



Reduction of body segmentation in the skeleton shrimp *Caprella scaura* (Amphipoda: Caprellidae) inferred from comparative internal anatomy of Caprelloidea

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Abstract

In bilaterians, particularly arthropods, body segments are often functionally differentiated along the anterior-posterior axis, resulting in lineage-specific morphologies. Although the acquisition of novel traits in body segments or appendages is considered a key driver of animal evolution, the loss or reduction of these structures has also contributed to the adaptation to new environments and emergence of novel body plans. Members of the family Caprellidae (Caprelloidea: Amphipoda: Crustacea), commonly known as skeleton shrimps, exhibit an unusual body plan characterized by highly elongated thoracic segments (pereonites) and a markedly reduced abdomen derived from the pleon (pleonites and urosomites). Caprellids also lack most appendages that are retained on the pleon in non-caprellid amphipods. Despite these distinctive features, the internal organization of organs within the reduced body segments of caprellids remains poorly understood. In this study, we conducted histological observations of *Caprella scaura* and found that organs essential for survival and reproduction, particularly the digestive and reproductive systems, are entirely located within the pereonites. Comparative observations of a related non-caprellid amphipod *Podocerus* sp., revealed a similar distribution of reproductive organs in the pereonites, whereas the pleon contained only extensions of the digestive organs. These results suggest that, in the common ancestor of Caprelloidea, essential organs were already positioned within the pereonites. Furthermore, previous studies indicate that pleonal appendages became functionally reduced in caprellids in association with specialization for an epiphytic lifestyle. The anatomical organization, together with functional changes in appendages, may have facilitated the evolution of the highly degenerated body plan characteristic of caprellids.

Keywords Anatomy · Abdomen · Caprellid · Podocerid · Body plan · Lifestyle

Introduction

Body segments are fundamental and evolutionarily important units, commonly observed in annelids, vertebrates, and arthropods (Carroll 1995; Davis and Patel 1999; Fusco and Minelli 2021). Among these groups, arthropods are the most successful animals on Earth, displaying remarkable diversity in both species number and morphological complexity (Akam 2000; Bar-On et al. 2018). Despite this diversity, all arthropods share a fundamental body organization: their bodies consist of serially repeated segments, each typically bearing a pair of appendages. Because of this conserved organization, body plans can be compared across even distantly related arthropod groups (Fusco and Minelli 2013). Consequently, the evolutionary acquisition

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of novel segmental traits and appendage morphologies has been studied extensively (Hannibal and Patel 2013; Clark et al. 2019).

In addition to the acquisition of novel traits, the loss or reduction of segments and appendages has also played an important role in arthropod evolution and diversification (Davis and Patel 1999; Smith et al. 2016). Among arthropods, several crustacean groups exhibit such reduced body plans. The general body plan of crustaceans consists of a head, a pereon (thoracic segments, or pereonites) and a pleon (Fig. 1). Note that although the pleon is often referred to as “abdomen”, this study uses the term pleon for segments with appendages, and abdomen for those without

appendages, according to previous studies (Barnard and Karaman 1991; Walossek and Müller 1997; Olesen and Walossek 2000). As an example of segment and appendage loss, cirripedes and ostracods completely lack pleons and pleonal appendages (Deutsch and Mouchel-Viehl 2003; Smith 2025). In decapods, a crab-like body plan which is characterized by a broad, flattened carapace and reduced, ventrally flexed pleon, has independently evolved and been lost multiple times within meioran crustaceans. This process is known as “carcinization” (Wolfe et al. 2021), which is considered to provide adaptive advantages related to protection, locomotion, and feeding (Luque et al. 2019; Wolfe et al. 2019). When segments containing essential organs

