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Review

A Review of the Ecomorphology of Pinnotherine Pea Crabs (Brachyura: Pinnotheridae), with an Updated List of Symbiont-Host Associations

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Abstract: Almost all pea crab species in the subfamily Pinnotherinae (Decapoda: Brachyura: Pinnotheridae) are considered obligatory endo- or ectosymbionts, living in a mutualistic or parasitic relationship with a wide variety of invertebrate hosts, including bivalves, gastropods, echinoids, holothurians, and ascidians. While the subfamily is regarded as one of the most morphologically adapted groups of symbiotic crabs, the functionality of these adaptations in relation to their lifestyles has not been reviewed before. Available information on the ecomorphological adaptations of various pinnotherine crab species and their functionality was compiled in order to clarify their ecological diversity. These include the size, shape, and ornamentations of the carapace, the frontal appendages and mouthparts, the cheliped morphology, the ambulatory legs, and the reproductive anatomy and larval characters. The phylogenetic relevance of the adaptations is also reviewed and suggestions for future studies are made. Based on an updated list of all known pinnotherine symbiont–host associations and the available phylogenetic reconstructions, it is concluded that, due to convergent evolution, unrelated species with a similar host interaction might display the same morphological adaptations.

Keywords: Decapoda; micro-computed tomography; morphology; parasitism; Pinnotherinae; symbiosis; symbiotic fauna

1. An Introduction to Pea Crabs

Symbiotic lifestyles, whether they are considered parasitic, commensal, or mutualistic, can be found in species of almost all major crustacean taxa. Only the remipedes (Remipedia) and horseshoe shrimps (Cephalocarida) form an exception, including no apparent taxa living in or on host organisms [1]. The true crabs (Decapoda: Brachyura) encompass 14 families with symbiotic species [2]. One of these families, the Pinnotheridae or ‘pea crabs’, currently holds around 320 recognized species [3,4], which can almost all be classified as obligatory endo- or ectosymbiotic [1]. The family is currently split into four subfamilies: Pinnotherinae, Pinnixinae, Pinnothereliinae, and Pinnixulalinae [5]. Members of Pinnotherinae are usually defined as small symbiotic crabs, living commensally or parasitically as endosymbionts between the branchial organs of bivalve, gastropod, and chiton molluscs, inside the pharyngeal basket of ascidians, inside the intestinal or respiratory system of holothurians and echinoids, and ectosymbiotic on the outer surface of various echinoids [6]. In addition, there are exceptional cases of pinnotherines living in brachiopods, on asteroids, and supposedly in decapod burrows and worm tubes [6,7]. The complicated multi-staged life history of only a few pinnotherines has been well

studied [8,9], but remains unknown for most other species. Pinnotherine species which have been identified as free-living are usually described from single specimens and one of the sexes only [6]. Although hard stage males and females are known to leave their (intermediate) host for numerous possible reasons (e.g., copulation during swarming [10]), it is most likely that soft staged individuals collected outside another invertebrate have been dislodged from their hosts [11], or are just venturing shortly outside their hosts [12].

Most members of the subfamilies Pinnixinae, Pinnothereliinae, and Pinnixulalinae [5] can be found as commensal symbionts living inside the holes and tubes of living annelid and sipunculid worms, and inside mud shrimp burrows (Decapoda: Axiidae and Upogebiidae). Although pinnixine, pinnothereline, and pinnixulaline crabs are known for their co-inhabiting behaviour, around 19 species are still considered to be free-living, whereas seven species are known as obligatory endo- or ectosymbionts. Closer inspection of the free-living species and their habitat is needed in order to confirm whether they are indeed free-living or if their host was simply not found and therefore not collected [13].

While pea crabs are regarded as one of the most specialized groups of symbiotic crabs [14], only few authors succeeded in testing or observing the functionality of their ecomorphological adaptations [15]. In the taxonomic literature, morphological adaptations are commonly only mentioned as part of species descriptions [7,16], while review papers mainly focus on the correlation between the sizes of the host and the symbiont [17], and on the morphology of the anatomical features associated with feeding habits and host choice, which are both thought to drive speciation [15].

Due to their small size and cryptic way of living, the adaptations pinnotherines have evolved in order to live in and on their host are barely understood [18]. This study aims to review the anatomy and hypothesized functional roles of the anatomical structures in pinnotherines, and to illustrate a number of these anatomical features. In this way, we hope to shed more light on the host specificity of the morphological adaptations and whether they have any phylogenetic relevance in the evolution of the whole subfamily. An updated, more extensive list of known symbiont–host relationships of the Pinnotherinae is also given (see Section 3.6), partly based on earlier works [1,6,11].

2. Studying Pea Crab Morphology

Traditionally, the morphological features of pea crabs were only illustrated using camera lucida illustrations [19] or photographs [20]. Most of the morphological features we can study using the previous literature is limited to only the third maxillipeds and the dorsal view of the entire female crab, whereas later, the (available) male crabs were also illustrated. More recent taxonomic works also included illustrations of the details of the ambulatory legs (especially the dactyli), chelae, and frontal view of the head region [19]. In more recent morphological papers, scanning electron microscopy (SEM) was used to capture the minute details on the claws [15]. In the present review, we aim not only to include the traditional methods in order to show the morphological features, but also a relatively new way to study both the internal and external morphology of pea crabs, by micro-computed tomography (μ -CT) scanning.

Three specimens from the Naturalis Biodiversity Center decapod collection (Leiden, the Netherlands; formerly Rijksmuseum van Natuurlijke Historie, RMNH) were selected for their distinct overall morphology, one representing the Pinnixinae (*Pinnixa cyllindrica* (Say, 1818)), and two representing the variety within the Pinnotherinae (*Nepinnotheres pinnotheres* (Linnaeus, 1758) for its basic pinnotherine body shape and *Xanthasia murigera* White, 1846 for its abnormal carapace ornamentations). The three specimens were illustrated using 3D models based on μ -CT: 3D models were made in the Naturalis Biodiversity Center CT-scanning and imaging facilities (Leiden, the Netherlands), using Avizo 9.5.0 volume-rendering software [21] and a Zeiss Xradia 520 Versa 3D X-ray microscope (CT-scanner), of specimens in 70% ethanol. The following settings were used: Optical magnification of 0.39, a scanning current of 87.0 μ A, a scanning voltage of 80.0 kV, an exposure time ranging from 1.3 to 1.5 ms, and pixel sizes ranging from 23.5 to 27.6.

The line drawings in this review were traced from previous literature. SEM pictures of claw morphologies and ornamentations were made at the Senckenberg Research Institute and Natural History Museum (Frankfurt, Germany), from the same samples and using the same methodology as described by Becker and Türkay [15].

To highlight the adaptive evolution of various anatomical features, we have organized the review into the five following sections: carapace shape, size, and ornamentation; frontal appendages and mouthparts; cheliped morphology; ambulatory leg adaptations; and sexual anatomy and larval characters. In addition, we have provided an updated list of all known pinnotherine symbiont–host associations (see Section 3.6).

3. Adaptations in Pinnotherine Morphology

3.1. Carapace Shape, Size, and Ornamentation

Most pinnotherine crabs are known for their strong sexual dimorphism, in which the females reach larger sizes than the conspecific males. This is most likely linked to their mating systems, in which the trait ‘pure-search polygynandry of sedentary females’ occurs [22–24]. This is, however, not apparent in all pinnotherine genera, where a different mating strategy is used. Both sexes of the species in the ectosymbiotic *Dissodactylus* complex (genera *Dissodactylus* and *Clypeasterophilus*) share a similar size and shape of the carapace and appendages. These genera are thought to use ‘pure-search polygynandry of mobile females’ as mating strategies [22,25]. The very subtle sexual dimorphism is thought to be the result of both sexes living on their host, rather than in their host, being able to leave their host and not being restricted to the space in the host’s cavities [26]. Similarly, female members of *Ostracotheres tridacnae* (Rüppell, 1830) and *Xanthasia murigera*, which inhabit giant clams (Tridacninae), are of the same size and shape as their male counterparts [27,28]. It is thought that males reach similar sizes as their female conspecifics due to their spacious *Tridacna* hosts allowing them to grow larger [12]. Furthermore, male and female members of the holothurian-associated genera *Alain* and *Holotheres* share a similar shape and size of the carapace, but males possess relatively stouter chelae and are only slightly (10–20%) smaller in carapace width and length than females [28,29]. In many pinnotherine species, the morphology of only one sex is known, resulting in limited knowledge on sexual dimorphism in those species [6]. In addition, although sexual dimorphism is most extreme in mollusc-inhabiting pea crabs (e.g., the genera *Pinnotheres*, *Fabia*, *Arcotheres*), it can be found all over the family tree, in association with almost all possible hosts (see Section 3.6).

Size differences between crab species is thought to be linked to specific morphological traits of their hosts, such as microhabitat space [15]. The largest species of pinnotherine crab, *Pinmaxodes gigas* Green, 1992, has a carapace width of 36 mm as is reported from the siphon of a large geoduck, the mudburrowing bivalve *Panopea* sp. [30]. The smallest pea crab species, *Nannotheres moorei* Manning & Felder, 1996, can be found in narrow hammer oysters (*Malleus candeanus* (d’Orbigny, 1853)) barely reaching a carapace width of 1.5 mm [31]. The smallest *Arcotheres* species (*A. pollus* Ah Yong & Ng, 2020) also lives inside a hammer-oyster (*M. albus* Lamarck, 1819) [32]. Host size does not just explain the interspecific size differences, but also intraspecific variation in the crabs. Cuesta et al. [33] studied the correlations between crabs of both sexes (*Pinnotheres bicristatus* García Raso & Cuesta, 2019) and one of their host bivalves, *Anomia ephippium* Linnaeus, 1758. A strong positive correlation was found between the sizes of the hosts and the sizes of the soft-shelled (post-hard) females, with larger hosts harbouring larger post-hard females. The larger size of the females can be explained by their sedentary lifestyle, not having to leave their host ever again. Additionally, being larger is also advantageous for reproductive purposes: larger body sizes can produce larger broods [34]. A similar, but weaker, positive correlation was found between the sizes of male crabs and their hosts; male crabs were always smaller than females in the same host size [33]. It is thought that smaller males looking for mates have access to a larger size range of host individuals [22]. In *Pinnotheres pisum*, *P. taichungae* K. Sakai, 2000,

and probably many more bivalve inhabitants, the size of the host is also positively correlated with the infestation rates within and between host species [35,36].

In addition to the study mentioned above [33], no correlation was found between the size of hard stage females and the size of their newly invaded hosts [37]. This suggests that intruding crabs do not select the biggest host available, but they will be limited in their growth by the size of the specific host. Similar results [15] were found in populations of other bivalve-associated pea crabs from all over the world: *Afropinnotheres monodi* Manning, 1993 [38], *Arcotheres sinensis* (Shen, 1932) [39], *Austinotheres angelicus* (Lockington, 1877) [40], *Calyptraeotheres garthi* (Fenucci, 1975) [41], *Pinnotheres pisum* (Linnaeus, 1767) [42], and *Pinnotheres tsingtaoensis* Shen, 1932 [26]. In addition to these mollusc-inhabiting species, Ahyong [12] found that *Austrotheres holothuriensis* (Baker, 1907) has a larger maximum size in spacious holothurians than in the mostly smaller ascidian host species. The specialist congeneric *A. pregenzeri* Ahyong, 2018, however, grows to similar sizes in its comparable ascidian hosts. Similarly, Becker and Türkay [43] found larger *Nepinnotheres pinnotheres* specimens infesting shells of *Pinna nobilis* Linnaeus, 1758, compared those from ascidian hosts. In general, larger hosts are thought to offer greater food resources than smaller hosts [15].

Based on their reproductive strategies, the shape and rigidness of the carapace can change throughout the multi-staged lifecycle of both female and male pea crabs. Campos [8] suggests two different ontogenetic pathways, based on his own observations and previous literature. In the first strategy, male and female crabs moult into their hard stages prior to host invasion and copulate after invasion of the host. After copulation, the female moults into her more globular post-hard (soft) stages and remains in the host. The hard stage male, characterized by having a well-calcified carapace, is fit for entering bivalve hosts [11] and is suggested to leave the host again [23] and copulate with other host-inhabiting hard stage females to increase its reproductive success [17]. Becker and Türkay [15] confirmed this theory for hard stage males of *Pinnotheres pisum*, observing the lack of distal segments in their ambulatory legs, likely due to them having been squashed by the closing of their bivalve hosts. During their time between hosts, male crabs of the same species might even use vectors like detached egg-cases of whelk snails (*Buccinum*) to cover greater distances [44].

This first strategy is found in most pinnotherine genera, but many details remain unknown for almost all species. The second strategy is similar, but differs in a few ways: juvenile crabs infest their (intermediate) hosts in the first post-planktonic stage and moult into a male or female hard stage crab. In this stage, morphological adaptations for swimming develop (e.g., hard carapace and ambulatory leg morphology, discussed later), and both male and female crabs leave their host for copulation in open water (often called swarming behaviour). Afterwards, females infest their terminal host and moult into more globular post-hard stages, while males might still switch between hosts in their terminal hard-stage. This strategy is thought to follow a seasonal pattern [30,45] and is known from members within the genera *Austrotheres* [12], *Calyptraeotheres* [9], *Fabia* [45], and *Tumidotheres* [8,30]. It is worth noting that swarming behaviour has been observed in *Fabia subquadrata* Dana, 1851, and *Tumidotheres maculatus* (Say, 1818) using 'night-light' fishing of a few swarming individuals, as described in Pearce [45]. Another unrelated species, *Tritodynamia horvathi* Nobili, 1905, which was transferred from the Pinnotheridae to another family [3], is known for its excessive swarming behaviour [46] and might have contributed to the theory that some pinnotherids swarm in a similar way [45].

Interspecific differences in carapace shape and rigidness of post-hard females can be traced back to their specific host range. Endosymbiotic pea crabs known from echinoderms and geoducks (e.g., genera *Alain*, *Buergeres*, *Holotheres*, *Holothuriophilus*, *Pinnaxodes*; see Section 3.6) share a firm, round to subangular carapace [30]. Similarly, members of the ectosymbiotic genera *Dissodactylus* and *Clypeasterophilus*, all known from the outer surface of flattened sea urchins such as sand dollars, share a flattened, extremely calcified, and somewhat widened carapace, which is thought to be useful for manoeuvring between the spines of sea urchins [47]. This somewhat flattened and wide carapace resembles that of the hard stage males and females of other genera associated with bivalves, like *Fabia subquadrata* and *Zaops ostreum* (Say, 1817) [48]. Most crabs of the remaining pinnotherine

genera known from molluscs and ascidians (with the exception of a few genera discussed below) live securely inside their host and share a globular soft-shelled carapace in the terminal female stages. This feature is usually accompanied by an enlarged pleon for egg development (Figure 1A–C) ([17]; see below). In a few cases, the carapace might be more calcified in specimens infesting certain bivalve groups, like the Arcidae [49]. The reason for this aberrant post-hard stage morphology is not known as for now.

In contrast to the morphological variation within the Pinnotherinae, members within the Pinnixinae, Pinixulalinae, and Pinnothereliinae all share a similar body shape. All representatives of these taxonomic groups have a flattened, wide carapace shape, and usually a third ambulatory leg that is larger in size than the other ones (Figure 1D–F) [18]. This body shape is thought to be the result of the symbiotic lifestyle of these crabs within the tubes and burrows of worms and decapods such as mud shrimps [50]. Although the crabs from these three subfamilies appear to be morphologically similar, Manning and Felder [51] discuss very slight intraspecific ecophenotypic variation, resulting from the crabs living in burrows from related but separate species of *Callinassa* mud shrimps. In addition, Palacios Theil and Felder [18] mentioned that the diversity of body shapes is the result of convergent evolution, resulting from host choices, rather than shared synapomorphies. Furthermore, a few non-pinnotherine pea crabs are known from atypical hosts: living inside and on hosts usually inhabited by pinnotherines. Other than their habitat preferences, none of these species resemble pinnotherines in their general morphology.

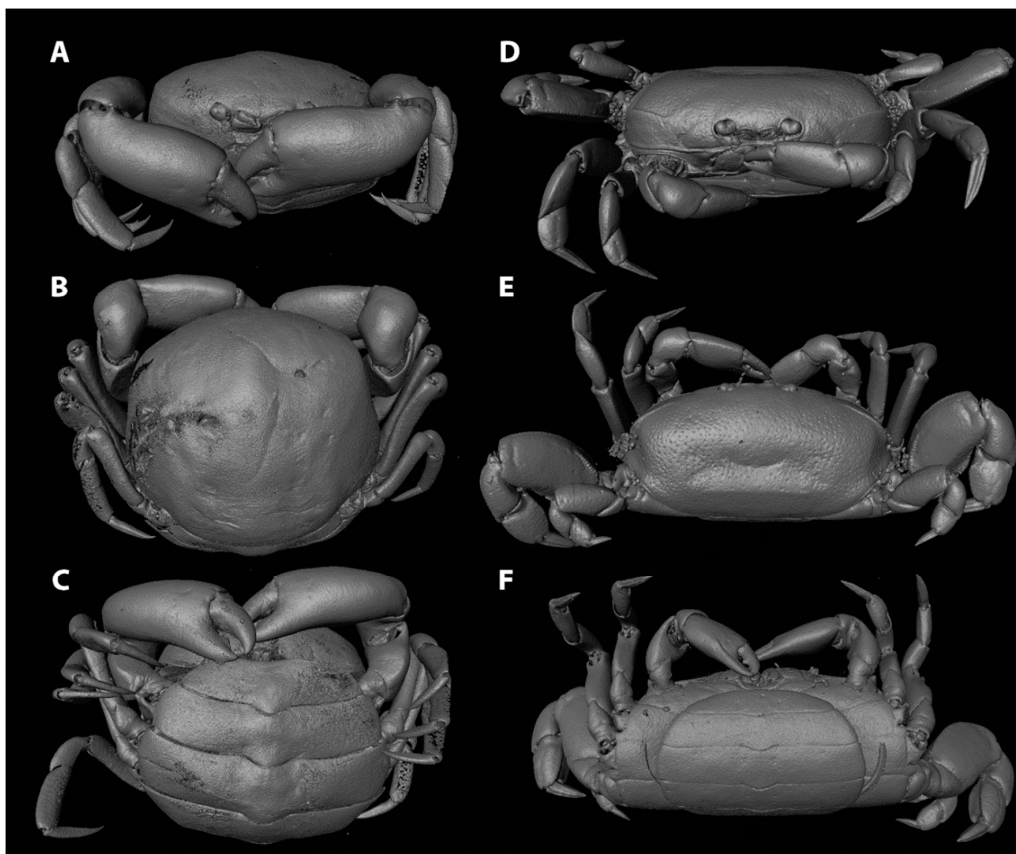


Figure 1. Three-dimensional models of two representatives of Pinnotheridae. (A–C) A typical (female) bivalve- and ascidian-inhabiting pinnotherine, *Nepinnotheres pinnotheres* (Linnaeus, 1758) (RMNH.CRUS.D.36): carapace width 1.8 mm. (D–F) A typical tube-dwelling pinnixine crab, *Pinnixa cyllindrica* (Say, 1818) (RMNH.CRUS.D.10104): carapace width 1.5 mm. Videos of the 3D models can be found in the Supplementary Data.

