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The History of Sexual Dimorphism in Ostracoda (Arthropoda, Crustacea) Since the Palaeozoic

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1. Introduction

Studies of the origin and history of sex in organisms are important for elucidating life-history strategies and reproductive modes, and are an essential component of the study of evolutionary biology [1]. Sexual dimorphism (*i.e.*, morphological differences between males and females) and its relationship to reproductive modes in both living and extinct/fossil organisms is a key aspect of such studies [2] [3].

Ostracods (Arthropoda) are the only organisms useful for investigations of the long-term history of sexual dimorphism during the last ca. 500 million years since the early Palaeozoic, *i.e.*, Ordovician (ca. 490 Ma = 490 million years ago) [4]. Ostracods are a class of small crustaceans (Figures 1 and 2) of which the adult form is around 1.0 mm in length, that inhabit most aquatic areas; *e.g.*, marine, brackish, and freshwater conditions (Figure 3) [5] [6]. Most ostracods have the ability to reproduce sexually, except for a part of species capable of reproducing asexually (parthenogenesis). The most distinctive feature of ostracods is the calcareous carapace (Figures 1 and 2). Species with strongly calcified carapaces are relatively easily fossilised, and ostracods are abundant in sediments globally starting from the early Ordovician [7]. In contrast, the proteinaceous (= 'chitinous') soft body with appendages (Figure 2) is rarely fossilised due to a lack of mineralised parts, and as a result an ostracod fossil typically consists only of the hard carapace. However, this is sufficient for both recent and fossil specimens to be identified to the species level, based on various carapace morphological characteristics (Figures 1 and 2).

Similar to other crustaceans such as decapods, ostracods grow by moulting (ecdysis; Figure 4). For example, in one ostracod order, the Podocopida, there are usually eight moult stages between egg and adult, with the last moulting being the first sexually mature stage. Carapace and appendage sexual dimorphism can be recognised during the last adult stage (Figures 5 and 6), and to a lesser degree in late juvenile stages [8–10].

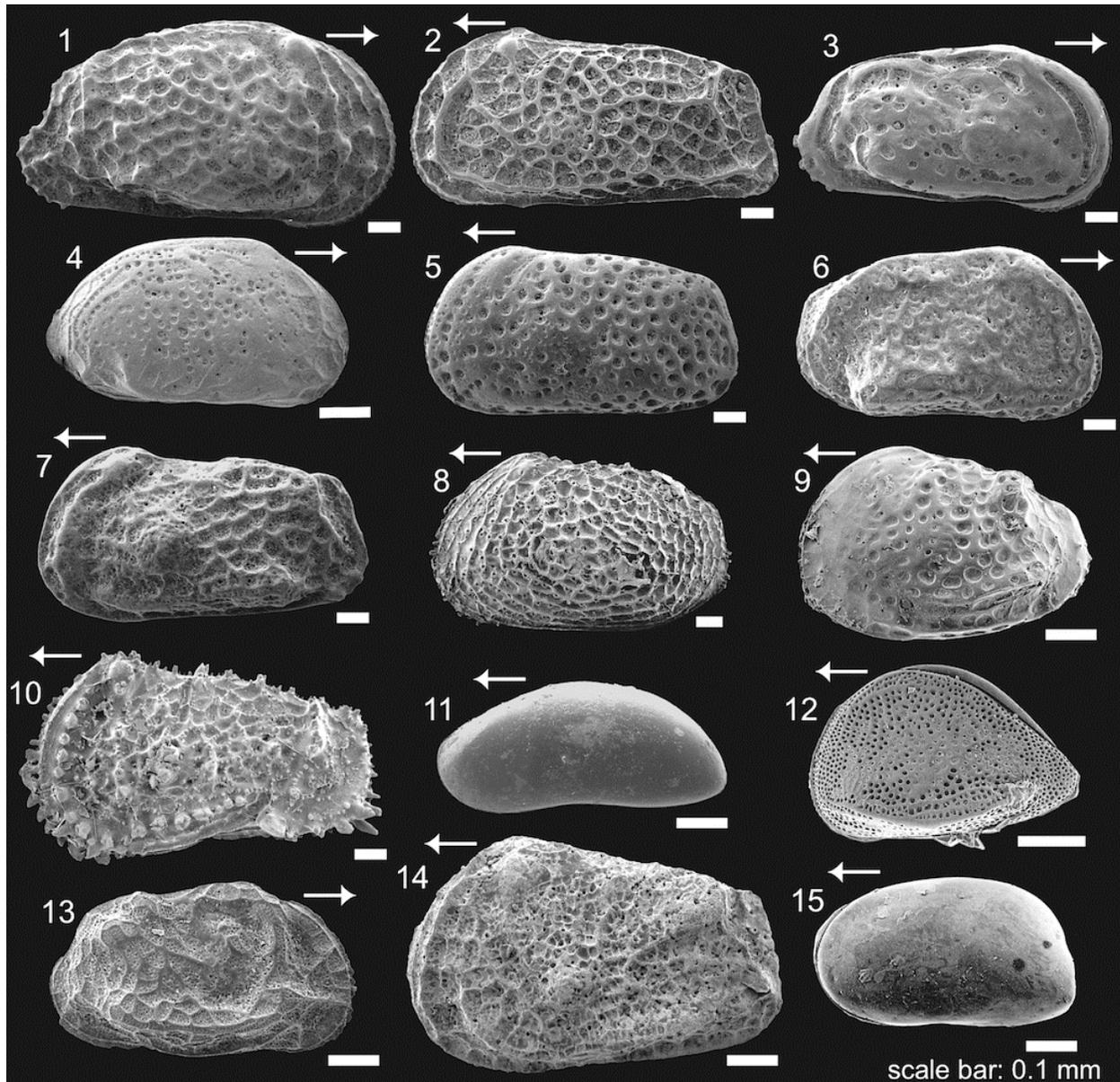


Figure 1. SEM images of fifteen ostracod species (Podocopida) from modern coast of southern Okhotsk Sea, modified from Ozawa (2012). 1: *Baffinicythere ishizakii*, RV, 2: *Baffinicythere robusticostata*, LV, 3: *Cornucoquimba alata*, RV, 4: *Howeina camptocytheroidea*, RV, 5: *Johnnealella nopporensis*, LV, 6: *Pectocythere* sp., RV, 7: *Laperousecythere robusta*, LV, 8: *Rabilimis septentrionalis*, LV, 9: *Robertsonites hanaii*, LV, 10: *Acanthocythereis dunelmensis* s.l., LV, 11: *Argilloecia toyamaensis*, LV, 12: *Cytheropteron carolae*, LV, 13: *Palmenella limicola*, RV, 14: *Elofsonella* cf. *concinna*, LV, 15: *Krithe* sp., LV. Arrows indicate anterior. LV: left valve, RV: right valve.

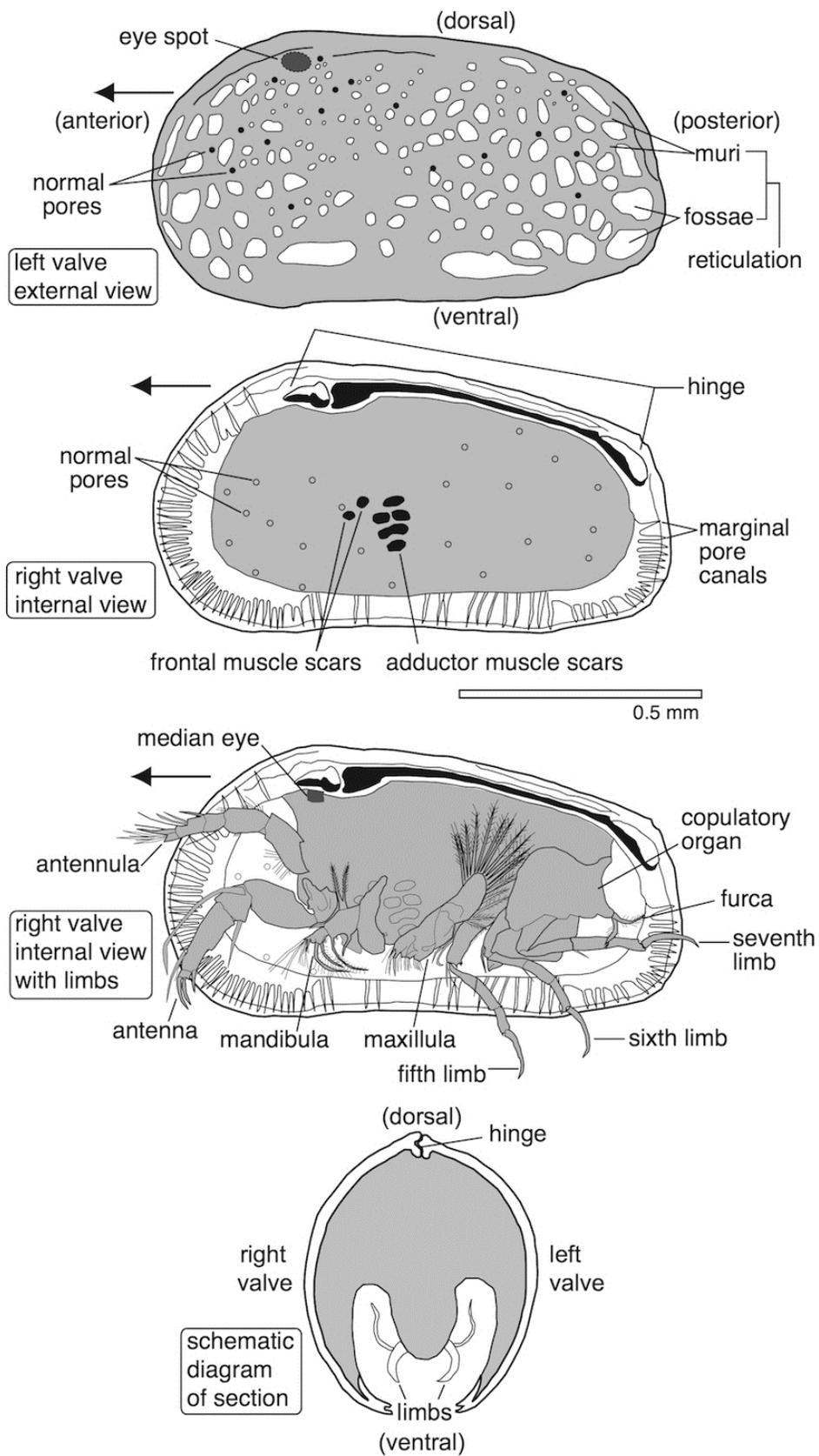


Figure 2. Morphology of ostracod male, based on *Hemicythere villosa* (Podocopida), modified from Horne *et al.* (2002)