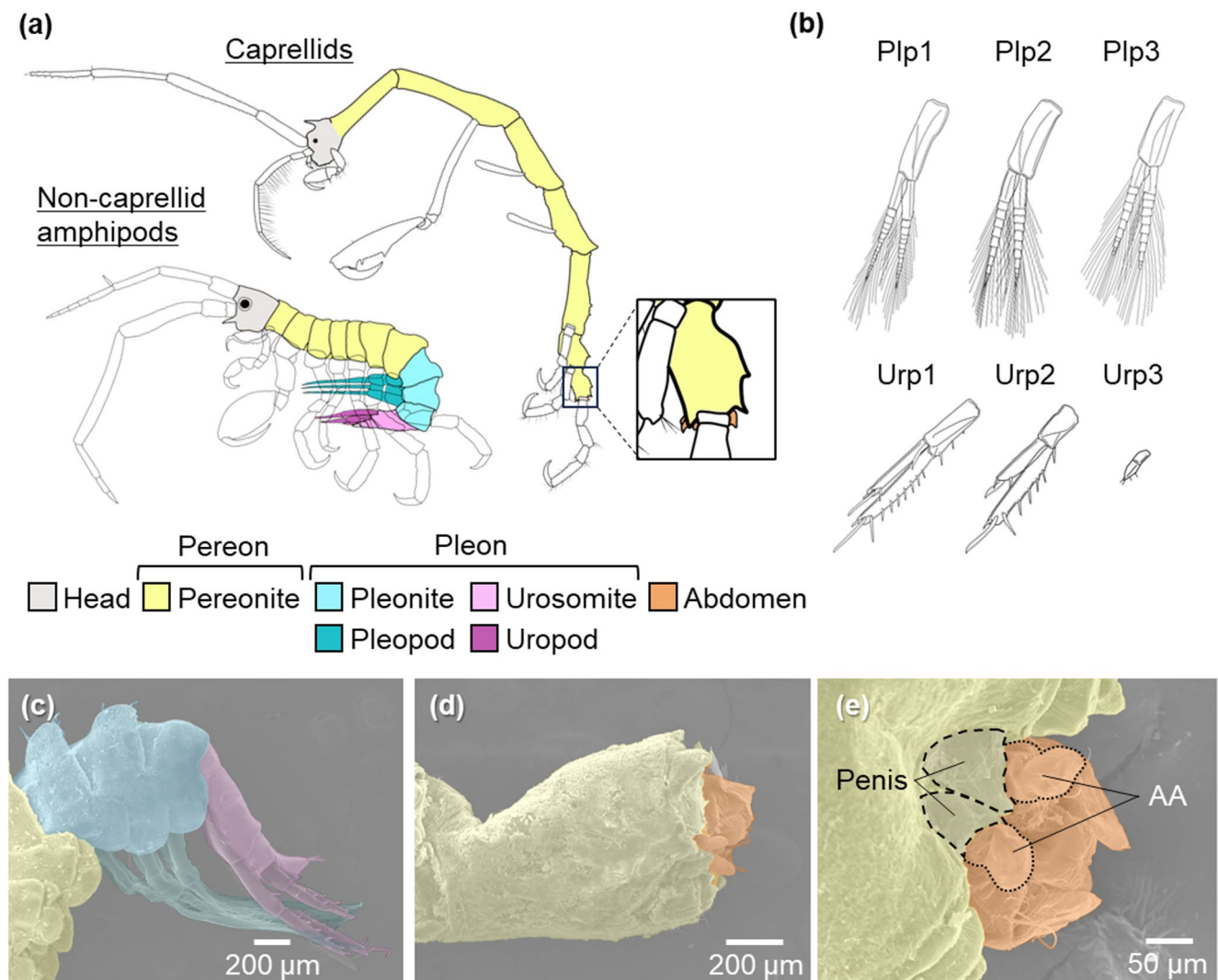


Fig. 1 Comparison between body plans of non-caprellid amphipods and caprellids. **a** Sketches of both a podocid (*Podocerus* sp.) as a representative of non-caprellid amphipods and a caprellid (*Caprella scaura*). The pereon is consisted of pereonites (thoracic segments), and the pleon is divided into anterior three pleonites and posterior three urosomites. In contrast to non-caprellid amphipods having the well-developed pleon, caprellids have only a minute abdomen. **b** Sketches

of pleopods and uropods of *Podocerus* sp. which are lost in caprellids. **c–e** SEM images of the pleon (pleonites and urosomites) of *Podocerus* sp. (**c**) and the abdomen of *C. scaura* (**d**, **e**). Methodology to obtain SEM images is shown in the Supplementary Information. **c**, **d** Left side view. **e** Ventral view. Note that only adult males have “abdominal appendages”. Abbreviations: AA, abdominal appendages; Plp1–3, the first to third pleopod; Urp1–3, the first to third uropod

related to digestion or reproduction are lost or reduced, strong selective pressures must act to prevent the loss of essential biological functions. However, how internal organ arrangement is modified in lineages with reduced segments remains poorly understood, in part due to the challenges of selecting suitable comparative model species. In addition, groups with degenerated body segments, such as cirripedes and decapods, have complicated life histories with drastic morphological changes triggered by larval settlement and metamorphosis.

Caprellids (Caprellidae: Caprelloidea: Amphipoda), commonly known as skeleton shrimps, represent a suitable model for investigating this question. Hereafter, the term “caprellid” refers to species within Caprellidae, whereas other amphipods are referred to as “non-caprellid amphipod.” The body of a typical non-caprellid amphipods consists of a head bearing antennal and feeding appendages, six pereonites with locomotory legs (pereopods), and six segments of the pleon which are divided into pleonites (the anterior region with swimming appendages, or pleopods) and urosomites (the posterior region with anchoring appendages, or uropods) (Barnard and Karaman 1991; Richter and Scholtz 2001; Sun and Patel 2019). By contrast, caprellids, particularly species of the genus *Caprella*, exhibit several unique traits, including a slender cylindrical body, fusion of the head and the first pereonite, rudimentary coxae, and the presence of only two pairs of gills (Fig. 1a). Most notably, caprellids have an extremely reduced abdomen, consisting of only a small segment attached to the posterior end of the pereonites, instead of fully developed pleon, i.e., pleonites and urosomites. They almost completely lack pleopods and uropods, only adult males having “abdominal appendages” (Fig. 1b–e; McCaine 1968; Arimoto 1976; Ito et al. 2011). This specialized body plan is thought to be linked to their epiphytic lifestyle, as caprellids cling to substrates such as seaweeds or bryozoans, in contrast to the free-living benthic or planktonic lifestyles of most amphipods (Ito et al. 2011; Copilaş-Ciocianu et al. 2020). Moreover, all amphipods are direct developers, lacking planktonic larval stages and metamorphosis (Poore 2005; Wilson 2009). These traits make caprellids valuable models for comparative studies of internal organ arrangement and segmental reduction.

Although the internal organization of non-caprellid amphipods has been described in detail for certain species (Hyne 2011; Štrus et al. 2019), knowledge of caprellid anatomy remains fragmentary, limited mostly to descriptions of the digestive tract and reproductive organs (Irie 1967; Keith 1974). To address this gap, we investigated the internal organ arrangement in *Caprella scaura* Templeton 1836 through histological observations. As a comparative model, we examined *Podocerus* sp. (Podoceridae: Caprelloidea), one of the closest relatives of caprellids with a

well-developed pleon. We propose that the evolution of the reduced abdomen in caprellids was facilitated by two key factors: (1) the essential organs, particularly those related to reproduction and digestion, were already confined within the pereonites in the common ancestor of caprellids and podocerids, and (2) the appendages, especially pleopods and uropods, lost in caprellids had functions that were either no longer necessary or even became obstructive together with the ecological shift, and could be compensated for by other appendages.

Materials and methods

Animals

Individuals of *Caprella scaura* were collected from piers belonging to the aquarium Yokohama-Hakkeijima Sea Paradise, on Hakkeijima Island, Yokohama, Kanagawa, Japan (35°20'08"N, 139°38'47"E) on 23 February and 28 April 2023. Since most caprellids cling to bryozoans—mainly *Bugula neritina* (Linnaeus 1758)—colonies attached to buoys and ropes were collected, and numerous *C. scaura* individuals were found among them. Specimens of *Podocerus* sp. were also collected for comparison. Sampling was conducted at Araiama beach, Miura, Kanagawa, Japan (35°09'43"N, 139°36'36"E) on 2 December 2024. Calcareous red algae (Rhodophyta) were collected from shallow rocky reefs and washed in plastic trays, from which *Podocerus* sp. individuals were released.

