Fig. 2A). The distal masticatory spine has sparse, slender setae from the second naupliar substage on (Fig. 3A).

Nauplius mandibles and maxillae

Aside from the second antenna, the mandible is the only other movable appendage in the nauplius stage, with a similar movement pattern as the second antenna. It can be separated into the mandible coxa and mandibular palp (Figs. 2A, 4A, 4B).

The mandible coxa starts as a bud at the first substage (Fig. 4C) but rapidly develops medially where the two molar surfaces finally touch at approximately the fourth substage (Fig. 4D, 4E). With exception of the first substage where there is no molar surface present, the general morphology of the molar surface remains similar during the nauplius stage. It is long and narrow, and has anterior cusps, a posterior dentiform structure and several rows of ornamented setae even before the left and right counterparts meet at midline. The spines on the molar surface are still simple (Fig. 4D).

The distal arc of the mandible coxa supports the mandibular palp, which projects at a right angle from the coxa (Fig. 2A). The mandibular palp is approximately the same length as the coxa and consists of three palpomeres, each bearing two spines (Fig. 4B). The spines on the first palpomere reach beneath the labrum during a posterior stroke. After the first naupliar substage, both spines on the first palpomere bear distal tufts of plumose setae. The proximal spine setae are unevenly distributed on the anterior surface and are directed to the mouth (Fig. 4B), similarly to the anterior tip of the naupliar process. The distal spine setae are arranged circularly around half the apex (Fig. 4B).

The naupliar maxillae are small setae in the early

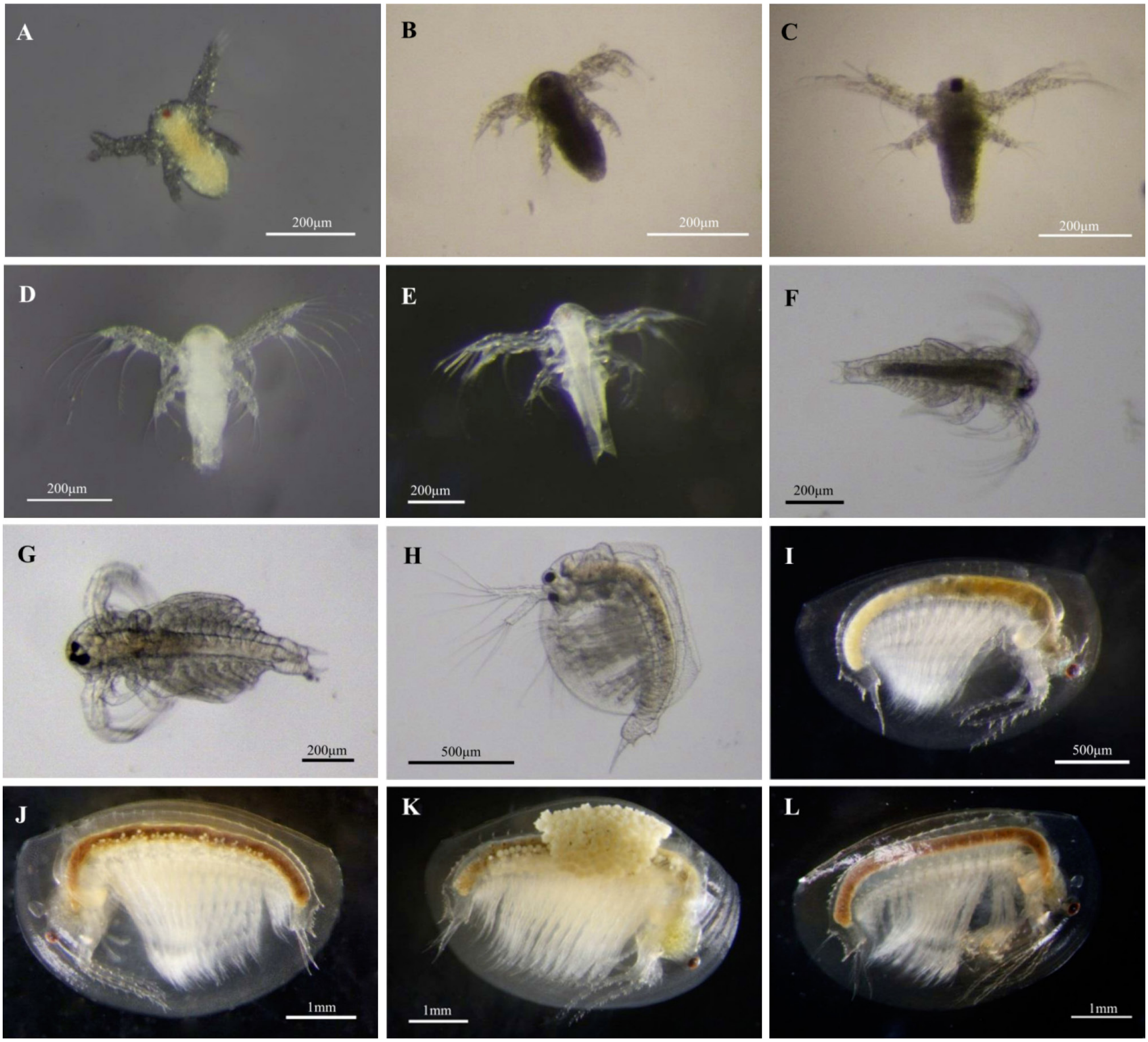

Fig. 1. Developmental stages of *Eulimnadia braueriana* observed under the light microscope. (A) Nauplius substage 1; (B) nauplius substage 2; (C) nauplius substage 3; (D) nauplius substage 4; (E) nauplius substage 5; (F) nauplius substage 6; (G) nauplius substage 7; (H) early juvenile substage; (I) late juvenile substage; (J) early adult stage (hermaphrodite); (K) fully grown hermaphrodite; (L) fully grown male.

substages (Fig. 4A, C). Maxilla buds appear at substage six. By the last substage (substage seven), the first maxillae have a slight food groove between them, with sparse setae vaguely directed to the mouth (Fig. 4F). The second maxillae are only visible in the last two substages as buds without setation (Fig. 4F).

Juvenile and adult second antenna

The second antenna of the juvenile and adult consists of the indistinctly segmented protopod, endopod and exopod (Fig. 2B, C).

The naupliar process and distal masticatory spine on the naupliar second antenna (Fig. 3A) gradually degenerate and disappear across the juvenile substages (Figs. 5A–C, 6A). The endopod and exopod are annulated, with two setae on each antennomere except the distal most one which has three setae, and elongate as the masticatory spines degenerate, matching the length of the protopod at the juvenile stage (Fig. 5C, D). The number of antennomeres increases with development, reaching seven on the endopod and eight on the exopod at maturation (Fig. 5E). The protopod anterior surface bears longitudinal rows of plumose setae (Fig. 5G).

During the early juvenile substages, the endopod and exopod bear long, distal setae (Fig. 5A). During the later juvenile substages, each antennomere bears one short and one long seta on the anterior and posterior surface, respectively (Fig. 5C). Eventually, four to five long setae distribute along the posterior surface of each adult antennomere (Fig. 5E, F).

Juvenile and adult mandibles and maxillae

The mandibular palp degenerates through the juvenile stage and is quickly outgrown by the coxa (Fig. 6A). The mandibular palp spines reduce and are no longer able to reach near the mouth, eventually disappearing before the animal reaches maturity.

The molar surface widens during the juvenile stage and the spines start to differentiate morphologically (Fig. 6B). The molars develop asymmetrically in the early juvenile substages. On the right molar surface, the cusps at the anterior region become broader at the border and both flagellated and simple processes are seen in the posterior region (Fig. 6B). The ventral border of the left molar surface consists of flagellated processes, with a particularly large process at the anterior end. Distinct from the naupliar molar surface (Fig. 4E), the setae that had been present near the posterior tooth decrease in number (Fig. 6B). The paragnath buds are seen during

