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Molting behavior, gastrolith formation, and mandibles of *Enoplometopus debelius* Holthuis, 1983 (Decapoda: Astacidea: Enoplometopidae) in an evolutionary context

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Abstract

Molting, gastrolith formation, and mandibular morphology are key features associated with growth, calcium regulation, and feeding ecology in decapod crustaceans. These aspects remain poorly understood in the reef lobster *Enoplometopus debelius* Holthuis, 1983. We investigated molting behavior, gastrolith structure, and mandibular sclerotization in *E. debelius* to evaluate their evolutionary significance within Astacidea. Molting occurred predominantly at night, and freshly molted individuals delayed consumption of exuviae for approximately two days. X-ray imaging revealed the presence of two pairs of gastroliths, in contrast to the single pair typically observed in other astacideans. Mandibular morphology showed strong mineralization of the incisor ridge, consistent with adaptations to marine feeding conditions. These findings suggest that *E. debelius* retains distinct morphological and functional traits that provide insight into the evolutionary diversification of Astacidea.

Keywords calcium storage, coral reefs, Crustacea, crustacean evolution, mandibular morphology, nocturnal behavior, X-radiography

Introduction

The infraorder Astacidea, which includes both freshwater and marine taxa, comprises the commercially important clawed lobsters (Nephropoidea), the reef lobsters (Enoplometopoidea), and the well-studied freshwater crayfishes (Astacoidea and Parastacoidea). *Enoplometopus* A. Milne-Edwards, 1862 represents a unique marine lineage of Astacidea that has received relatively little scientific attention (Poupin, 2003; De Grave *et al.*, 2009; Chan, 2010). *Enoplometopus* was initially classified within the genus *Nephrops* Leach, 1814 of the family Nephropidae, based primarily on adult external morphology (Randall, 1839).

Subsequent investigations proposed alternative classifications for *Enoplometopus* based on larval morphology, gill structure, and claw formation. Gurney (1938) noted that *Enoplometopus* exhibits chelae only on the first pair of walking legs, while the second and third pairs show incomplete claw closure. He also identified similarities between the gill structure and larval morphology of *Enoplometopus* and Axiidae, suggesting that the genus should be placed within that family. Holthuis (1946) initially classified *Enoplometopus* within the homarid superfamily, but reassigned it to Thalassinidea (Holthuis, 1974) without providing a particular justification. De Saint Laurent (1973) re-examined *Enoplometopus* and, recognizing its distinct morphology and geographical distribution, proposed a new superfamily, Enoplometopoidea, within Astacidea. De Saint Laurent (1988) Subsequently established the family Enoplometopidae. Cladistic analyses and molecular phylogenetic studies later supported this classification (Ahyong & O'Meally, 2004). Further research confirmed that Enoplometopoidea represents the most basal lineage within Astacidea (Tsang *et al.*, 2008), a conclusion reinforced by comparisons between the morphology of modern species of *Enoplometopus* with fossil evidence (Devillez, 2019).

Among Astacidea, crayfishes (Astacoidea, Parastacoidea) are widely studied due to their accessibility and economic

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importance in aquaculture (Huxley, 1880; Holdich & Lowery, 1988), whereas species of Nephropidae have been the focus of research primarily because of their commercial fisheries value (Factor, 2013). Research on *Enoplometopus* has been comparatively limited, with most studies focusing on taxonomy, species diversity, and distribution (Poupin, 2003; Chan & Ng, 2008), as well as specific aspects such as larval development (Abrunhosa *et al.*, 2007) and spermatophore morphology (Matthews, 1954). *Enoplometopus debelius* Holthuis, 1983, a coral reef species found in the tropical Pacific, also recorded from Japan (Kubo, 1952).