This *Podocerus* sp. is treated in the current study as an undescribed species. Although 69 species of the genus *Podocerus* have been described worldwide, only five have been recorded from the Japanese Archipelago (Arai et al. 2022; Horton et al. 2025). Molecular phylogenetic analysis of COI sequences to infer the phylogenetic position of *Podocerus* sp. (NCBI Accession Number: LC908961), indicated that this species was closely related to *Podocerus setouchiensis* Arai et al. 2022 (see [Supplementary Information](#)). However, genetic resources for podocerids are limited in the National Center for Biotechnology Information database. In addition, although the sequence identity between *Podocerus* sp. from Araiama and *P. setouchiensis* was relatively high (97%), the genetic distance, calculated by Kimura-2-parameter model was too high to regard these two species as the same species (2.4%; e.g., Lefebvre et al. 2006; Costa et al. 2009). Morphological differences were also noted between *Podocerus* sp. and *P. setouchiensis*, including the number of setae along the telson margin and the setal condition on the propodus of the first and second gnathopods in adult males. These results suggest that the Araiama specimens represent a distinct species, but the taxonomic identity of *Podocerus*

sp. remains unresolved until more detailed observations on morphological and molecular analyses are conducted.

Collected animals of both *C. scaura* and *Podocerus* sp. were anesthetized with eugenol-based FA100 (DS Pharma Animal Health Co., Ltd., Osaka, Japan) and photographed using an Olympus SZX 16 stereomicroscope equipped with a DP28 digital camera (Olympus, Tokyo, Japan). Body length which was the sum of the length of the head and that of the first to seventh pereonite (Otomo et al. 2022), was measured using Image J ver. 1.53e (Schneider et al. 2012). Specimens were fixed and decalcified in Bouin's solution before dehydration for histological preparations. To ensure that only sexually mature specimens were examined, the postembryonic stage of *C. scaura* was determined following Otomo et al. (2022), and only individuals of *Podocerus* sp. forming precopulatory guarding pairs were selected.

Histological observations

Fixed samples were dehydrated in an ethanol series (70%, 90%, 95%, and 100% (twice); 30 min at each concentration), transferred to xylene, and embedded in paraffin. Sagittal and transverse serial sections (5–7 μ m thick) were cut using a Spencer Lens microtome (Buffalo, USA) and stained with hematoxylin and eosin. Sections were examined using an Olympus BX51 optical microscope equipped with a DP74 digital camera (Olympus, Tokyo, Japan).

Fluorescent staining of nuclei and F-actin

To examine detailed structures of male reproductive organs in *C. scaura*, fluorescent staining was performed. Reproductive organs were dissected from the fifth to seventh

pereonites of an adult male, fixed in 4% paraformaldehyde buffered with filtered seawater, and washed three times in PBT (0.3% v/v Triton X-100 in PBS) for 15 min each. Nuclei were stained with 4',6-diamidino-2-phenylindole (DAPI; 2 μ g/mL; Sigma, St. Louis, MO, USA), and F-actin was stained with rhodamine-phalloidin (1:40; Invitrogen, Paisley, UK) by incubating samples for 1 h at room temperature. Samples were washed three times in PBT (15 min each), mounted in VECTASHIELD Mounting Medium (Vector Laboratories, Burlingame, CA), and observed under a confocal laser scanning microscope (CLSM; FV3000; Olympus, Tokyo, Japan).

Results and discussion

Internal structure of adult males

The digestive system of *Caprella scaura* was generally similar to that described in other caprellid species (Keith 1974). The foregut, led from the mouth to the cardiac chamber of the stomach, extended from the head to the first pereonite. Posterior to the foregut, the midgut continued through to the anus, which opened at the posterior end of the abdomen. A pair of hepatopancreas (digestive glands) was connected to the ventrolateral sides of the midgut and extended close to the posterior end of the seventh pereonite (Fig. 2a, b).

Sagittal sections of adult males revealed organs strongly stained with hematoxylin and eosin, located from the posterior fifth to the seventh pereonite (Fig. 2a, c). These organs could be distinguished morphologically into three components: (1) an elongated oval organ at the posterior end of the fifth pereonite, (2) a tubular structure, and (3) a large round

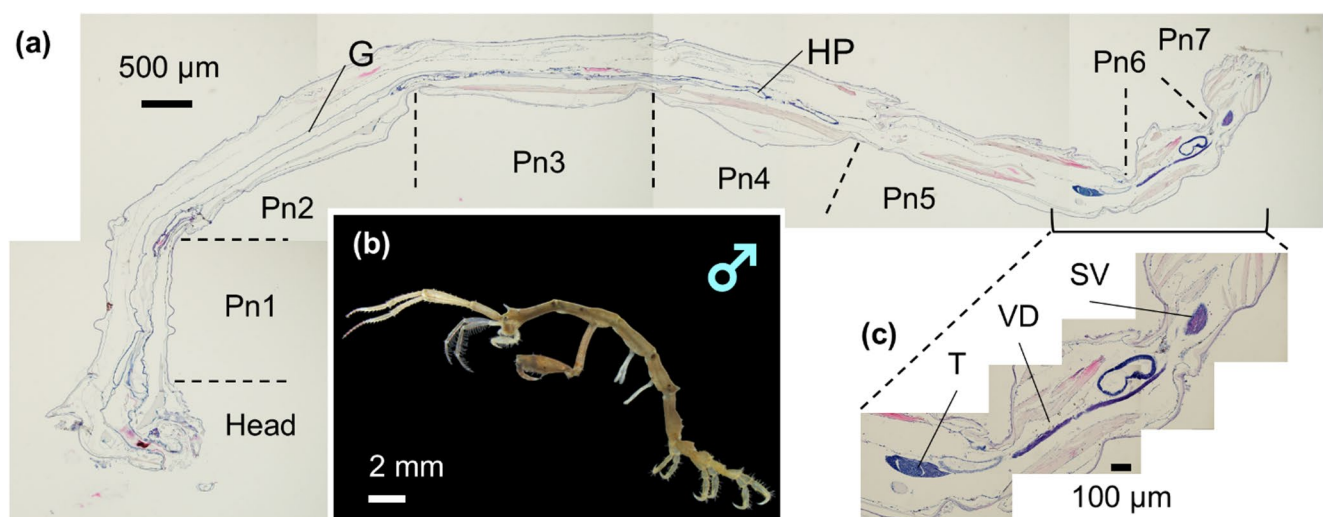


Fig. 2 Sagittal section of an adult male of *Caprella scaura*. **a** Sagittal section of the whole body. **b** Sectioned individual when alive. **c** Magnified view of male reproductive organs located on the fifth to seventh

pereonite. Abbreviations: G, gut; HP, hepatopancreas; Pn1–7, the first to seventh pereonite; SV, seminal vesicle; T, testis; VD, vas deferens

organ in the anterior part of the seventh pereonite. Because the penis of caprellids is located on the ventral posterior end of the seventh pereonite (Fig. 1e), these structures were identified as male reproductive organs.