A few, presumably not closely related, pinnotherine genera share various structural ornamentations on their carapaces. These ornamentations are described in the taxonomic literature as tubercles, plates, lamellae, and upturned margins. The functionality of these ornamentations is still unknown [52], but these structures might be the result of adaptive evolution [27]. Both species of the genus *Austrotheres* have a subhexagonal carapace shape, with a distinct (in *A. pregenzeri*) to weak (in *A. holothuriensis*) epigastric ridge, which is covered with tubercles in *A. pregenzeri* (Figure 2A) [12]. Members of *Durckheimia* display two upturned margins: one medial plate and one anterior plate, often with a sharp medial notch, continuing into two lateral margins (Figure 2B) [27,53]. Similarly, crabs of the monospecific genus *Visayeres* share the medial plate of the supposedly related species of *Durckheimia*, showing a conical dorsal surface [54]. Members of the genera *Serenotheres* and *Limotheres* share a somewhat pentagonal carapace shape, with a pronounced rostrum (more pronounced in *Limotheres*) and an angled dorsal surface, which forms a weak (*Limotheres*) or strong (*Serenotheres*) eave-like (overhanging) structure anteriorly with the ‘true’ frontal margin that is much lower than the front of the dorsal margin (Figure 2C,D) [27,52,55].

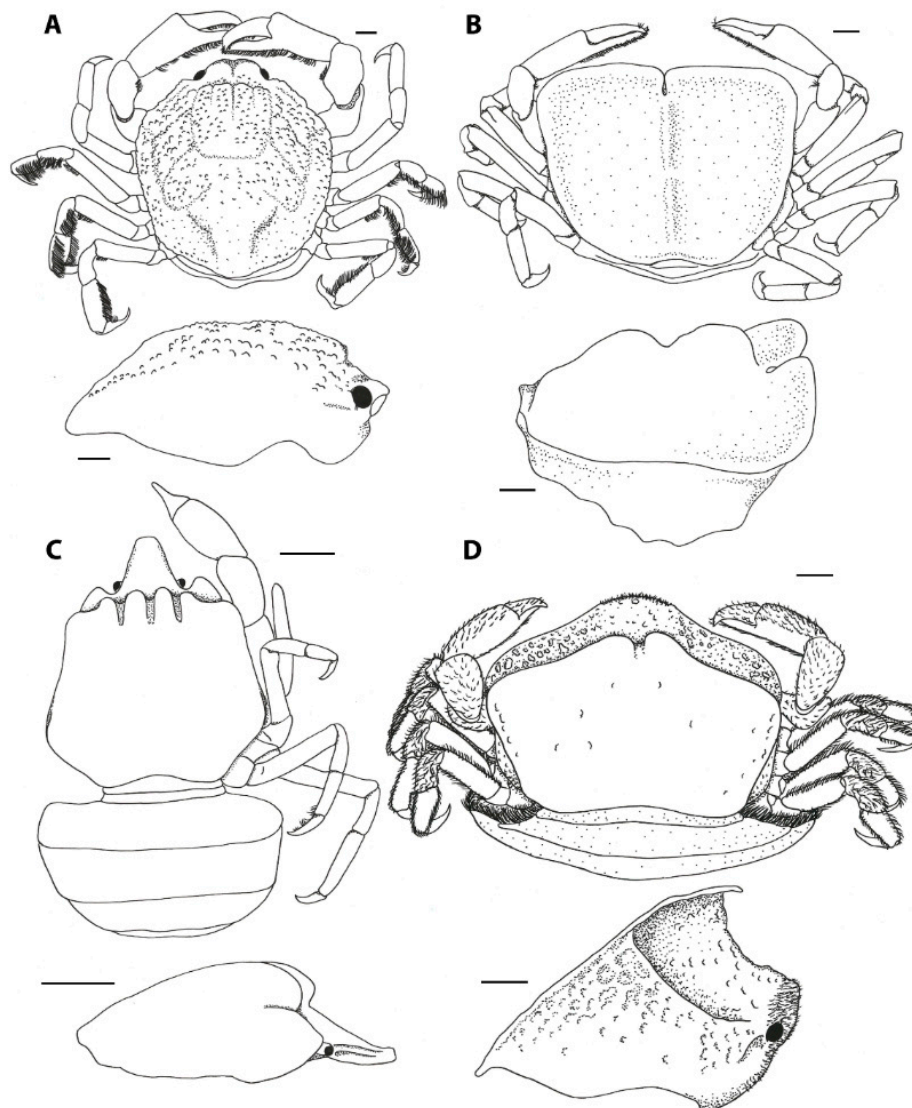


Figure 2. Dorsal and lateral views of representatives of Pinnotherinae with ornamented carapace morphologies. (A) *Austrotheres pregenzeri* Ahyong, 2018, after Ahyong [12]. (B) *Durckheimia lochi* Ahyong & Brown, 2003, after Ahyong and Brown [53]. (C) *Limotheres nasatus* Holthuis, 1975, after Holthuis [55]. (D) *Serenotheres besutensis* (Serène, 1967) after Ahyong and Ng [27]. Scale bars: 1 mm.

Lastly, both members of the monotypic genera *Tridacnatheres* and *Xanthasia* share a unique ornamentation of the carapace: a sharp, upturned (in *Xanthasia*) or weak, folded (in *Tridacnatheres*) ridge at the carapace margin, which terminates anteriorly in the hepatic region, in addition to a strong (in *Xanthasia*) or weak (in *Tridacnatheres*) rostro-dorsal and medial mushroom-like tubercle (Figure 3) [27]. Virtual sections of CT-scan volumes of *X. murigera* reveal that ornamentations have a well-calcified outer surface, but no associated tissues were identified underneath. The stomach of the crab is partly calcified and is obviously attached to the inner surface of the rostro-dorsal tubercle (Figure 3C). Using this imaging method, no other organs were apparently associated in a similar way with the other ornamental structures. The carapace of *Xanthasia* (and, to a lesser extent, that of *Tridacnatheres*) resembles those found in various unrelated leucosiids (purse crabs, such as *Alox*, *Ebelia*, and *Ixa*), hymenosomatids (pillbox crabs, such as *Halicarcinus*), and epialtids (symbiotic spider crabs, such as *Oxypleurodon*).

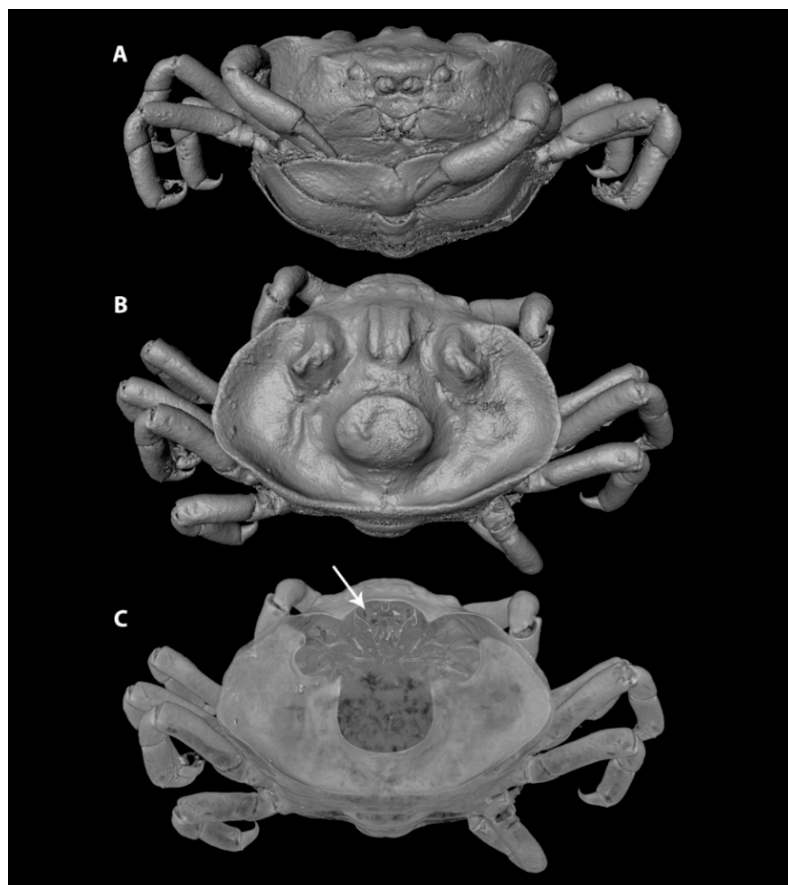


Figure 3. Three-dimensional model of a female *Xanthasia murigera* White, 1846 (RMNH.CRUS.D.27677): carapace width 1.2 mm. (A) Dorsal view. (B) Lateral view. (C) Volume horizontally cut through carapace showing the stomach inside the most rostro-dorsal tubercle (arrow). Videos of this 3D model can be found in the Supplementary Data.

Although the functionality of this wide range of morphological features is currently unknown, patterns in carapace ornamentation can be linked to host specificity. Most of the above-mentioned species live in various, often spacious, hosts: members of *Austrotheres* live in holothurians and (large) ascidians, but are known to venture outside their hosts [12]; members of *Durckheimia* and *Limotheres* live in scallops of the family Limidae; all species of *Serenotheres* and *Visayeres* live inside boring mussels (Lithophaginae); and the members of *Xanthasia* and *Tridacnatheres* live inside giant clams (genus *Tridacna*). The bivalve hosts mentioned above are not necessarily inhabited exclusively by these pea crab genera (see Section 3.6). The unique ornamentations on the carapaces can play parts

in structural and/or chemical mimicry to confound the host. For example, host mucus may stick to the carapace of the crab easily due to its crevices. Owing to the presence of host mucus on the crab, the crab may not be perceived as a foreign object. While both passive and active mimicry as camouflage have been studied in crustaceans in detail [56], their use of structural and chemical mimicry to avoid being noticed by a host has not received detailed examination hitherto. Other crustaceans possibly utilizing similar strategies might be found in the palaemonid shrimp genera associated with bivalves like *Anchistus*, *Conchodytes*, and *Pontonia* [57]: these genera possess less spines on their carapaces than their ectosymbiotic relatives, probably evolved to be smoother due to their endosymbiotic lifestyle [58]. In addition, cleaning shrimp of the species *Ancylomenes pedersoni* (Chace, 1958) and other cleaning shrimp symbiotic to anemones might use a similar strategy: in order to not get stung and devoured by the anemone, the shrimps need to acclimate themselves by acquiring host tissue, a phenomenon, which is also well known from clownfish (Amphiprioninae) [59].

The variation in body shape is also translated into the variation of rostrum shape and size. Although the functionality is unknown, species of some pea crab genera possess an elongated rostrum, like *Austrotheres* [12], *Limotheres* [55], *Serenotheres* (e.g., [27]) and, to a lesser degree, in *Abyssotheres* [60] and *Nepinnotheres* (e.g., [7]). Members of the (paraphyletic) genus *Fabia* and the related genus *Bonita* possess an extension of the rostrum towards the midline of the carapace: two longitudinal sulci split the anterior side of the carapace in three portions [16,61].

Although other symbiotic crab families are known for their host-specific and cryptic lifestyle using camouflage (e.g., Pilumnidae, Eumedoninae, such as *Ceratocarcinus*, *Harrovia*, *Zebrida*) [2,62], most pinnotherines do not display intricate camouflage patterns. Most species have evolved to be clear, transparent or unicoloured (mostly white, yellowish, or brown, purple to black in some species of *Arcotheres*) [63]. Adult female individuals of some endosymbiotic species are so translucent that the inner organs shine through, most conspicuously the orange-coloured mature ovaries (such as in *Nepinnotheres*, *Pinnotheres*, and *Zaops*) [15,16,33].

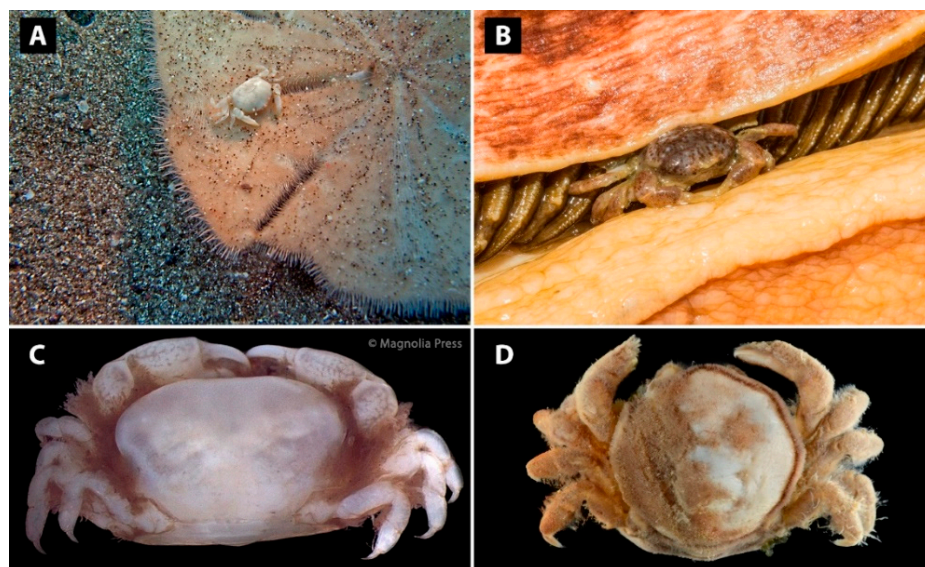


Figure 4. External features of some representatives within the Pinnotherinae. (A) Crabs of *Dissodactylus mellitae* (Rathbun, 1900) on a sand dollar (from [64], photo credit M. Faasse). (B) Red-mottled colouration of *Opisthopus transversus* Rathbun, 1894 living in the folds of a gumboot chiton (*Cryptochiton stelleri* Von Middendorff, 1847) (photo credit M. Harms). (C) Dense setation at the lateral carapace margins in *Holothuriophilus trapeziformis* Nauck, 1880 (reproduced from [65]). (D) Overall setation within *Nepinnotheres edwardsi* (De Man, 1887) (SS-4433), setae removed on the right side (reproduced from The Biodiversity of Singapore database-photo credit: A. Anker). Photographs reproduced with permission from the respective photographers and copyright holders.

Additionally, males of *Nepinnotheres pinnotheres* (as *Pinnotheres veterum* Bosc, 1801) were reported to change their colour at night [66]. A few cases in which crypsis seems obvious, concern the genera *Dissodactylus* and *Clypeasterophilus*, which are thought to mimic shell fragments or coral rubble in soft sediments [67]. The white colouration might also mimic shell fragments attached to the host, as some sea urchins (e.g., sand dollars) cover themselves in rubble (Figure 4A; [68]) and some regular echinoids hold debris over their test using tube feet. The Caribbean species *Clypeasterophilus rugatus* (Bouvier, 1917) even has black-and-white coloured bands on its ambulatory legs [68], similar to Indo-West Pacific *Zebrida* crabs (Pilumnidae: Eumedoninae) [62]. More elaborate colourations can be found in the males of *Pinnotheres bicristatus* [33], *Pinnaxodes gigas* and *P. floridensis* Wells & Wells, 1961, and *Opisthopus transversus* Rathbun, 1894 (Figure 4B) [30]. While the cause or potential function of the colouration in *Pinnotheres bicristatus* is not mentioned in the description [33], the colouration of the other three species is discussed in taxonomic works. The species display orange-red spots on the dorsal surface of their ambulatory legs and carapace, while the ventral side of these structures display orange-grey spots, which may be caused by carotenes derived from their host [69]. *Pinnotheres gigas* is known from various geoduck species while *P. floridensis* has only been found in a single species of holothurian. In contrast, *O. transversus* is known from a wide range of hosts, including holothurians (see Section 3.6). Although the species might partly share a similar microhabitat (geoducks siphons somewhat resemble the digestive organs of holothurians) and may have a similar diet (as demonstrated in the third maxillipeds, see below; [30]), this does not fully explain their colouration, because there are other species living inside holothurians with similar mouthparts that lack such colour patterns (e.g., *Holotheres*). The holothurian-associated pinnixine crab species *Pinnixa barnharti* Rathbun, 1918, is known to have a similar orange-red colouration, which may also be linked to its diet. This crab species is known to compete with *O. transversus* for shelter, so probably also for food sources [50].

Setal coverage can be found in many crustacean lineages and, similarly, a wide range in different setal coverage patterns can be found in the Pinnotherinae. Most species are glabrous or only have a sparsely setose integument, in combination with some setae for feeding practises (see below: Sections 3.3 and 3.4). A few exceptions are the conspicuously tomentose holothurian-associated genera *Alain*, *Holotheres*, *Holothuriophilus* (Figure 4C), and *Trichobezoares*, which possess a very setose carapace or carapace margins [29,65,70]. Ahyong [12] mentions that since these genera do not appear to be related, the setation may be an adaptation for holothurian infestation. Few other representatives with setose carapaces belong to *Arcotheres* (e.g., *A. pollus* [32]), *Afropinnotheres* (e.g., *A. monodi* [7]), *Mesotheres* (e.g., *M. barbatus* (Desbonne, in Desbonne & Schramm, 1867) [71]), *Nepinnotheres* (e.g., *N. pinnotheres*, *N. edwardsi* (De Man, 1887) (Figure 4D), and *N. villosulus* (Guérin, 1832) [15,72,73]), *Pinnotheres* (e.g., *P. pilulus* Tai, Feng, Song & Chen, 1980 [74]), and *Tumidotheres* (*T. maculatus* [75]). The actual function of full or partial coverage with setae remains unknown, but Becker and Türkay [15] suggest that *Nepinnotheres pinnotheres* uses the short setae to collect mucus from the body walls of ascidian hosts, since it lacks the setal comb on the chelipeds (see below: Section 3.3). Similarly, Kruczynski [75] observed individuals of *Tumidotheres maculatus* continuously cleaning their carapaces to collect bivalve gill mucus. The setose pinnixine crab *Glasella leptosynaptae* (Wass, 1968) has been reported from the body of holothurians, with the original description stating that it usually occurs near the anterior end, but never near the mouth of the holothurian. Wass [76] mentioned that the ridges and setae on the carapace may enable the crab to cling to rough-surfaced holothurians, since the crab was always found with its dorsal surface pressed against the body wall of the host [76]. Long setae on the dactylus and propodus of the third maxillipeds of this species indicate a filter-feeding diet, but no observations were made. The full body setation of the previously mentioned pinnotherine species might also play a role in chemical mimicry or defense: host mucus might attach to the short setae in order to conceal the crab, or to make the crab less palatable when venturing outside of the host [77].