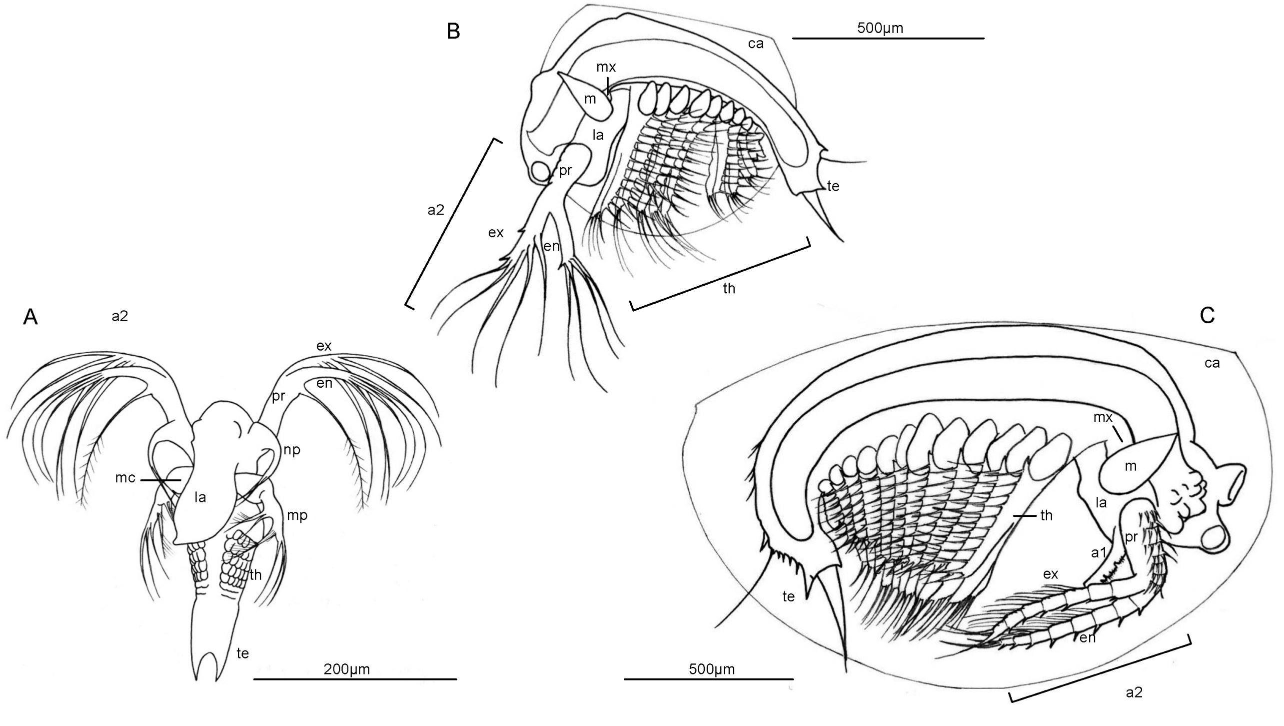

Fig. 2. *Eulimnadia braueriana* diagram. (A) nauplius substage; (B) early juvenile substage; (C) late juvenile and early adult stage (structures for reproduction not implied). a1, first antenna; a2, second antenna; ca, carapace; en, endpod; ex, exopod; la, labrum; m, mandible; mc, mandible coxa; mp, mandible palp; mx, maxillae; np, naupliar process; pr, protopod; te, telson; th, thoracopod(s).

the late juvenile stage, located anterior of the first maxillae right beneath the mandibles (Fig. 6C).

In the adult, molar surface morphology is more differentiated (Figs. 7A, 8). The central region constitutes the largest area on the molar surface; it is smooth and perforated (Fig. 8A). The border on the anterior side shows flagellated processes (Fig. 8B, C). Processes on the anterior end are broad and flat while those on the posterior end are slender (Fig. 8D). The transitional zone starts next to the posterior end (Fig. 8A). Here, the flagellated processes are substituted by blunt protrusions. The peripheral region is narrow and has simple processes (Fig. 8E). The posteriodorsal area is relatively small and bears only one single large tooth (Fig. 8F). It separates the peripheral region and the 'region with bordering flagellated processes.'

The first maxillae are fully developed in the juvenile stage, equipped with long plumose setae that reach to the mandible coxa (Fig. 9). The second maxillae are flat and also bear dense setae that are directed anteriomedially (Fig. 9A). They are approximately half as large as the first maxillae. Lateral to the second maxillae are the labral gland openings (Fig. 9A). The paragnaths, which started to develop in the juvenile stage, are conical, directed medially and slightly dorsally in adults (Fig. 9D). In ventral view, they are usually obstructed laterally by the mandible coxa.

Adult mandibles of *Branchinella kugenumaensis* and *Lynceus biformis*

The mandibles of *B. kugenumaensis* also have molar surfaces with obvious morphological distinction in different areas (Figs. 7B, 10). At the dorsoposterior surface where *E. braueriana* has a posterior tooth (Fig. 8F), *B. kugenumaensis* has a row of flagellated, conical teeth (Fig. 10C). The teeth decrease in size to the anterior margin and decrease both in size and complexity posteriorly until they are simple cusps on the posterior most margin and slender, flagellated spines at the dorsoanterior border (or 'the region of bordering flagellated process'; Fig. 10A). Several small protrusions are present at the transition area between the dorsoposterior border and the central region (Fig. 10C). The peripheral region consists of spines with

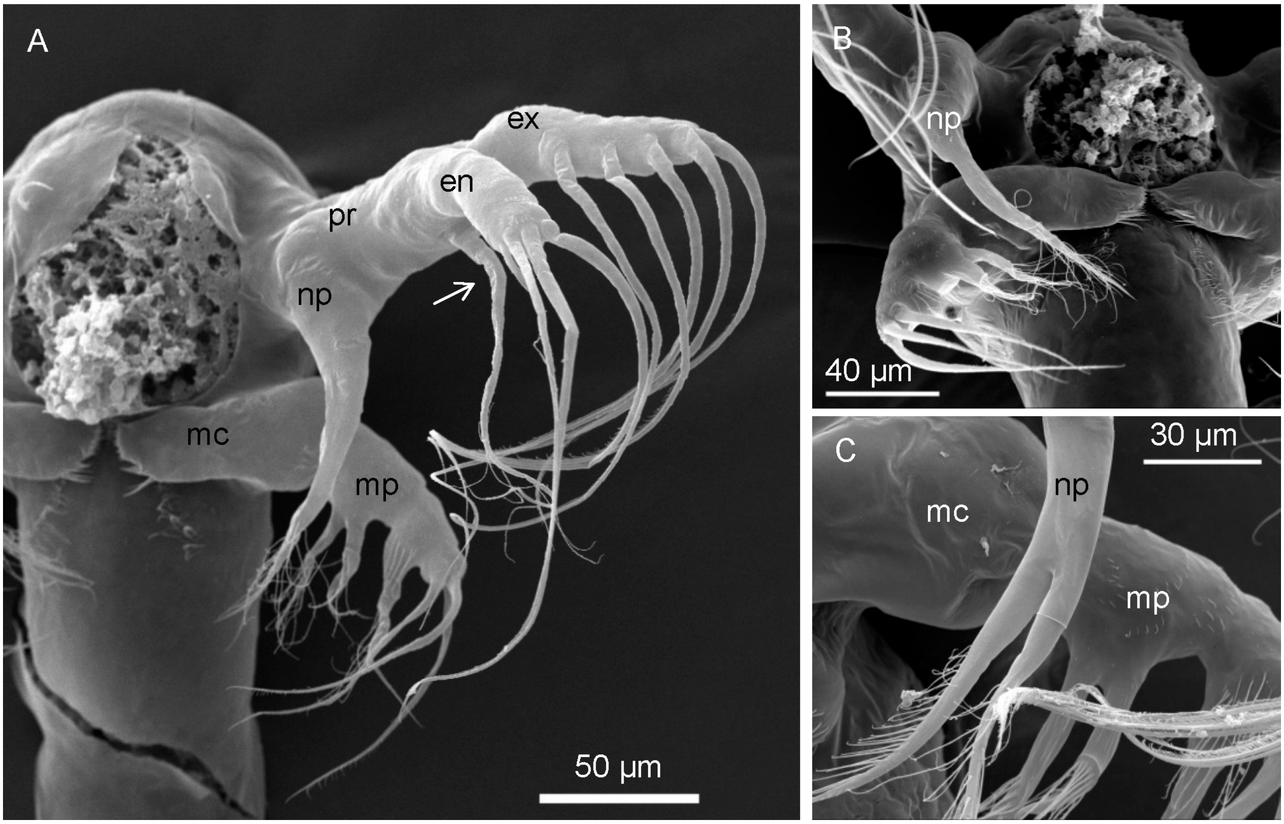

Fig. 3. Nauplius second antennae. (A) Overall appearance of the second antenna (nauplius substage 3). The entangling of setae is an artifact. (B) Naupliar process at nauplius substage 3. (C) Naupliar process at nauplius substage 6. en, endpod of second antenna; ex, exopod of second antenna; mc, mandible coxa; mp, mandible palp; np, naupliar process; pr, protopod of second antenna; arrow, distal masticatory spine.