To further characterize these organs at the cellular level, the fifth to seventh pereonites of adult males were dissected and observed with CLSM. Two paired sets of reproductive organs were present on both sides of these segments (Fig. 3a–c). CLSM observations showed that the elongated oval organ could be divided into three regions along the anterior–posterior axis, based on cell morphology (Fig. 3d, e). The anterior region contained large, round cells; the middle region contained smaller, irregularly shaped cells about half the size of those in the anterior region; and the posterior region contained elongated cells with pointed ends. Previous studies on non-caprellid amphipods reported that

testes contained spermatogonia, spermatocytes, and sperm arranged linearly along the anterior–posterior axis (Nichols 1909; Charniaux-Cotton 1962). Amphipod sperm are filamentous with a tail-like appendage but lack flagella (Reger 1966; Pitnick et al. 2009). Based on these knowledge, the anterior, middle, and posterior cells were identified as spermatogonia, spermatocytes, and sperm, respectively. Thus, the elongated oval organ in the fifth pereonite was identified as the testis of *C. scaura*. The tubular and roundish organs located posterior to the testis were filled with sperm (Fig. 3f, g), and were identified as the vas deferens and seminal vesicle, respectively.

In addition, transverse sections revealed a small round organ attached near the distal end of the vas deferens in the seventh pereonite (Fig. 4). This structure was identified as the androgenic gland (AG). The AG is a male-specific gland that secretes

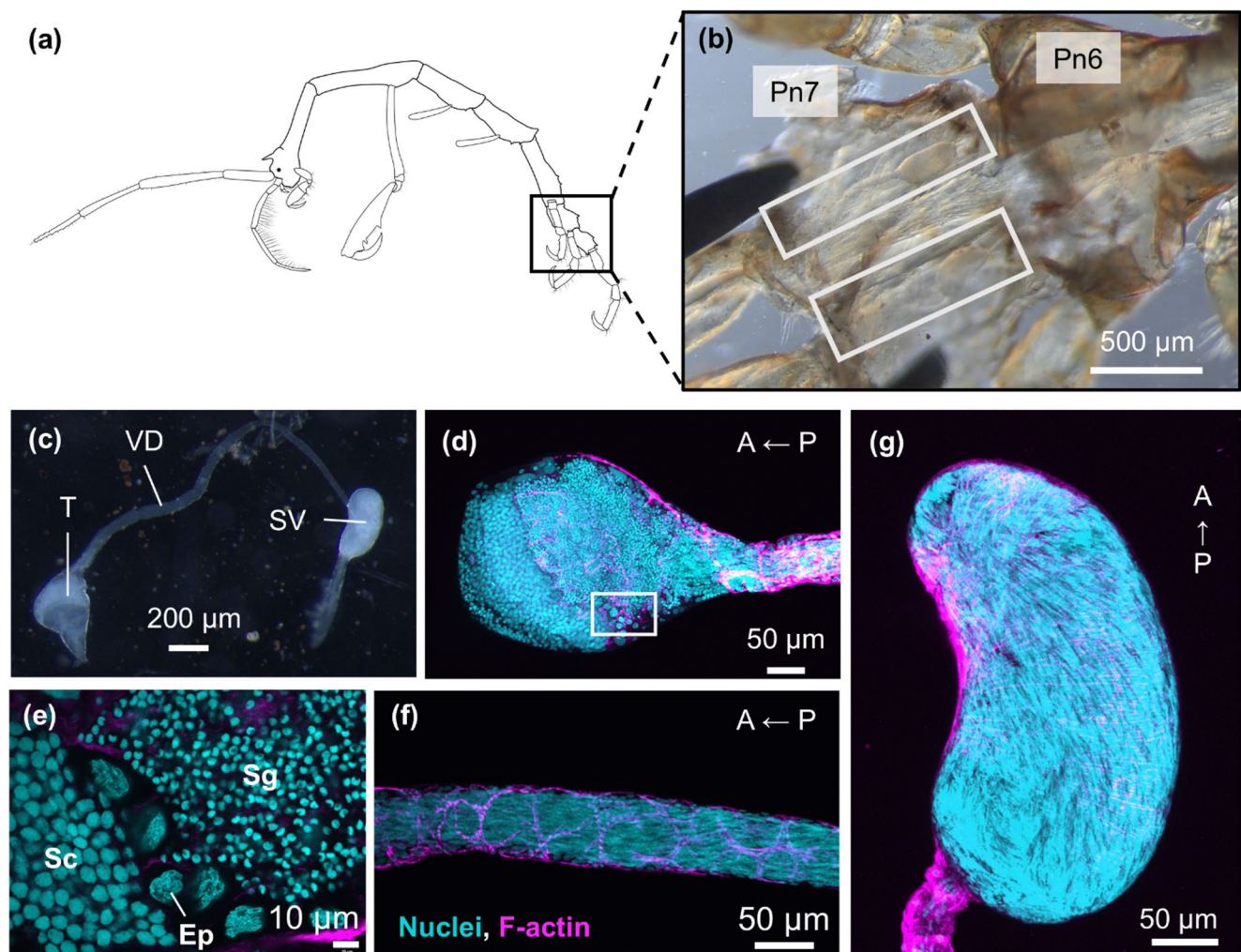


Fig. 3 Detailed observations on male reproductive organs of *Caprella scaura*. **a** Diagram of dissected part. **b** Dorsal view of dissected sixth and seventh pereonites. A pair of male reproductive organs are located on both sides (white boxes). **c** An extracted male reproductive organ. **d–g** Fluorescent images, with nuclei (cyan) and F-actin (magenta) stained by DAPI and rhodamine-phalloidin, respectively. **(d)** Testis.

The white box indicates the magnified part in (e). **(e)** Magnified image of the border between spermatocytes (Sc) and spermatogonia (Sg), including epidermal cells (Ep), in the testis. **(f)** Vas deferens. **(g)** Seminal vesicle. Abbreviations: Pn6,7, the sixth and seventh pereonite; SV, seminal vesicle; T, testis; VD, vas deferens

the androgenic gland hormone (AGH), which regulates masculinization and the development of sexually dimorphic traits in crustaceans. In both decapods and amphipods, the AG is typically located near the subterminal region of the vas deferens (Charniaux-Cotton 1962; Taketomi et al. 1990; Levy and Sagi 2020; Farhadi et al. 2021). The position and morphology of this structure in *C. scaura* are consistent with those characteristics.