3.2. Frontal Appendages and Mouthparts

The process of host recognition is one of the most studied subjects in symbiotic crustacean research [78]. Studying this process is necessary to understand the evolution, ecology, but also the functional morphology of symbiotic crustaceans. The morphological features thought to be linked to host recognition in pinnotherines are all located anteriorly, namely the eyes for visual cues, and both antennulae and antennae for picking up and emitting chemical cues. The eyes were at first considered to play a role in host recognition; however, the ectosymbiotic *Dissodactylus primitivus* Bouvier, 1917, was shown to find its host using only chemical cues (see below) [78]. Although related species within the genera *Dissodactylus* and *Clypeasterophilus* are known to hop on and off their hosts and are therefore atypical within the Pinnotherinae [79], the lack of functionality of their relatively small eyes remains unexplained [78]. Most pinnotherine species have small eyes, but there is quite a lot of variation in their placement and size, which may be linked to their specific host range (variation in general eye shape can also be found in other symbiotic crustaceans, such as palaemonid shrimp [80,81]). The placement of the eyes and their visibility in dorsal view have been used as taxonomic characters, although size is usually only briefly mentioned. One species stands out, since it hints to evolutionary processes known from animals in caves and deep-sea environments: *Arcotheres latifrons* (Bürger, 1895) is an eyeless species [19]. Since the host of this species is unknown, it is impossible to say if the host plays a role in the reduction and eventual disappearance of the eyes. The species, however, is known from a single specimen only, which supports the idea that the lack of eyes in this specimen is an anomaly. The larval development of other *Arcotheres* species has been studied before and no larval stage is known to lack eyes (e.g., [17]).

Species within the *Dissodactylus* complex are commonly used as model organisms to examine host recognition in pinnotherids [78,82], but more species have been studied in this regard [15]. The antennulae were identified as the principal structures of chemoreception in all studied species [10,15] and no variation among different pinnotherine lineages is known. In addition to the setae on the antennulae, other setae types have a chemoreceptive function in brachyuran crabs as well [83] and male crabs often possess elongated setae near the eyes, such as in *Austinotheres angelicus* [84] and *Dissodactylus primitivus* [78]. Located near the antennulae are the antennae, which emit chemical (excretory) cues. Some pinnotherine species are attracted to conspecifics (e.g., *Tunicotheres moseri* (Rathbun, 1918) [15]), which is likely due to chemical cues emitted from the antennal glands (green glands). The morphology of antennae was discussed by previous authors for their supposed taxonomic relevance [71,85].

The third maxillipeds cover the other mouthparts and are also located anteriorly. These structures are thought to play a major role in feeding and are among the most important structures mentioned in studies on pinnotherid taxonomy and evolution. The pinnotherid third maxillipeds evolved to display two distinct features that most other crab families do not display and appear to be heavily modified for symbiotic life [86]: (1) the ischium and merus are fused into an ischiomerus, with a suture only visible in *Pinnaxodes* (Figure 5A, [87]), but hardly apparent in all other genera; and (2) the dactylus is reduced in various species, leaving a two-segmented palp (Figure 5D, [88]), or dislocated to the base of the propodus forming a 'subchelate' third maxilliped [7]. The features of the third maxilliped have been used as characters to distinguish species and genera [7,12,27,89], but the systematic relevance of the third maxilliped morphology was recently questioned, because of the high intrageneric variation in the genera *Nepinnotheres* [32], *Calyptraeotheres*, and *Dissodactylus*. Additionally, the third maxilliped appears to provide little significance in recognising phylogenetic lineages [85]. The three-segmented palp (consisting of a carpus, propodus and dactylus, articulated with a fused ischiomerus) is known from most genera and is thought to be plesiomorphic. A two-segmented palp (consisting of a carpus and propodus) is known from a few genera (*Austrotheres*, *Calyptraeotheres*, *Discorsotheres*, *Dissodactylus*, *Gemmotheres*, *Latatheres*, *Nannootheres*, *Ostracotheres* (Figure 5D), and *Tunicotheres*) and is thought to be an apomorphic character [12,85]. Additionally, a three-segmented palp has been observed in one

specimen of *Discorsotheres spondyli* (Nobili, 1905) (a species with a known two-segmented palp) and is thought to be an anomaly [12].

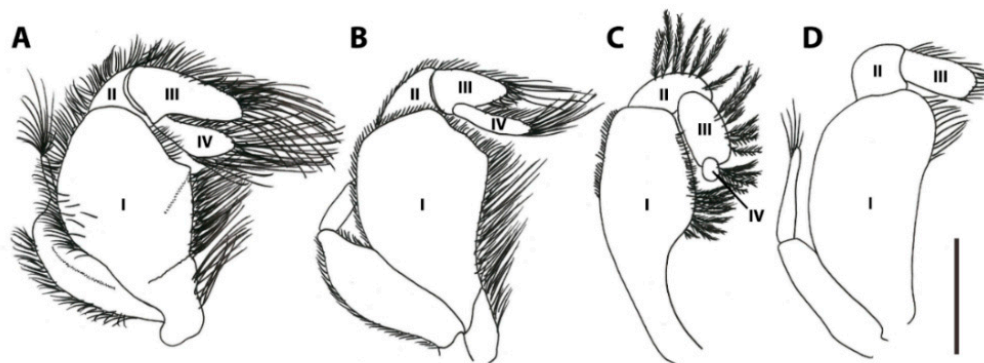


Figure 5. Morphology of the third maxillipeds in pinnotherines. (A) *Pinnaxodes floridensis* Wells & Wells, 1961, after Wells and Wells [90]. (B) *Afropinnotheres ratnakara* Ng & Kumar, 2015, after Ng and Kumar [91]. (C) *Dissodactylus schmitti* Griffith, 1987, exopod not illustrated, after Griffith [92]. (D) *Ostracotheres cynthiae* Nobili, 1906, after Ahyong [12]. Roman numerals indicate different segments: I: fused ischium and merus, II: carpus, III: propodus, IV: dactylus. Scale bars: (A,B,D): 1 mm; (C): 0.5 mm.

Although the palp might not have the once-thought systematic significance [7], it may be relevant for studies focusing on functional morphology. The palps are usually covered with long (feathery) setae and are thought to be used for various feeding strategies: they may be used by bivalve-associated pea crabs, enabling them to grasp host mucus from their own ambulatory legs or chelae, or directly from the hosts' gills [15]. Another strategy would be to filter planktonic food from the bypassing water, as suggested for some holothurian-associated genera (such as *Pinnaxodes* (Figure 5A), *Holotheres*, and *Holothuriophilus* [41,70,90]). Species of the bivalve-associated *Afropinnotheres* are known for their disproportionately large dactyli of the third maxillipeds (Figure 5B) and might use the third maxillipeds in a similar way [7]. Similarly, Christensen and McDermott [23] suggested that pea crabs living in the atrial cavities of ascidians (in this case *Pinnotheres pugettensis* Holmes, 1900, *P. taylora* Rathbun, 1918, and *Nepinnotheres pinnotheres*) use similar strategies for feeding. On the other hand, species of the ascidian-associated *Tunicotheres* bear no dactyli on the third maxillipeds, so this is likely not the case [88]. The authors also mentioned that immature crabs of *Zaops ostreum* possess feathery mouthparts and lose them in later stages, while switching feeding strategy (see below: Section 3.4; [23]). Most species within the tube- and burrow-dwelling subfamilies Pinnixinae, Pinnixulalinae, and Pinnothereliinae have extremely long setae on their dactyli of the third maxillipeds, thought to be used for feeding [23]. More evidence for an ecomorphological role of the palp of the third maxilliped can be found in some species lacking a dactylus (or having a seemingly dysfunctional dactylus): species of *Dissodactylus* and *Clypeasterophilus* bear very small dactyli on their third maxillipeds (Figure 5C) and are known to feed on the spines and tube feet of their sea urchin hosts (see below), instead of eating planktonic material and/or mucus [93]. Similarly, members of the bivalve- and ascidian-associated *Calyptraeotheres* and gastropod-associated *Orthotheres* also appear to possess very small dactyli on their third maxillipeds [92], whereas most other mollusc- and ascidian-associated genera would possess well-developed dactyli.

Pea crabs have a wide range of epipod shapes for internal grooming of the gills, but their morphologies are probably not directly related with their host choice and dietary habits [94]. Pohle [94] found groups of anchor-shaped outgrowths (setules) in setae on the epipods of the maxilla, maxillulae, and maxillipeds, in members of the genera *Opisthopus*, *Dissodactylus*, *Pinnaxodes*, and the unrelated (non-pinnotherine) *Pinnotherelia* [94]. Pohle did not only study the epipods of pinnotherines, but also the number of gills [95]. Pohle and Marques [95] found that the number of gill pairs in pinnotherid crabs could vary between species, while the number is constant in most other brachyuran

families. Representatives from the genera *Opisthopus*, *Pinnaxodes*, *Calyptraeotheres*, *Tumidootheres*, *Orthootheres*, *Tunicotheres*, and *Nepinnotheres* appear to have four pairs of gills, while members of *Durckheimia*, *Ostracotheres*, *Xanthasia*, *Limotheres*, *Arcotheres*, and *Zaops* appear to have three pairs of gills. The genera *Dissodactylus*, *Clypeasterophilus*, and *Pinnotheres* have three or four gill pairs, depending on the species. Pohle and Marques [95] mentioned that this low number of gills is probably the result of a symbiotic lifestyle, rather than the crabs' size: the smaller species within the genus *Aphanodactylus* (Pinnotheroidea: Aphanodactylidae) were found to have more gill pairs than the larger bivalve-associated pinnotherines.

Although they are seldomly illustrated, the other five pairs of mouthparts (mandibles, maxillae, maxillulae, and first and second pair of maxillipeds) may possess phylogenetically significant anatomical characters (as in palaemonid shrimps [58]). In addition, they may be linked to dietary preferences: symbiotic amphipods appear to have specialised mouthparts, depending on their host and dietary preferences [96]. Similarly, crabs feeding on bivalve mucus may possess other mouthpart characters than crabs feeding on sea urchin spines.

3.3. Cheliped Morphology

While crabs from other brachyuran lineages may use their chelipeds for feeding, defense, intraspecific aggression, and/or courtship [83], the chelipeds of pinnotherine species were previously believed to only play a role in feeding strategies [15]. Similar to the morphology of the carapace, the chelae display a wide range of shapes and sizes, including ornamentations like setation and specialised feeding structures. For instance, the relatively largest (relative to body size) and most robust chelae (robustness: chela circumference/length; [97]) can be found in species associated with holothurians and hosts with a similar internal morphology. The robust chelae are most pronounced in members of *Austrotheres*, *Holothuriophilus*, *Holotheres* (Figure 6A), *Buergeres*, *Pinnaxodes*, and *Trichobezoares* (e.g., [30,70]). Similar robust chelae, however, can also be found in the free-living genus *Hospitootheres*, the tunicate-associated genus *Tunicotheres*, and a few members of the bivalve-associated genera *Tumidootheres* and *Nepinnotheres* [7,88,98]. The function of the robust chelae of the before-mentioned genera is not well understood, but the specialised third maxillipeds and position within the host of the holothurian-associated genera (see above: Section 3.2) suggest that the chelae do not play a major role in the feeding strategies [90]. In support of this hypothesis, it is worth noting that *Buergeres deccanensis* (Chopra, 1931) is known to inflict damage to its host, by piercing the body wall with its chelae while inhabiting the respiratory system [99].

The somewhat robust chelipeds of the species within the ectosymbiotic sea urchin-associated genera *Dissodactylus* and *Clypeasterophilus* have been studied in detail [97]. The species within these two genera display a range of different sizes of the chelipeds and morphologies of the cutting edges of both fingers, which is thought to be linked to the dietary habits [97] and the ability to attach themselves to the hosts [47,100]. Telford [97] stated that the porosity of the urchin's spines is directly linked to the robustness and cutting morphology of the associated crabs' chelae. For example, the species *Dissodactylus mellitae* (Rathbun, 1900) possesses very robust chelae, which are perfectly adapted for clipping more porous spines. Another species, *Clypeasterophilus rugatus* (mentioned by Telford [97] as *D. calmani* Rathbun, 1918), has comparatively slender chelae, thought to be adapted for feeding on soft tube-feet (podia). Telford [97] mentioned that the most common host of *C. rugatus*, the echinoid *Clypeaster rosaceus* (Linnaeus, 1758), is the host with the least porous spines, which are the most difficult to clip. In addition, *D. primitivus* was thought to be the least adapted and most evolutionarily primitive of the studied species [97], and *C. rugatus* the species with the most derived (or adapted) traits [92], but these hypotheses are rejected in recent molecular analyses [5], placing *C. rugatus* at a basal position of the clade.

Very slender chelipeds can be found in most of the bivalve-associated genera, reaching most extreme shapes in *Amusiotheres* (Figure 6B), *Durckheimia*, *Discorsotheres*, *Solenotheres*, and *Tacitootheres* [12,19,27,101,102]. The lack of prominent teeth on the cutting surfaces of the

chela, and the elongated mani in most of these species, suggest that chelae are not used for cutting, but for brushing mucus and grooming (e.g., *Pinnotheres pisum* [15]). A common associated feature with such elongated chelae is a setal ornamentation of the inner surface of the palm and pollex. This brush-like row of setae can be found in female specimens of many genera associated with bivalves: *Abyssotheres*, *Afropinnotheres*, *Amusiotheres*, *Arcotheres*, *Austrotheres*, *Bonita*, *Fabia* (Figure 6C), *Gemmotheres*, *Discorsotheres*, *Durckheimia*, *Latatheres*, *Nannotheres*, *Nepinnotheres* (but not *N. pinnotheres*), *Pinnotheres* (Figure 6D), *Sindheres*, *Tacitotheres*, *Viridotheres*, *Visayeres*, *Xanthasia*, *Waldotheres*, and *Zaops* [7,12,15,16,19,27,30,31,54,60,61,102–105]. This adaptive feature can also be found in two genera associated with gastropods, *Ernestotheres* and *Calyptraeotheres* [7,89], and in the sea urchin-associated *Dissodactylus latus* Griffith, 1987 [93]. After being mentioned in taxonomic papers several times, Becker and Türkay [15] showed the setae row for the first time in detail, using SEM, and found the setae to be of the long regularly orientated pappo-serrate type in *Pinnotheres pisum* (Figure 6D). The same species was observed and even photographed feeding from strands of nutrient-rich mucus hanging from the gills of their bivalve hosts, using the setal comb. Similarly, the pinnixine crab *Scleroplax faba* (Dana, 1851) is also known to feed from mucus strands from bivalve hosts, similar to bivalve-inhabiting pinnotherines [50]. This species possesses a setose surface on the inner surface of the chelae, but lacks the specialised setal comb discussed above.

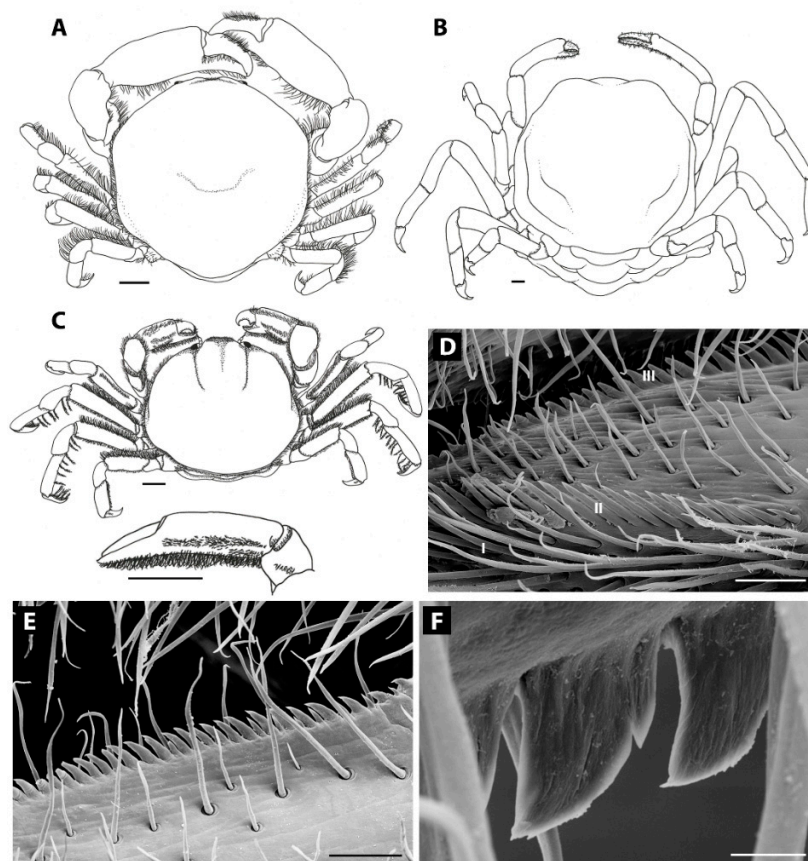


Figure 6. Morphology of the chelipeds and associated ornamentations in pinnotherines. (A) Enlarged chelae in *Holotheres danielae* Ahyong, 2010, after Ahyong [106]. (B) *Amusiotheres obtusidentatus* (Tai et al., 1980), after Ng and Ho [102]. (C) *Fabia subquadrata* Dana, 1851, note the setal comb on the inner side of the claw, after Campos [16]. (D) *Pinnotheres pisum* (Linnaeus, 1767), note the pappo-serrate setal comb (I), the short row of soft denticles on the inner surface of the pollex tip (II), and the similar denticles on the cutting edges of the claw (III). E: *Pinnotheres pectunculi* Hesse, 1872, with a row of soft denticles. F: *Pinnotheres pectunculi* Hesse, 1872, detail of one of the scales, note the rough surface and the serrated tips. Scale bars: (A–C) 1 mm; (D,E) 100 μ m; (F) 10 μ m.