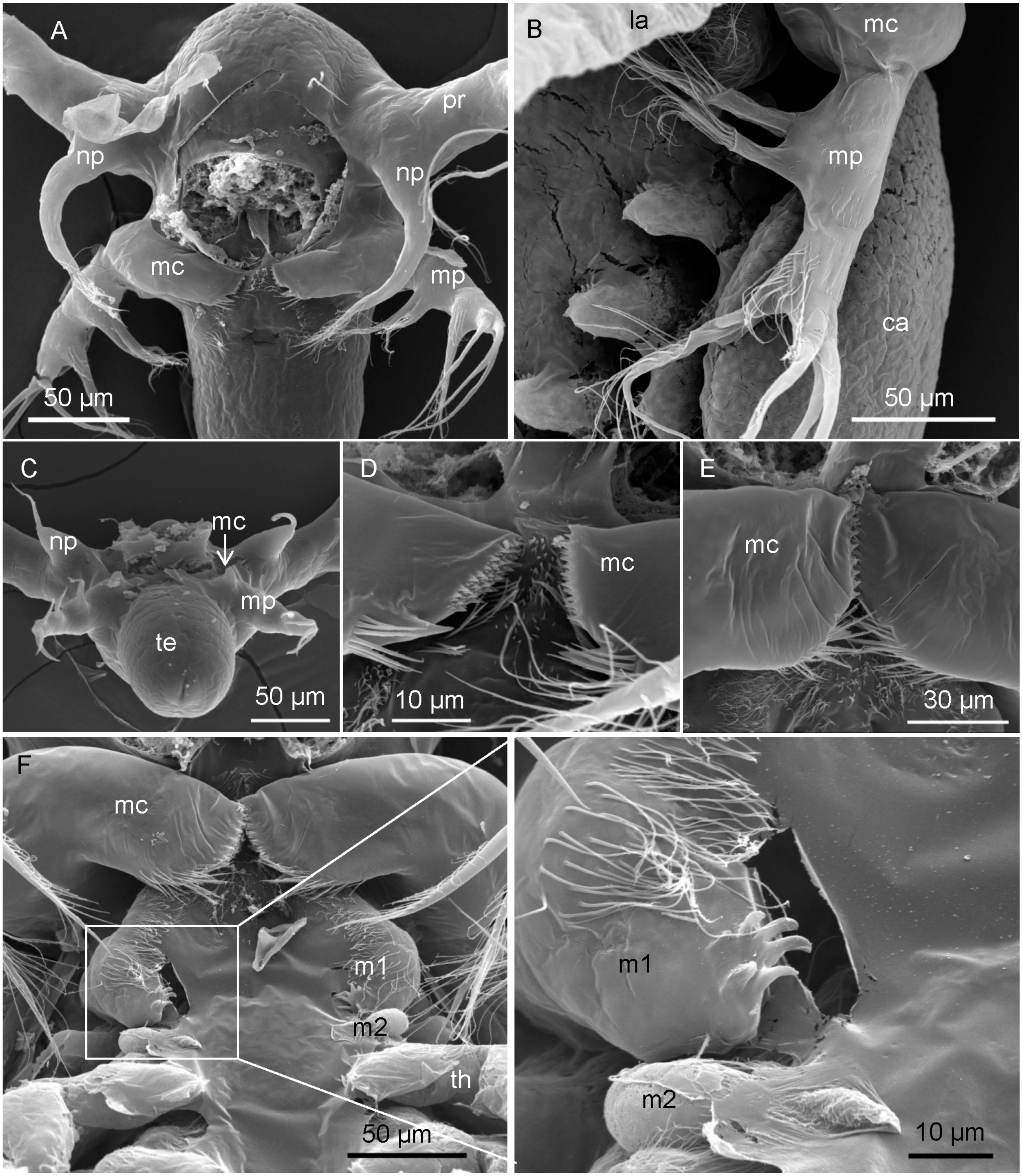

Fig. 4. Nauplius mandibles and maxillae. (A) Relative locations of feeding structures (substage 2). (B) Mandibular palp (substage 7). (C) Mandible coxa at substage 1 (posterior view). (D) Molar surface at substage 3. (E) Mandible coxa at the last nauplius substage (substage 7). (F) Relative location of mandible and maxillae (substage 7). ca, carapace; la, labrum; mc, mandible coxa; mp, mandible palp; m1, first maxilla; m2, second maxilla; np, naupliar process; pr, protopod; te, telson; th, thoracopod.

multiple flagellations which decrease in diameter and complexity anteriorly (Fig. 10B). Immediately medial to the thin anterior spines are several rows of teeth that are rectangular in distal view and bear a variety of conical cusps (Fig. 10C). Near the central region, these cusps are less developed and are arranged in closer proximity to each other. The central region is broad, smooth and perforated as in *E. braueriana* (Fig. 10A).

Lynceus biformis has quite different molar surface than that of *E. braueriana* and *B. kugenumaensis* (Fig.

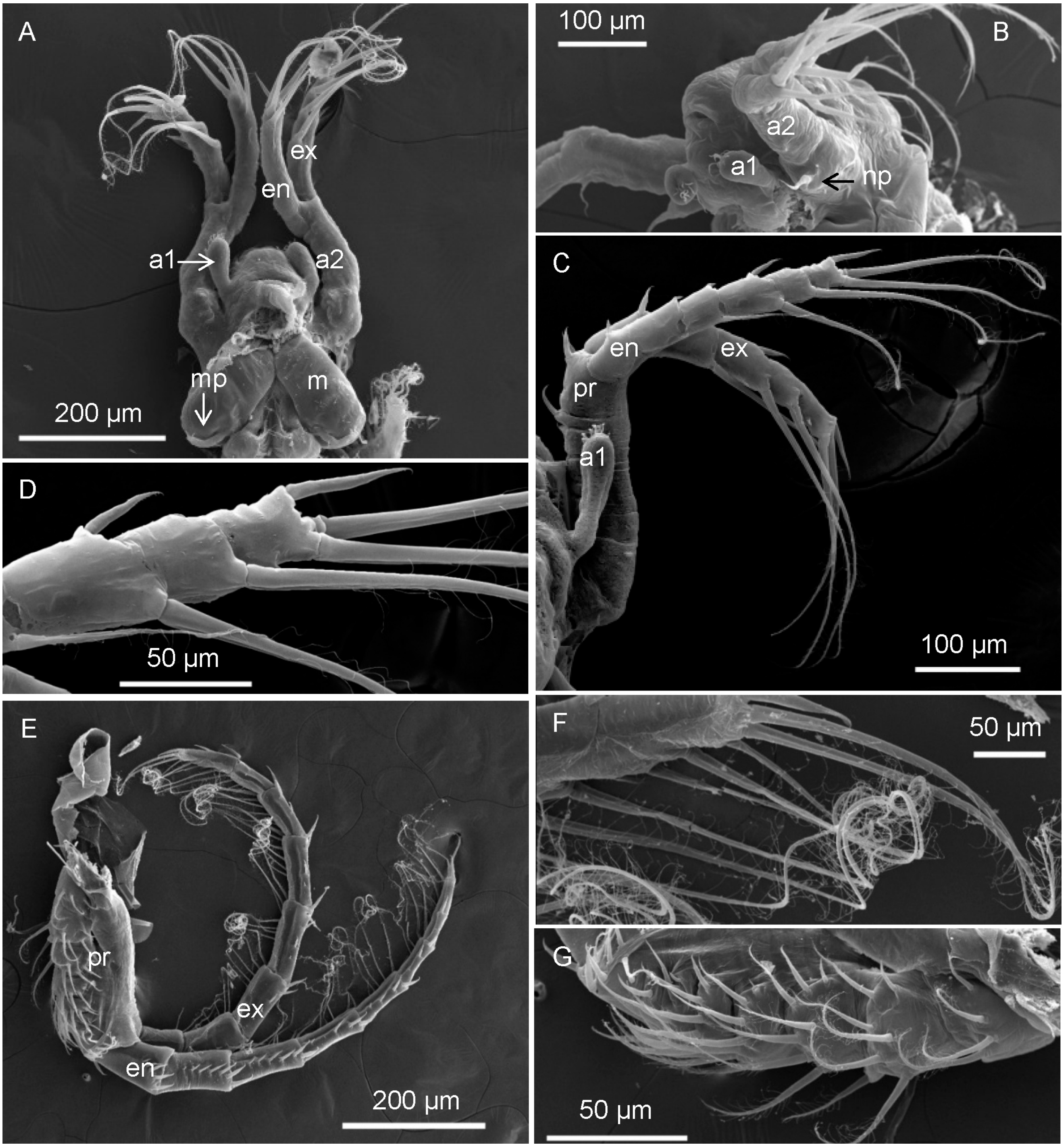

Fig. 5. Juvenile and adult second antennae. (A) Early juvenile antenna (ventral view). (B) Degenerating naupliar process. (C) Late juvenile antenna without masticatory spines (ventral view). (D) Endopod setae (late juvenile). (E) Adult second antenna (medial view). (F) Setae on the endopod (adult stage). (G) Setae on the protopod. a1, first antenna; a2, second antenna; en, endpod; ex, exopod; m, mandible; mp, mandible palp; np, naupliar process; pr, protopod.