This study firstly identified the position and structure of the AG in caprellids. The AG and AGH are known to play

pivotal roles not only in sex differentiation and the expression of male secondary characters, but also in the regulation of reproductive and agonistic behaviors in males (Ra'anan and Sagi 1985; Okumura and Hara 2004; Levy and Sagi 2020; Farhadi et al. 2021; Toyota et al. 2023). Although functions of AGH have been studied mainly on decapods, the presence of AG in *C. scaura* suggests that the AGH also plays crucial roles in male sexual development of caprellids, as implied by Otomo et al. (2022).

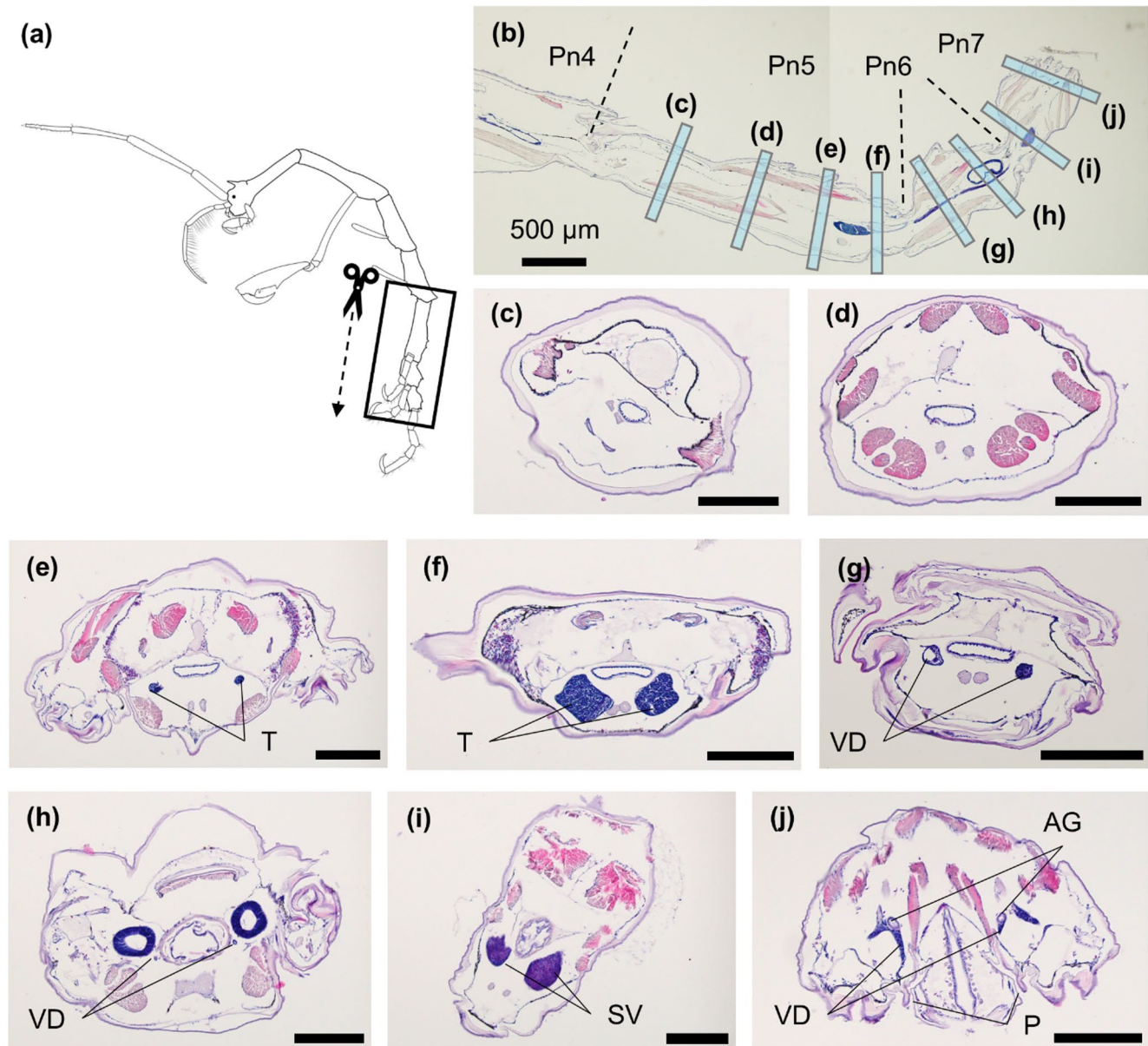


Fig. 4 Transverse sections of an adult male of *Caprella scaura* for identification of the androgenic gland. **a** Diagram of the sectioning part and direction. **b** Sectioned positions of transverse sections showed in (c–j). **c–j** Transverse sections of each part showed in (b). Images of

(c–j) are oriented as anterior is proximal, upper is up, and right is left. Scale bars indicate 200 μm. Abbreviations: AG, androgenic gland; P, penis; Pn4–7, the fourth to seventh pereonite; SV, seminal vesicle; T, testis; VD, vas deferens

Internal structure of adult females

Female internal structures were examined in sagittal and transverse sections. The ovaries were located bilaterally in the third and fourth pereonites (Fig. 5). Numerous oocytes were present within the ovaries, and all oocytes within a female appeared to be in the same developmental stage depending on the criteria of vitellogenesis in crustaceans including amphipods (Charniaux-Cotton 1985), suggesting that they are released simultaneously during a single spawning event. Although the oviduct was not directly observed, it likely extended from the posterior end of the ovary to the ventral region of the fifth pereonite, where the female gonopore is located.

Internal structure of *Podocerus* sp.

The digestive system of *Podocerus* sp. was consistent with descriptions of other non-caprellid amphipods (Fig. 6a, b; Martin 1964; Hyne 2011; Štrus et al. 2019). It consisted of the foregut, midgut, and hindgut, with paired hepatopancreas branching from the foregut in the first pereonite. The pleonites and urosomites, which together form the pleon, contained only extensions of the midgut and hindgut, as well as hepatopancreas, with the anus opening at the end of the third urosomite.

Male reproductive organs consisted of a testis, vas deferens, and seminal vesicle, extending from the second to the seventh pereonite, with the penis located on the ventral end of the seventh pereonite (Fig. 6c, d). Female reproductive

organs included paired ovaries spanning the second to sixth pereonites, with genital openings located ventrally at the posterior end of the fifth pereonite (Fig. 6e, f). As observed in *C. scaura*, all oocytes of *Podocerus* sp. seem in the same developmental stage (Charniaux-Cotton 1985).