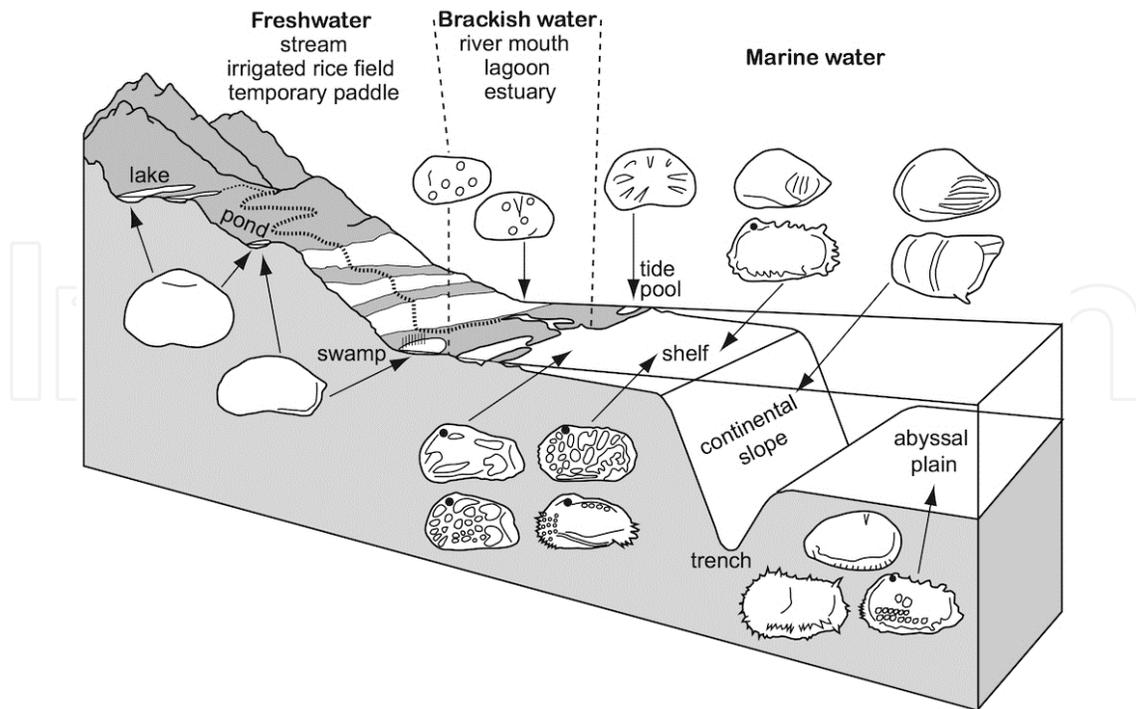


Figure 3. Schematic hypothetical profile of terrestrial aquatic to abyssal habitats of living ostracods progressing toward coastline, modified from Benson (2003).

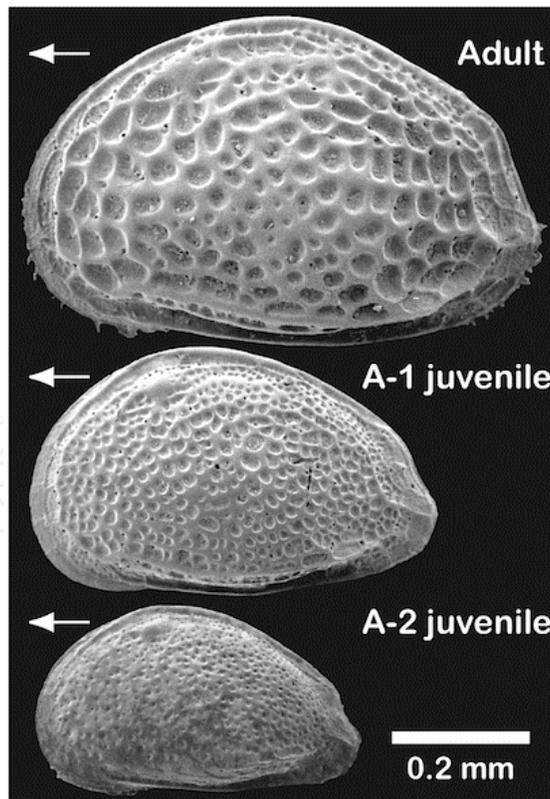


Figure 4. SEM images of last three molting stages in *Aurila* sp. of Ozawa and Kamiya (2009) (Podocopida) from the modern coast of northeastern Japan Sea, modified from Ozawa (2012). Arrows indicate anterior.

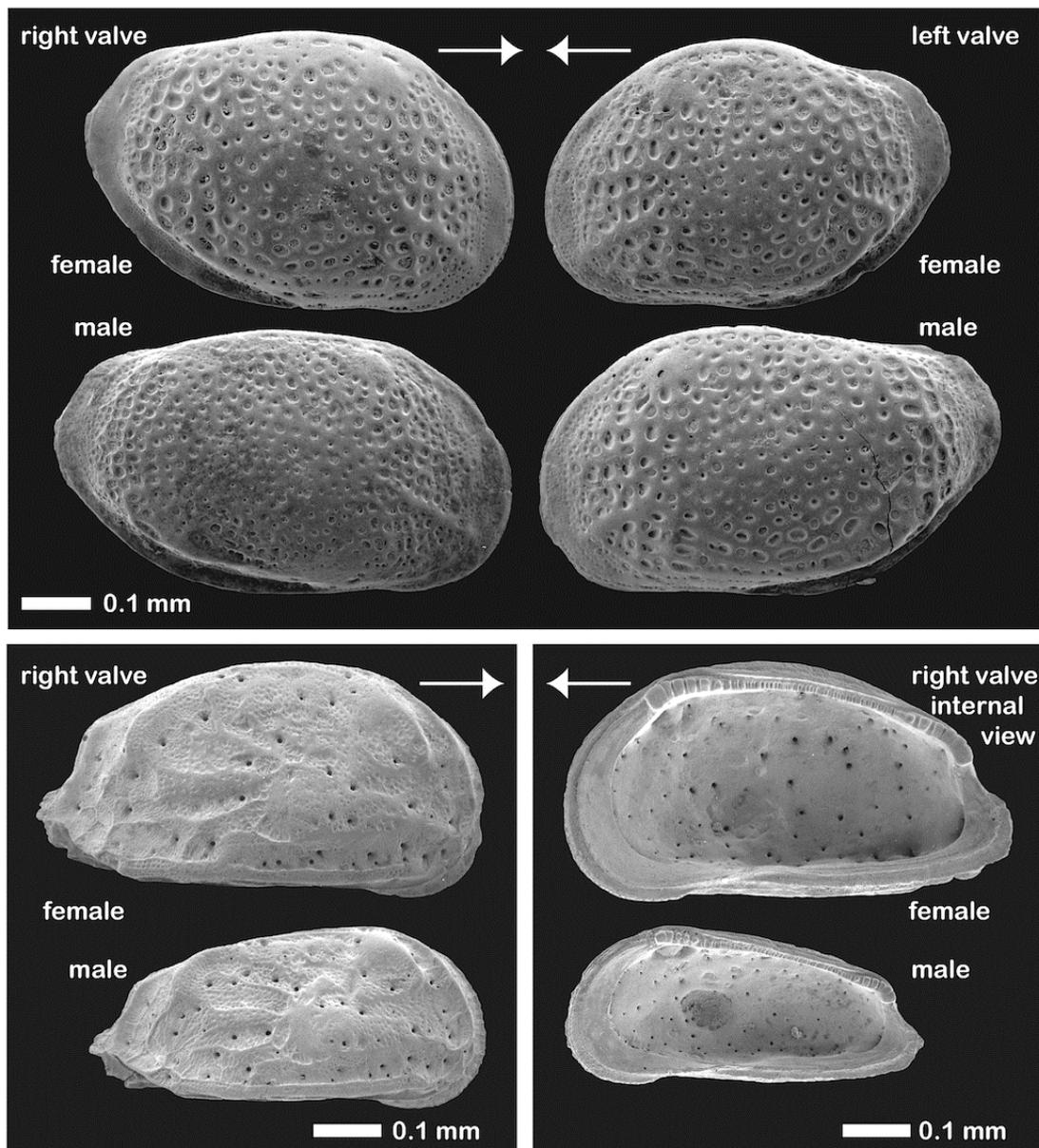


Figure 5. SEM images of carapaces in male and female of *Loxoconcha kamiyai* (upper two rows) and *Finmarchinella hanaii* (lower two rows) (Podocopida) from Quaternary deposits of central Japan, modified from Ozawa (2012). Arrows indicate anterior.