Despite its taxonomic significance, key biological aspects of *E. debelius* remain unexplored. Molting is a critical process for growth, development, and exoskeletal renewal among decapods. It is closely linked to calcium regulation via gastrolith formation (Greenaway, 1985; Luquet & Marin, 2004). In Nephropoidea and the freshwater Astacidea, a single pair of gastroliths is typically formed within the stomach wall to store calcium before molting (Travis, 1960; McWhinnie, 1962; Ueno, 1980). This condition has also been documented in the freshwater crayfish *Cherax quadricarinatus* (von Martens, 1868) (Shechter *et al.*, 2008). Whether *Enoplometopus* possesses a single or multiple pairs of gastroliths has remained unknown. Its gastrolith morphology also remains unknown. Understanding the mechanism of calcium storage in *Enoplometopus* is of relevance for understanding the origin and evolution of the group.

Mandibular morphology also provides critical insights into evolutionary adaptations among crustaceans, with sclerotization reflecting dietary shifts and environmental constraints (Kawai & Patoka, 2020; Kawai, 2022). Studies suggest that marine Nephropidae exhibit highly sclerotized incisor ridges, whereas freshwater Astacoidea and Parastacoidea show reduced sclerotization, with more developed molar ridges and incisor mineralization (Bouchard, 1977; Hobbs, 1991; Bentov *et al.*, 2012; Huang & Kawai, 2020). No comparative study has examined the mandibles of the species of Enoplometopoidea. Since X-ray imaging can reveal mineralization patterns based on relative gastrolith size (molt mineralization index, MMI; Shechter *et al.*, 2008), an inter-superfamily comparison could provide novel insights into the evolutionary pressures shaping feeding adaptations.

We investigated the molting behavior, gastrolith formation, and mandible morphology of *E. debelius* to explore its position within Astacidea. Through X-ray imaging and behavioral observations, we assessed whether two-pair gastrolith formation represents an ancestral trait and examined how mandible sclerotization patterns correspond to ecological transitions from marine to freshwater habitats. By integrating morphological and behavioral data, we aimed to elucidate the evolutionary pathways that have shaped Astacidea, particularly in the context of calcium regulation and feeding ecology.

Materials and Methods

Molting behavior

We used a rearing tank (359 mm wide, 220 mm deep, 262 mm high) containing two individuals (one male and one female) of *E. debelius* to study molting behavior. The post-orbital carapace length (POCL) of the individuals was measured with a caliper as the distance from the posterior margin of the orbit to the posterior median margin of the carapace. Sex determination followed Holthuis (1983). Females were identified by the presence of an elliptical sperm receptacle with a vertical slit, whereas males possess enlarged first pleopods ending in an equilateral triangular shape.

The tank substrate consisted of commercial coral gravel (0.5–1 cm in diameter) spread to a thickness of approximately 1 cm. We installed a circulation-type filtration system (Tetra Auto One-Touch Filter AT-50; Tetra, Tokyo, Japan) in the tank. Water exchange was conducted weekly, replacing approximately half of the water volume, using artificial seawater (Tetra Marine Salt). The animals were fed a commercial diet (Hikari Crab Cuisine, Kyorin., Tokyo, Japan) once daily at 0700. The amount of food provided was slightly more than they could consume overnight. The tank contained five polyvinyl chloride (PVC) pipes (inner diameter 20 mm or 50 mm, length 50 mm or 150 mm) for hiding. No artificial lighting was used, the tank following the natural photoperiod. The water temperature was maintained at a constant 25°C year-round using a heater and air conditioning.

Molting activity and post-molt behavior were observed twice daily at 0700 and 1500, with additional observations conducted randomly at other times. These observation times were selected to distinguish between post-night and daytime (prior to sunset) conditions, with 0700 h corresponding to post-dawn observations and 1500 h representing daytime conditions.

The molting process began with an individual remaining stationary on the substrate in a normal position, defined as a posture in which the chelipeds are extended forward, the dorsal surface facing upward, and the abdomen extended. This was followed by splitting at the junction between the cephalothorax and abdomen. When molting was detected, the time of day was recorded, along with whether the molted individual consumed its exuviae. The number of days required for complete consumption of the exuviae was also recorded.