Additionally, rows of soft denticles, accompanied by soft setae on both sides of the claw, were found on the cutting edges of both the pollex and the movable finger of *Pinnotheres pisum* [15], *P. pectunculi* Hesse, 1872 (Figure 6E,F), and *Nepinnotheres pinnotheres* (Becker, pers. obs.). The mechanical properties of the denticles were revealed during preparation for SEM (Figure 6D–F), as the denticles appeared soft during preparation, making the preservation and study difficult (C.B. pers. obs.). These three species were also found to possess a short row of similar, but longer, denticles on the inner side of the tip of the pollex (Figure 6D). A quick survey of the available taxonomic literature reveals more species that possess the small denticles on the cutting edges of the chelae: *Pinnotheres haiyangensis* Shen, 1932, *P. dilatatus* Shen, 1932, and *P. luminatus* Tai et al., 1980, were all illustrated by Tai and Yang [74] with small denticles on the inner surface of both the pollex and the movable finger. More recently, *Sindheres karachiensis* Kazmi & Manning, 2003, was illustrated and described with special attention to the denticles, looking similar to those mentioned above [105]. A thorough survey of these and other species is needed to confirm if the row of denticles is homologous to the row found in *Pinnotheres pisum*, *P. pectunculi* and *Nepinnotheres pinnotheres*, and whether this character is present in more pinnotherine species. The function of these denticles is not known, but the position and the softness of the structures suggest that they are not used for scraping host mucus (C.B. pers. obs.). The soft denticles might, however, play a role in chemoreception, where the crabs use their chelae's soft denticles to 'taste' their food before digesting it. Similar soft denticles can be found in many more crab species and this feature is not limited to pinnotherids (C.B. pers. obs.). The denticles in the studied pinnotherids can be observed to have a rough surface and serrate tips, potentially bearing pores similar to the ones found on the chelae of the hermit crab *Pagurus hirsutiussculus* (Dana, 1851) [107]. This row of denticles resembles structures found on the first chelipeds of some palaemonid shrimp species, living in association with bivalves and ascidians (C.H.J.M. Fransen, pers. comm.).

3.4. Ambulatory Leg Adaptations

In all symbiotic brachyuran crab lineages, most adaptive features can be found in the morphology of the ambulatory legs [2]. A few examples are the last pair of ambulatory legs of sponge crabs (Dromiidae) and carrier crabs (Dorippidae), the subchelate ambulatory legs of zebra crabs (Pilumnidae: Eumedoninae), and flexible dactylo-propodal articulation of coral-clinging crabs (Tetraliidae) [2]. The Pinnotheridae form no exception, since the most apparent feature of the tube-dwelling pinnixine, pinnixulaline, and pinnothereliine crabs are the wide third pair of ambulatory legs for gripping the walls of shared burrows and tubes [18]. The Pinnotherinae have more subtle morphological adaptations of the ambulatory legs, which are discussed below.

The most apparent ontogenetic changes can be seen in the morphology of the ambulatory legs. In both reproductive strategies [8], the hard stage males possess long plumose swimming setae, usually on the second and third ambulatory legs (e.g., described from *Pinnotheres pisum* [108] and *Zaops ostreum* [109]). The hard stage crabs swim between hosts and use their long setae for swimming by "bending their chelae slightly inward and by holding the first and fourth ambulatory legs stationary in an inverted V-shape, and by fast stroking both sides of the second and third ambulatory legs back and forth sequentially" [110]. In some species, swarming of post-hard staged males and females is known, even after the initial infestation. In this case, the crabs also develop new swimming setae (known from members of *Calyptraeothers* [9], *Tumidothers* (Figure 7A) [8,30], *Austrothers* [12], *Fabia* [45], and seemingly from species of *Afropinnotheres* [7], *Ostracothers* [12], *Nepinnotheres* [32], and *Pinnotheres* [110]). In addition, some species are known to develop similar secondary swimming setae, but in a later moulting stage: Watanabe and Henmi [17] found that one female crab (an unidentified species within the genus *Arcothers*) developed swimming setae in a post-hard stage, after forming simple setae at first. A similar development was found in post-hard stages of *Pinnotheres pisum* [111], but the author does not mention whether the setae are of simple or plumose type [17]. The secondary development of plumose swimming setae in post-hard stages might be a strategy for crabs to leave their host when circumstances are unfavourable (e.g., when starving; [17]).

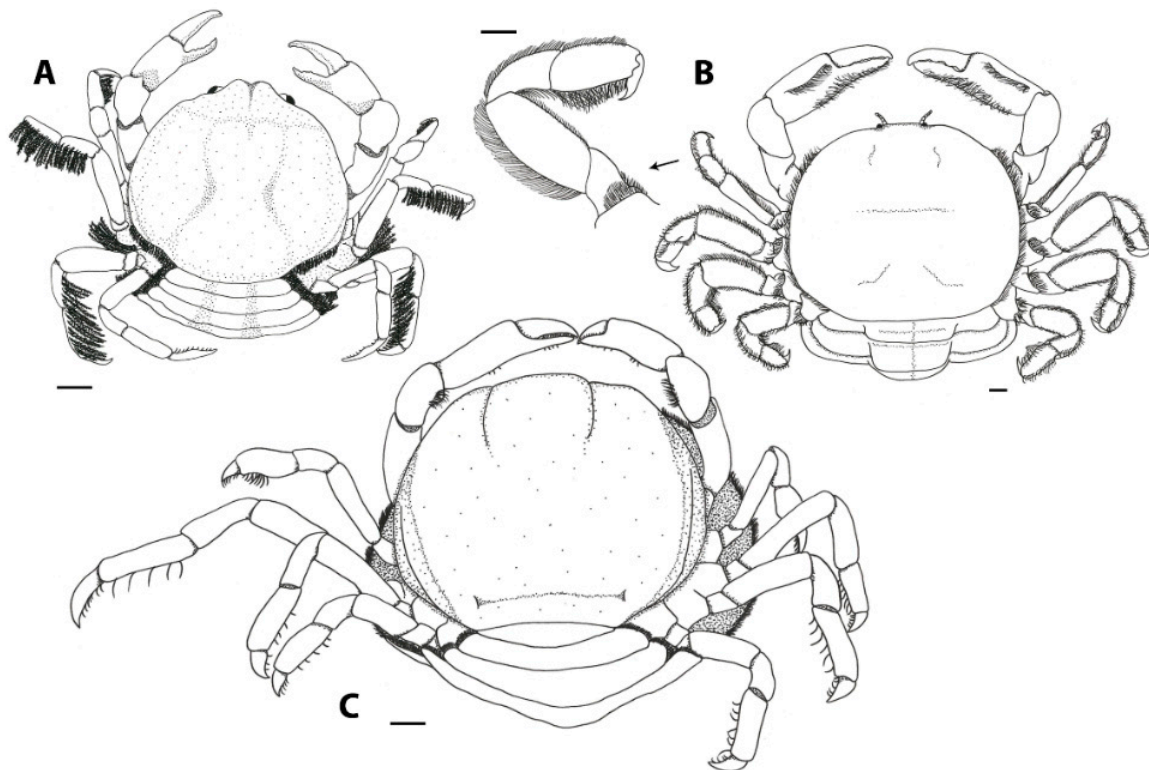


Figure 7. Morphology of the ambulatory legs in pinnotherines. (A) *Tumidotheres margarita* (Smith, 1869), after Campos [8]. (B) *Ernestotheres conicola* (Manning & Holthuis, 1981), note the flattened ambulatory legs, after Manning [7]. (C) *Fabia carvachoi* (Campos, 1996), after Campos [16]. Scale bars: (A–C) 1 mm.

Similar to the overall shape and size of the chelipeds, the ambulatory legs of pinnotherines also display a wide range of shapes and sizes. The widest legs among pinnotherines, just like the most robust chelae, are again found in holothurian- and geoduck-associated genera like *Pinnaxodes* and *Holothuriophilus* [30]. Members of the gastropod-associated genera *Mesotheres*, *Ernestotheres* (Figure 7B), and to some extent *Orthotheres*, have flattened, broad ambulatory legs [7,71,112], probably to cling to their large, mobile hosts. In contrast, members of *Waldotheres*, *Amusiotheres*, *Tacitotheres*, *Zaops*, and most other bivalve-associated genera have elongated, slender, and feeble ambulatory legs. This indicates that they do not leave their sedentary host, and rarely move around within the host [8]. Members of *Zaops* might form an exception in having swollen propodi of the ambulatory legs, similar to the ambulatory legs of *Raytheres* [84]. It remains unknown whether the swollen propodi are an adapted feature.

The different sizes of ambulatory legs in pinnotherines have also been studied in detail, with special focus on the elongation of just one leg after the hard stages [113–117]. This asymmetry of the ambulatory legs is thought to be linked to the feeding habits and the initial settlement of the female crabs inside the host [15]. In laboratory experiments, Watanabe and Henmi reared a member of the genus *Arcotheres* and found that the longer ambulatory leg of this species developed on the side of the crab which was directed to the opening of the bivalve host (Watanabe and Henmi, pers. comm. in [15]). While the elongation of the single leg segments may vary between species and genera, in most cases, the dactylus and propodus of the elongated ambulatory leg possess morphological adaptations, seemingly for ‘reeling in’ mucus strands (discussed below), similar to the modified cheliped mentioned above. Asymmetry of the ambulatory legs is not limited to, but is most apparent in the bivalve-associated genera *Amusiotheres*, *Discorsotheres*, *Fabia* (Figure 7C), *Solenotheres*, *Tacitotheres*, and *Zaops* [12,71,116]. Extremely asymmetrical legs can also be found in the limpet-associated *Enigmatheres* [61].

Most variation in the ambulatory legs can be found in the most distal segment, the dactylus. For instance, the previously mentioned ectosymbiotic genera *Dissodactylus* and *Clypeasterophilus* have bifurcate (‘forked’) dactyli in their first, second, and third pair of ambulatory legs (Figure 8C), which are

thought to aid in moving between the spines of their host urchins and sand dollars [20,92,100,118]. Similarly, one species within *Abyssotheres* (*A. abyssicola* (Alcock & Anderson, 1899)) has an “obtuse projection on the dorsal surface of the dactylus of the walking legs”, but this seems to be a unique feature, even within the genus [119]. Morphological adaptations in the dactyli of other species can also be linked to their host choice and position inside the host: the holothurian-associated *Holotheres halingi* [120] and its congeners possess falcate, sharp dactyli in all ambulatory legs, used to cling to the inner surface of the host. The description of *Holotheres halingi* mentions the species to be favouring lateral contact more than bottom contact, and the species seems to be unable to walk due to its enlarged pleon and modified ambulatory legs [120]. Morphologically similar falcate dactyli can be found in a wide range of pinnotherine genera, not limited to holothurian symbionts: *Discorsotheres*, *Durckheimia*, *Latatheres*, *Orthotheres*, *Ostracotheres*, *Serenotheres*, *Solenotheres*, *Tridacnatheres*, *Visayeres* (Figure 8A), *Xanthasia*, and some species of *Nepinnotheres* [12,19,27,54,101].

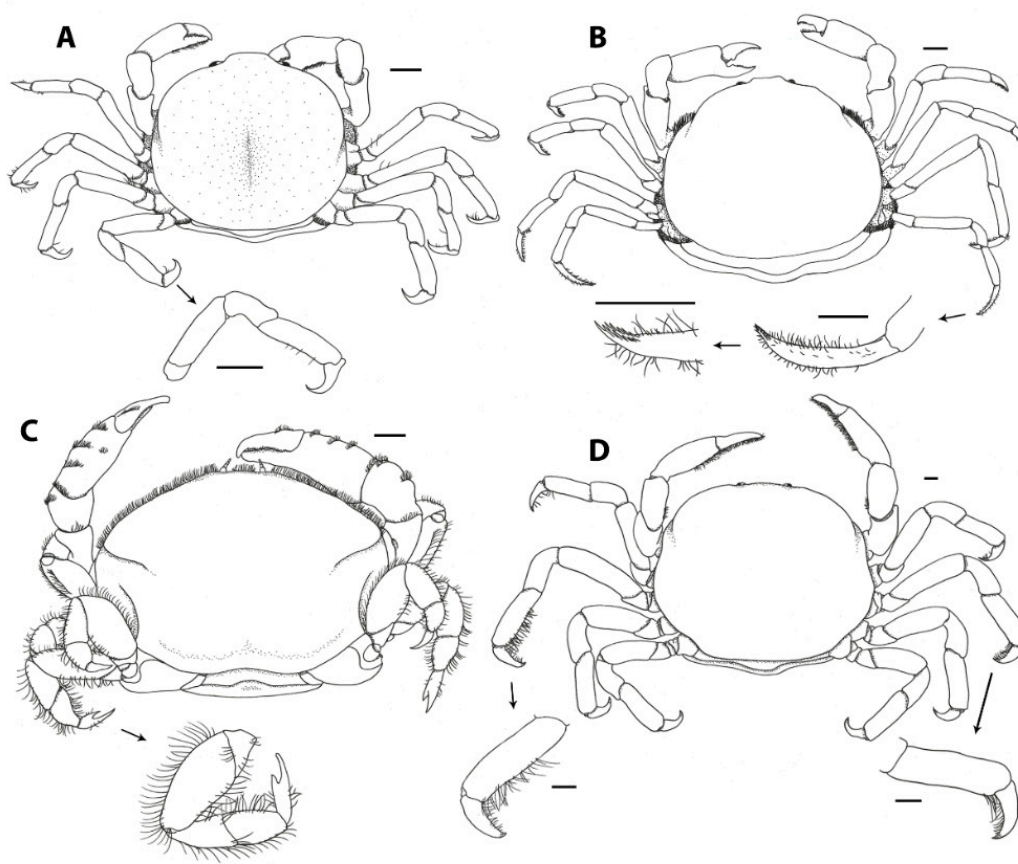


Figure 8. Morphology of the ambulatory legs and dactyli in pinnotherines. **A:** *Visayeres acron* Ahyong & Ng, 2007, with falcate ambulatory leg dactyli, after [54]. **B:** *Arcotheres similis* (Bürger, 1895), with sword-shaped last ambulatory leg dactyli, with microstructured dactylus tip, after [19]. **C:** *Dissodactylus schmitti* Griffith, 1987, with bifurcate second and third ambulatory leg dactyli, after [93]. **D:** *Discorsotheres spondyli* (Nobili, 1905), with asymmetrical setation on the propodus and dactylus of the second pair of ambulatory legs, after [12]. Scale bars: (A–D) 0.5 mm.

Members of the bivalve-associated genus *Arcotheres* are unique with regard to a few morphological features [115], most obvious in the form of the dactyli of the last pair of ambulatory legs. The dactyli are described as ‘sword-shaped’ [115], being straighter and more elongated (longer or of equal length as the attached propodus) than the dactyli of the other ambulatory legs (Figure 8B) [19]. The dactyli of the last pair of ambulatory legs are often ornamented with rows of short, simple setae (e.g., *A. ridgewayi*

(Southwell, 1911), illustrated in [121]) and a row of denticles (e.g., most conspicuous in *A. placunae* (Hornell & Southwell, 1909), illustrated in [122], and *A. vicajii* (Chhapgar, 1957) [123]).

The functions of these setae and denticles are not known, but since the last pair of ambulatory legs is generally shorter than the third pair in *Arcotheres*, it is improbable that crabs use these legs to 'reel in' host mucus. The denticles, however, resemble those on the chelipeds' cutting edges mentioned above (see Section 3.3), and may be used to scrape or groom their host, or even their own bodies for gathering mucus: some species are illustrated with their last pair of ambulatory legs being folded up against the dorsal side of their carapace (e.g., *A. borradailei* (Nobili, 1906) [121]). In addition, the denticles might be used for chemoreception, by 'tasting' food with its ambulatory legs, as observed in *Zaops ostreum* [109], or for providing grip inside the host: similar rows of scales can be found on the dactyli of the ambulatory legs of some palaemonid shrimp species, also living in bivalves and ascidians [57,58,124]. Furthermore, all members of the gastropod-associated *Calyptraeotheres*, except *C. garthi*, also possess sword-like, setose dactyli on their last ambulatory legs [89,125–128]. The function and microstructure of the appendages remain unknown. Moreover, some species of *Pinnotheres* also possess a similar dactylus on both their last ambulatory legs (see Section 3.6).

In addition to *Arcotheres* and *Calyptraeotheres*, species in many other genera possess inconspicuous ornamentations on their leg segments, but the arrangement may vary between genera. For example, simple setae are found on the dactyli of the fourth ambulatory legs of species within *Gemmotheres* and *Tunicotheres* [88], and similar setae are found on the propodus and dactylus of members of the genus *Discorsotheres*, with some species even showing asymmetry between the leg setation (Figure 8D) [12]. The functionality of this specific setation is probably linked to the feeding strategy of these species, although this has only been observed in *Zaops ostreum* [23,109]. The observed crabs feed in a similar way as *Pinnotheres pisum* [15] by gathering mucus strings, but Stauber [109] observed that they "catch newly formed mucus with the (distally setose) ambulatory legs, then reach underneath the pleon with their chelipeds, comb the legs, and pass the food on to the mouth" [23].

The detailed illustrations and ecological information provided by Zmarzly [50] allow for a quick survey of the potentially adapted morphology of symbiotic pinnixine species. Both the pinnixine crab species *Scleroplax faba* and *S. littoralis* (Holmes, 1895) are known as endosymbionts in holothurians and bivalves respectively, and possess falcate dactyli on their ambulatory legs, thought to aid in attaching themselves to their host. *Scleroplax faba* also appears to possess uniform ambulatory leg lengths, atypical for members of the Pinnixinae, Pinnothereliinae, and Pinnixulalinae.

3.5. Sexual Anatomy and Larval Characters

The reproductive strategies of Pinnotherinae, their larval development and sexual anatomy show several traits that seem important with regard to their symbiotic lifestyle. It is, however, hard to distinguish between adaptations that are characteristic for small-sized crabs in general and those that are specific to symbiotic lifestyles. Hines [129] has shown that the investment in egg production (body weight/brood weight) in *Zaops ostreum* (as *Pinnotheres ostreum*) and *Fabia subquadrata* is highly increased compared to free-living crab species. Hartnoll [130] reviewed the reproductive investment among a range of brachyuran crabs and concluded that metabolic costs drive trade-offs between growth (body size) on the one hand and reproductive investment (relative brood size) on the other. A large body size reduced the risk of predation, but may lead to reaching sexual maturity later in ontogeny and, also, to producing smaller broods (in relation to body size) as more energy resources go into growth [130]. Female bivalve-dwelling pinnotherines with a life cycle similar to *Pinnotheres pisum*, remaining solely within their host after starting metamorphosis, are not exposed to predators. Such species can, thus, 'afford' to invest a greater deal of energy resources in reproduction. By not being very mobile, they also save on metabolic costs for locomotion and do not need to search for food as they directly obtain it from their host.