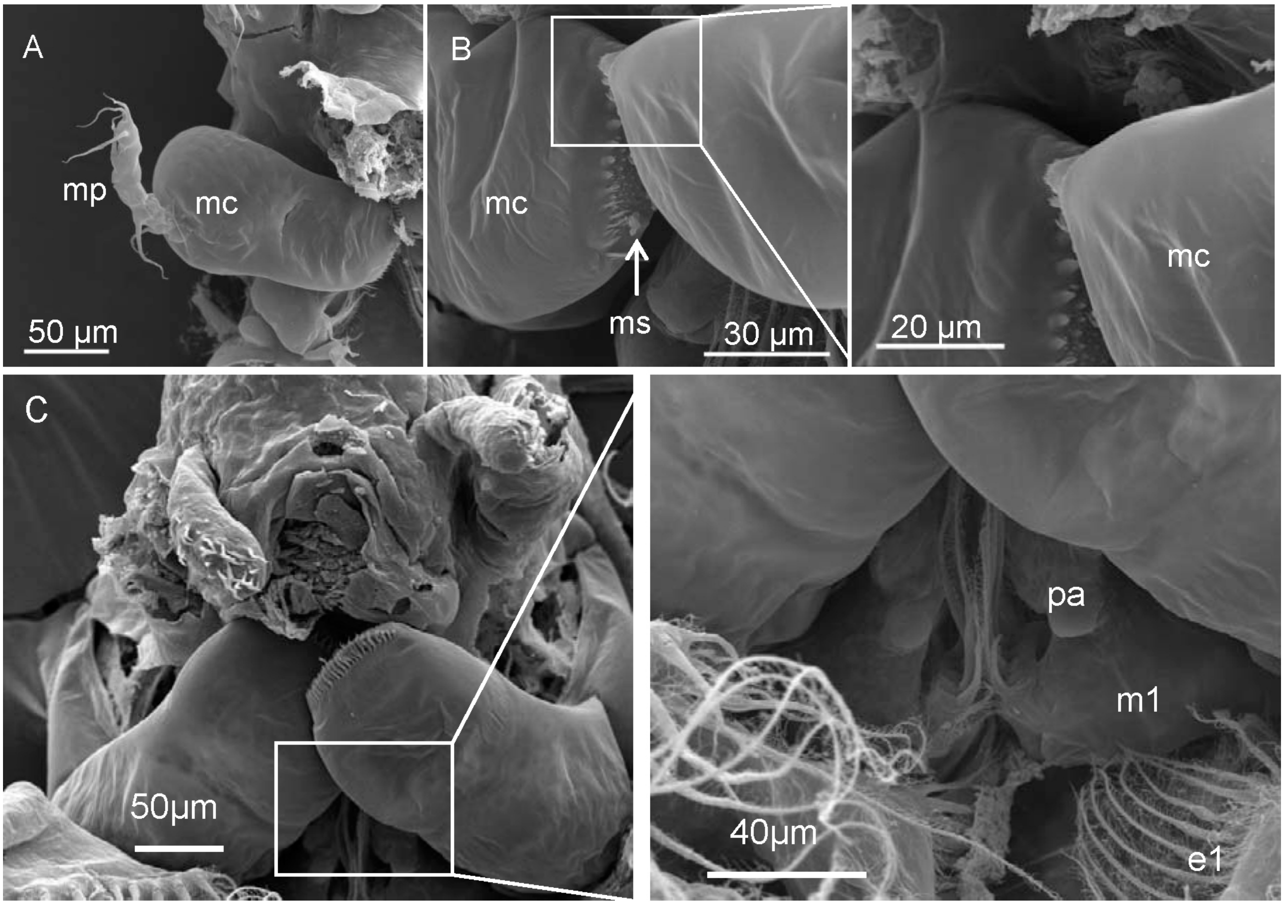

Fig. 6. Juvenile mandibles. (A) Degenerating mandibular palp (early juvenile, ventral view). (B) Early juvenile molar surface with preliminary asymmetry. (C) Late juvenile mandibles with the developing paragnaths. e1, endite I; m1, first maxilla; mc, mandible coxa; mp, mandible palp; ms, molar surface; pa: paragnath.

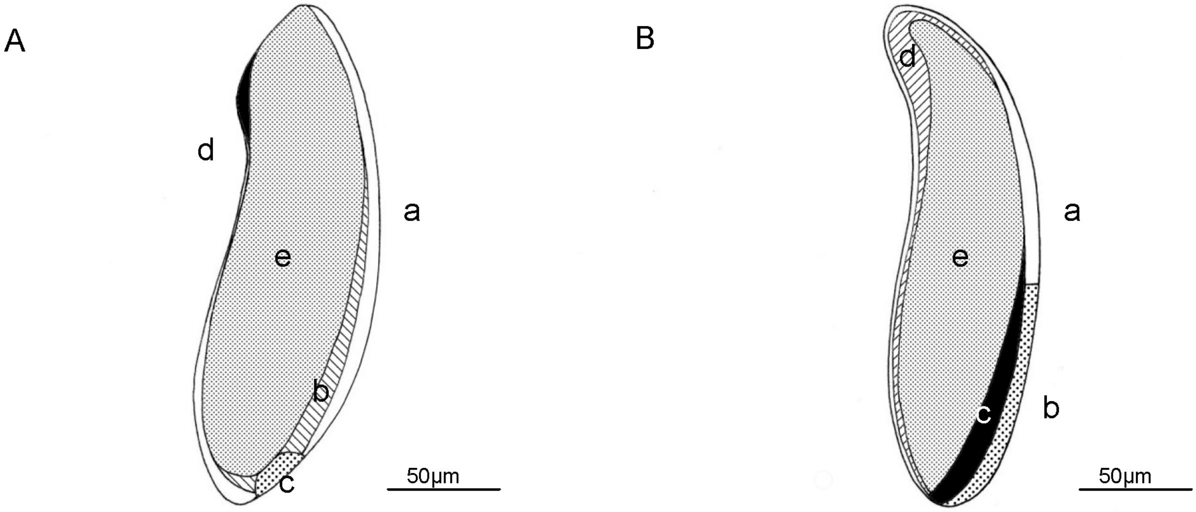

Fig. 7. Diagram of adult right molar surface (left as ventral, and up as anterior). Area with the same color represents similar morphology. Molar surface of (A) *Eulimnadia braueriana*; (B) *Branchinella kugenumaensis*. a, anterior bordering flagellated region; b, posterior bordering flagellated region; c, transitional zone; d, peripheral region; e, center region.

11). The molar surface is long and narrow (Fig. 11A), with 11 dorsoventral ridges and grooves (Fig. 11B). The ridges are crescent shaped with higher spines on the two ends and lower spines in the middle.

Juvenile and adult thoracopods

In the first juvenile substage, *E. braueriana* has seven pairs of movable thoracopods which decrease in size and development posteriorly (Fig. 2C). A fully developed thoracopod consists of five medial endites (Fig. 12A), a basolateral epipod (Fig. 12B), a distolateral exopod and a distal endopod (Fig. 12C). The first two thoracopods pairs in adult males are specialized as claspers (Fig. 1L), whereas in hermaphrodites, the ninth and tenth thoracopods pairs have dorsally extended exopodal filaments for egg attachment. In unspecialized thoracopods, the epipod is the only lobe without marginal setae (Fig. 12B). The exopod has a dorsal and a ventral extension (Fig. 12C). Both extensions bear loosely distributed marginal setae. The endites and the endopod have dense, plumose marginal setae (Fig. 12D, E) forming a mesh with the setae of the adjacent thoracopods. Endite I (also called the proximal endite) is slightly elongated and subacute (Fig. 12A, D). It bears dense plumose setae on the ventral side, two slightly thicker setae on the distal side, and two short, stout setae with a row of triangular teeth on the posterior side (Fig. 12D). The remaining endites all have two parallel rows of dense, plumose setae (Fig. 12E). There

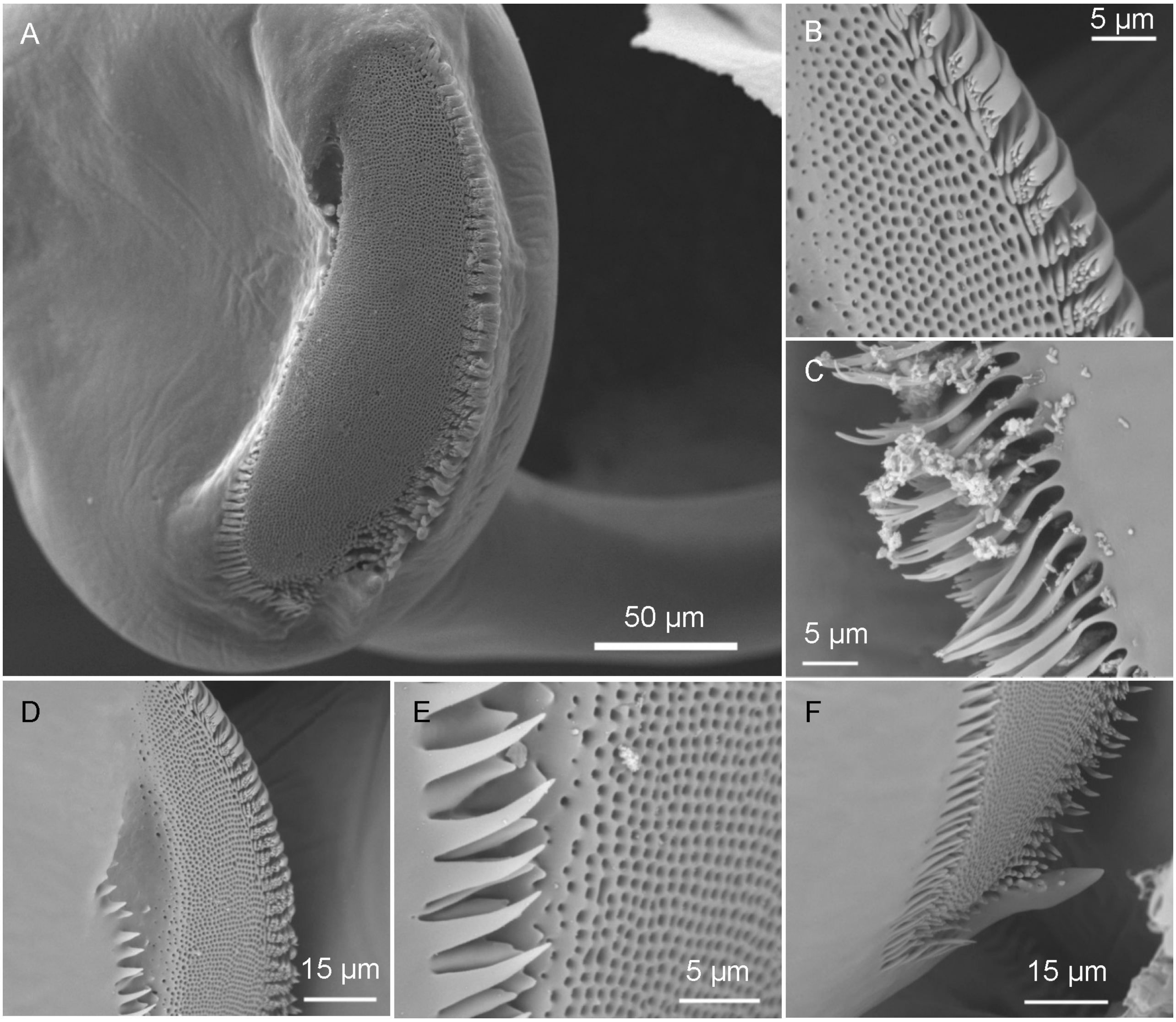

Fig. 8. *Eulimnadia braueriana* adult molar surface. (A) Right molar surface (left as ventral, and up as anterior). (B) Anterior bordering flagellated region. (C) Posterior bordering flagellated region. (D) Anterior part of the molar surface. (E) Peripheral region. (F) Posterior tooth.

is a palp on endite V of the first six thoracopod pairs (Fig. 12C), bearing long, robust, pectinate distal setae on the distal end (Fig. 12F).