Observations were conducted from 1 April 2021 to 30 September 2021, and from 1 May 2022 to 31 December 2023. Beginning on 1 May 2022, the pair was replaced by a new pair every six months. This was done to minimize potential behavioral modification associated with prolonged captivity and repeated molting cycles under artificial conditions. As a result, a total of four males and four females (eight individuals in total) were kept under laboratory conditions. The carapace length of the individuals at the time of introduction to the tank had a mean of 16.4 mm (standard deviation 3.6 mm) (10.5 mm – 19.0 mm).

Molting events recorded during the two observation periods were pooled, and the timing of each molt was analyzed.

Observation of gastrolith

To prevent aggression between individuals immediately after molting, we kept individuals of *E. debelius* separately in water-permeable plastic containers (100 mm wide, 50 mm deep, 50 mm heigh), with six containers placed in a single tank. The individual was replaced if molting occurred. Aeration was provided for each container, and a PVC pipe

(inner diameter 20 mm, length 50 mm) was placed in each container as a shelter.

We used a total of 22 individuals (10 males and 12 females) in the experiment. The mean POCL of males and females combined was 14.6 mm (standard deviation 2.4 mm) (10.3 mm – 18.5 mm). Individuals were different from those used in the molting-behavior observations. Feeding regime, water exchange, temperature, and photoperiod were the same as those used for the molting behavior observations.

We promptly removed individuals when exuviae were observed. We froze and dissected individuals that had molted within 8 h after completion of molting, and gastroliths removed from the stomach. One male and one female were fixed in 70% ethanol and examined by X-ray imaging (Best-X-DC, New Life Radiology, Turin, Italy).

For comparison, we kept individuals of three crayfishes, *Procambarus clarkii* (Girard, 1852), *Enoplometopus occidentalis* (Randall, 1839), and *Enoplometopus daumi* Holthuis, 1983, under the same conditions described above for *E. debelius*. All gastrolith observations described for *E. debelius* and the three species of crayfishes were based on post-ecdysis individuals examined immediately after molting. This criterion was applied consistently across species to ensure comparability of gastrolith condition and to standardize the description of molting stage throughout the study.

Observation of the mandible

We selected two representative specimens from at least 15 individuals of *E. debelius*. Comparatively large individuals were selected to facilitate observation. One male and one female were frozen and fixed in 70% ethanol, and X-ray images of the mandibles were obtained. For comparison, one male and one female each of *P. clarkii* and *Metanephrops japonicus* were treated in the same way, and their mandibles examined by X-ray imaging.

Statistical analysis

Differences in molting frequency between daytime and nighttime were evaluated using a chi-square goodness-of-fit test. Differences between sexes in molting timing were analyzed using a chi-square test for independence. The assumptions of the chi-square test, including expected frequencies, were satisfied. Significance was evaluated at $P = 0.05$. Statistical analyses were performed using Statcel 4 software (OMS Publishing, Saitama, Japan).

Results

Molting behavior

Each individual studied molted at least once, and all molting events consistently occurred outside shelters. The process began with the individual assuming a stationary posture in the normal position (see above). At this point, the junction between the cephalothorax and the abdomen split, causing the cephalothorax shell to lift. The soft body subsequently emerged (Fig. 1A). By further bending the abdomen, the soft body moved upwards, exposing the eyes, antennae, walking legs, and other appendages, as well as the abdomen (Fig. 1B).