In organisms—other from ostracods—with abundant fossil records, there are very few cases of likely sexual dimorphism. One such case is the speculated “sexual dimorphism” of extinct ammonites (molluscs) discovered since the 1860s [11]. Many occurrences of ammonite fossils have been reported globally, and with respect to shell size, two different forms exist in particular groups of ammonites: the larger ‘macroconch’ and smaller ‘microconch’ within a probable single species from such genera as *Graphoceras*, *Ludwigina*, *Perisphinctes*, and *Yokoyamaceras* from Jurassic and Cretaceous strata [12–14].

However, ammonite sexual dimorphism has long been debated. In addition, whether microconchs of ammonites are males or females remains speculative [11] [15]; therefore,

which ammonite form constitutes the male shell remains uncertain. In contrast, because ostracods are living organisms, we can examine their soft body and appendages in detail, including rarely fossilised parts such as the copulatory organs of males and females. Furthermore, we have excellent an fossil record of ostracods extending back to the early Palaeozoic, so we can compare modes of sexual dimorphism by comparing living to extinct fossil species. Therefore, we are able to determine the detailed characteristics associated with sexual dimorphism and their function in ostracods more easily than in extinct organisms such as ammonites.

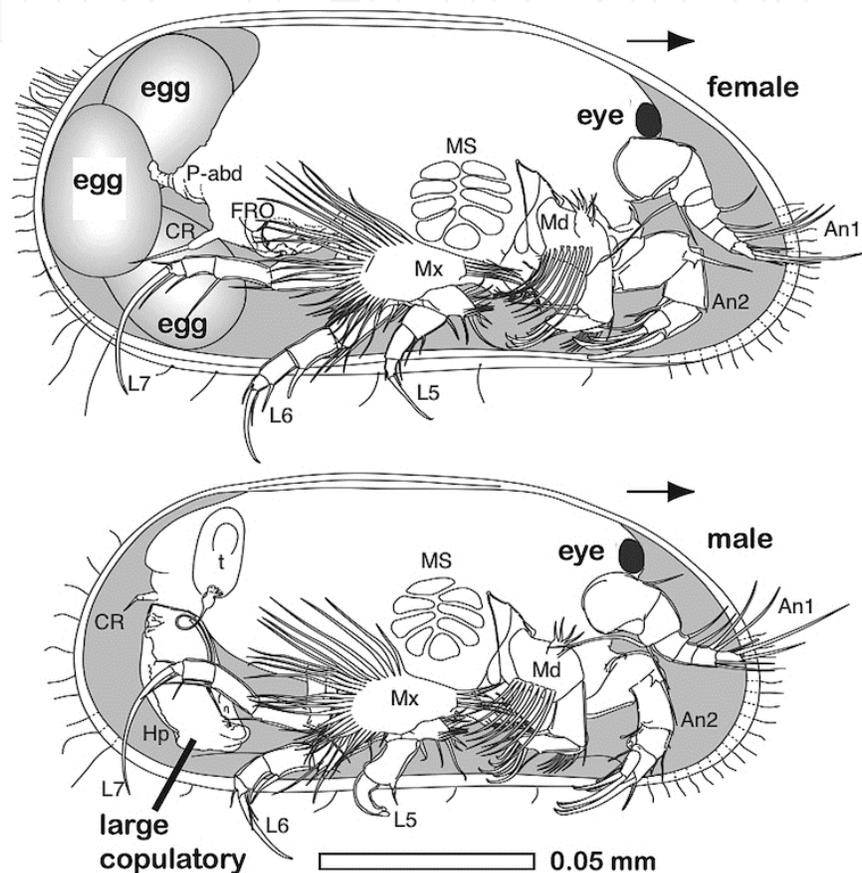


Figure 6. Morphology of female and male with right valve removed (one of each pair of appendages drawn for clarity) of *Vestalenula cornelia* (Podocopida) from modern springs in Yaku-shima Island of southwestern Japan, modified from Smith *et al.* (2006). Arrows indicate anterior.

Due to these unique traits, ostracods are the only organisms on earth that are useful for studying the history of sexual dimorphism since the Ordovician. Representative examples of sexual dimorphism within ostracods, mainly in species from Japan, are first introduced. This chapter then introduces one example of a sexually dimorphic feature accompanied by heterochrony (paedomorphosis). Recently, our research group found a rare case of sexual dimorphism in ostracod hingements with a paedomorphic character within only one phylogenetic group of one family. This morphology could be an important characteristic for evaluation of the history of sexual dimorphism in ostracods since the early Palaeozoic [16]. The author discusses this together with the history of ostracod sexual dimorphism from the

Palaeozoic to Recent, reviewing another case of ostracod sexual dimorphism with paedomorphosis reported by [17].

2. General features of ostracods for taxonomy, ecology, and morphology

Ostracods are a class of small crustaceans (Figures 1 and 2), the adult form of which is typically ca. 1.0 mm in length. They are not generally well known to many people except for researchers of fossils or living crustaceans due to their small size and lack of commercial significance compared to other crustaceans; *e.g.*, shrimps and crabs.

Class Ostracoda consists of the following six orders: Podocopida, Platycopida, Palaeocopida, Leperditicopida, Myodocopida, and Halocypridina [10]. This chapter focuses mainly on ostracod species belonging to the order Podocopida, which consists of more than 20,000 named living and fossil species distributed globally, because Podocopida is the most diversified taxonomic group in class Ostracoda (Figure 3) [10]. The well-known bioluminescent organism 'the sea firefly' (called 'umi-hotaru' in Japanese) is a kind of ostracod but belongs to another order, Myodocopida.

Ostracods occur in most aquatic environments on earth (Figure 3), such as the deep sea to a depth of several thousands of meters, through to shallow seas on the continental shelf [5]. They also live in rock pools in intertidal zones, brackish water areas at river mouths, lagoons and estuaries, freshwater lakes, ponds, irrigated rice fields, and temporary puddles. Most species are benthic throughout their lives, and crawl on or through the surface sediment and among aquatic plants [10]. A number of interstitial species, which live between sediment particles, are also distributed globally [18] [19].

The most distinctive feature of ostracods is the calcareous bivalved carapace (or shell), consisting of two valves that completely envelop the soft body and all appendages (Figures 1 and 2) [10]. Various types of appendage are protruded between opened valves for locomotion, feeding, and reproduction. The two valves (termed right and left) are connected by a hingement running along the dorsal margin (Figure 2). The word ostracod (or 'ostracode') is derived from Greek word 'ostrakon', which means 'a shell'. This carapace (or shell) has various morphological characteristics (Figures 1 and 2) that allow detailed taxonomic and phylogenetic studies to be performed on both living and fossil specimens [20–22].

Like other crustaceans such as decapods, ostracods grow by moulting (ecdysis; Figure 4). For example, in Podocopida, there are usually eight moult stages between egg and adult [20]. Species with strongly calcified carapaces, such as most marine species, are relatively easily fossilised. Ostracods are abundant in sediments globally, beginning in the early Ordovician (ca. 490 Ma) [7]. The proteinaceous (= 'chitinous') soft body and appendages are rarely fossilised due to a lack of mineralised parts, with rare exceptions, such as preservation of the soft parts of Silurian fossils [23]. Therefore, an ostracod fossil typically consists only of the hard-calcified carapace; however this is sufficient for identification of both modern and fossil specimens to the species level based on various carapace morphological characteristics.

In particular, the surface ornamentation (reticulation, fossae, muri, eye tubercle, ridges and so on), hingement type, muscle scar morphology (Figures 1 and 2), and pore shape and numbers are useful for ostracod taxonomy [24]. With living specimens, the morphology of male copulatory organs and other appendages are also used for species identification, similar to identification techniques used for other crustaceans, such as decapods [24–26]. Fossil ostracods are commonly utilised by palaeontologists as important palaeoenvironmental and stratigraphic (geological age) indices, and have long been used in oil and gas exploration [4] [27–29].

3. Representative examples of ostracod sexual dimorphism in extinct and living species

Like other crustaceans such as crabs, ostracods grow by moulting (ecdysis; Figure 4). For example, in Podocopida, there are usually eight moult stages between egg and adult, and the last moulting is the first sexually mature stage [20]. The adult stage is termed 'A', whereas juvenile stages are numbered; *e.g.*, 'A-1' (*i.e.*, one stage before the adult) and 'A-2' (two stages before the adult), as shown in Figure 4 [20]. Sexual dimorphism (morphological differences between males and females) is commonly found on carapaces and appendages [4, 9, 30], as shown in Figures 5 and 6, and is especially recognisable during the last adult stage (A), and to a lesser degree in the later juvenile stages, such as A-1.

This article introduces representative examples of sexual dimorphism in the last adult stage from the Palaeozoic to Recent, primarily in representative Podocopida from within and around Japan.