Adult thoracopods of *B. kugenumaensis* and *L. biformis*

The eleven pairs of *B. kugenumaensis* thoracopods are biramous, with six medial endites, a distal endopod, a lateral exopod and the basolateral praepipod and epipod (Fig. 13A). The setae on the lateral lobes are sparse compared to the long, dense and plumose setae of the medial endites (Fig. 13A, B). The first three endites are broad (Fig. 13B), whereas the distal three are much smaller and bear setae with shorter setulae (Fig. 13C). The endite setation is similar to that of *E. braueriana* (Fig. 12A).

Lynceus biformis thoracopods bear dense setae

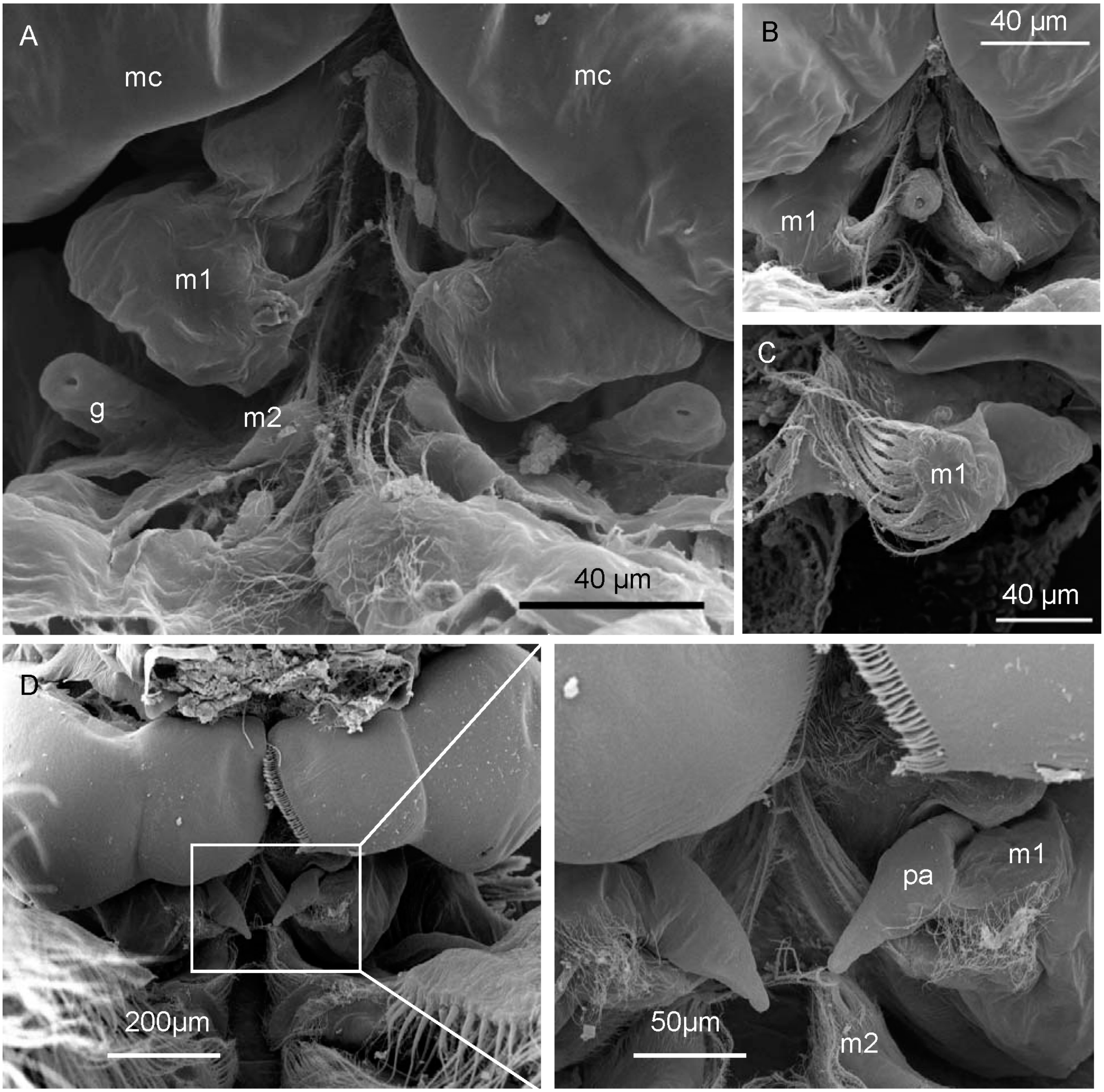

Fig. 9. *Eulimnadia braueriana* fully developed maxillae. (A) Relative location of feeding structures. (B) First maxillae with transported particles. (C) Setae of the first maxillae. (D) Location of the paragnaths, whose direction may have been slightly affected during sample preparation. g, labral gland; mc, mandible coxa; m1, first maxillae; m2, second maxillae; pa: paragnath.

on both the medial and lateral lobes (Fig. 14A). There are five medial endites, a distal endopod, a basolateral epipod and a distolateral exopod with a dorsal extension. In males, the first thoracopod pair is specialized as claspers; in females, the ninth to twelfth thoracopods are specialized for egg attachment. The thoracopods diminish in size posteriorly (Fig. 14A). On the distal end of the endopod and endite IV and V, *L. biformis* possess robust pectinate setae (Fig. 14B). The thoracopods of *L. biformis* are similar to those of *E. braueriana* but have notably more robust pectinate setae.

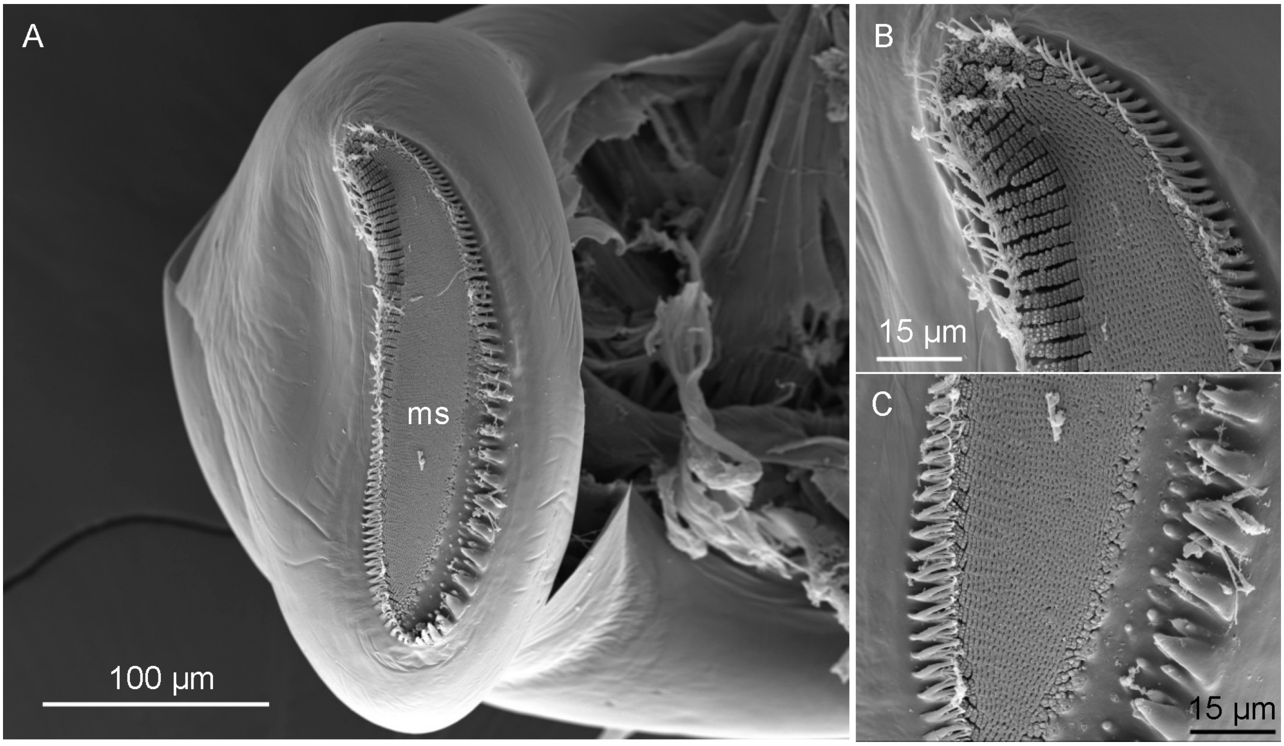

Fig. 10. *Branchinella kugenumaensis* molar surface. (A) Right molar surface (up as anterior). (B) Anterior part of the molar surface. (C) Posterior part of the molar surface. ms, molar surface.