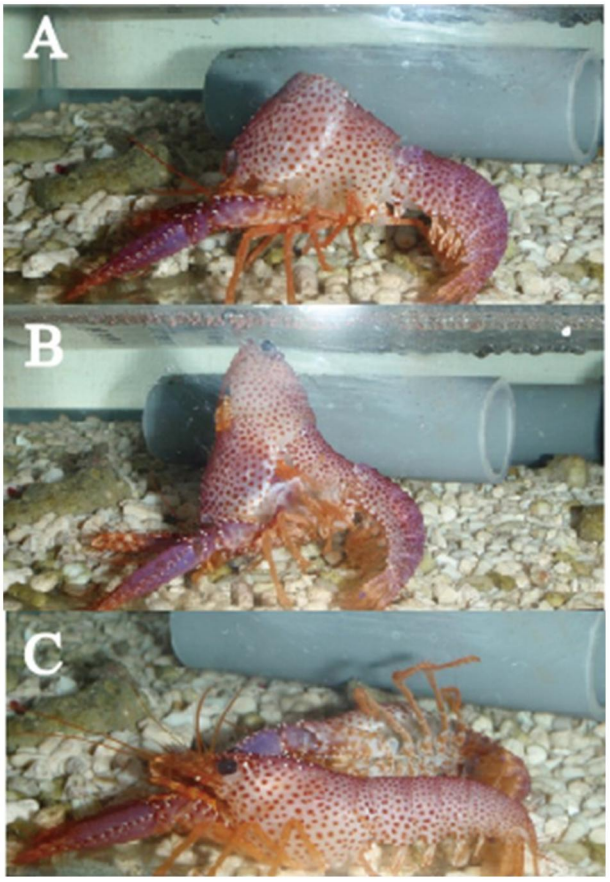

Figure 1 Molting behavior of *Enoplometopus debelius*: initial (**A**), middle (**B**), and final (**C**) stages. Male, POCL 19.0 mm.

Once the walking legs were freed, the molting individual completely exited the old exoskeleton (Fig. 1C). The duration from the initial appearance of the soft body at the junction between the cephalothorax and abdomen to its complete emergence from the exuviae was approximately three minutes.

The following behaviors were commonly observed immediately after *E. debelius* molted. On the day of molting and the following day, freshly molted individuals did not consume their exuviae. Starting from the second day onward, they began to eat the exuviae (Fig. 2), and by days 3 to 5, they had consumed more than two-thirds of the exiviae. Apart from the period immediately after molting, male and female individuals typically remained hidden in separate shelters (Fig. 3, top). Males did not share a shelter with females after molting. Only during the 3 to 4 d immediately following a female's molt, males and females cohabited in the same shelter (Fig. 3, bottom). No consistent guarding behavior by males toward females or specific orientation of individuals within the shelters was observed. No copulation or spermatophore transfer was directly observed during the study period. Three males and three females molted during daytime, whereas seven males and nine females molted at night. The proportion of individuals that molted at night was 70% for males, 75% for females. A chi-square goodness-of-fit test performed to compare the molting frequencies between daytime (6 individuals) and nighttime (16 individuals) showed a significant difference in molting distribution ($\chi^2 = 4.55$, $P = 0.033$),

Figure 2 Consumption of exuviae by a female *Enoplometopus debelius* (POCL 20.1 mm) after four days of molting.