3.1. Carapace shape and size

3.1.1. Palaeozoic example in an extinct group

A well-known example of ostracod sexual dimorphism of the carapace exists in species of the family Beyrichiidae of the order Palaeocopida from the Ordovician to the Permian (Figure 7) [4] [31]. In many species of this family, distinct sexual dimorphism is seen in the adult stage; *i.e.*, females possess a large bulbous swelling in the antero-ventral part of each valve. These swellings that open internally into the domicilium found in species of this family are known as brood pouches (or cruminae) [25].

Species of this family were already extinct at the end of Palaeozoic, so various functions for this kind of pouch, including brood care, have been speculated [15]. Valves and carapaces of juvenile stages within this pouch were found in two species of the genus *Beyrichia* (*B. kloedini* and *B. jonesii*) in the family Beyrichiidae [25]. Based on the example of those two species, it became clear that these were probably brood pouches. An alternative (or perhaps double) function as buoyancy aids has been proposed by some researchers; thus firm evidence that all pouch types were used only for brood care has not yet been found [25]. It has been

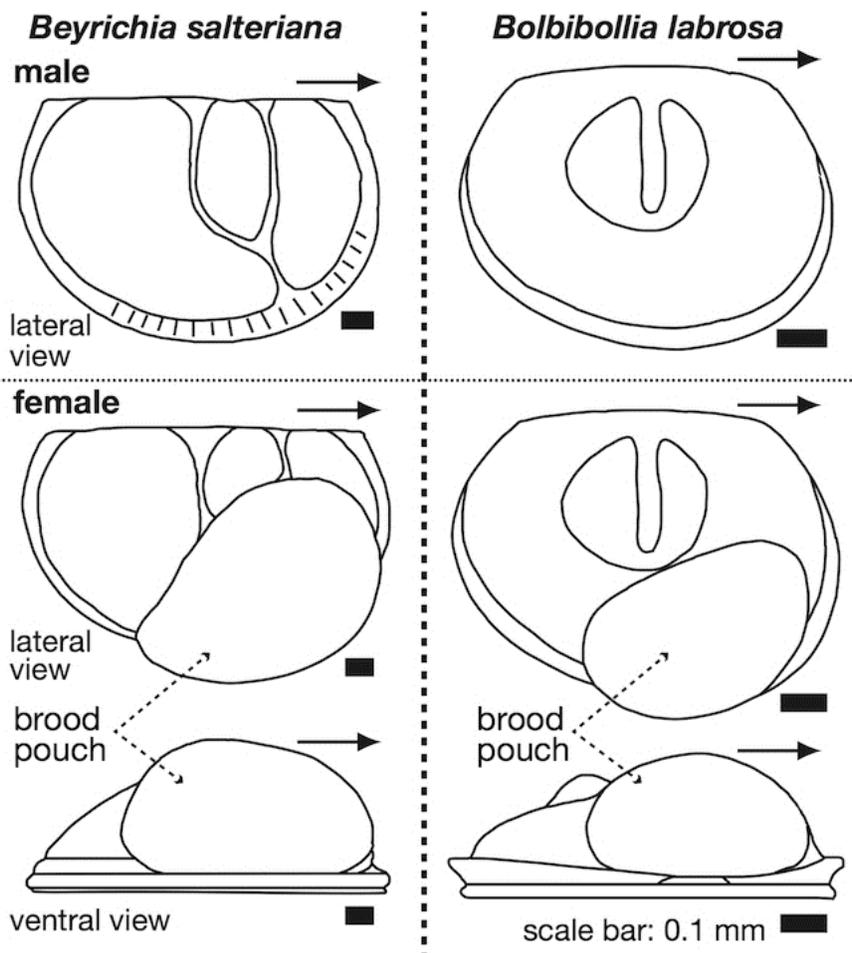


Figure 7. Carapace outlines of female and male of *Beyrichia salteriana* and *Bolbibollia labrosa* in Family Beyrichiidae (Palaeocopida) from Silurian deposits of Sweden and Canada respectively, modified from Benson *et al.* (1961). Arrows indicate anterior.

inferred that species of this family inhabited Palaeozoic shallow-marine shelf-water environments [7]. Thus, a reasonable interpretation of pouch function in this family is needed to clarify the detailed evolutionary processes of the ecology and reproductive modes of Palaeocopida in Palaeozoic shallow-marine water areas.

3.1.2. Mesozoic example in an extinct species

Carapace shape and size sexual dimorphism is common in ostracods, and males can be larger or smaller than females [4]. One example from the Mesozoic is a non-marine species of the podocopid genus *Cypridea* [15] [32]. This genus occurred only during the Jurassic and Cretaceous, and is not found in Cenozoic deposits. The shape and size of *Cypridea subvaldensis* (Figure 8) from Cretaceous sediments in northeastern China was studied, and the differences between the two forms were recognised to represent sexual dimorphism within a single species [32].

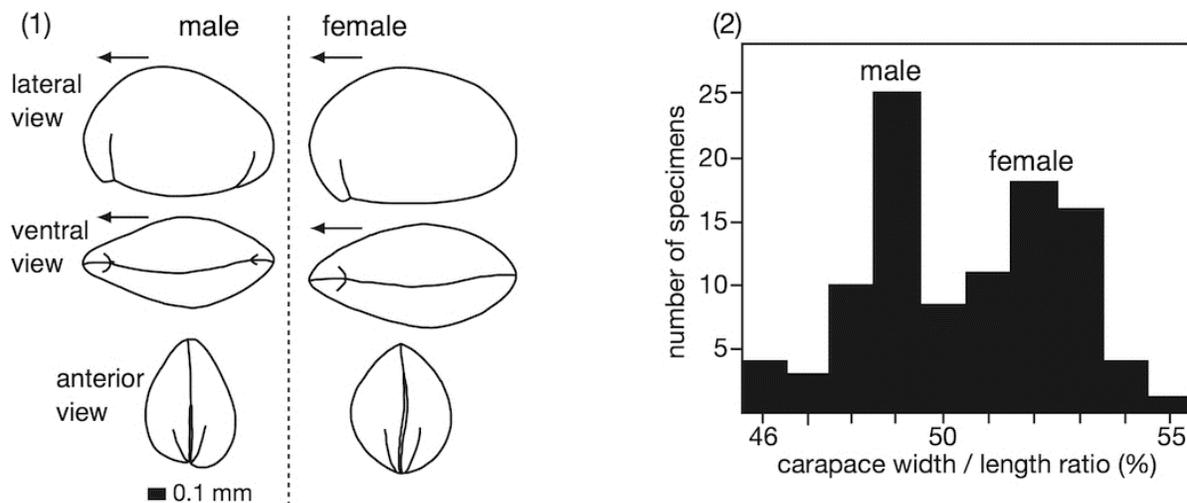


Figure 8. (1) Carapace outlines of female and male of *Cypridea subvaldensis* (Podocopida) in lateral, ventral and anterior views from Cretaceous deposits in northeastern China, modified from Hanai (1951). Arrows indicate anterior. (2) Frequency of carapace length/ width ratio (%) for specimens of *Cypridea subvaldensis* in Cretaceous fossil assemblages from northeastern China, modified from Hanai (1951).

Carapace sizes (length and width) of approximately 100 specimens of this species in one fossil assemblage from sedimentary rocks at one site were measured [32]. Based on the frequency of the carapace length/ width ratio, Hanai suggested that the two different-sized forms represent male and female forms within a single species. He proposed that the male carapace is smaller and narrower than that of the female, with a more arch-shaped outline along dorsal margin. This was based on the carapace shapes of the sexes of the single living species of a related genus, *Chlamydotheca*, in which the male form is slightly smaller and has a more arch-shaped dorsal margin than the female form.

3.1.3. Cenozoic and recent examples

A number of Japanese Cenozoic and living Podocopida genera, such as *Finmarchinella*, *Loxoconcha*, *Semicytherura* and *Vestalenua* (e.g., Figures 5 and 6), can be recognised by their distinct carapace shape and size sexual dimorphism [2, 9, 16, 17, 33]. In many cases, the male forms of these podocopids have relatively longer and narrower carapaces than the females (Figures 5 and 6) [34–36]. For example, in one modern species, *Bicornucythere bisanensis*, which is found in shallow brackish water areas in Japan, the male carapace is slightly more slender than that of the female (Figure 9) [8, 37, 38].

Primarily in podocopid species, female carapaces show greater posterior inflation than those of males, as in species of the genera *Metacypris* and *Xestoleberis* from Japan (Figure 10) [26] [39]. This kind of sexual dimorphism is more distinct in the adult than the juvenile stages [9]. In some cases, the male carapaces may be inflated posteriorly to accommodate relatively large copulatory organs, or it may have a more pronounced posterior keel, whereas in podocopid and myodocopid taxa with brood care, female carapaces are larger and more inflated than in the male [25] [40]. Eggs and the first two- or three-stage juveniles are retained within the posterior part of the domicilium. The shape of adult male valves of

many Myodocopida species differ greatly from those of juveniles and females, and females are sometimes smaller than males even if there is brood care within the group [10].