Appendage morphologies on the pleon and their functions

Caprellids completely lack pleopods and uropods which are retained in non-caprellid amphipods, including podocerids (Fig. 1b; Barnard and Karaman 1991; Sun and Patel 2019). It is known that only adult males of some caprellid genera, including *Caprella*, have “abdominal appendages” on the proximal part of their abdomen. Although they are deduced as for mating because these structures can be seen only in adult males (Fig. 1e; McCaine 1968; Caine 1991; Arimoto 1976), their functions remain unclear. So further studies are needed on the evolutionary and developmental background of these appendages, and their functions are not argued in this study.

In typical non-caprellid amphipods, pleopods are feather-like shaped and used for swimming through rapid beating, while also facilitating respiration by generating currents that enhance oxygen exchange at the coxal gills (Dahl 1977; Boudrias 1991; Steele and Steele 1991). Uropods, being rigid and inflexible, are primarily used for anchoring, crawling, and burrowing (Meadows and Reid 1966; Steele 1988; Kutschera et al. 2012). Most amphipods are free-living benthic animals that actively crawl and swim,

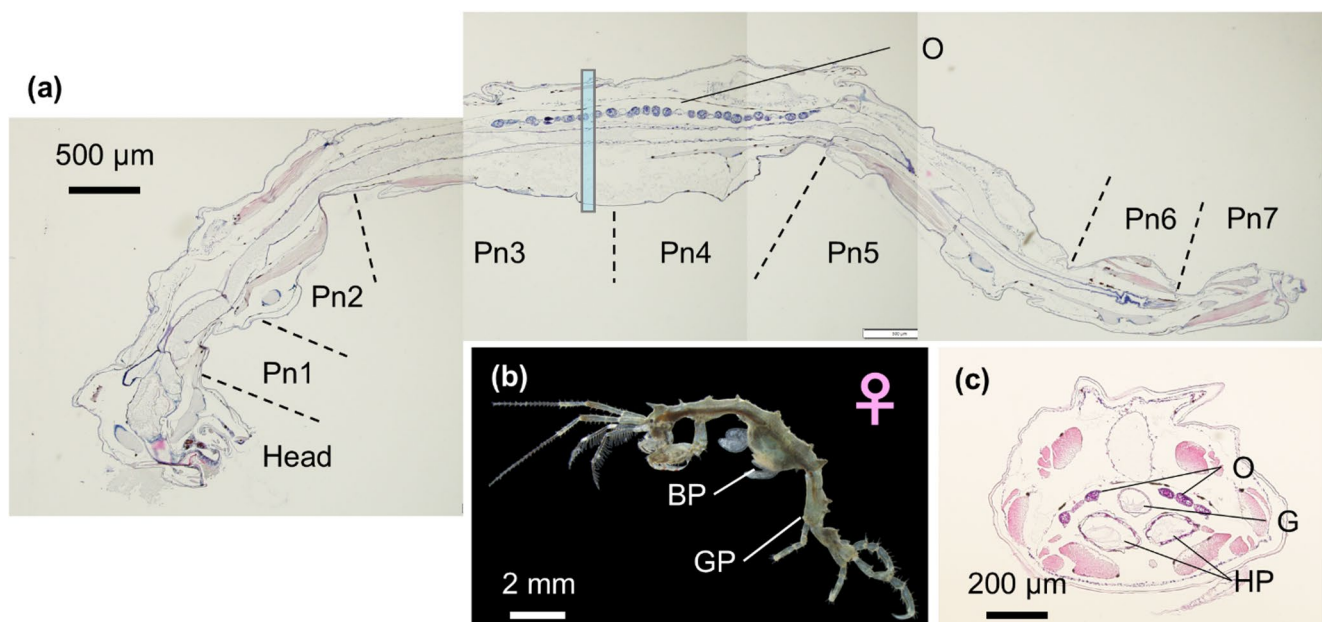


Fig. 5 Sagittal section of an adult female of *Caprella scaura*. **a** Sagittal section of the whole body. The blue box indicates the sectioned part of (c). **b** Sectioned individual when alive. **c** Transverse section of the third pereonite whose sectioned position is showed in (a) as the blue

box. The image is oriented as anterior is proximal, upper is up, and right is left. Abbreviations: BP, brood pouch; G, gut; GP, gonopore; HP, hepatopancreas; O, ovary; Pn1–7, the first to seventh pereonite