Egg production, however, is also constrained by female body size in general and particularly by the space that is available for yolk accumulation inside the body. This may explain that pinnotherids,

despite being generally small in order to be able to enter and fit inside their hosts, have a preference for large- over small-sized host species within their specific host range, as the same species reaches larger body sizes in more spacious hosts [15]. This again has an effect on the fecundity (eggs per brood) which is positively correlated with body size (carapace width) within a species (e.g., *Dissodactylus primitivus*, *D. crinitichelis* Moreira, 1901 [131]; *Austinotheres angelicus* [40]).

Another important adaptation regarding brood size is the large pleon of female pinnotherids which functions in incubating the eggs until larvae hatch. The pleon is extremely enlarged in bivalve-associated Pinnotherinae resembling *Pinnotheres pisum*: the pleon covers the whole ventral side of the crab, reaches the mouthparts anteriorly and even covers the proximal segments of the ambulatory legs [132]. In fact, the pleon is enlarged to a degree that it seriously hampers locomotion of adult female *P. pisum* (C.B., pers. obs.). Due to spending their whole adult life inside the host, where females are protected from predators and have plenty of food, locomotion is not crucial for survival. A comparison of brood sizes (mass of brood and number of eggs), pleon width, and body size (body mass and carapace width) among various species may yield insights into the degree of reproductive investment, and the adaptations in relation to different hosts and life history strategies of Pinnotherinae. Unfortunately, the current knowledge on pleon sizes among pea crabs is very limited as no study has focused on this character so far, and only few taxonomic descriptions show the female in ventral aspect or details of the pleon in the presented line drawings (but see *Pinnaxodes floridensis* [90]). It is, however, obvious that the female pleon of ectosymbiotic pinnotherine genera (*Dissodactylus* and *Clypeasterophilus*) is not as wide as in most endosymbiotic taxa. As in all brachyuran crabs, a sexual dimorphism in pleon width is also obvious in these genera, with the male having a narrow pleon and the female possessing a wide pleon for breeding. The female pleon in *Dissodactylus* and *Clypeasterophilus* is, however, not enlarged to a degree that it is visible from the dorsal view [133] and does not appear to prevent locomotion. The members of the ectosymbiotic genera need to retain the ability to move around on the host and escape predators.

Although the size relations and the outer morphology of the pleon have barely been studied, the internal morphology has caught interest in the past. In most brachyuran crabs, the ovaries are restricted to the cephalothorax and do not extend into the pleon [134]. In the bivalve-dwelling *Pinnotheres pisum* and *P. pectunculi*, and the ascidian and bivalve-dwelling *Nepinnotheres pinnotheres*, ovaries extend into the pleon and run along both sides of the digestive system [135]. To date, it is unknown which other pinnotherine genera show the same extension of ovaries, but it is very likely the case for many endosymbiotic species with an extremely wide pleon. A study of male *P. pisum* and *N. pinnotheres* has shown that a corresponding adaptation is present in males: parts of the vas deferens, where gametes develop and seminal plasma is produced, reach into the narrow male pleon as well [136]. This shows that the large size of the female pleon alone may not explain the adaptation of extending reproductive organs beyond the cephalothorax.

Interestingly, another symbiotic group of crabs shows the same adaptation as Pinnotherinae, at least in the females: several species of Cryptochiridae (gall crabs) associated with stony corals have ovaries extending into the pleon to a varying degree [137]. Also, in the free-living mangrove crab *Goniopsis cruentata* (Latreille, 1803), mature ovaries extend into the first pleomers [138]. This species is relatively small sized with females reaching maturity (L_{50}) at 22.6 mm carapace width [139]. The trait of reproductive organs being extended from the cephalothorax into the pleon shows how hard it is to identify the responsible driver for evolutionary changes. Small body sizes and symbiotic/parasitic lifestyles similarly lead to peculiar sexual adaptations and an increase of the investment in reproduction [140,141]. Most endosymbionts have smaller body sizes than their free-living relatives, thus, adaptations cannot be linked to body size or symbiotic lifestyle alone.

Other characters which may have significance with regard to the pinnotherid's symbiotic lifestyle can be found in the larval development and morphology: most brachyuran zoea larvae possess paired lateral spines, and a dorsal and rostral spine [142], which are either regarded as buoyancy structures for planktonic dispersal or as an antipredatory adaptation. Within the Pinnotherinae,

larvae of *Pinnaxodes chilensis* (H. Milne Edwards, 1837) [143], *Clypeasterophilus rugatus* [144], *Nepinnotheres pinnotheres* (as *Pinnotheres veterum* Bosc, 1801) [145], and *Afropinnotheres monodi* [146] also possess these spines, and confirm to the general brachyuran larval morphology. Several other species and genera of Pinnotherinae are known to lack the dorsal spine, such as *Pinnotheres pisum* and *P. pectunculi* [132], some are even completely spineless (e.g., *Zaops ostreum* [147]).

In the latter species, behavioural experiments revealed a specific behaviour when exposed to predators: zoea larvae of *Z. ostreum*, quickly sank to the sea floor when the pleon was flexed tightly against the body [147]. This behaviour was interpreted as an antipredatory defense [147], but may also have benefits for pea crab larvae settling in a habitat with suitable hosts or in a large aggregation of hosts as in mussel or oyster beds. It is worth noting that pinnotherines are not the only group in which some species show a reduction of spines in zoeal stages; this adaptation is also found in species of Leucosiidae and Hymenosomatidae [142,145], and may have evolved for similar reasons, either as an antipredatory strategy or for the control of larval settlement in suitable habitats (in both cases by being able to sink faster and more directional).

Some species of Pinnotherinae show an abbreviated larval development or even parental care. The larval development tends to be abbreviated in pinnotherines, by having only two to four zoeal stages, while most brachyuran crabs have five. In *Tunicotheres moseri*, symbiotic with ascidians [148], and *Mesotheres barbatus* (as *Orthotheres barbatus* (Desbonne in Desbonne & Schramm, 1867) [149]), only two zoea stages were found. *Tunicotheres moseri* also shows brood care: after the larvae hatch from the eggs, they are not dispersed, but remain under the female pleon until they reach the first crab stage [150].

3.6. Updated List of Symbiont-Host Associations

Updated symbiont-host association list for all recognized (valid) species within the Pinnotherinae are showed in Table 1.

Table 1. Updated symbiont-host association list for all recognized (valid) species within the Pinnotherinae (previous lists include [11,26,151]). Pinnotherine taxonomy follows WoRMS [4] and the Systema Brachyurorum [3], unless stated otherwise in the subscripts (see below). References including the most complete information about host specificity can be found for all species. If recent works list new host species, but neglect the already known hosts from older literature [6], both the older and more recent references are included. Host nomenclature follows identifications provided in the references, also updated with WoRMS [4]. Where host groups or host species are unknown, a question mark is provided; where identifications of host species were unable to link with a recognized species, identifications are provided with a question mark between parentheses: (?). Notes on the host specificity or taxonomy can be found below, indicated with superscript numbers. Distribution abbreviations: IWP-Indo-West Pacific, EP-East Pacific, ATL-Atlantic Ocean (please note that Atlantic and East Pacific distributions also include non-tropical waters).

| Species | Host | Host Species | Distr. | References |
|---|-------------------|---|---------|------------|
| <i>Abyssotheres</i>¹ | | | | |
| <i>A. abyssicola</i> (Alcock & Anderson, 1899) | Bivalvia | <i>Acesta indica</i> (Smith, 1899) | IWP | [119] |
| <i>A. aesticola</i> Komatsu & Ohtsuka, 2009 | Bivalvia | <i>Acesta philippinensis</i> (Bartsch, 1913) | IWP | [60] |
| <i>Afropinnotheres</i> | | | | |
| <i>A. crosnieri</i> Manning, 1993 | ? | ? | ATL | [7] |
| <i>A. dofleini</i> Lenz, 1914 ¹ | Bivalvia, Ascidia | <i>Atrina squamifera</i> (Sowerby, 1835), <i>Perna perna</i> (Linnaeus, 1758), <i>Pinna</i> sp.; <i>Ascidia sydneyensis</i> (Stimpson, 1855), <i>Pyura stolonifera</i> (Heller, 1878) | ATL/IWP | [29] |
| <i>A. guinotae</i> Manning, 1993 | Bivalvia | 'unnamed bivalve mussel' | ATL | [7] |
| <i>A. larissae</i> (Machkevskiy, 1992) | Bivalvia | <i>Crassostrea tulipa</i> (Lamarck, 1819) | ATL | [7] |
| <i>A. monodi</i> Manning, 1993 | Bivalvia | <i>Cerastoderma edule</i> (Linnaeus, 1758), <i>Cerastoderma glaucum</i> (Bruguière, 1789), <i>Chamelea gallina</i> (Linnaeus, 1758), <i>Donax trunculus</i> Linnaeus, 1758, <i>Eastonia rugosa</i> (Helbling, 1779), <i>Mactra stultorum</i> (Linnaeus, 1758), <i>Mytilus galloprovincialis</i> Lamarck, 1819, <i>Polititapes aureus</i> (Gmelin, 1791), <i>Ruditapes decussatus</i> (Linnaeus, 1758), <i>Scrobicularia plana</i> (da Costa, 1778), <i>Spisula solida</i> (Linnaeus, 1758), <i>Venerupis corrugata</i> (Gmelin, 1791) | ATL | [152] |
| <i>A. ratnakara</i> Ng & Kumar, 2015 | Bivalvia | <i>Atrina vexillum</i> (Born, 1778), <i>Perna perna</i> (Linnaeus, 1758) | IWP | [91,121] |
| <i>Alain</i> | | | | |
| <i>A. crosnieri</i> Manning, 1998 | Holothuria | <i>Molpadia</i> sp. | IWP | [153] |
| <i>A. raymondi</i> Ahyong & Ng, 2008 | Holothuria | 'unidentified deep-water holothurian' | IWP | [28] |
| <i>Alainotheres</i> | | | | |
| <i>A. leloeffi</i> (Crosnier, 1969) ² | ? | ? | ATL | [7] |
| <i>Amusiotheres</i> | | | | |
| <i>A. hanumantharaoi</i> Devi & Shyamasundari, 1989 | Bivalvia | <i>Amusium pleuronectes</i> (Linnaeus, 1758) | IWP | [154] |
| <i>A. obtusidentatus</i> (Tai et al., 1980) | Bivalvia | <i>Amusium pleuronectes</i> (Linnaeus, 1758), <i>Ylistrum japonicum</i> (Gmelin, 1791) | IWP | [102] |

Table 1. Cont.

| Species | Host | Host Species | Distr. | References |
|--|----------|---|--------|------------|
| <i>Arcotheres</i> | | | | |
| <i>A. alcocki</i> (Rathbun, 1909) | Bivalvia | <i>Atrina vexillum</i> (Born, 1778), <i>Meretrix</i> sp., <i>Meretrix casta</i> (Gmelin, 1791), <i>Mytilus</i> sp., <i>Pinna atropurpurea</i> (Sowerby, 1825), <i>Tegillarca granosa</i> (Linnaeus, 1758) | IWP | [6,155] |
| <i>A. arcophilus</i> (Bürger, 1895) | Bivalvia | <i>Arca</i> sp. | IWP | [6] |
| <i>A. atrinae</i> (T. Sakai, 1939) | Bivalvia | <i>Atrina japonica</i> (Reeve, 1858) | IWP | [156] |
| <i>A. boninensis</i> (Stimpson, 1858) | Bivalvia | <i>Saccostrea echinata</i> (Quoy & Gaimard, 1835) | IWP | [6] |
| <i>A. borradaii</i> (Nobili, 1906) | Bivalvia | <i>Mya</i> sp., <i>Pinna</i> sp. | IWP | [6] |
| <i>A. coarctatus</i> (Bürger, 1895) | Bivalvia | <i>Polymesoda</i> spp. | IWP | [19] |
| <i>A. cyclinus</i> (Shen, 1932) | Bivalvia | <i>Barbatia virescens</i> (Reeve, 1844), <i>Cyclina sinensis</i> (Gmelin, 1791), <i>Meretrix meretrix</i> (Linnaeus, 1758) | IWP | [74] |
| <i>A. exiguus</i> (Bürger, 1895) | ? | ? | IWP | [19] |
| <i>A. guinotae</i> Campos, 2001 | Bivalvia | <i>Barbatia</i> sp. | IWP | [115] |
| <i>A. latifrons</i> (Bürger, 1895) | ? | ? | IWP | [19] |
| <i>A. latus</i> (Bürger, 1895) ³ | Bivalvia | <i>Atrina vexillum</i> (Born, 1778), <i>Pinna</i> sp. | IWP | [19] |
| <i>A. modiolicola</i> (Bürger, 1895) | Bivalvia | <i>Mactra violacea</i> (Gmelin, 1791), <i>Marcia opima</i> (Gmelin, 1791), <i>Modiolus philippinarum</i> (Hanley, 1843) | IWP | [6,19] |
| <i>A. nudifrons</i> (Bürger, 1895) | ? | ? | IWP | [19] |
| <i>A. obesus</i> (Dana, 1852) | Bivalvia | <i>Arca</i> sp., <i>Cytherea</i> sp., <i>Gafrarium</i> spp., <i>Sunetta subquadrata</i> (Sowerby, 1851) | IWP | [6,49] |
| <i>A. ocularius</i> Komai et al., 2020 | Bivalvia | <i>Andara</i> spp. | IWP | [49] |
| <i>A. palaensis</i> (Bürger, 1895) | Bivalvia | <i>Anadara antiquata</i> (Linnaeus, 1758), <i>Arca</i> sp., <i>Barbatia foliata</i> (Forsskål in Niebuhr, 1775), <i>Mactra grandis</i> Gmelin, 1791, <i>Placuna ephippium</i> (Philipsson, 1788), <i>Tegillarca granosa</i> (Linnaeus, 1758) | IWP | [6] |
| <i>A. pernicola</i> (Bürger, 1895) | Bivalvia | <i>Perna</i> sp. | IWP | [19] |
| <i>A. placunae</i> (Hornell & Southwell, 1909) | Bivalvia | <i>Placuna placenta</i> (Linnaeus, 1758) | IWP | [6] |
| <i>A. placunicola</i> Ng, 2018 | Bivalvia | <i>Placuna ephippium</i> (Philipsson, 1788) | IWP | [157] |
| <i>A. pollus</i> Ahyong & Ng, 2020 | Bivalvia | <i>Malleus albus</i> (Lamarck, 1819) | IWP | [32] |
| <i>A. purpureus</i> (Alcock, 1900) | Bivalvia | <i>Ostrea</i> sp., <i>Protapes gallus</i> (Gmelin, 1791) | IWP | [158] |
| <i>A. rayi</i> Ahyong & Ng, 2007 | Bivalvia | ? | IWP | [19] |
| <i>A. rhombifer</i> (Bürger, 1895) | Bivalvia | <i>Tucetona auriflua</i> (Reeve, 1843) | IWP | [19] |
| <i>A. ridgewayi</i> (Southwell, 1911) ³ | Bivalvia | <i>Pinna atropurpurea</i> (Sowerby, 1825) | IWP | [19] |
| <i>A. rotundatus</i> (Bürger, 1895) | Bivalvia | <i>Circe</i> sp. | IWP | [19] |
| <i>A. shahi</i> Trivedi et al., 2018 | Bivalvia | <i>Magallana bilineata</i> (Röding, 1798) | IWP | [122] |
| <i>A. similis</i> (Bürger, 1895) | Bivalvia | <i>Ostrea</i> sp., <i>Placuna placenta</i> (Linnaeus, 1758) | IWP | [6] |
| <i>A. sinensis</i> (Shen, 1932) | Bivalvia | <i>Alectryonella plicatula</i> (Gmelin, 1791), <i>Chlamys nipponensis</i> (?), <i>Magallana angulata</i> (Lamarck, 1819), <i>Magallana gigas</i> (Thunberg, 1793), <i>Meretrix lusoria</i> (Röding, 1798), <i>Modiolus auriculatus</i> (Krauss, 1848), <i>Mytilus unguiculatus</i> Valenciennes, 1858, <i>Mytilus edulis</i> Linnaeus, 1758, <i>Ruditapes philippinarum</i> (Adams & Reeve, 1850), <i>Venerupis aspera</i> (Quoy & Gaimard, 1835) | IWP | [6,159] |
| <i>A. spinidactylus</i> (Gordon, 1936) | Bivalvia | <i>Modiolus philippinarum</i> (Hanley, 1843), <i>Modiolus</i> sp. | IWP | [6] |
| <i>A. tivalae</i> (Gordon, 1936) | Bivalvia | <i>Tivela stefaninii</i> (Nardini, 1933) | IWP | [6] |
| <i>A. vicajii</i> (Chhapgar, 1957) | Bivalvia | <i>Marcia recens</i> (Holten, 1802), <i>Mercenaria</i> sp., <i>Meretrix casta</i> (Gmelin, 1791), <i>Perna viridis</i> (Linnaeus, 1758) | IWP | [123,155] |
| <i>A. winckworthi</i> (Gordon, 1936) | Bivalvia | <i>Protapes gallus</i> (Gmelin, 1791) | IWP | [6] |

Table 1. Cont.