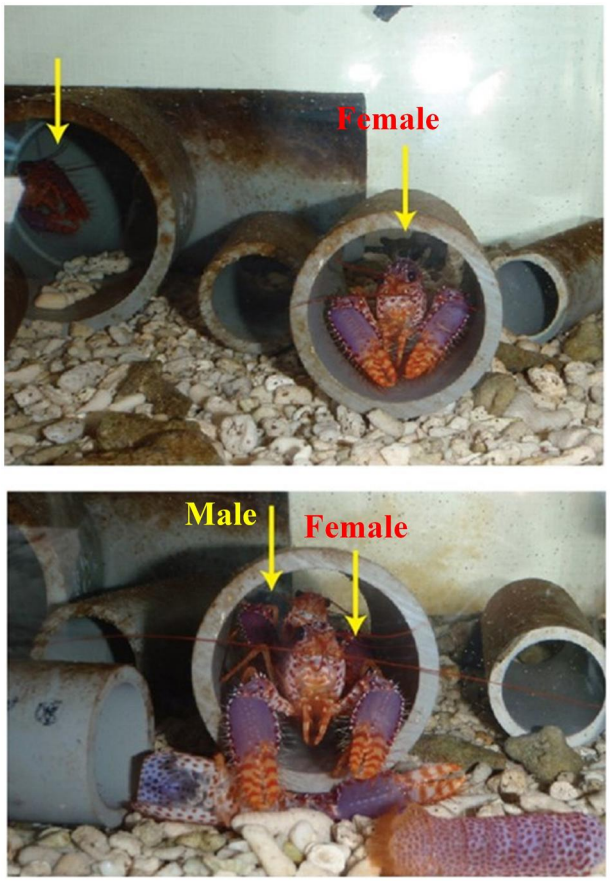

Figure 3 Post-ecdysis behavior of *Enoplometopus debelius*: upper, before molting of female POCL 20.1 mm; lower, one day after molting of the female and non-molting male POCL 19.0 mm.

suggesting that molting occurred more frequently at night. There was no significant difference between males and females in both daytime (3 males, 3 females) and nighttime molting (7 males, 9 females) ($\chi^2 < 0.01$, $P > 0.99$). The observed molting distribution did not significantly differ from the expected values, indicating no statistical association between molting timing and sex.

Observation of gastrolith

A pair of gastroliths in pre-molt individuals of *C quadricarinatus* appeared as white, hard material observed through X-ray exposure in the stomach wall (Fig. 4A). In a post-molt individual of *E. debelius*, a relatively large pair of white, hard substances was observed in the stomach, accompanied by a smaller pair of similar material (Fig. 4B, C). A pair of gastroliths was present in the stomach in all post-molt *P. clarkii* individuals, appearing milky white and hemispherical, with a slight indentation at the center of the circular surface (Fig. 5A). Similarly, two pairs of gastroliths were found in the stomach of all individuals of *Enoplometopus daumi, E. debelius*, and *E. occidentalis*, both appearing milky white. One pair was relatively large and spherical, featuring a slight indentation on the circular surface, while the other pair was smaller and oval-shaped (Fig. 5B–D).

Observation of the mandible

X-ray images of *E. debelius, M. japonicus*, and *P. clarkii* are shown in Figure 6. The incisor ridge appeared less distinctively white in the following order: *E. debelius, M. japonicus*, and *P. clarkii*. The white region was clearly visible in *E. debelius*, but it became less distinct in *M. japonicus*, and no white areas were visible in *P. clarkii* (Fig. 6). The molar ridge was distinct in *E. debelius* (Fig. 6B), faint in *M. japonicus* (Fig. 6D), and although a white area was present in *P. clarkii*, it was limited to a narrow region (Fig. 6F).

Discussion

Molting behavior

Molting in *E. debelius* was consistently observed to occur primarily at night, which is in agreement with previous observations in a freshwater crayfish (Murakami & Kawai, 2022). No significant difference between sexes in molting timing was detected, suggesting that diel molting patterns are not sex-dependent under the present conditions.

A notable behavioral pattern was the temporary cohabitation of males and females immediately following female molting. Because individuals otherwise remained isolated, this short-term association likely reflects part of reproductive behavior. Post-molt female receptivity is well known in decapod crustaceans, and mating shortly after ecdysis has been reported in several taxa, including *Homarus americanus* (Atema, 1986; Factor, 2013). Although we were unable to make observations of copulation or spermatophore transfer, the observed cohabitation is consistent with a premating molt scenario. Further behavioral and experimental studies are required to confirm whether chemical communication or pheromonal cues are involved.