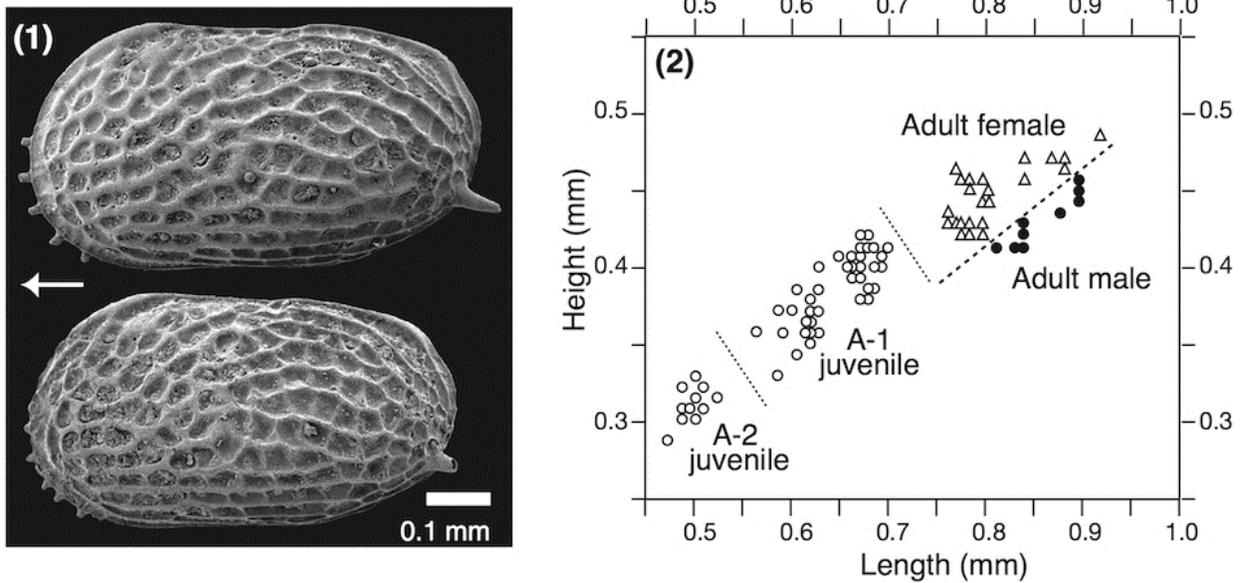


Figure 9. (1) SEM images of carapaces in male (upper) and female (lower) of *Bicornucythere bisanensis* (Podocopida) from Quaternary deposits of central Japan, modified from Ozawa (2009). Arrows indicate anterior. (2) Diagram for valve size (length and height) of this species in adult female, adult male, A-1 and A-2 juveniles, modified from Ozawa (2009).

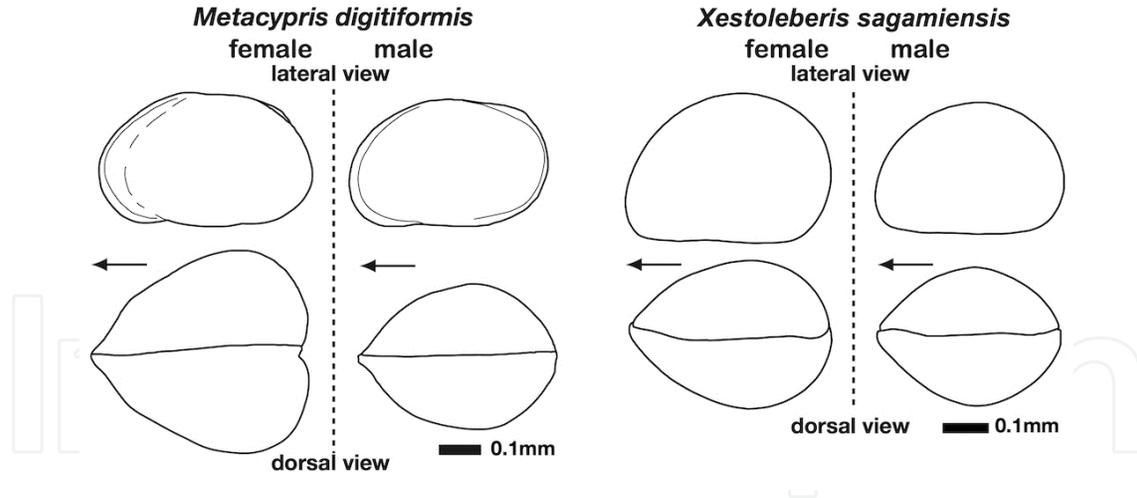


Figure 10. Carapace outlines of female and male in lateral and dorsal views of *Metacypris digitiformis* and *Xestoleberis sagamiensis* (Podocopida) from modern water areas of central Japan, redrawn from Smith and Hiruta (2004) and Sato and Kamiya (2007) respectively. Arrows indicate anterior.

The sexual behaviour of ostracods is diverse, and seven different types of brood care have been recognised in various lineages from Palaeozoic to Recent [25] [41]. These various types have arisen independently in several marine and non-marine lineages of ostracods, so diverse carapace shapes acting as brood pouches are found. The ability of the ostracod female to brood eggs or juveniles within the carapace might protect the young from severe

environmental fluctuations and predation [25]. Brood care may be advantageous for the dispersal of some groups of non-marine water ostracods, such as species in the subfamily Timiriaseviinae (e.g., genus *Metacypris*), the eggs of which may not be desiccation-resistant. The variety of brood care modes and carapace brood pouches that evolved in unrelated ostracod lineages is one of the most remarkable reproductive characteristics of ostracods, because other crustaceans exhibit a limited number of brood-care solutions [25] [42].

3.2. Carapace surface ornamentation

The podocopid species *Callistocythere pumila* favours very shallow brackish water environments around 1 m depth in inner bay and open lagoon areas near river mouths in Japan [43] [44]. It can be recognised by its conspicuous sexual dimorphism of carapace surface ornamentation (Figure 11). The female form has relatively distinct ornamentations on the entire carapace, such as numerous deep fossae [43] [44]. However, the male form has an extensive weakly ornamented area, especially in the median part of the carapace on a relatively slender valve (Figure 11).

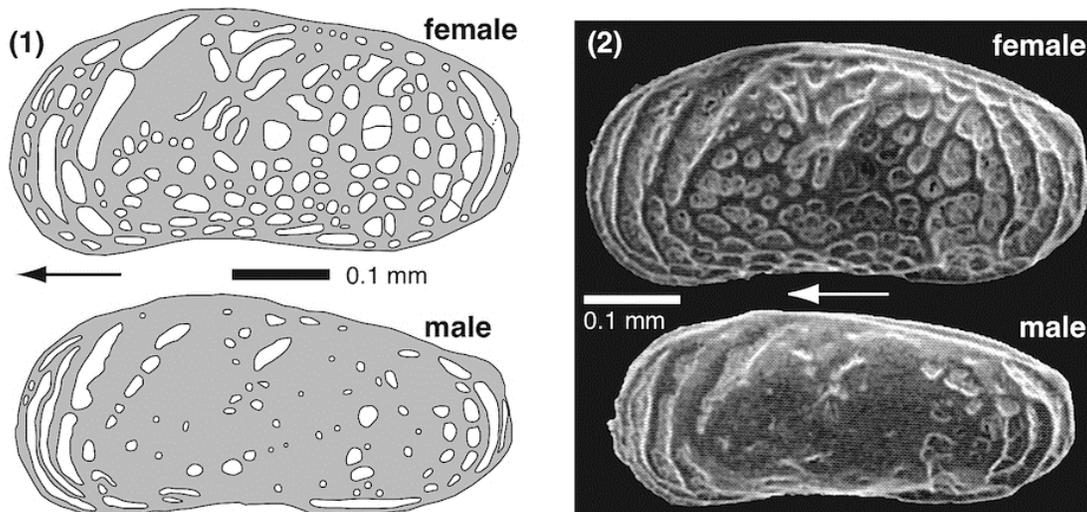


Figure 11. (1) Schematic patterns of fossae on carapace surface in female and male of *Callistocythere pumila* (Podocopida) in lateral view from modern brackish water area of central Japan, redrawn from Tsukagoshi (1998). (2) SEM images of carapaces in male and female of this species in lateral view, from modern brackish water area of central Japan, modified from Kamiya *et al.* (2001). Arrows indicate anterior.

The carapace morphology of this species occupies an intermediate taxonomic position between two genera, *Callistocythere* and *Leptocythere*; the female and male forms resemble the former and latter genera, respectively [43]. Due to these morphological differences between males and females, they were originally described as a different species [45] [46]. However, those two forms have recently been considered to represent males and females of a single species, *Callistocythere pumila*, based on the detailed description of soft parts [43]. As yet no reasonable interpretation of the function of sexually dimorphic ornamentation has been postulated. The significance of this dimorphism for the ecology or life-history of *C. pumila* requires investigation to clarify the detailed evolutionary processes of the ecology of Cenozoic brackish water podocopids.

3.3. Appendages

3.3.1. The example of *Bicornucythere bisanensis*

Bicornucythere bisanensis (Podocopida) predominantly inhabits shallow brackish water areas in inner bay areas near river mouths in and around Japan [47]. Sexual dimorphism of the appendages of this species has been known since the 1910s [45, 48, 49]. The right fifth limb (= first thoracic leg) of the male is uniquely thicker and slightly shorter than the left fifth limb [30] [50]. The central podomere of the right fifth limb is very inflated, and is 1.5-times the thickness of that of the female. Thus, the fifth limb of the male in this species shows asymmetry, and this unique morphology has not been observed in the female. This is a representative example of sexual dimorphism in podocopid appendages.