| Species | Host | Host Species | Distr. | References |
|--|---------------------|---|--------|------------|
| Austinotheres | | | | |
| <i>A. angelicus</i> (Lockington, 1877) | Bivalvia | <i>Modiolus capax</i> (Conrad, 1837), <i>Ostrea angelica</i> Rochebrune, 1895, <i>Saccostrea palmula</i> (Carpenter, 1857) | EP | [6,40] |
| Austrotheres | | | | |
| <i>A. holothuriensis</i> (Baker, 1907) | Holothuria, Ascidia | <i>Herdmania grandis</i> (Heller, 1878), ‘holothurians’ | IWP | [12] |
| <i>A. pregenzeri</i> Ahyong, 2018 | Ascidia | <i>Herdmania grandis</i> (Heller, 1878) | IWP | [12] |
| Bonita | | | | |
| <i>B. mexicana</i> Campos, 2009 | Bivalvia | <i>Pseudochama exogyra</i> (Conrad, 1837) | EP | [61] |
| Buergeres | | | | |
| <i>B. choprai</i> Ahyong & Ng, 2020 | Holothuria | <i>Actinopyga echinites</i> (Jaeger, 1833) | IWP | [32] |
| <i>B. deccanensis</i> (Chopra, 1931) | Holothuria | <i>Holothuria scabra</i> Jaeger, 1833 | IWP | [99] |
| <i>B. holothuriae</i> (Semper, 1880) | Holothuria | <i>Stichopus horrens</i> Selenka, 1867 | IWP | [70] |
| <i>B. ortmanni</i> (Bürger, 1895) | Holothuria | <i>Holothuria fursocinerea</i> Jaeger, 1833 | IWP | [70] |
| Calyptraothes | | | | |
| <i>C. camposi</i> Ayón-Parente & Hendrickx, 2014 | Gastropoda | <i>Crepidula striolata</i> Menke, 1851 | EP | [128] |
| <i>C. garthi</i> (Fenucci, 1975) | Gastropoda | <i>Bostrycapulus odites</i> Collin, 2005, <i>Crepidula argentina</i> Simone, Pastorino & Penchaszadeh, 2000, <i>Crepidula cachimilla</i> Cledón, Simone & Penchaszadeh, 2004, <i>Crepidula plana</i> Say, 1822, <i>Crepidula protea</i> (d’Orbigny, 1841), <i>Crepidula unguiformis</i> Lamarck, 1822, <i>Crepidula</i> sp., <i>Trochita pileus</i> (Lamarck, 1822) | ATL | [125,160] |
| <i>C. granti</i> (Glassell, 1933) | Gastropoda | <i>Bostrycapulus odites</i> Collin, 2005, <i>Crepidula cachimilla</i> Cledón, Simone & Penchaszadeh, 2004, <i>Crucibulum spinosum</i> (Sowerby, 1824), <i>Crepidula striolata</i> Menke, 1851, <i>Lottia mesoleuca</i> (Menke, 1851) | EP | [41,89] |
| <i>C. hernandezii</i> Hernández-Ávila & Campos, 2006 | Gastropoda | <i>Crucibulum auricula</i> (Gmelin, 1791) | ATL | [126] |
| <i>C. pepeluisi</i> Campos & Hernández-Ávila, 2010 | ? | ? | EP | [127] |
| <i>C. politus</i> (Smith, 1870) | Gastropoda | <i>Calyptrea</i> sp., <i>Crepidatella dilatata</i> (Lamarck, 1822) | EP | [125] |
| Clypeasterophilus | | | | |
| <i>C. juvenilis</i> (Bouvier, 1917) | Echinoidea | <i>Clypeaster subdepressus</i> (Gray, 1825), <i>Meoma ventricosa</i> (Lamarck, 1816) | ATL | [161] |
| <i>C. rugatus</i> (Bouvier, 1917) | Echinoidea | <i>Clypeaster rosaceus</i> (Linnaeus, 1758), <i>Encope michelini</i> Agassiz, 1841 | ATL | [161] |
| <i>C. stebbingi</i> (Rathbun, 1918) | Echinoidea | <i>Clypeaster subdepressus</i> (Gray, 1825) | ATL | [161] |
| <i>C. ususfructus</i> (Griffith, 1987) | Echinoidea | <i>Clypeaster europacificus</i> Clark, 1914, <i>Clypeaster speciosus</i> Verrill, 1870 | EP | [161] |

Table 1. Cont.

| Species | Host | Host Species | Distr. | References |
|--|------------|---|--------|------------|
| Discorsotheres | | | | |
| <i>D. camposi</i> Ahyong, 2018 | Bivalvia | <i>Spondylus</i> spp. | IWP | [12] |
| <i>D. spondylia</i> (Nobili, 1905) | Bivalvia | <i>Spondylus exilis</i> cf. (Sowerby, 1895) | IWP | [12] |
| <i>D. subglobosus</i> (Baker, 1907) | Bivalvia | <i>Equichlamys bifrons</i> (Lamarck, 1819), <i>Modiolus areolatus</i> (Gould, 1850), <i>Pecten fumatus</i> Reeve, 1852, <i>Spondylus tenellus</i> Reeve, 1856 | IWP | [12] |
| <i>D. subquadrata</i> (T. Sakai, 1939) | Bivalvia | <i>Magallana nippona</i> (Reki, 1934), <i>Mytilus edulis</i> Linnaeus, 1758, <i>Spondylus squamosus</i> Schreibers, 1793 | IWP | [12] |
| Dissodactylus ⁴ | | | | |
| <i>D. crinitichelis</i> Moreira, 1901 | Echinoidea | <i>Clypeaster rosaceus</i> (Linnaeus, 1758), <i>Clypeaster subdepressus</i> (Gray, 1825), <i>Encope emarginata</i> (Leske, 1778), <i>Encope michelini</i> Agassiz, 1841, <i>Leodia sexiesperforata</i> (Leske, 1778), <i>Mellita quinquesperforata</i> (Leske, 1778), <i>Mellita</i> sp., <i>Meoma ventricosa</i> (Lamarck, 1816) | ATL | [161] |
| <i>D. glasselli</i> Rioja, 1944 | Echinoidea | <i>Encope micropora californica</i> Verrill, 1870, <i>Lanthonia grantii</i> (Mortensen, 1948), <i>Lanthonia longifissa</i> (Michelin, 1858), <i>Mellita kanakoffi</i> Durham, 1961 | EP | [161] |
| <i>D. latus</i> H. Griffith, 1987 | Echinoidea | <i>Clypeaster subdepressus</i> (Gray, 1825), <i>Encope michelini</i> Agassiz, 1841, <i>Leodia sexiesperforata</i> (Leske, 1778) | ATL | [161] |
| <i>D. lockingtoni</i> Glassell, 1935 | Echinoidea | <i>Encope grandis</i> Agassiz, 1841, <i>Encope micropora californica</i> Verrill, 1870, <i>Leodia sexiesperforata</i> (Leske, 1778), <i>Encope</i> spp., <i>Lanthonia grantii</i> (Mortensen, 1948), <i>Lanthonia longifissa</i> (Michelin, 1858), <i>Mellita kanakoffi</i> Durham, 1961 | EP | [161] |
| <i>D. mellitae</i> (Rathbun, 1900) | Echinoidea | <i>Clypeaster subdepressus</i> (Gray, 1825), <i>Encope michelini</i> Agassiz, 1841, <i>Leodia sexiesperforata</i> (Leske, 1778), <i>Mellita isometra</i> Harold & Telford, 1990, <i>Mellita quinquesperforata</i> (Leske, 1778) | ATL | [161] |
| <i>D. nitidus</i> Smith, 1870 | Echinoidea | <i>Encope grandis</i> Agassiz, 1841, <i>Encope micropora californica</i> Verrill, 1870, <i>Encope</i> spp., <i>Lanthonia longifissa</i> (Michelin, 1858) | EP | [161] |
| <i>D. primitivus</i> Bouvier, 1917 | Echinoidea | <i>Meoma ventricosa</i> (Lamarck, 1816), <i>Plagiobrissus grandis</i> (Gmelin, 1791) | ATL | [161] |
| <i>D. schmitti</i> H. Griffith, 1987 | ? | ? | EP | [93] |
| <i>D. xantusi</i> Glassell, 1936 | Echinoidea | <i>Clypeaster subdepressus</i> (Gray, 1825), <i>Encope grandis</i> Agassiz, 1841, <i>Encope micropora californica</i> Verrill, 1870, <i>Encope michelini</i> Agassiz, 1841, <i>Encope</i> spp., <i>Leodia sexiesperforata</i> (Leske, 1778), <i>Mellitella stokesii</i> (Agassiz, 1841), <i>Lanthonia longifissa</i> (Michelin, 1858) | EP | [161] |
| Durckheimia | | | | |
| <i>D. caeca</i> Bürger, 1895 | Bivalvia | <i>Chama pacifica</i> Broderip, 1835, <i>Lima lima</i> (Linnaeus, 1758), <i>Lima vulgaris</i> (Link, 1807) | IWP | [27] |
| <i>D. carnipes</i> De Man, 1889 | ? | ? | IWP | [27] |
| <i>D. lochi</i> Ahyong & Brown, 2003 | Bivalvia | <i>Ctenoides ales</i> , <i>Lima vulgaris</i> (Link, 1807) | IWP | [27] |
| Enigmatheres | | | | |
| <i>E. canfieldi</i> (Rathbun, 1918) | Gastropoda | <i>Megathura crenulata</i> (Sowerby, 1825) | EP | [61] |
| Ernestotheses | | | | |
| <i>E. conicola</i> Manning, 1993 | Gastropoda | <i>Conus</i> sp. | ATL | [7] |

Table 1. Cont.

| Species | Host | Host Species | Distr. | References |
|---|-----------------|--|--------|------------|
| Fabia ⁵ | | | | |
| <i>F. byssomiae</i> (Say, 1818) | Bivalvia | <i>Hiatella arctica</i> (Linnaeus, 1767), <i>Anadara notabilis</i> (Röding, 1798) | ATL | [16] |
| <i>F. carvachoï</i> Campos, 1996 | Bivalvia | <i>Semele flavescens</i> (Gould, 1851) | EP | [16] |
| <i>F. concharum</i> (Rathbun, 1894) | Bivalvia | <i>Cryptomya californica</i> (Conrad, 1837), <i>Donax gouldii</i> Dall, 1921, <i>Leukoma staminea</i> (Conrad, 1837), <i>Modiolus capax</i> (Conrad, 1837), <i>Modiolus modiolus</i> (Linnaeus, 1758), <i>Mya arenaria</i> Linnaeus, 1758, <i>Parapholas californica</i> (Conrad, 1837), <i>Pholadidea loscombiana</i> Turton, 1819, <i>Tapes</i> sp., <i>Tivela stultorum</i> (Mawe, 1823) | EP | [16] |
| <i>F. emiliai</i> (Melo, 1971) | Bivalvia | <i>Anadara brasiliana</i> (Lamarck, 1819), <i>Glycymeris longior</i> (Sowerby, 1833), <i>Glycymeris</i> sp. | ATL | [116] |
| <i>F. felderi</i> Gore, 1986 | ? | ? | ATL | [116] |
| <i>F. hemphilli</i> (Rathbun, 1918) | ? | ? | ATL | [116] |
| <i>F. malaguena</i> (Garth, 1948) | ? | ? | EP | [162] |
| <i>F. subquadrata</i> Dana, 1851 | Bivalvia | <i>Cyclocardia ventricosa</i> (Gould, 1850), <i>Leukoma staminea</i> (Conrad, 1837), <i>Modiolus capax</i> (Conrad, 1837), <i>Modiolus modiolus</i> (Linnaeus, 1758), <i>Mya arenaria</i> Linnaeus, 1758, <i>Mytilus californianus</i> Conrad, 1837, <i>Mytilus edulis</i> Linnaeus, 1758, <i>Saxidomus gigantea</i> (Deshayes, 1839), <i>Tresus capax</i> (Gould, 1850), <i>Tivela stultorum</i> (Mawe, 1823), <i>Tresus nuttallii</i> (Conrad, 1837) | EP | [30] |
| <i>F. tellinae</i> Cobb, 1973 | Bivalvia | <i>Laciolina magna</i> (Spengler, 1798) | ATL | [16] |
| Gemmotheres | | | | |
| <i>G. chamae</i> Roberts, 1975 | Bivalvia | <i>Chama</i> spp. | ATL | [85] |
| Holotheres | | | | |
| <i>H. danielae</i> Ahyong, 2010 | Holothuria | <i>Acaudina molpadioides</i> (Semper, 1867) | IWP | [106] |
| <i>H. flavus</i> (Nauck, 1880) | Holothuria | 'unidentified holothurian' | IWP | [70] |
| <i>H. halangi</i> (Hamel et al., 1999) | Holothuria | <i>Holothuria scabra</i> Jaeger, 1833 | IWP | [120] |
| <i>H. semperi</i> (Bürger, 1895) | Holothuria | <i>Holothuria fursocinerea</i> Jaeger, 1833, <i>Holothuria scabra</i> Jaeger, 1833 | IWP | [70] |
| <i>H. setnai</i> (Chopra, 1931) | Holothuria | <i>Actinopyga mauritiana</i> (Quoy & Gaimard, 1834) | IWP | [6] |
| Holothuriophilus ⁶ | | | | |
| <i>H. pacificus</i> (Poeppegg, 1836) | Holothuria | <i>Athyonidium chilensis</i> (Semper, 1868) | EP | [6] |
| <i>H. trapeziformis</i> Nauck, 1880 | Holothuria | <i>Holothuria inornata</i> (Semper, 1868) | EP | [41] |
| Hospitotheres | | | | |
| <i>H. powelli</i> ² Manning, 1993 | Decapod burrows | <i>Balsscallichirus balssi</i> (Monod, 1933), <i>Leptalpheus</i> sp. nov. (?) | ATL | [7] |
| Juxtafabia | | | | |
| <i>J. muliniarum</i> (Rathbun, 1918) | Bivalvia | <i>Chione californiensis</i> (Broderip, 1835), <i>Chionista fructifraga</i> (Sowerby, 1853), <i>Chione tumens</i> Verrill, 1870, <i>Leukoma grata</i> (Say, 1831), <i>Tagelus affinis</i> (Adams, 1852), <i>Polymesoda inflata</i> (Philippi, 1851) | EP | [163] |
| Latatheres | | | | |
| <i>L. affinis</i> (H. Milne Edwards, 1853) | ? | ? | IWP | [12] |
| <i>L. tomentipes</i> (Takeda & Konichi, 1994) | Bivalvia | 'unidentified bivalve mollusc' | IWP | [12] |

Table 1. Cont.

| Species | Host | Host Species | Distr. | References |
|---|-------------------|---|--------|------------|
| Limotheres | | | | |
| <i>L. nasatus</i> Holthuis, 1975 | Bivalvia | <i>Ctenoides mitis</i> (Lamarck, 1807) | ATL | [55] |
| Mesotheres | | | | |
| <i>M. barbatus</i> (Desbonne, 1867) | Gastropoda | <i>Cittarium pica</i> (Linnaeus, 1758) | ATL | [6] |
| <i>M. serrei</i> (Rathbun, 1909) | Gastropoda | <i>Strombus</i> sp. | ATL | [6] |
| <i>M. strombi</i> (Rathbun, 1905) | Gastropoda | <i>Pleuroploca</i> sp., <i>Strombus alatus</i> Gmelin, 1791, <i>Strombus pugilis</i> Linnaeus, 1758, <i>Strombus</i> sp., <i>Triplofusus giganteus</i> (Kiener, 1840) | ATL | [6,71] |
| <i>M. unguifalcula</i> (Glassel, 1936) ⁷ | Gastropoda | <i>Strombus</i> sp., <i>Turbo</i> sp. | EP | [164] |
| Nannotheres | | | | |
| <i>N. moorei</i> Manning & Felder, 1996 | Bivalvia | <i>Malleus candeanus</i> (d'Orbigny, 1853) | ATL | [31] |
| Nepinnotheres ⁵ | | | | |
| <i>N. affinis</i> (Bürger, 1895) | Bivalvia | <i>Chlamys hastata</i> (Sowerby, 1842), <i>Ostrea</i> sp., <i>Pinna</i> sp. | IWP | [6] |
| <i>N. africanus</i> Manning, 1993 | ? | ? | ATL | [7] |
| <i>N. androgynus</i> Manning, 1993 | Bivalvia | <i>Panopea glycymeris</i> (Born, 1778) | ATL | [7] |
| <i>N. atrinicola</i> (Page, 1983) | Bivalvia | <i>Atrina zelandica</i> (Gray, 1835), <i>Austrovenus stutchburyi</i> (Wood, 1828), <i>Modiolus areolatus</i> (Gould, 1850) | IWP | [165] |
| <i>N. cardii</i> (Bürger, 1895) | Bivalvia | <i>Fragum unedo</i> (Linnaeus, 1758), <i>Maetra chinensis</i> Philippi, 1846, <i>Mytilus unguiculatus</i> Valenciennes, 1858, <i>Meretrix meretrix</i> (Linnaeus, 1758), <i>Ostrea denselamellosa</i> Lischke, 1869, <i>Pinna bicolor</i> Gmelin, 1791, <i>Spisula sachalinensis</i> (Schrenck, 1862) | IWP | [6] |
| <i>N. edwardsi</i> (De Man, 1887) | Bivalvia | <i>Atrina vexillum</i> (Born, 1778), <i>Ostrea</i> sp., <i>Pinna</i> sp. | IWP | [6] |
| <i>N. fulvia</i> Ahyong & Ng, 2020 | Bivalvia | <i>Fulvia australis</i> (Sowerby, 1834) | IWP | [32] |
| <i>N. glaberrimus</i> (Bürger, 1895) | Bivalvia | <i>Arca</i> sp., <i>Ctenoides suavis</i> Masahito, Kuroda & Habe in Kuroda & al., 1971, <i>Geloina coaxans</i> (Gmelin, 1791) | IWP | [6] |
| <i>N. latipes</i> (Jacquinot, 1846) | Bivalvia | <i>Modiolus</i> sp., <i>Pinna</i> sp., <i>Saccostrea scyphophilla</i> (Peron & Lesueur, 1807) | IWP | [166] |
| <i>N. margaritiferae</i> (Laurie, 1906) | Bivalvia | <i>Mytilus</i> sp., <i>Pinctada imbricata</i> (Röding, 1798) | IWP | [6] |
| <i>N. novaezelandiae</i> (Filhol, 1885) | Bivalvia | <i>Aulacomya atra</i> (Molina, 1782), <i>Austrovenus stutchburyi</i> (Wood, 1828), <i>Magallana gigas</i> (Thunberg, 1793), <i>Mytilus galloprovincialis</i> Lamarck, 1819, <i>Paphies ventricosa</i> (Gray, 1843), <i>Perna canaliculus</i> (Gmelin, 1791) | IWP | [165] |
| <i>N. pectinicola</i> (Bürger, 1895) | Bivalvia | <i>Decatopecten radula</i> (Linnaeus, 1758) | IWP | [6] |
| <i>N. pinnotheres</i> (Linnaeus, 1758) | Bivalvia, Ascidia | <i>Atrina pectinata</i> (Linnaeus, 1767), <i>Pinna nobilis</i> Linnaeus, 1758; <i>Ascidia mentula</i> Müller, 1776, <i>Halocynthia papillosa</i> (Linnaeus, 1767), <i>Microcosmos</i> spp. | ATL | [15,152] |
| <i>N. rathbunae</i> (Schmitt, 1973) | Bivalvia | <i>Donax</i> sp. | IWP | [6] |
| <i>N. rouxi</i> (H. Milne Edwards, 1853) | ? | ? | IWP | [6] |
| <i>N. sanqueri</i> Manning, 1993 | ? | ? | ATL | [7] |
| <i>N. tellinae</i> (Manning & Holthuis, 1981) | Bivalvia | <i>Austromacoma nymphalis</i> (Lamarck, 1818) | ATL | [7] |
| <i>N. villosulus</i> (Guérin, 1832) | Bivalvia | <i>Atrina chinensis</i> (Deshayes, 1841), <i>Pinctada margaritifera</i> (Linnaeus, 1758) | IWP | [6] |