The delayed consumption of exuviae may be explained by two non-exclusive factors. First, immediately after molting, individuals possess a soft exoskeleton, including incompletely sclerotized mouthparts and mandibles, which likely limits their ability to mechanically process and consume the

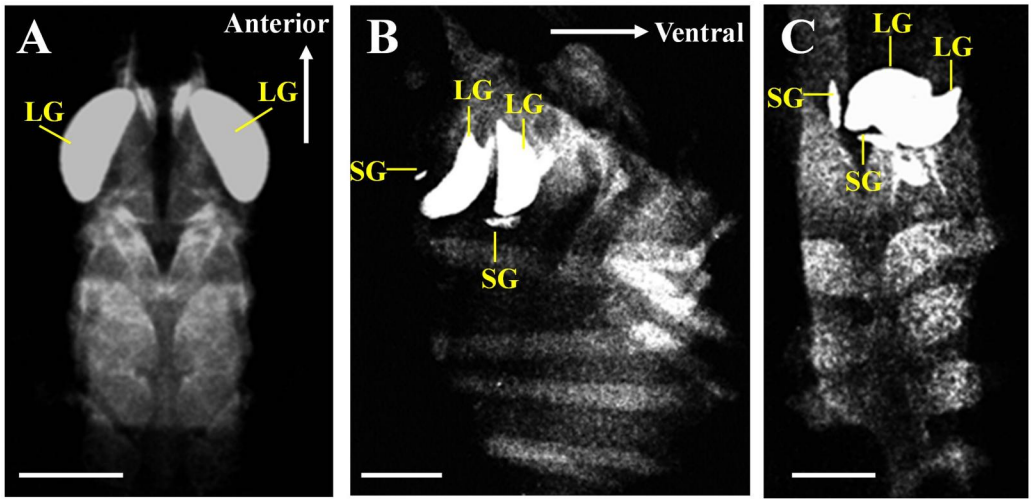

Figure 4 X-ray images of gastroliths (ventral view) of *Cherax quadricarinatus* (**A**), lateral (**B**) and ventral views of *Enoplometopus debelius* (**C**). Scale bar: 1 cm.

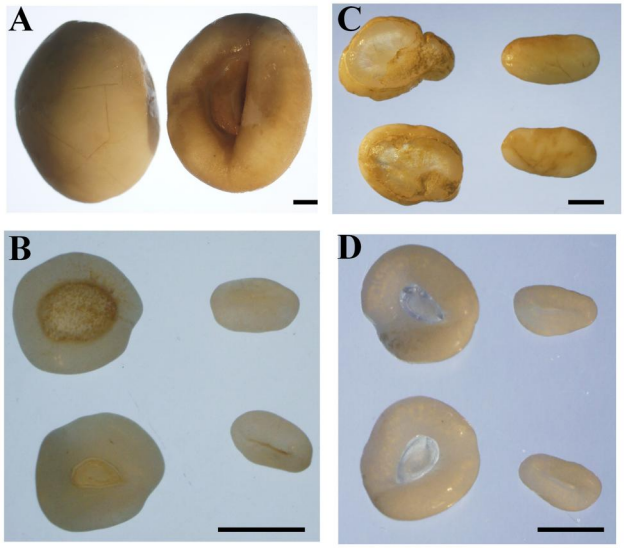

Figure 5 Gastrolith formation in 8 h post-molt of *Procambarus clarkii* (female, POCL 34.1 mm) (**A**), *Enoplometopus daumi* (male, POCL 12.0 mm) (**B**), *E. occidentalis* (female, POCL 26.0 mm) (**C**), and *E. debelius* (male, POCL 10.8 mm) (**D**). Left: dorsal side; right, ventral side (A); upper, dorsal side; lower, ventral side (B–D). Scale bar: 1 mm.

exuviae (Atema, 1986). This mechanical limitation does not necessarily apply to all behaviors. Feeding on exuviae requires sufficient hardening and functional recovery of the mandibles, whereas mating-related behavior is not strictly dependent on such mechanical conditions. Females of some decapods are known to molt prior to mating and are capable of copulation during the soft post-molt period (Atema, 1986). Feeding ability may be limited during this period. The inability to consume exuviae immediately after molting does not contradict the possibility that reproductive interactions may occur during the same interval. The observed temporary cohabitation of males and females following female molting is consistent with this interpretation, although direct evidence of copulation was not obtained. These interpretations remain tentative and should be verified through targeted behavioral observations.