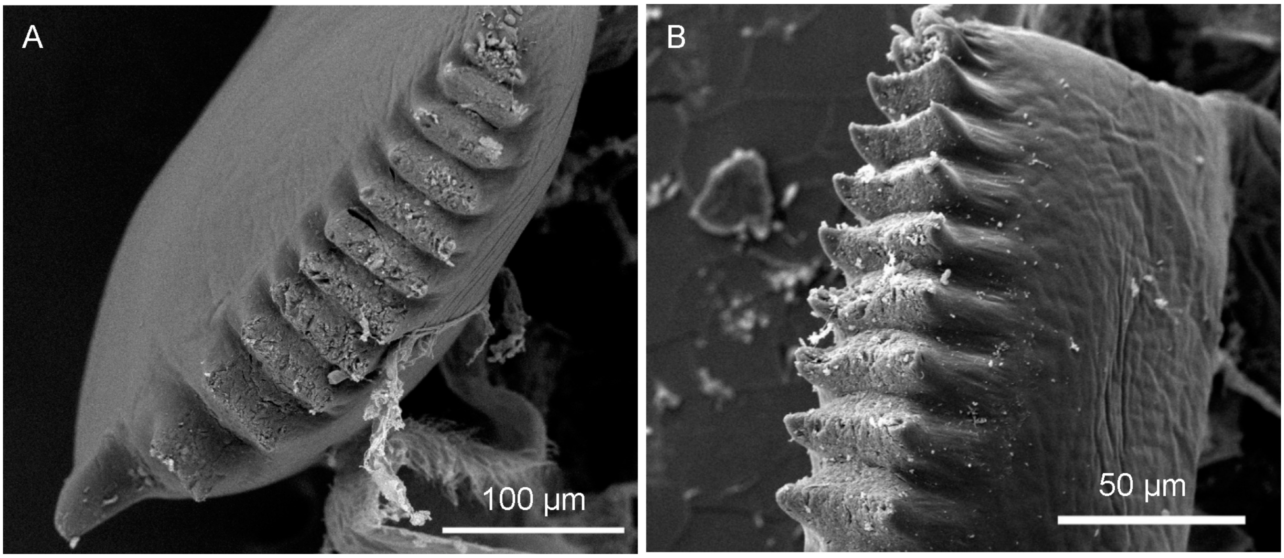

Fig. 11. *Lynceus biformis* molar surface. (A) Right molar surface. (B) Ridges of the molar surface.

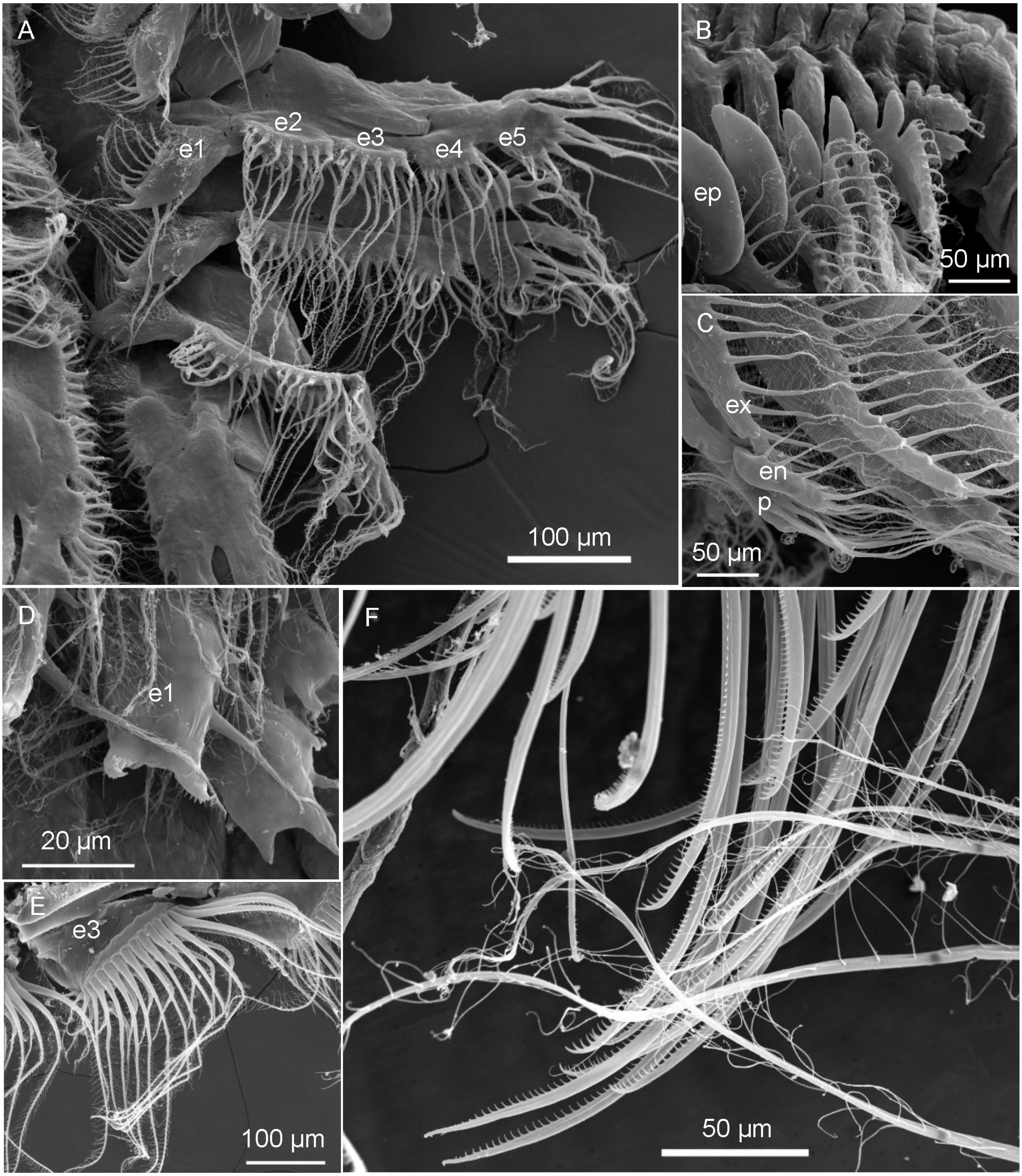

Fig. 12. *Eulimnadia braueriana* juvenile and adult thoracopods. (A) Medial-anterior view. (B) Lateral view: epipod and exopod. (C) Lateral view of thoracopods: endopod and exopod. (D) Anterior view of the first endite (dorsal is to the left) (E) Setae of the second to fifth endite (anterior view). (F) Pectinate setae on the palp of the fifth endite. e1–5, endite I–V; en, endopod; ep, epipod; ex, exopod; p, palp on endite V.

DISCUSSION

Eulimnadia braueriana feeding structures undergo significant changes with development (summarized in Table 1). In the nauplius stage, the second antenna and mandibles are the only movable appendages functioning in feeding. They remain relatively simple in structure in the nauplius stage. The endopods and exopods of naupliar second antenna elongate, becoming segmented and setose in juveniles and adults. Juvenile and adult mandibular structures enlarge and develop morphologically differentiated molar surface. The thoracopods bud in the nauplius stage and have five endites with dense setae when reaching full

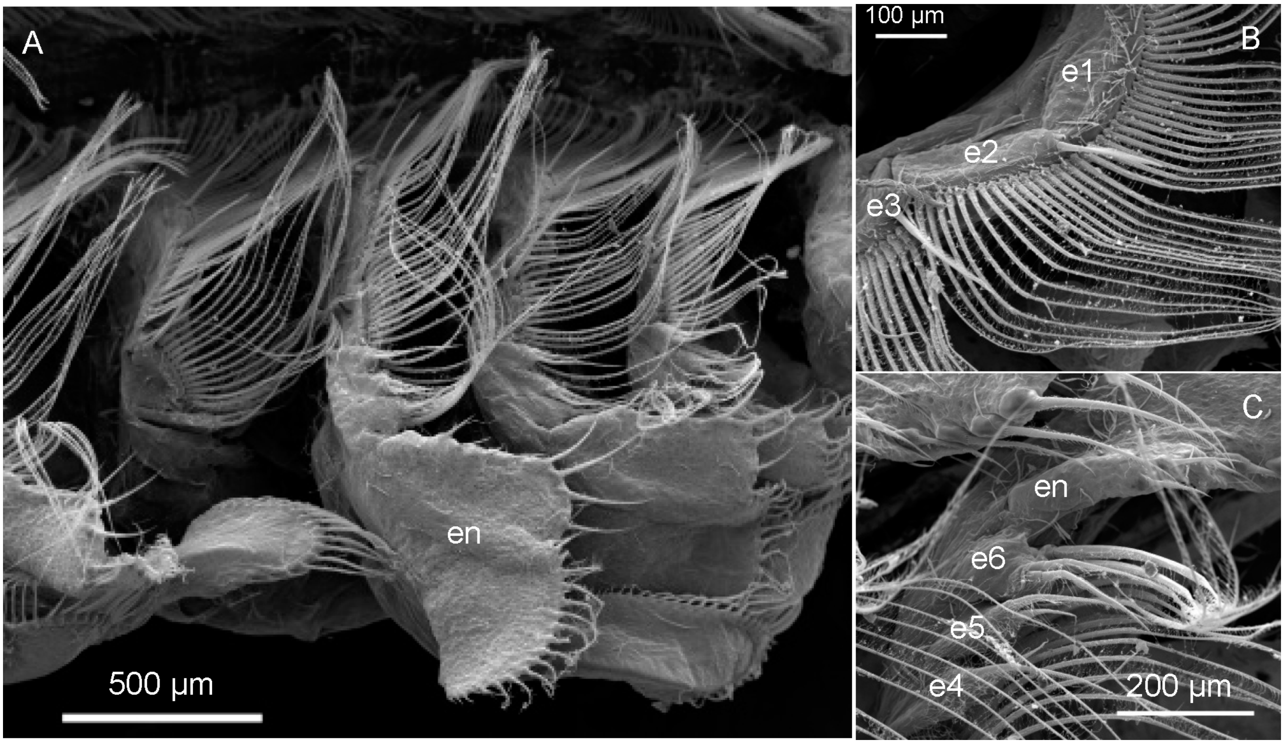

Fig. 13. *Branchinella kugenumaensis* thoracopods. (A) Medial-ventral view. (B) Endites I–III. (C) Setae of endites IV–VI and endopod. e1–6, endite I–VI; en, endopod.