The ecological function of this dimorphism has been clarified by [30] [50]. They observed its mating behaviour under experimental conditions from detailed video recordings. According to their observations (Figure 12), this short and thick podomere in the right fifth limb of the male is an adaptation for courting behaviour, where the male rotates the female's carapace three or four times using the right fifth limb just before mating (Figure 12). Thus, this right limb (especially the central podomere) is thicker and shorter than both the male left limb and the female's fifth limb to facilitate holding and rotating the female carapace. The thick podomere of the male right fifth limb is markedly more muscular than either that of the left side and those of the female, facilitating this behaviour [15, 30, 37].

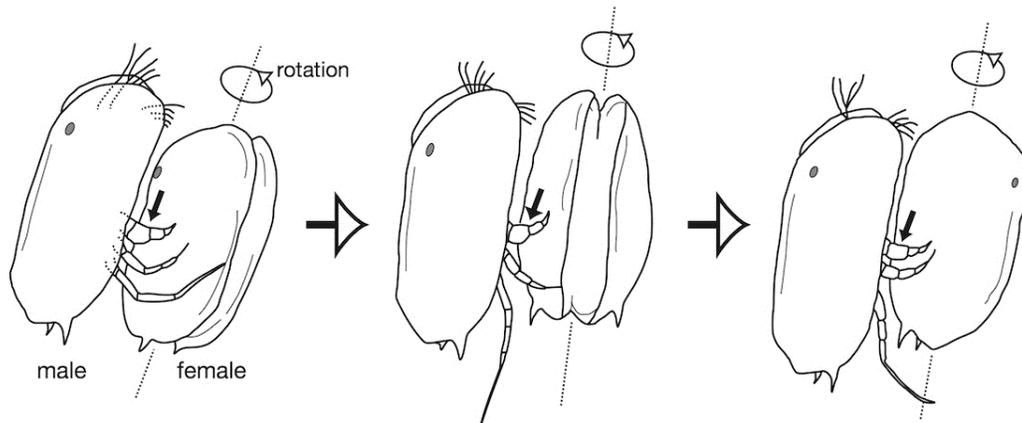


Figure 12. Schematic profile of courting behaviour (= rotation of female carapace by male's fifth limb) just before mating behaviour, indicating the location of its fifth limb by black arrows, for modern *Bicornucythere bisanensis* (Podocopida) from modern inner bay area of central Japan, modified from Abe and Vannier (1991).

3.3.2. The example of *Vargula hilgendorfi*

Several examples of sexual dimorphism of appendages other than the fifth limb in living marine species have been reported for *Vargula hilgendorfi* (Myodocopida) [51]. This species inhabits shallow marine water environments, and the relative size of the furca at the posterior part of the soft body compared to the length of the entire carapace differs between the sexes. The male's furca is relatively larger than that of the female. According to detailed

observations of its ecological behaviour under experimental conditions [51], this species pushes off from sea-bottom sediments just before swimming in water, especially using the furca (Figure 13). Based on observations of video recordings, the male tends to swim around much more actively than the female; thus explaining the function of the relatively large furca in the male [37].

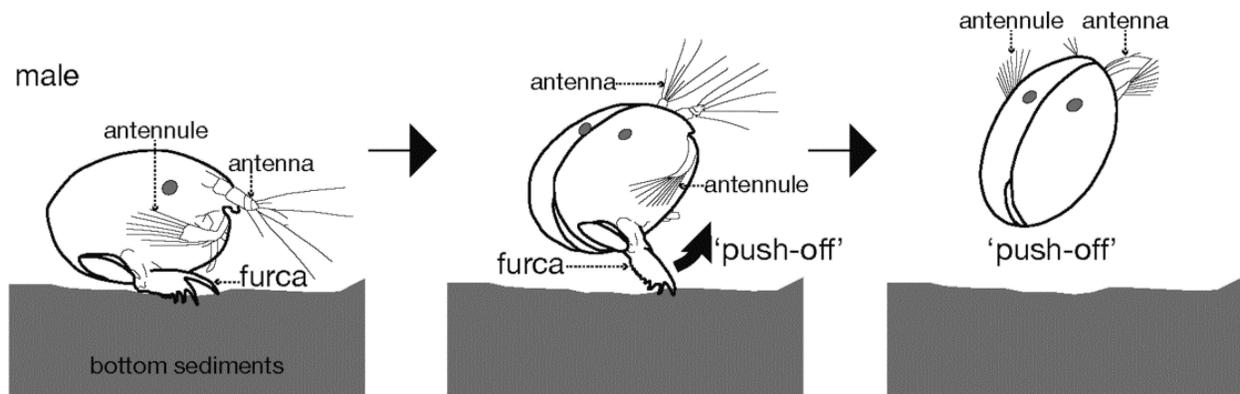


Figure 13. Schematic profile of ‘push-off’ behaviour just before swimming for modern *Vargula hilgendorfi* (Myodocopida), indicating the location of its furca by black arrows, modified from Vannier and Abe (1993).

A further four examples of sexually dimorphic appendages and eyes are found on *Vargula hilgendorfi*, as follows: (a) the existence or absence of two suckers on the first appendage (antennule), (b) different numbers of bristles on the first appendage, (c) different sizes of the basal part of the second appendage (antenna), (d) different sizes of compound eyes [37, 51]. The probable function of (a) is support by the male form of the female carapace during mating behaviour. However, the functions of the other sexually dimorphic characteristics (b)–(d) remain unclear. The Myodocopida first appeared during the early Palaeozoic (Ordovician), and still inhabit many marine environments [7]. Therefore, these other sexually dimorphic characteristics are interesting examples of myodocopid ostracod morphology, and indicate the evolutionary processes associated with their ecology, including mating behaviour and reproduction modes, since the Palaeozoic.

4. Sexual dimorphism in the inner carapace, with Paedomorphosis

Sexually dimorphic and paedomorphic morphological characteristics of the inner carapace were recently reported in two unrelated podocopid taxonomic groups from Japan [16] [17]. These, together with their ecological and evolutionary significance for ostracods since the Palaeozoic, are reviewed below.

4.1. Hingement morphology and dimorphism

The genus *Loxocorniculum* of the family Loxoconchidae was established [65] based primarily on modern *Loxocorniculum fischeri* from the Caribbean Sea, and is characterised by a horn-like protuberance on the postero-dorsal corner of the carapace. However, except for the

horn-like protuberance, the carapace appearance of species of this genus, including *Loxocorniculum mutsuense* from Japan, is very similar to that of the genus *Loxoconcha* as noted by Ishii *et al.* [63]. The phylogenetic independence of *Loxocorniculum* in Japan as a genus distinct from *Loxoconcha* has been debated [16]. Therefore this chapter tentatively includes *Loxocorniculum mutsuense*, first proposed as a new species from Japan by [66], in the genus *Loxoconcha* following the opinion of Ishii *et al.* [63].

The ostracod genus *Loxoconcha* (family Loxoconchidae) is widely distributed in shallow marine environments from tropical to subarctic regions [52–54]. This is one of the most diversified ostracod genera, which comprises ca. 600 species [7]. This genus is common in and around Japan [55–59], and about 40 living and fossil species have been described [60]. Thus, *Loxoconcha* is one of the most important Japanese ostracod genera.

A new fossil species *Loxoconcha kamiyai* from Pleistocene strata from the eastern coast of the Sea of Japan (Figure 14) was described, and its carapace morphology examined [16]. Palaeobiogeography of *L. kamiyai* was discussed, and its phylogenetic relationship to related

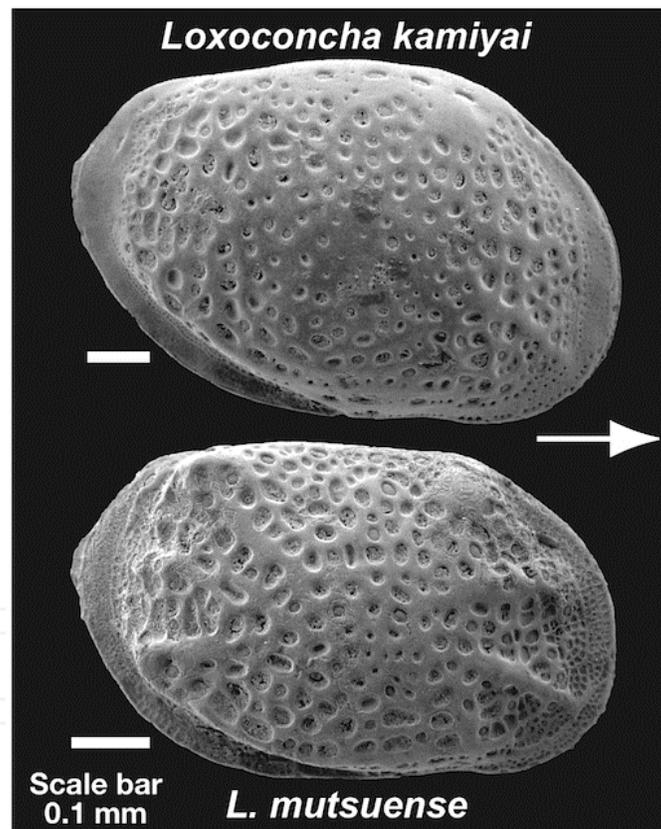


Figure 14. SEM images of two *Loxoconcha* species (Podocopida) from Quaternary deposits of central Japan, modified from Ozawa (2010). Arrows indicate anterior.

loxoconchid species was assessed, based on the pore distribution pattern (a type of ostracod sensory organ; Figure 15). The number, distribution, and differentiation of pores on the ostracod carapace surface during ontogeny have been studied to determine phylogenetic relationships among species [61]. The reconstruction of ostracod phylogeny based on pore

analyses was first proposed by [21] for 14 species of the genus *Cythere*. His work was followed by [26] [62–64] for species of other genera. This method of phylogenetic reconstruction, proposed by [21], was termed ‘differentiation of distributional pattern of pore (DDP) analysis’ [61]. The pore distribution in *L. kamiyai* was examined by this method [16], and the results were compared to the pore data of 17 other *Loxoconcha* species (Figure 16).