Gastrolith formation and evolutionary implications

Our research revealed that *E. debelius* possesses two pairs of gastroliths, consisting of one large hemispherical pair and one smaller oval pair. This condition differs from the single pair typically reported in members of Nephropoidea and the freshwater Astacidea (Travis, 1960; McWhinnie, 1962; Ueno, 1980), and thus represents a potentially important morphological feature within Astacidea.

From a phylogenetic perspective, Enoplometopoidea has been regarded as the basal lineage within Astacidea (Tsang *et al.*, 2008; Wolfe *et al.*, 2019). Two alternative interpretations can be considered to explain such hypothesis. First, the presence of two pairs of gastroliths in *E. debelius* may represent a retained ancestral condition, whereas the single pair observed in other astacidean lineages would then be interpreted as a derived state resulting from reduction. Alternatively, the two-pair condition in Enoplometopoidea may represent a lineage-specific specialization that evolved independently from the single-pair condition observed in other astacidean groups.

The available fossil evidence does not conclusively support either scenario. Fossil crayfish gastroliths resembling the single-pair condition have been reported (Audo *et al.*, 2023), suggesting that the reduction to a single pair may have occurred early in astacidean evolution. Importantly, this hypothesis is not intended to imply that freshwater calcium limitation drove the initial reduction to a single pair of gastroliths; rather, calcium limitation is considered here as a secondary ecological factor that may have influenced subsequent functional refinement after the trait had already evolved. Without fossil evidence demonstrating a two-pair condition, the hypothesis of ancestral retention in *E. debelius* remains speculative.

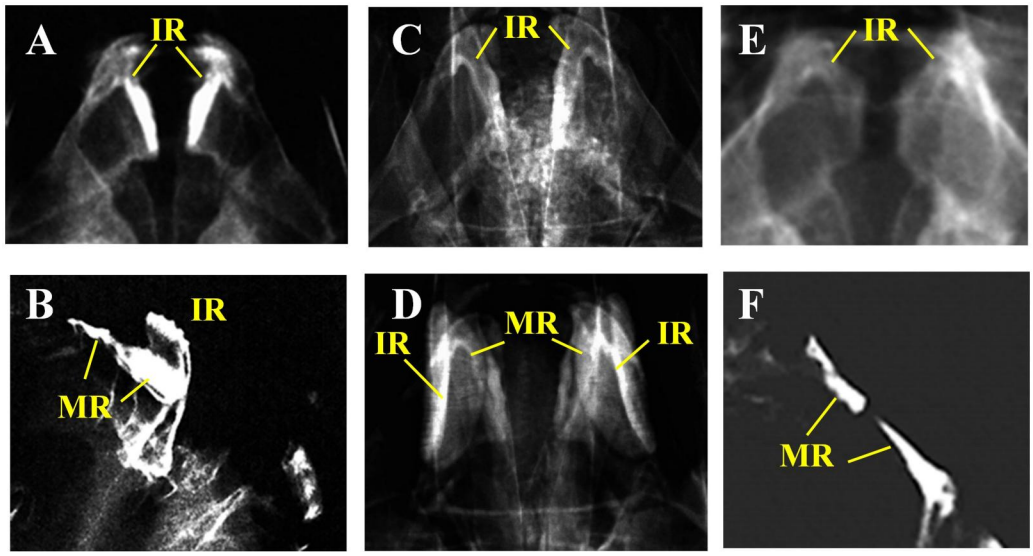

Figure 6 X-ray image (ventral view) of mandibles of *Enoplometopus debelius* (male, POCL 14.3 mm) (**A**), *Metanephrops japonicus* (male, POCL 38.1 mm) (**B**), and *Procambarus clarkii* (male, POCL 15.5 mm) (**C**). Distocaudal view of the mandible of *E. debelius* (**D**), *Metanephrops japonicus* **(E)**, and *Procambarus clarkii* (**F**). IR, incisor ridge; MR, molar ridge.