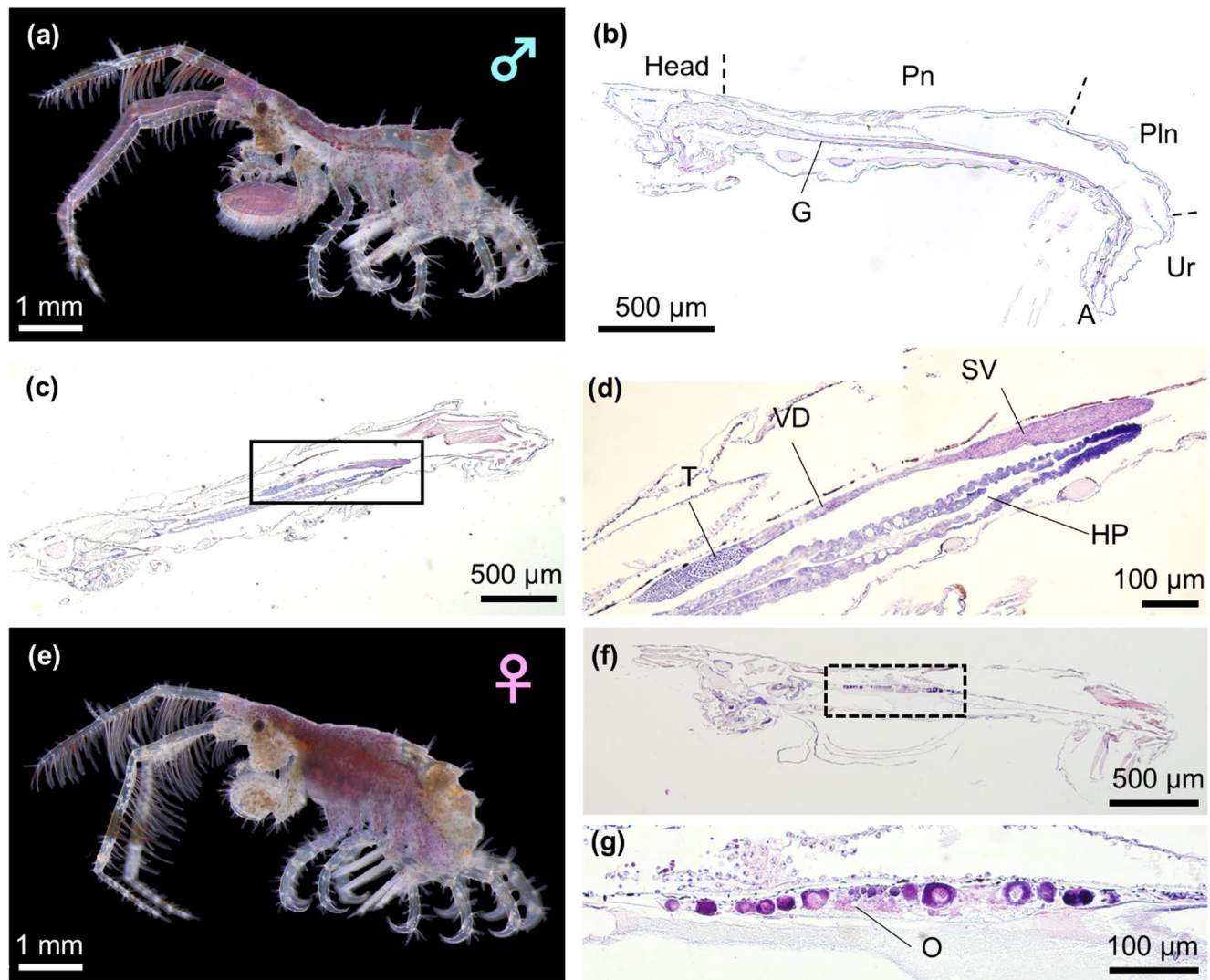


Fig. 6 Arrangement of internal organs of *Podocerus* sp. **a–d** Adult male. (a) Sectioned individual when alive. (b) Sagittal section containing only digestive organs. **c, d** Male reproductive organs. The black box in (c) indicates the magnified part showed in (d). **e–g** Adult female. (e) Sectioned individual when alive. (f, g) Female reproduc-

tive organs. The black dotted box in (f) indicates the magnified part showed in (g). Abbreviations: A, anus; G, gut; HP, hepatopancreas; O, ovary; Pln, pleonite; Pn, pereonite; SV, seminal vesicle; T, testis; Ur, urosomite; VD, vas deferens

whereas caprellids cling to substrates such as algae or bryozoans using their pereopods, and swim only rarely (Copilaş-Ciocianu et al. 2020). When caprellids swim, it is typically for predator avoidance and is achieved through body undulations or setae on the second antennae (Caine 1978, 1979, 1989). Respiration in caprellids is supported instead by two pairs of gills on the third and fourth pereonites (Takeuchi et al. 2003). Thus, the pleopods and uropods should be useless for an epiphytic lifestyle of caprellids. Their functions were either lost or reassigned to other appendages, such as the first gnathopods and posterior pereopods (Takeuchi and Hirano 1995).

On the other hand, pleopods and uropods may even represent a functional hinderance to a clinging lifestyle. In non-caprellid

amphipods, including podocerids, the pleon is generally folded ventrally beneath the pereon, such that it lies between the substrate and the pereon (Dahl 1977; Barnard et al. 1988). Given that caprellids, and also cyamids (Cyamidae) which are included in Caprelloidea, typically grasp the substrate primarily with their posterior pereopods (Takeuchi and Hirano 1995; Ito et al. 2011), the presence of a pleon could interfere with firm attachment to the substrate. If so, positive natural selection may have favored the reduction or loss of these segments, together with their appendages. This hypothesis is further supported by the swimming behavior of the caprogammarid *Caprogammarus gurjanovae* Kudrjashov and Vassilenko, 1966 (Ito et al. 2011). Caprogammarids possess a well-developed pleon and pleopods and actively swim by beating their pleopods. It has

been proposed that the pleon and pleopods of caprogammarids were secondarily regained after having been lost in the basal branch of caprellids and caprogammarids (Ito et al. 2011). Together, these observations suggest that ecological shift and associated behavioral differences — specifically, transitions between benthic clinging and active swimming — are linked to the presence or absence of the pleon, pleopods, and uropods.

Comparative anatomy and evolution of degenerative abdomen of caprellids

This study revealed the arrangement of internal organs in caprellids, showing that almost all parts of the digestive and

reproductive systems are contained within the pereonites, while the highly reduced abdomen houses only the posterior extension of the gut and anus. Although earlier studies described specific structures such as the pharynx (Keith 1974) and male reproductive organs (Irie 1967), this is the first report on the complete internal anatomy of caprellids. Furthermore, this study clarifies the differences between *C. scaura* and *Podocerus* sp. in the arrangement of internal organs and the appendage morphologies with their suggested functions inside each segment (Fig. 7).

Podocerus sp., which retains well-developed pleon, i.e., pleonites and urosomites, was examined as a comparative model to infer the evolutionary transition to the reduced