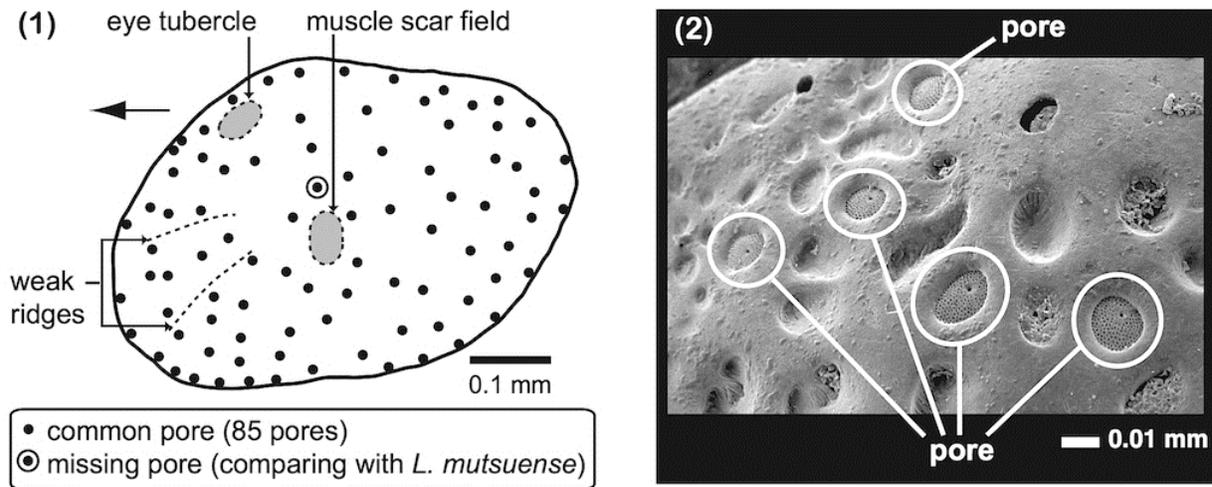


Figure 15. (1) Distribution pattern of pores in adult left valve of *Loxoconcha kamiyai* (Podocopida), modified from Ozawa and Ishii (2008). Position of one missing pore of this species is determined by comparison with the distribution pattern of pores of *Loxoconcha mutsuense* (= *Loxocorniculum mutsuense*; Podocopida) in Ishii *et al.* (2005). Arrows indicate anterior. (2) Close-up view of SEM images of pores in antero-dorsal marginal area on left valve of *Loxoconcha kamiyai* (Podocopida) from Quaternary deposits of central Japan, modified from Ozawa (2010).

On the basis of the DDP results for its adult and A-1 juvenile stages, *L. kamiyai* was determined to be the species most closely related to *Loxoconcha mutsuense* (= *Loxocorniculum mutsuense*). Both species have the same total number of pores on the carapace at the A-1 juvenile stage (75 pores per valve; Figure 16). The difference in total number of pores in the adult stage is only one between these two species, missing on the central area in *L. kamiyai* (Figure 15). These results strongly suggest its closest phylogenetic affinity to another species, *L. mutsuense*, in the same family [16].

Both *Loxoconcha kamiyai* and *Loxoconcha mutsuense* show a unique and remarkable sexual dimorphism in the adult stage, especially in the anterior element of the hingement (Figures 17 and 18). On the right valve, the anterior hingement element of the adult male is commonly smaller and rounder than that of the adult female. Its shape is very similar to the small, round anterior element of its A-1 juvenile stage [16]. The anterior element of the female hingement is larger and more rectangular than that of either the male or the A-1 juvenile (Figures 17 and 18).

These morphological characteristics of *Loxoconcha kamiyai* are seen in specimens from diverse geological ages and geographical regions (Figure 19); in fossil specimens from Pliocene sediments (4–3 Ma) in the Nagano and Niigata Prefectures of central Japan (age from [67–69]) and Pleistocene strata around 1.5 and 0.9 Ma from the Noto Peninsula and

Sado Island in central Japan (age from [70] [71]). The same hingement character is found in *L. mutsuense* of various geological ages in fossil specimens from many areas (Figure 20), such as Pleistocene strata around 1.5 and 0.9 Ma in central Japan [16], and also in modern specimens from shallow marine environments off the northeastern and southwestern Japanese coast [66] [72].

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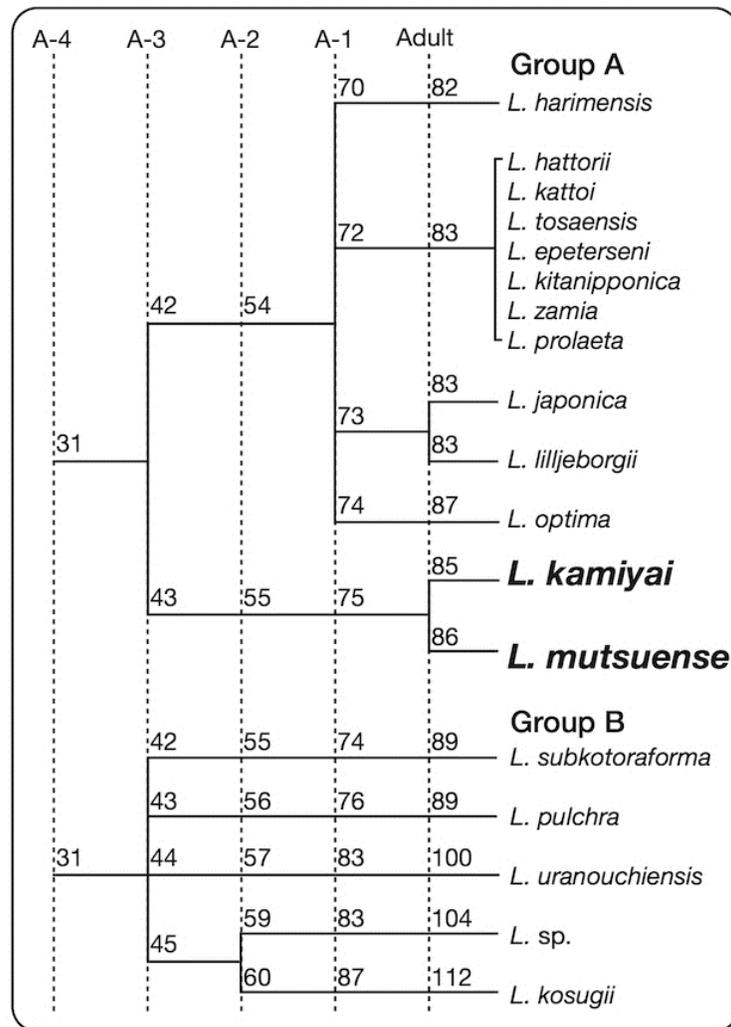


Figure 16. Results of DDP analysis for eighteen *Loxoconcha* species (Podocopida), modified from Ishii *et al.* (2005) and Ozawa and Ishii (2008). Numbers indicate total numbers of pores for each lineage and stage. Trees drawn by hand.