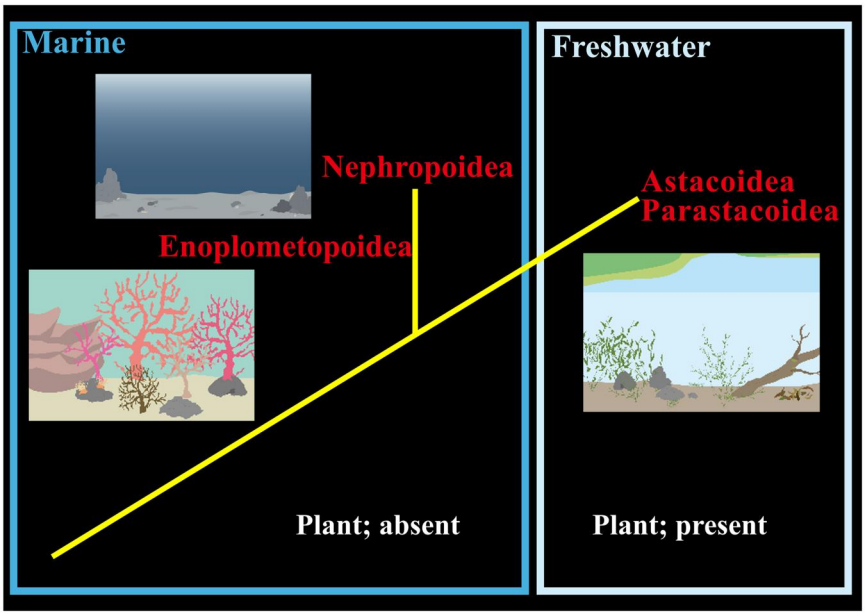

Figure 7 Schematic representation of mandible evolution in Astacidea, from corneous mandibles in marine environments to non-corneous mandibles in freshwater environments.

Environmental factors may also play a role in shaping gastrolith morphology. Freshwater crayfishes inhabit environments where calcium availability is often limited, and efficient internal calcium storage is essential (Greenaway, 1985; Luquet & Marin, 2004). By contrast, *E. debelius* inhabits coral reefs, where calcium is abundant. While this difference may influence calcium storage strategies, it does not directly explain the presence of two pairs of gastroliths. The functional significance of this condition thus remains unclear.

Overall, the two-pair gastrolith condition in *E. debelius* should be interpreted cautiously, as either a retained ancestral trait or an independent adaptation. Resolving this question will require additional data from fossil records, developmental studies, and comparative analyses across Astacidea.

Mandibular morphology and ecological adaptations

Our results show clear differences in mandibular mineralization between *E. debelius*, *M. japonicus*, and *P. clarkii*. In particular, the incisor ridge was most strongly mineralized in *E. debelius*, whereas it was reduced in the two freshwater taxa. These results are consistent with previous morphological studies (Huang & Kawai, 2020; Kawai, 2022).

Mandibular sclerotization is generally interpreted as an adaptation to diet and feeding mechanics (Bouchard, 1977; Hobbs, 1991; Kawai *et al.*, 1995). Marine taxa such as Enoplometopoidea and Nephropoidea are thought to feed on relatively hard or structurally complex food items, including benthic invertebrates associated with coral reefs and other benthic environments (Kawai & Patoka, 2020). By contrast, freshwater crayfishes primarily consume detritus and plant-derived material, which requires less mechanical resistance but need more grinding capacity (Bouchard, 1977; Hobbs, 1991; Kawai *et al.*, 1995). Our X-ray observations support such interpretation. The well-developed and mineralized incisor ridge in *E. debelius* is consistent with the need to process harder food materials, whereas the reduced mineralization observed in freshwater taxa reflects a shift toward softer or fibrous diets. Mechanical testing of mandible strength would nevertheless be required to quantitatively validate this functional interpretation.

We did not make any dietary observations and therefore the relationship between mandibular morphology and diet remains inferential. Future studies integrating gut content analysis, feeding experiments, and mechanical testing will be necessary to confirm the functional significance of these morphological differences in the mandible.

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