Table 1. Cont.

| Species | Host | Host Species | Distr. | References |
|---|--|--|--------|------------|
| Opisthopus | | | | |
| <i>O. transversus</i> Rathbun, 1894 ⁸ | Polyplacophora, Gastropoda, Bivalvia, Polychaeta, Holothuria | <i>Cryptochiton stelleri</i> (Middendorff, 1847); <i>Aplysia vaccaria</i> Winkler, 1955, <i>Bulla gouldiana</i> Pilsbry, 1895, <i>Megastraea undosa</i> (Wood, 1828), <i>Megathura crenulata</i> (Sowerby, 1825), <i>Navanax inermis</i> (Cooper, 1862), <i>Neverita lewisii</i> (Gould, 1847); <i>Crassadoma gigantea</i> (Gray, 1825), <i>Dinocardium robustum</i> (Lightfoot, 1768), <i>Megapitaria squalida</i> (Sowerby, 1835), <i>Modiolus</i> sp., <i>Mytilus edulis</i> Linnaeus, 1758, <i>Nuttallia nuttalli</i> (Conrad, 1837), <i>Pholas</i> sp., <i>Platyodon</i> sp., <i>Tivela stultorum</i> (Mawe, 1823), <i>Tresus nuttallii</i> (Conrad, 1837), <i>Zirfaea pilsbryi</i> Lowe, 1931, <i>Zirfaea</i> sp.; <i>Arenicola</i> sp., <i>Chaetopterus variopedatus</i> (Renier, 1804); <i>Apostichopus californicus</i> (Stimpson, 1857), <i>Apostichopus parvimensis</i> (Clark, 1913), <i>Caudina</i> sp. | EP | [6,30] |
| Orthoheres | | | | |
| <i>O. bayou</i> Ng & Ho, 2016 | Gastropoda | <i>Haliotis asinine</i> Linnaeus, 1758 | IWP | [112] |
| <i>O. haliotidis</i> Geiger & Martin, 1999 | Gastropoda | <i>Haliotis asinina</i> Linnaeus, 1758 | IWP | [112] |
| <i>O. turboe</i> T. Sakai, 1969 | Gastropoda | <i>Turbo argyrostomus</i> Linnaeus, 1758 | IWP | [112] |
| Ostracotheres | | | | |
| <i>O. cynthiae</i> Nobili, 1906 | Ascidia | <i>Herdmania momus</i> (Savigny, 1816), <i>Herdmania</i> sp. | IWP | [12] |
| <i>O. tridacnae</i> (Rüppel, 1830) | Bivalvia | <i>Tridacna maxima</i> (Röding, 1798), <i>Tridacna squamosina</i> Sturany, 1899 | IWP | [12] |
| Pinnaxodes ⁶ | | | | |
| <i>P. bipunctatus</i> (Nicolet, 1849) | Echinoidea | 'probably sea-urchins' | EP | [167] |
| <i>P. chilensis</i> (H. Milne Edwards, 1837) | Echinoidea | <i>Caenocentrotus gibbosus</i> (Agassiz in Agassiz & Desor, 1846), <i>Loxechinus albus</i> (Molina, 1782), <i>Tetrapygus niger</i> (Molina, 1782) | EP | [167] |
| <i>P. floridensis</i> H.W. Wells & M.J. Wells, 1961 | Holothuria | <i>Holothuria princeps</i> Selenka, 1867 | ATL | [6] |
| <i>P. gigas</i> Green, 1992 | Bivalvia | <i>Panopea generosa</i> Gould, 1850, <i>Panopea globose</i> Dall, 1898, <i>Pinna rugosa</i> Sowerby, 1835, <i>Atrina pectinata</i> (Linnaeus, 1767), <i>Barnea</i> sp., <i>Crenomytilus grayanus</i> (Dunker, 1853), <i>Gregariella difficilis</i> (Deshayes, 1863), <i>Mactra antiquata</i> Spengler, 1802, <i>Meretrix lamarckii</i> Deshayes, 1853, <i>Mytilus</i> sp., <i>Ruditapes philippinarum</i> (Adams & Reeve, 1850); <i>Holothuria hilla</i> Lesson, 1830, <i>Stichopus gyryfer</i> Selenka, 1867 | EP | [30] |
| <i>P. major</i> Ortmann, 1894 | Bivalvia, Holothuria | <i>Crenomytilus grayanus</i> (Dunker, 1853), <i>Gregariella difficilis</i> (Deshayes, 1863), <i>Modiolus modiolus</i> (Linnaeus, 1758), <i>Mya arenaria</i> Linnaeus, 1758, <i>Mytilus edulis</i> Linnaeus, 1758, <i>Mytilus galloprovincialis</i> Lamarck, 1819, <i>Mytilus unguiculatus</i> Valenciennes, 1858 | IWP | [6,87,168] |
| <i>P. mutuensis</i> T. Sakai, 1939 | Bivalvia | <i>Anomalocardia flexuosa</i> (Linnaeus, 1767), <i>Cyrtopleura costata</i> (Linnaeus, 1758) | IWP | [70,168] |
| <i>P. tomentosus</i> Ortmann, 1894 | Bivalvia | <i>Anomalocardia flexuosa</i> (Linnaeus, 1767), <i>Cyrtopleura costata</i> (Linnaeus, 1758) | ATL | [169] |
| Pinnotheres ⁵ | | | | |
| <i>P. bicristatus</i> García Raso & Cuesta, 2019 | Bivalvia | <i>Anomia ephippium</i> Linnaeus, 1758, <i>Ostrea edulis</i> Linnaeus, 1758 | ATL | [33,37] |
| <i>P. bidentatus</i> T. Sakai, 1939 ⁹ | 'Free living' | ? | IWP | [110] |
| <i>P. corbiculae</i> T. Sakai, 1939 ¹⁰ | Bivalvia | <i>Corbicula japonica</i> Prime, 1864 | IWP | [6] |
| <i>P. coutierei</i> Nobili, 1905 | ? | ? | IWP | [6] |

Table 1. Cont.

| Species | Host | Host Species | Distr. | References |
|---|-------------|--|--------|------------|
| <i>P. dilatatus</i> Shen, 1932 | Bivalvia | <i>Venerupis aspera</i> (Quoy & Gaimard, 1835) | IWP | [6] |
| <i>P. excussus</i> Tai et al., 1980 | Bivalvia | <i>Gafrarium</i> sp. | IWP | [74] |
| <i>P. globosus</i> Hombron & Jacquinot, 1846 ³ | Bivalvia | <i>Meretrix</i> sp., <i>Pinna</i> sp., <i>Sunetta subquadrata</i> (Sowerby, 1851) | IWP | [6] |
| <i>P. gordonae</i> Shen, 1932 ¹¹ | Bivalvia | <i>Anomia cytaeum</i> Gray, 1850, <i>Fulvia undatopicta</i> (Pilsbry, 1904), <i>Mytilus unguiculatus</i> Valenciennes, 1858, <i>Ruditapes philippinarum</i> (Adams & Reeve, 1850), <i>Venerupis aspera</i> (Quoy & Gaimard, 1835), <i>Venerupis philippinarum</i> (Adams & Reeve, 1850) | IWP | [6] |
| <i>P. guerini</i> H. Milne Edwards, 1853 | Bivalvia | 'oysters' | ATL | [6] |
| <i>P. haiyangensis</i> Shen, 1932 | Bivalvia | <i>Laternula gracilis</i> (Reeve, 1860) | IWP | [6] |
| <i>P. hickmani</i> (Guiler, 1950) | Bivalvia | <i>Eumarcia fumigata</i> (Sowerby, 1853), <i>Modiolus</i> sp., <i>Mytilus</i> sp., <i>Neotrigonia margaritacea</i> (Lamarck, 1804), <i>Plebidonax deltoides</i> (Lamarck, 1818) | IWP | [53] |
| <i>P. hirtimanus</i> H. Milne Edwards, 1853 | ? | ? | ATL | [6] |
| <i>P. kamensis</i> Rathbun, 1909 | ? | ? | IWP | [6] |
| <i>P. kutensis</i> Rathbun, 1909 | ? | ? | IWP | [6] |
| <i>P. lanensis</i> Rathbun, 1909 | ? | ? | IWP | [6] |
| <i>P. laquei</i> T. Sakai, 1961 ¹² | Brachiopoda | <i>Laqueus rubellus</i> (Sowerby, 1846), 'other brachiopods' | IWP | [170] |
| <i>P. lithodomi</i> Smith, 1870 | Bivalvia | <i>Leiosolenus attenuates</i> (Deshayes, 1836), <i>Lithophaga aristata</i> (Dillwyn, 1817) | EP | [6] |
| <i>P. luminatus</i> Tai et al., 1980 | Bivalvia | <i>Asaphis violascens</i> (Forsskål in Niebuhr, 1775) | IWP | [74] |
| <i>P. lutescens</i> Nobili, 1905 | ? | ? | IWP | [6] |
| <i>P. mactricola</i> Alcock, 1900 | Bivalvia | <i>Mactra violacea</i> (Gmelin, 1791) | IWP | [6] |
| <i>P. maindroni</i> Nobili, 1905 | ? | ? | IWP | [6] |
| <i>P. nigrans</i> Rathbun, 1909 | ? | ? | IWP | [6] |
| <i>P. obscuridentata</i> Tai & Song, 1986 | ? | ? | IWP | [171] |
| <i>P. obscurus</i> Stimpson, 1858 | ? | ? | IWP | [6] |
| <i>P. onychodactylus</i> Tesch, 1918 | ? | ? | IWP | [6] |
| <i>P. paralatissimus</i> Tai & Song, 1986 | ? | ? | IWP | [171] |
| <i>P. parvulus</i> Stimpson, 1858 | Bivalvia | <i>Pecten albicans</i> (Schröter, 1802), <i>Pinna</i> sp., <i>Saxidomus purpurata</i> (Sowerby, 1852), <i>Sunetta subquadrata</i> (Sowerby, 1851) | IWP | [6] |
| <i>P. pectunculi</i> Hesse, 1872 | Bivalvia | <i>Clausinella fasciata</i> (da Costa, 1778), <i>Glycymeris glycymeris</i> (Linnaeus, 1758), <i>Venus casina</i> Linnaeus, 1758, <i>Venus verrucosa</i> Linnaeus, 1758 | IWP | [15] |
| <i>P. perezi</i> Nobili, 1905 | Bivalvia | <i>Pholas</i> sp. | IWP | [6] |
| <i>P. pholadis</i> De Haan, 1835 | Bivalvia | <i>Barnea manilensis</i> (Philippi, 1847), <i>Chlamys nipponensis</i> (?), <i>Meretrix lusoria</i> (Röding, 1798), <i>Mimachlamys sanguinea</i> (Linnaeus, 1758), <i>Mytilus edulis</i> Linnaeus, 1758, <i>Pecten albicans</i> (Schröter, 1802), <i>Ruditapes philippinarum</i> (Adams & Reeve, 1850), <i>Spisula sachalinensis</i> (Schrenck, 1862) | IWP | [6] |
| <i>P. pichilinquai</i> Rathbun, 1923 | ? | ? | EP | [6] |

Table 1. Cont.

| Species | Host | Host Species | Distr. | References |
|---|-------------------|--|--------|------------|
| <i>P. pilulus</i> Tai et al., 1980 | Bivalvia | <i>Martesia</i> sp. | IWP | [74] |
| <i>P. pisum</i> (Linnaeus, 1767) | Bivalvia | <i>Acanthocardia echinata</i> (Linnaeus, 1758), <i>Cerastoderma edule</i> (Linnaeus, 1758), <i>Chamelea gallina</i> (Linnaeus, 1758), <i>Clausinella fasciata</i> (da Costa, 1778), <i>Donax vittatus</i> (da Costa, 1778), <i>Dosinia lupinus</i> (Linnaeus, 1758), <i>Ensis ensis</i> (Linnaeus, 1758), <i>Ensis magnus</i> Schumacher, 1817, <i>Gari fervensis</i> (Gmelin, 1791), <i>Modiolus modiolus</i> (Linnaeus, 1758), <i>Mytilus edulis</i> Linnaeus, 1758, <i>Mytilus galloprovincialis</i> Lamarck, 1819, <i>Nucula nitidosa</i> Winckworth, 1930, <i>Ostrea edulis</i> Linnaeus, 1758, <i>Spisula</i> spp. | ATL | [15] |
| <i>P. pugettensis</i> Holmes, 1900 | Ascidia, Bivalvia | <i>Halocynthia aurantium</i> (Pallas, 1787), <i>Halocynthia igaboja</i> Oka, 1906, <i>Ascidia paratropa</i> (Huntsman, 1912); <i>Mya arenaria</i> Linnaeus, 1758 | EP | [6] |
| <i>P. quadratus</i> Rathbun, 1909 | Bivalvia | <i>Arca</i> sp. | IWP | [6] |
| <i>P. sebastianensis</i> (Rodrigues da Costa, 1970) | Bivalvia | <i>Atrina rigida</i> (Lightfoot, 1786) | ATL | [6] |
| <i>P. serrignathus</i> Shen, 1932 | ? | ? | IWP | [6] |
| <i>P. shoemaker</i> Rathbun, 1918 | ? | ? | ATL | [6] |
| <i>P. siamensis</i> Rathbun, 1909 | ? | ? | IWP | [6] |
| <i>P. taichungae</i> K. Sakai, 2000 ⁹ | Free living | ? | IWP | [6] |
| <i>P. taylori</i> Rathbun, 1918 | Ascidia | 'transparent tunicates' | EP | [6] |
| <i>P. trichopus</i> Tesch, 1918 | Bivalvia | <i>Pinctada</i> sp. | IWP | [6] |
| <i>P. tsingtaoensis</i> Shen, 1932 | Bivalvia | <i>Hiatula acuta</i> (Cai & Zhuang, 1985), <i>Laternula peichiliensi</i> (?), <i>Mactra quadrangularis</i> Reeve, 1854 | IWP | [26,74] |
| Raytheres | | | | |
| <i>R. clavapedatus</i> (Glassell, 1935) | Bivalvia | <i>Leiosolenus attenuates</i> (Deshayes, 1836) | EP | [6] |
| Serenotheres | | | | |
| <i>S. besutensis</i> (Serène, 1967) | Bivalvia | <i>Lithophaga</i> sp. | IWP | [27] |
| <i>S. janus</i> Ng & Meyer, 2016 | Bivalvia | <i>Leiosolenus obesus</i> (Philippi, 1847) | IWP | [52] |
| Sindheres | | | | |
| <i>S. karachiensis</i> Kazmi & Manning, 2003 | Bivalvia | <i>Gastrochaena</i> sp. | IWP | [105] |
| Solenotheres | | | | |
| <i>S. prolixus</i> Ng & Ngo, 2010 | Bivalvia | <i>Solen corneus</i> Lamarck, 1818 | IWP | [101] |
| Tacitotheres | | | | |
| <i>T. glaber</i> (Bürger, 1895) | Bivalvia | <i>Tapes conspersus</i> (Gmelin, 1791), <i>Tapes literatus</i> (Linnaeus, 1758) | IWP | [6] |
| <i>T. laevis</i> (Bürger, 1895) | Bivalvia | <i>Coralliophaga</i> sp. | IWP | [6] |
| <i>T. longipes</i> (Bürger, 1895) | ? | ? | IWP | [6] |
| Trichobezoares | | | | |
| <i>T. pilumnoides</i> (Nobili, 1906) ¹³ | Holothuria | <i>Holothuria scabra</i> Jaeger, 1833 | IWP | [29] |
| <i>T. villosissimus</i> (Doflein, 1904) | Holothuria | <i>Actinopyga mauritiana</i> (Quoy & Gaimard, 1834) | IWP | [29] |

Table 1. Cont.

| Species | Host | Host Species | Distr. | References |
|---|----------|--|--------|------------|
| Tridacnatheres | | | | |
| <i>T. whitei</i> (de Man, 1888) | Bivalvia | <i>Pinna</i> sp., <i>Tridacna gigas</i> Linnaeus, 1758, <i>Tridacna squamosa</i> Lamarck, 1819 | IWP | [27] |
| Tumidotheres | | | | |
| <i>T. carabiensis</i> Palacios Theil & Felder, 2019 | Bivalvia | <i>Atrina rigida</i> (Lightfoot, 1786), <i>Barbatia candida</i> (Helbling, 1779), <i>Isognomon alatus</i> (Gmelin, 1791), <i>Pinctada imbricata</i> Röding, 1798, <i>Pteria colymbus</i> (Röding, 1798) | ATL | [98] |
| <i>T. maculatus</i> (Say, 1818) ¹⁴ | Bivalvia | <i>Aequipecten tehuelchus</i> (d'Orbigny, 1842), <i>Anomia simplex</i> d'Orbigny, 1853, <i>Argopecten gibbus</i> (Linnaeus, 1758), <i>Argopecten irradians</i> (Lamarck, 1819), <i>Atrina rigida</i> (Lightfoot, 1786), <i>Atrina seminuda</i> (Lamarck, 1819), <i>Atrina serrata</i> (Sowerby, 1825), <i>Chama macerophylla</i> Gmelin, 1791, <i>Modiolus americanus</i> (Leach, 1815), <i>Modiolus modiolus</i> (Linnaeus, 1758), <i>Mya arenaria</i> Linnaeus, 1758, <i>Mytilus edulis</i> Linnaeus, 1758, <i>Mytilus platensis</i> d'Orbigny, 1842, <i>Ostrea puelchana</i> d'Orbigny, 1842, <i>Perna perna</i> (Linnaeus, 1758), <i>Placopecten magellanicus</i> (Gmelin, 1791) | ATL | [98] |
| <i>T. margarita</i> (Verrill, 1869) | Bivalvia | <i>Argopecten irradians concentricus</i> (Say, 1822), <i>Argopecten ventricosus</i> (Sowerby, 1842), <i>Barbatia reeveana</i> (d'Orbigny, 1846), <i>Crassadoma gigantea</i> (Gray, 1825), <i>Limaria pacifica</i> (d'Orbigny, 1846), <i>Pinctada mazatlanica</i> (Hanley, 1856) | EP | [8] |
| <i>T. orcutti</i> (Rathbun, 1918) | ? | ? | EP | [6] |
| Tunicotheres | | | | |
| <i>T. moseri</i> (Rathbun, 1918) | Ascidia | <i>Molgula occidentalis</i> Traustedt, 1883, <i>Phallusia nigra</i> Savigny, 1816, <i>Polycarpa spongiabilis</i> Traustedt, 1883 | ATL | [8] |
| Viridotheres | | | | |
| <i>V. asaphis</i> Ahyong, 2020 | Bivalvia | <i>Asaphis violascens</i> (Forskål in Niebuhr, 1775) | IWP | [172] |
| <i>V. buergeri</i> (Rathbun, 1909) | ? | ? | IWP | [6] |
| <i>V. cygnus</i> Ahyong, 2020 | Bivalvia | <i>Maetra pura</i> Reeve, 1854, | IWP | [166] |
| <i>V. gracilis</i> (Bürger, 1895) | Bivalvia | <i>Marcia opima</i> (Gmelin, 1791), <i>Solen</i> sp. | IWP | [6] |
| <i>V. kupang</i> Ahyong, 2018 | ? | ? | IWP | [173] |
| <i>V. lilliyae</i> (Manning, 1993) | ? | ? | ATL | [7] |
| <i>V. marionae</i> Manning, 1996 | Bivalvia | <i>Europocardium caparti</i> (Nicklès, 1955) | ATL | [103] |
| <i>V. otto</i> Ahyong & Ng, 2007 | ? | ? | IWP | [19] |
| <i>V. sanguinolariae</i> (Pillai, 1951) | Bivalvia | <i>Hiatula diphos</i> (Linnaeus, 1771) | IWP | [6] |
| <i>V. takedai</i> Ahyong et al., 2012 | Bivalvia | <i>Nipponoclava gigantea</i> (Sowerby, 1888) | IWP | [174] |
| <i>V. viridis</i> (Manning, 1993) | ? | ? | ATL | [7] |
| Visayeres | | | | |
| <i>V. acron</i> Ahyong & Ng, 2007 | Bivalvia | <i>Lithophaga</i> sp. | IWP | [54] |
| Waldotheres | | | | |
| <i>W. mccainae</i> (Schmitt, 1973) | Bivalvia | <i>Donax rugosus</i> Linnaeus, 1758 | ATL | [7] |