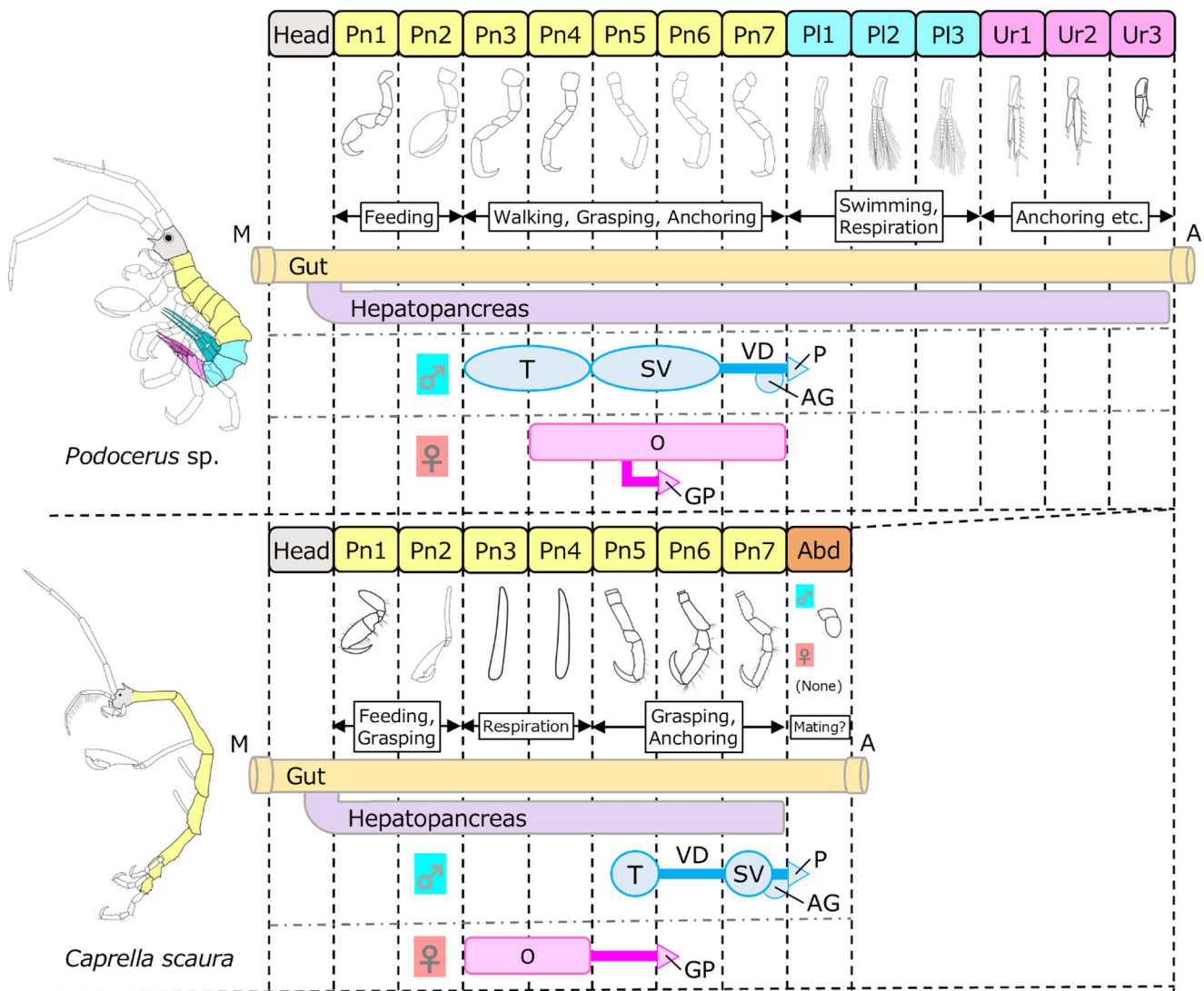


Fig. 7 Summary and comparison of the arrangement of internal organs of *Podocerus* sp. and *Caprella scaura*. Appendage morphologies with their functions and internal organs on each segment are depicted. Note that the pleon (pleonites and urosomites) and its appendages present in *Podocerus* sp. are almost absent in *C. scaura*, except for “abdominal appendages” present only in adult males which are possibly used for

mating. There are only extensive parts of the gut and hepatopancreas in the pleon of *Podocerus* sp. Reproductive organs of both sexes are contained in pereonites in both species. Abbreviations: A, anus; Abd, abdomen; AG, androgenic gland; GP, gonopore; M, mouth; O, ovary; P, penis; Pl, pleonite; Pn, pereonite; SV, seminal vesicle; T, testis; Ur, urosomite; VD, vas deferens

abdomen of caprellids. Observations revealed that the pleon of *Podocerus* sp. contained only extensions of the gut and hepatopancreas, with the anus opening at the posterior end of the third urosomite. Reproductive organs of both sexes were confined to the pereonites (Figs. 6, 7). This arrangement closely resembles that of other non-caprellid amphipods (Ford et al. 2005; Hyne 2011). The family Podoceridae, to which *Podocerus* sp. belongs, is nested within the superfamily Caprelloidea, together with the families Caprellidae, Caprogammaridae, Cyamidae, and Dulichiidae. Phylogenetic studies suggest that podocerids and dulichiids, which have well-developed pleon, represent the more ancestral forms within Caprelloidea (see [Supplementary Information](#); Myers and Lowry 2003; Ito et al. 2008; Lowry and Myers 2013). These observations indicate that in the common ancestor of Caprelloidea (including *Podocerus* sp. and *C. scaura*), the essential organs were already confined within the pereonites.

It can be considered that the evolution of segmental reduction faces strong selective constraints if those segments contain essential organs and appendages. In caprellids, however, reduction of the pleon and pleonal appendages was possible because (1) the essential internal organs were already located in the pereonites in their ancestors (at least in the last common ancestor with Podoceridae) and (2) the presence of the pleon, pleopods and uropods became unnecessary, or even obstructive together with the ecological shift from free-living benthic to epiphytic lifestyle, and their functions were transferable to other appendages.

A similar logic may apply to other crustaceans with reduced pleons, particularly the phenomenon of carcinization in decapods. In macrurans (e.g., shrimps and lobsters), pleons house extensions of both digestive and reproductive organs (Felgenhauer 1992). In brachyuran crabs, however, reproductive organs are confined to the cephalothorax, and the pleon is reduced and folded ventrally, retaining only gonopods (reproductive appendages) and part of the digestive tract. This shift likely reflects the transition from a swimming macruran lifestyle to a benthic crab-like ecology (Luque et al. 2019; Wolfe et al. 2019). Similar to the case in caprellids, such drastic morphological changes may be related to the ancestral condition of the pleon and to ecological, and possibly behavioral, shifts that occurred in brachyurans. By contrast, cirripedes, and also ostracods, completely lack pleons and pleonal appendages, but their highly specialized internal anatomy and unresolved phylogenetic position complicate direct comparisons. So, although the extreme reduction of segments is known in cirripedes, it has not fully explained under the same framework (Hilgard 1960; Mouchel-Vielh et al. 1998; Chan et al. 2021; Ip et al. 2021; Bernot et al. 2023). Further phylogenetic and evolutionary developmental studies will be required to clarify the evolutionary and developmental mechanisms underlying loss of pleons and pleonal appendages in these crustaceans.

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Author contributions YO and TM designed the experiments. YO and HK arranged and conducted field collections. YO, KO and RK carried out experiments. YO and TM analyzed the data and wrote the original manuscript. YO and TM managed the processes of review and editorial revision. All authors have read and provided their consent for the previous and final manuscript versions.

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Data availability The sequence data obtained in this study is deposited in NCBI with its accession number provided in the text.

Declarations

Competing interests The authors declare no competing interests.

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