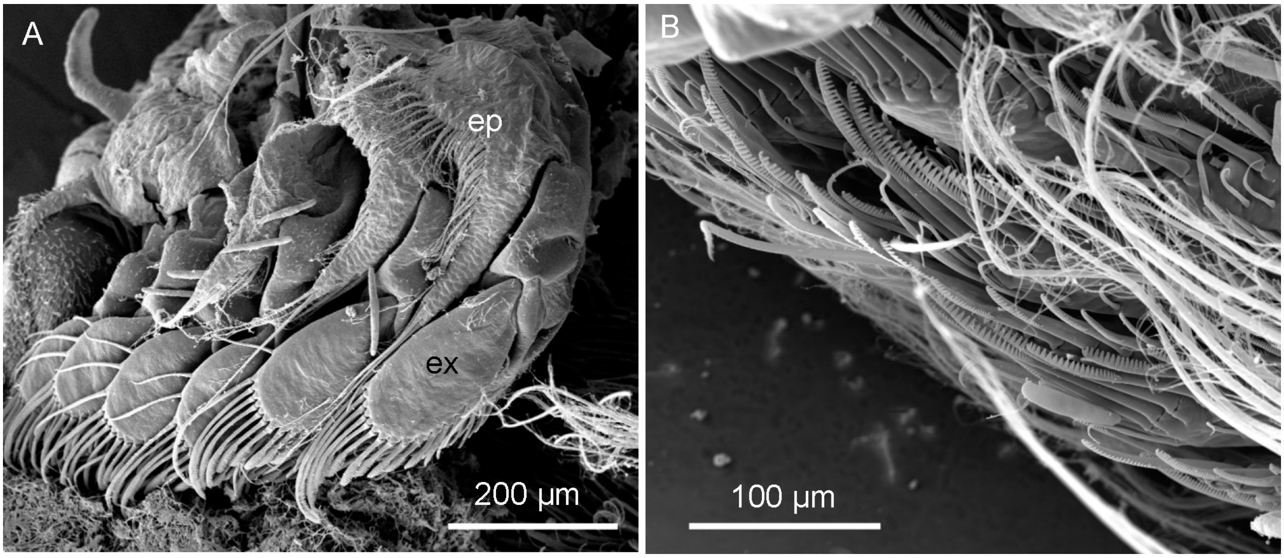

Fig. 14. *Lynceus biformis* thoracopods. (A) Lateral view. (B) Pectinate setae (ventral view). ep, epipod; ex, exopo.

development in the juvenile and adult stage. *Eulimnadia braueriana* adult thoracopods are generally similar to those of *Branchinella kugenumaensis* and *Lynceus biformis* in morphology. The adult molar surface, on the other hand, is quite distinct in *L. biformis*, while they are similar between *E. braueriana* and *B. kugenumaensis*.

Gut content analysis is a common approach to study feeding ecology of zooplankton and provides specific information on ingested content. It is, however, affected by the processing and digestion rate of the studied organism, possibly leading to unidentified or misidentified food particles. Additionally, gut contents only reflect what had been ingested during a certain time period at that specific environment. Morphology serves as an alternative approach to zooplankton's feeding ecology, particularly for the ventrally bent and carapace-covered clam shrimps such as *E. braueriana* where direct feeding actions are hard to observe. Although feeding structure morphology cannot reveal specific food choice, it shows the overall food handling and ingesting ability. The results are also less influenced by environmental characteristics during a specific period. From feeding structure morphology, we can infer the feeding mechanism of a species and the ingested food type in any given environment. Morphological examination can be seen as a complementary method to gut content analysis for studying feeding mechanism of zooplankton as well as other arthropods.

Eulimnadia braueriana's feeding mechanism is a dynamic process through ontogeny. At the first naupliar substage, yolk is visibly contained in the trunk. The whole trunk appears yellowish, and the yolk is so dense that the gut is not visible. Moreover, the mandible coxae are only buds, indicating that this substage is exclusively lecithotrophic. Yolk is gradually consumed but still persists through several successive naupliar substages. The two molar surfaces meet at approximately the fourth substage, which was also observed in the same species (Olesen and Grygier 2003) and in *Limnadia stanleyana* King, 1855 (Anderson

Table 1. Summary of the relevant feeding structures of *Eulimnadia braueriana*

Developmental stage	Substage	Structures					Inferred feeding mode
		Second antenna	Molar surface	Mandibular palp	Maxillae	Thoracopods	
Nauplius	I	Naupliar process without setulae	Bud like	Smooth setae without setulae	NA	NA	Filter-feeding
	II	Naupliar process with setulae	Uniform spines	Setae of the first segment differentiated and directed to mouth part	Small setae on flat surface		
	III		Uniform spines at the anterior part, posterior tooth present, several rows of setae at the posterior part				
	IV	Naupliar process bifid					
	V					Bud like	
	VI						
	VII				Small setae on elaborated surface pointing medially		
Juvenile	Early	Naupliar process degenerating	Spines differentiating, left and right molar surface asymmetric	Degenerated	Dense plumose setae on both first and second maxillae	7–9 pairs	Filter-feeding and scraping
	Late	Naupliar process absent		NA		10–11 pairs	
Adult		Naupliar process absent	Spines fully differentiated, left and right molar surface asymmetric	NA		12–18 pairs with pectinate structure on the first several pairs	

NA: not available.

1967). These morphological characteristics of the early naupliar substages mean that *E. braueriana* nauplii could be exclusive lecithotrophic until the third naupliar substage, relying entirely on yolk nutrition. Traces of yolk, however, can sometimes still be seen in substage five. Naupliar substages four and five may be a transition period in which the nauplius is partially lecithotrophic before foraging independently. Afterwards, the last two naupliar substages become totally planktotrophic. For planktotrophic nauplii, the main naupliar structures that gather and transfer food particles to the mouth are the second antennal masticatory spines and the mandibular palp spines. This coordinated second antenna-mandible system is suggested as a mechanism to filter planktonic particles (Olesen 2004). The second antennal posterior stroke not only facilitates locomotion, but also filters and conveys the particles to the mouth. The appendage setae also possess setulae that filter particles from the water. Throughout the naupliar substages, *E. braueriana* changes from exclusively lecithotrophic to planktotrophic filter feeding.

This coordinated second antenna-mandible system of *E. braueriana* undergoes transition during the juvenile stage. With the degeneration of the naupliar process and distal masticatory spine, the second antenna loses its feeding function. In Spinicaudata juveniles and adults, the second antenna is the only structure responsible for locomotion (Cannon 1932; Olesen 2009). The developed setose, movable thoracopods and the maxillae take over the feeding role upon entering the juvenile stage. In general, the anterior cephalic food handling structures are substituted by posterior cephalic as well as thoracic structures in the juvenile stage. This posterior shift of feeding structures was also observed in other arthropods (Averof and Patel 1997; Møller et al. 2007), implying a significant change in feeding mechanisms.

Eulimnadia braueriana juveniles and adults share similar feeding structure morphology. At the early juvenile substage, the molar surface is less differentiated and individuals only possess half the thoracopod number as the adults. Relevant feeding structures become fully developed at the later juvenile substages. On each thoracopod, *E. braueriana* endites possess two parallel rows of dense, plumose setae. Similar endite morphology has been observed in other filter feeding branchiopods (Cannon 1932). Such dense setae form a "wall" of the food groove, creating an internal water current that helps transport food particles towards the mandibles. The endite palps also bear pectinate setae that are similar to the scraping setae of *Lynceus* (Martin 1989; Fryer and Boxshall 2009). As these palpal setae of *E. braueriana* are the distal most limb structures which are able to touch external surfaces, we suspect they have similar scraping function as in *Lynceus*.

Pectinate setae in *E. braueriana* and *Lynceus* have similar morphology but they differ in location and abundance. In *E. braueriana*, they are only present on the endite V palp. In *Lynceus*, however, they are present on the two distal-most endites and the endopod (Fryer and Boxshall 2009). The *Lynceus* scraping setae also outnumber those of *E. braueriana*. Since scraping setae have less dense setulae, they may not be as efficient in filtering as the plumose setae. The arrangement of setae implies that the *Lynceus* is less filtratory compared to *E. braueriana* but has greater scraping ability. In contrast, *E. braueriana*, having less scraping setae and more abundant plumose setae, may have limited scraping abilities but relies more on filtering.