Table 1. Cont.

| Species | Host | Host Species | Distr. | References |
|---------------------------------|----------|---|--------|------------|
| Xanthasia | | | | |
| <i>X. murigera</i> White, 1846 | Bivalvia | <i>Hippopus</i> sp., <i>Tridacna crocea</i> Lamarck, 1819, <i>Tridacna gigas</i> (Linnaeus, 1758), <i>Tridacna maxima</i> (Röding, 1798), <i>Tridacna squamosa</i> Lamarck, 1819 | IWP | [27] |
| Zaops | | | | |
| <i>Z. angelae</i> Manning, 1993 | Bivalvia | <i>Brachidontes modiolus</i> (Linnaeus, 1767) | ATL | [98] |
| <i>Z. geddesi</i> (Miers, 1880) | Bivalvia | <i>Crassostrea rhizophorae</i> (Guilding, 1828) | ATL | [6] |
| <i>Z. ostreum</i> (Say, 1817) | Bivalvia | <i>Anomia peruviana</i> d'Orbigny, 1846, <i>Crassostrea rhizophorae</i> (Guilding, 1828), <i>Crassostrea virginica</i> (Gmelin, 1791), <i>Mytilus edulis</i> Linnaeus, 1758, <i>Pecten</i> spp. | ATL | [6] |

¹: Ng and Kumar [91] showed *Afropinnotheres* to be present in the Indian Ocean, with the description of *A. ratnakara*, but most other species of *Afropinnotheres* are from the west coast of Africa, with *A. monodi* even reaching as far as Europe [152]. *Afropinnotheres dofleini* was described from South Africa, connecting the two distribution patterns [91]. ²: All twelve specimens listed in the original description of *Hospitotheres powelli* were found in the soft-soiled estuary in Bonny River (Nigeria), found in decapod burrows [7]. The specimens supposedly shared these burrows with *Leptalpheus* sp. nov. and *Balsscallichirus balssi* (as *Callianassa balssi*). The actual host of this species might be a bivalve (Galeommatodea, Myidae and Lucinidae), living inside the same burrows as the decapods [175]. Consequently, the hypothetical host might have been destroyed during collection. Crabs identified as *H. powelli* appear to share many features with mollusk-inhabiting pea crabs, but closer inspection is needed. Another West African species, *Alainotheres leloeuffi*, shares a similar description of the habitat and was described based on one male specimen from a sandy sublittoral habitat in Ivory Coast. The only description of the habitat from the male holotype lacks information about a potential host, but mentioned it was dredged from “the reddish-brown sea floor (depth: 20 m)”. Dredging is known to destroy delicate invertebrates, including the shells of bivalves, and might have dislodged the crab from its original host [176]. Another possibility is that the male crab had left its host to search for host-infesting females. ³: The holotype of the first described species from Singapore, *Pinnotheres globosum* Hombron & Jacquinot, 1846 is considered lost, and the designation of a neotype will be published in 2020 (following [177]). *Arcotheres latus* (Bürger, 1895) and *A. ridgewayi* (Southwell, 1911) were found to be synonymous with *P. globosum* (now probably in *Arcotheres*) [177]. Until a revision is published, we list all three species separately. ⁴: Although *Dissodactylus meyerabichi* is regarded a junior synonym of *D. nitidus*, some databases still include the species as an accepted name [3,4]. Following Griffith [93], we do not include this species in Table 1. *Dissodactylus* may also include six additional species described as *Dissodactylus* zoea stages from Japan [178]. Schmitt et al. [6] listed the six species as ‘Species incertae’, provisionally in a separate genus, *Dissodactylozoea*. The identity of these specimens remains unknown. ⁵: Although *Fabia*, *Nepinnotheres*, and *Pinnotheres* have been the subject of many revisions, erecting new genera accounting for previously included species [16,88,179], the three genera still prove to be polyphyletic [5]. The molecular phylogeny reconstruction of Palacios Theil et al. [5] included two species of *Fabia* and *Nepinnotheres*, all being placed in different lineages. Additional molecular and morphological studies are needed to properly revise the two genera, but the distribution of the members of *Fabia* and *Nepinnotheres* can provide hints of a more natural classification. Within *Fabia*, four species are from the eastern Pacific (including the type species *F. subquadrata*) and five are from the tropical Western Atlantic (including the other analysed species). Within *Nepinnotheres*, five species are from the Atlantic coast of Africa (with *N. pinnotheres*’ also reaching Europe), while the remaining thirteen species can be found in the (greater) Pacific region, from India to New Zealand and the Philippines. Although Palacios Theil et al. [5] include only one species of *Pinnotheres* in their phylogenetic analyses, the genus is (still) urgently in need of a thorough revision, as stated by previous authors [7,113,180]. Evidence for the heterogeneity of the genus is the extreme morphological variation in the currently 45 recognised species, in addition to the absence of illustrations, host-information, and collection materials. A quick review of the illustrations of some of the better-known Indo-West Pacific species suggest already four species needing to be included in *Arcotheres* due to their sword-like dactyli on the last ambulatory legs: *P. obscuridentata* [171], *P. excussus* [74], and *P. parvulus* [156].

Proper examination is needed to refer the four (and possibly more) species to *Arcotheres* (as in [32,121]).⁶: There are some unanswered questions about the taxonomy of *Holothuriophilus* and *Pinnaxodes*, most recently highlighted by Ng and Kumar [91]. *Holothuriophilus pacificus* and *H. trapeziformis* are listed as the only species within *Holothuriophilus* [3,4], but previous authors [87,169] mentioned *Pinnaxodes mutuensis* and *P. tomentosus* to also be included in *Holothuriophilus* (see [65]). Jiang and Liu [181], Marin [168], and subsequently Ng and Kumar [91] include the two species in *Pinnaxodes*, based on morphological differences between the two genera (see [70]). We follow Ng and Kumar [91] in including the two species in *Pinnaxodes*. After Ng and Manning suggested it [70], Palacios Theil et al. [5] showed the southeastern Pacific species *Holothuriophilus pacificus* and *Pinnaxodes chilensis* to be related. The molecular phylogeny did not include the Indo-West Pacific and Western Atlantic species of *Pinnaxodes*, which are needed to solve this taxonomic problem. While both species of *Holothuriophilus* live in holothurians in the southeastern Pacific, members of *Pinnaxodes* have been found in a wide range of hosts organisms, from the Western Atlantic, Indo-West Pacific, and eastern Pacific. *Pinnaxodes chilensis* can be found inside the rectums of several species of urchins [87,167], while *P. bipunctatus* was described “probably from a sea urchin” and has not been examined since [167]. Campos [167] placed the species in *Pinnaxodes* after detailed examination of the description, and suggested it is related to *P. chilensis*. *Pinnaxodes floridensis* can be found in western Atlantic waters, inside the respiratory system of holothurians [87]. This species was described by Wells and Wells [90] after examination of 174 specimens, and found to “live commensally, not harming the [holothurian] host”. Although the Western Atlantic distribution raises questions about the generic status of this species, Takeda and Masahito [87] relate the species to the western Pacific *P. major*. *Pinnaxodes major* was reported as an inhabitant of a holothurian [182], which would be in line with the hosts of the other species of *Pinnaxodes* and *Holothuriophilus*. This species, however, can also be found in a wide range of shallow-water mussels and fan shells [87], as in *P. mutuensis* and *P. tomentosus*. In contrast, *P. gigas*, a species more recently described by Green [183] from the northeast Pacific has been found only once in fan shells [30]. Preferred hosts are geoduck clams. The host choice and potential switching (from a holothurian host to a geoduck within one life cycle) are discussed by Campos [30].⁷: *Mesotheres unguifalcula* can be found on the Pacific coasts of Mexico, in the stomachs of large gastropods from the genera *Strombus* and *Turbo*. Campos [164] mentioned the discovery of *M. unguifalcula*: “According to Glassell [184] the host for this species was not determined, but he recorded for the female topotypes that were collected “on the ambulacral groove of starfish.” I consider that this needs confirmation.” [164]. No other specimen has been collected from sea stars after 1936, so this might be an oddity or a rare encounter of an intermediate host.⁸: *Opisthopus transversus* can be found in a wide range of hosts [185]: inside the folds and openings of chitons, gastropods, bivalves, and holothurians. Campos et al. [185] suggested the crab to also live inside annelid worms like *Chaetopterus variopedatus*, which contrasts with the lifestyle of the above mentioned *Hospitotheres* and most pinnixine genera. Schmitt et al. [6] mentioned the species as living as a commensal symbiont inside the tubes of living *C. variopedatus*, and cite Hopkins and Scanland [69]. Hopkins and Scanland [69] described the hosts of *O. transversus* and stated that they found the largest specimens inside large species of gastropods and bivalves, somewhat smaller specimens inside holothurians and the smallest specimens inside the small gastropod *Bulla*, and inside worm tubes of living *C. variopedatus*. Hopkins and Scanland [69] suggested that the juvenile crabs to seek shelter until they can compete with the other crabs inhabiting the worm tubes (here *Pinnixa barnharti* and *Polynyx* sp. (Porcellanidae)). In failing to do so, the crabs will inhabit the available holothurians and gastropods. These observations might however suggest the worms to be an intermediate host for the crabs until they can move to their terminal host. In the absence of a particular obligate host choice of *O. transversus* is a derived or primitive character is not known as for now, but can be studied using molecular techniques [5].⁹: *Pinnotheres taichungae* was originally identified as *Pinnotheres bidentatus* [110], an ambiguous species from two localities in Japan [186]. The specimens described by T. Sakai (both sexes) and later by K. Sakai (only males) as *P. bidentatus* have been regarded as free-living [156,186]. Similarly, *P. taichungae* is also known as a free-living species: “Female crabs of this species may not necessary behaving as its congeners - commensal in bivalves, they may emerge into water columns during flooding tides, presumably, buried to substrata during ebb tides, since the water margin retreats up to 3 km on the shoreline at this time.” (about *P. taichungae*, as *P. bidentatus*, [110]). As McDermott [11] already stated, free living pinnotherines have probably been dislodged from their host in the collection procedure. The swimming setae on all ambulatory legs described by Hsueh and Huang [110] suggest the specimens to be hard staged males and females, maybe leaving their hosts for copulation [10].¹⁰: *Pinnotheres corbiculae* can only be found in the brackish-water clam *Corbicula japonica*, which makes it the only pinnotherid crab living in a brackish environment. T. Sakai [156]

described the species from 'Yamato-sizimi' clams (*C. japonica*), from the southern Sendai river (Kagoshima prefecture, Japan), and mentions another uncertain locality from Nagasaki. He mentioned the species to be the only pinnotherid living inside freshwater clams, but recent studies suggest *C. japonica* only to be found in brackish water in Japan and Korea where populations cannot live for long durations in environments with salinity greater than 21 psu or less than 0.3 psu [187]. *Pinnotheres corbiculae* has not been collected after the original description and appears to only be present in southern Japan. More specimens are needed find if *P. corbiculae* can be found in *C. japonica* in other parts of Japan, if water salinity is related to infestation rate, and if the species has evolved morphological adaptations to live in brackish environments.¹¹: *Pinnotheres gordonii* was found by Ng et al. [3] to represent the female of *Pinnotheres gordonae*.¹²: The unique host-choice of this crab was described by T. Sakai in 1961 (see [182]). Not baring any morphological adaptations, *Pinnotheres laquei* can be found in a common Japanese brachiopod, *Laqueus rubellus*, and supposedly in more species of brachiopods [170]. Although the external morphology of this brachiopod resembles bivalves, the internal morphology is unique to the group. Feldmann et al. [170] described the positioning and commensal lifestyle of *P. laquei* in its host, and mentions this species to be the only crab (and one of a few invertebrates) to live in association with a brachiopod.¹³: While the original description by Nobili [188] of *Trichobezoares pilumnoides* did not mention any hosts, Laurie [189] two female specimens from holothurians and one female specimen from a sponge [29]. Laurie's observation is probably a rare finding of a soft-shelled female leaving the holothurian host. There is an additional (new) species that is found in sponges from the Caribbean [68], but the sex of this species is undetermined and this might also be just a male crab wandering between hosts.¹⁴: *Tumidotheres maculatus* can be found in a wide range of bivalve hosts, but also in the tubes of worms and sometimes free-living in sandy substrates [6]. All other species of *Tumidotheres* are only found in bivalves, and since *T. maculatus* is found to be closely related to its congeners [5,98], it is safe to say that the free-living and specimens of this species inhabiting worm tubes were collected during a swarming event, as described by Derby and Atema [10] and Campos [8]. We therefore chose to only list the bivalve associates.

4. Phylogenetic Significance of Adaptive Features and Future Perspectives

The phylogenetic significance of the morphological adaptations can be examined by linking the adaptations with recent molecular phylogenetic reconstructions [5,18]. Most adaptive features seem to be the result of convergent evolution, rather than shared synapomorphies [5], and these are: the size, ornamentations, colour patterns, and setation of the carapace, in addition to the differences between male and female carapaces; the morphology of the eyes, rostrum, third maxillipeds [85], and the specialised feeding structures on the chelipeds. More data are needed to confirm if the adaptive features of the ambulatory legs bear any phylogenetic significance (especially the features of the dactyli).

Although many more species need to be included in future molecular analyses, a few adaptive features could be phylogenetically relevant characters that are taxonomically important. The development of swimming setae in both males and females in their hard stages for copulation in open water (the ‘second strategy’ in [8]) can be found in some genera listed within the West Atlantic and eastern Pacific ‘Pinnotherinae II’ group (sensu [5]). The swimming setae can be found in *Calyptraeotheres*, *Fabia* (specifically *F. subquadrata*), and *Tumidotheres*, and may be used by *Fabia emiliai* (de Melo, 1971) and *Juxtafabia muliniarum* (Rathbun, 1918), judging from the swimming setae seen in the presented figures [116,163]. This strategy is not known from the other species clustering in the same lineage: *Tunicotheres moseri*, *Holothuriophilus pacificus* (Poëppig, 1836), *Pinnaxodes chilensis*, and the species in the *Dissodactylus* complex.

All these species have a firm to hard carapace in the ‘post-hard’ stages of the female, which is not the case in the other analysed branches of pinnotherine evolution and might be an adaptation associated with open-water copulation. Such ‘swarming’ behaviour is also known from some *Austrotheres* species, and female swimming setae are known from some members of *Afropinnotheres*, *Nepinnotheres*, *Ostracotheres*, and *Pinnotheres* (all not included in the phylogenetic reconstructions [5]). Those are all species from the Indo-West Pacific and will probably be placed elsewhere on the tree later on.

Another character was found in all branches of the ‘Pinnotherinae II’ [5]: the relatively large and robust chelae present in all species within the *Dissodactylus* complex (all members within *Dissodactylus* and *Clypeasterohilus*), all species of *Tunicotheres*, *Tumidotheres*, *Holothuriophilus*, *Pinnaxodes*, *Calyptraeotheres*, and *Fabia subquadrata*, *F. emiliai*, and *Juxtafabia muliniarum*. Although the feeding strategies and the use of chelae might differ between species (e.g., strictly parasitic feeding on host tissues in *Dissodactylus* using their chelae, ‘grooming’ in *Fabia* using the setal comb, and filter feeding in *Pinnaxodes* using the third maxillipeds), the chelae are very different from the feeble chelipeds of other crabs included in the phylogenetic reconstruction [5] like the Vietnamese bivalve-associated *Solenotheres prolixus* Ng & Ngo, 2010, the Chinese/Thai *Amusiotheres obtusidentatus* (Tai et al., 1980), and the European *Pinnotheres pisum*.

The large, robust chelae are not limited to the ‘Pinnotherinae II’ species (for example, *Nepinnotheres pinnotheres*, and *Alain raymondi* Ahyong & Ng, 2008 also possess relatively large chelae), and one species with slender chelae, *Zaops ostreum*, might be more closely related to *Tumidotheres* than previously thought [98] and might cluster within the ‘Pinnotherinae II’.

Although most recent evolutionary studies on pea crabs have been focussing on a small subgroup of the Pinnotherinae [98], or the other pinnotherid subfamilies [18], the study by Palacios Theil et al. [5] provides a sufficiently large base for further studies on the complete pinnotherine evolution. Genetic barcodes of more species, especially those from the Indo-West Pacific, are needed to solve taxonomic problems, but also to build a complete and robust phylogeny.

A large-scale revision of Indo-West Pacific pinnotherids will be published in the near future [49]. Using a combination of phylogenetic reconstructions with morphometric analyses and detailed host information, detailed insights regarding patterns of convergent evolution and adaptive radiation of morphological structures can be obtained. such studies will constitute a crucial contribution to our understanding of pinnotherid biodiversity.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1424-2818/12/11/431/s1>, A video of the rotating 3D models of the CT-scanned material from Figures 1 and 3 can be found in the supplementary data.

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