Among the Spinicaudata, similar "scrapers" have been described in *Imnadia* (Botnariuc 1947; Straskraba 1965) and *Metalimnadia* (Roessler 1991). Scrapers are also found on the endites of the second trunk limb in radopod cladocerans (Anomopoda) (Dumont and Silva-Briano 1998; Kotov 2000; Edgecombe et al. 2003; Van Damme and Eggermont 2011). The radopod cladocerans also bear filtering related structures such as filter plates, combs, and setae on the trunk limbs (Kotov et al. 2003; Van Damme et al. 2005 2013; Van Damme and Eggermont 2011). Studies on these crustaceans imply that Laevicaudata, Spinicaudata, and Radopoda all have species that possess scraping abilities. The Spinicaudata and Radopoda may utilize both filter-feeding and scraping modes (Table 2). While the Cyclestherida is a considered link between Spinicaudata and Cladoceran (Olesen 1999) and the Ctenopoda is suggested to have evolved earlier than Anomopoda (Dumont and Silva-Briano 1998), there is currently no description of *Cylestheria hislopi* endite setae, and the ctenopods are reported as filter-feeders. Far more studies on branchiopod feeding structure morphology are needed before any conclusions can be reached concerning feeding mode evolution through phylogeny.

Feeding processes include food collection from the environment and food transportation to ingestion. In *E. braueriana*, filtered or scraped particles are transported proximally into the food groove by the endites. Inside the food groove, particles are either transported by the water current or mechanically pushed anteriorly by the beating thoracopods (Martin 1989). The stout, pointed endite I may function in pushing larger particles forward (Cannon 1932). The gap between the anterior most thoracopods and the mandibles is closed by the first and second maxillae, as well as the paragnaths. The labral gland opening lateral to the second maxillae may produce a secretion to entangle the food particles into a mass for easier transportation (Cannon and Leak 1932; Zeni and Zaffagnini 1992). The first maxillae have setae morphologically similar to the dense, plumose setae of the endites. They may have similar filtering and particle-transporting function as the endites (Fryer 1983; Fryer and Boxshall 2009). The labrum and paragnaths, *i.e.*, the upper and lower lip respectively, seal the space around the mouth cavity. Overall, food particles are gathered by thoracopods and then transported in the food groove formed by coordinated thoracopod movements and the two pairs of maxillae in *E. braueriana*.

After being collected and transported, the food mass then passes the molar surface of *E. braueriana* from posterior to anterior. The large tooth on the mandible posteriodorsal side has been suggested to be homologous with the *pars incisivus*, which usually has biting functions (Richter 2004; Edgecombe et al. 2003). It could be capable of crushing larger particles before they reach the finer structures further anterior on the molar surface (Edgecombe et al. 2003). The *E. braueriana* molar surface has similar structures as some filter-feeding anostracans (Brendonck 1994; Mura 1996), while it is clearly different from the laevicaudatan molar surface. Comparing the *E. braueriana* molar surface to that of radopod cladocerans, the cladoceran molar surface has deeper ridges at the central region and prominent posterior tooth or teeth (Kotov 2000; Edgecombe et al. 2003). *Cyclestheria hislopi*, on the other hand, is morphologically intermediate between *E. braueriana* and Radopoda. The *Cylcestheria hislopi* molar surface also has ridges at the central region, similar to those of the radopods, but they are clearly confluent. The spines on the anterioventral margin increase in length anteriorly but are overall similar to the slender spines of the *E. braueriana* molar surface (Edgecombe et al. 2003). Although it is debatable whether the molar surface form is informative of clam shrimp feeding mechanisms (Mura 1996), *E. braueriana* thoracopod morphology implies that filtering function is an essential part in its adult feeding.

Eulimnadia braueriana initially adopts planktonic filtering in the late nauplius substages and then shifts to filtering with some scraping in the adult stage. Although they possess filtering related feeding structures in all stages, the naupliar substages might filter different resources than the juveniles and adults considering the pelagic living of nauplii compared to the benthic living juveniles and adults (Liu et al. 2016). In addition to the difference in body size and thus the manageable size of food particles, the feeding structures become more diverse through ontogeny. The fully developed mandible, maxillae and the thoracopods with dense, plumose and pectinate setae can utilize a wider food variety, including planktonic and sessile materials. Moreover, since the nauplii showed opposite phototaxis compared with the juveniles and adults (Liu et al. 2016), they probably feed on resources in microhabitats distinct from that of juveniles and adults. The *E. braueriana* nauplii may pelagically forage fine suspended particles near the water surface, while the juveniles and adults mainly forage larger particles and sessile materials in the benthic layer.

Sympatric species may show differentiated resources utilization, particularly regarding large

Table 2. Comparison of the main feeding structures among adults of diplostracans and their inferred feeding modes

	Structures		Inferred feeding mode
	Molar surface morphology	Scraping setae location	
Spinicaudata *Eulimnadia braueriana* Ishikawa, 1895[1]	Perforated central region, peripherally flagellated processes, with one posterior tooth	Palp of endite V of thoracopod 1–6 in hermaphrodites and 3–6 in males	Filter-feeding and scraping
Laevicaudata *Lynceus biformis* (Ishikawa, 1895)[1, 2] *Lynceus simiafaensis* (Hadring, 1941)[3]	Dorsoventral ridges with a dorsal and a ventral cusp on each ridge	Endite IV and V, and endopod of thoracopod 1–8 in females and 2–8 in males	Scraping
Cyclestherida *Cyclestheria hislopi* (Baird, 1859)[2, 4]	Perforated central region with parallel ridges, pectinate cuticular projections at the ventral margin	Undescribed	Filter-feeding
Cladocera Radopoda[5, 6, 7, 8]	Dorsoventral ridges with branched projections at margin, protrusion or teeth at the posterodorsal margin	7–8 scrapers on endites of trunk limb 2	Filter-feeding and scraping

[1]This study; [2]Richter 2004; [3]Fryer and Boxshall 2009; [4]Olesen et al. 1996; [5]Dumont and Silva-Briano 1998; [6]Kotov 2000; [7]Edgecombe et al. 2003; [8]Van Damme et al. 2011.

branchiopods in rapidly fluctuating temporary wetlands. The coexisting anostracan *B. kugenumaensis* has similar dense, plumose endite setae as *E. braueriana*, but not the scraping setae. Molar surface morphologies are also alike between these two species. Their filtering feeding ability might be similar, but they have different vertical utilization distribution (Wang et al. 2012). Different from *B. kugenumaensis*, adult *L. biformis* share similar vertical distribution as *E. braueriana* (Wang et al. 2012; Liu et al. 2016). The pectinate setae on the endites and exopod of both *L. biformis* and *E. braueriana* also imply similar scraping function. Their molar surfaces, however, show that they may have some degree of food resource partitioning. A distinct border of the molar surface composed of flagellated or simple processes exists in *E. braueriana*, but the largest area is the smooth, perforated central region of the mandible. On the other hand, the molar surface of *L. biformis* does not show any wide, smooth area, neither does it have slender processes. *Lynceus biformis* molar surface is uniformly constituted of rough dorsoventral ridges. Another difference is that the *Lynceus*' left and right molar surfaces are symmetric, implying that no biting but only grinding is involved in its feeding activity (Richter 2004). Combining differentiated spatial distribution (Wang et al. 2012 2018) and feeding structure morphologies, we suggest that *E. braueriana*, *L. biformis* and *B. kugenumaensis* feed on different resources in Siangtian Pond. Planktonic filter feeding and benthic scraping could be the main feeding mode of *B. kugenumaensis* and *L. biformis*, respectively. *Eulimnadia braueriana*, on the other hand, could be a mixture of planktonic filtering and scraping feeder in the benthic environment.

CONCLUSIONS

We approached ontogenic feeding mechanisms of *E. braueriana* through feeding structure morphology and made a preliminary comparison among adult feeding structures of all three large branchiopod species inhabiting Siangtian Pond. Morphology of *E. braueriana* feeding structures developed gradually, with the most prominent changes happening during the early juvenile substages. *Eulimnadia braueriana* shifts from lecithotrophic to planktonic living during the nauplius stage and retains its filter feeding ability since then. In adults, the pectinate scraping setae are morphologically like those of laevicaudatans. Based on the feeding structures, previous demonstrated phototaxis, and spatial distribution, *E. braueriana* nauplii and juveniles / adults could feed on different food resources, although this species is basically a filter feeder. *Eulimnadia braueriana* has similar filtering structures as the co-occurring *Branchinella kugenumaensis*, while having obvious differences in scraping setae and molar surface compared with *Lynceus biformis*. The results of interspecific morphology difference imply that these three sympatric species may have levels of feeding mechanism differentiation, as well a separation in spatial habitat utilization. As a whole, morphology serves as a feasible way to study the feeding ecology of crustaceans such as branchiopods.

Acknowledgments: We thank Dr. Lien-Siang Chou of the Institute of Ecology and Evolutionary Biology, National Taiwan University for the support during the study period. We are grateful to Ms. Ya-Chan Yang of Technology Commons, College of Life Science, National Taiwan University for excellent technical assistance with scanning electron microscopy. This study was funded by a student research program of Yangmingshan National Park (A0089).

Authors' contributions: JYL and CCW designed the research approach. JYL prepared the materials and did the experiments and analysis. All authors drafted the manuscript.

Competing interests: The authors declare that they have no conflicts of interests.

Availability of data and materials: Not applicable.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable. Specimens collected from the field were approved by Yangmingshan National Park (Issue No. 20140546).

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