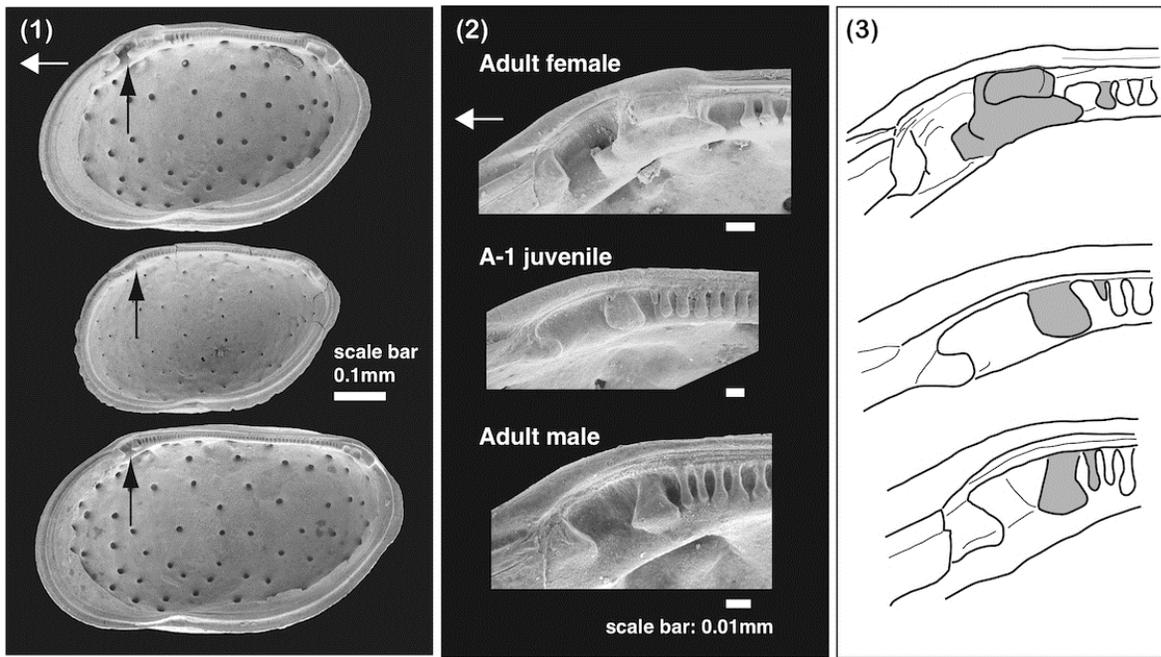


Figure 17. Comparison of lateral view (adult female, A-1 juvenile, adult male) of inner right valve of *Loxoconcha kamiyai* (Podocopida) from Quaternary deposits of central Japan, modified from Ozawa and Ishii (2008). (1): SEM images of lateral view from inside; arrows indicate locations of anterior hingement element, (2): SEM images of close-up view of anterior hingement element, (3): Sketch of anterior hingement element (= 2). Upper row: adult female, middle row: A-1 juvenile, lower row: adult male. White arrows indicate anterior.

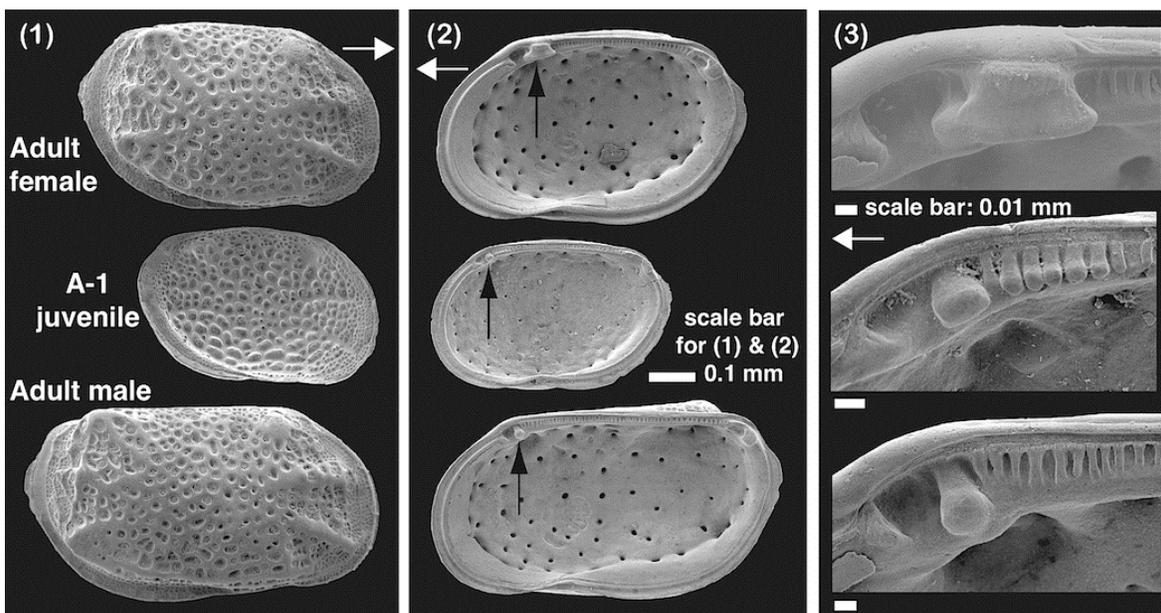


Figure 18. Comparison of SEM images of lateral view (adult female, A-1 juvenile, adult male) for right valve of *Loxoconcha mutsuense* (= *Loxocorniculum mutsuense*; Podocopida) from Quaternary deposits of central Japan, modified from Ozawa and Ishii (2008). (1): External lateral view, (2): Internal lateral view; arrows indicate locations of anterior hingement element, (3): Close-up view of anterior hingement element. Upper row: adult female, middle row: A-1 juvenile, lower row: adult male. White arrows indicate anterior.

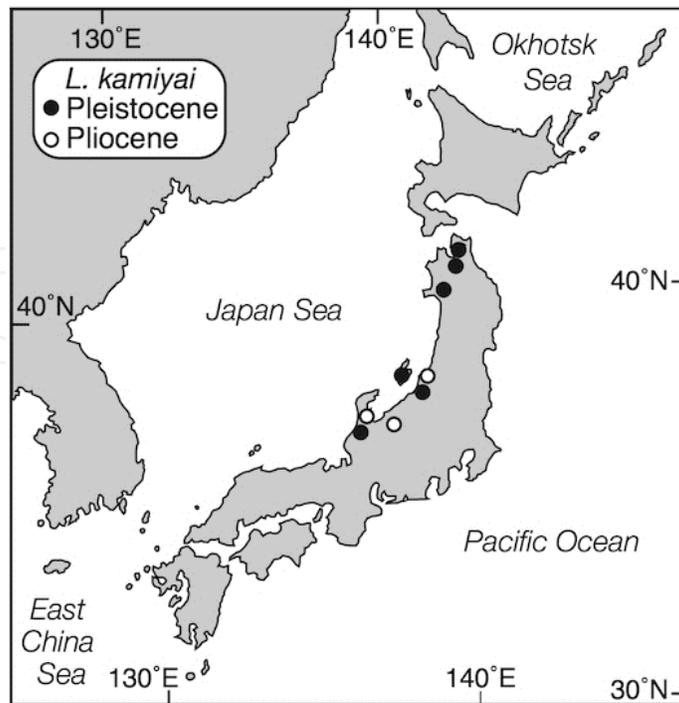


Figure 19. Geographical and geological occurrences of *Loxoconcha kamiyai* (Podocopida) based on data from previous studies, modified from Ozawa (2010).

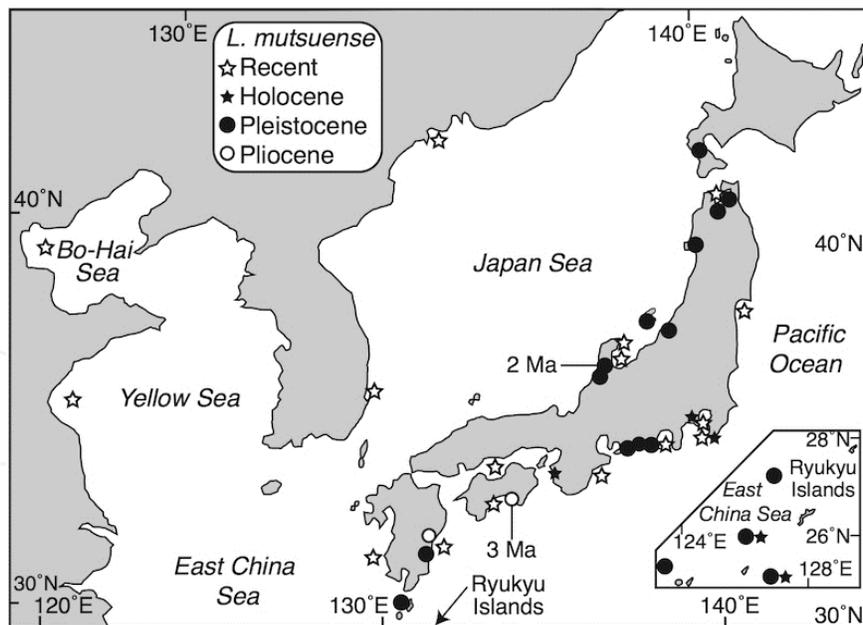


Figure 20. Geographical and geological occurrences of *Loxoconcha mutsuense* (= *Loxocorniculum mutsuense*; Podocopida) based on data from previous studies, modified from Ozawa (2010), adding with distributional data from southwestern Japan of Irizuki (2004).

This hingement sexual dimorphism in modern specimens of *Loxoconcha mutsuense* (= *Loxocorniculum mutsuense*) from the coast of northeastern Japan was mentioned only briefly

in [66]. Ishizaki referred to a “hinge structure delicate in male but stronger (bold) in female with prominent tooth within anterior socket of right valve” ([66], p. 90) in the systematic description of this species. However, he did not show clear illustrations of these dimorphic characteristics for comparison. *L. mutsuense* from the coast of southwestern Japan was re-described in a carapace sketch from an internal view of the female right valve [72]. Okubo’s illustration (Fig. 17b in [72], p. 425) clearly shows the large anterior hingement tooth on the female. However, he also did not refer to this characteristic or the morphology of the male’s hingement in the text. Considering the findings of [16], Ozawa and Ishii concluded that this sexually dimorphic morphology is a stable characteristic within each species, and not a geographical or geological variation or a deformity within a single species.

Using the female’s hingement as a standard, the male morphology in these two species can be explained as a type of heterochrony of [73] [74]; *i.e.*, paedomorphosis [16]. Paedomorphic examples of podocopid hingements have been found in two species in 11 pairs from five families—the Cytheridae, Leptocytheridae, Hemicytheridae, Cytheruridae, and Loxoconchidae—within the superfamily Cytheridea from the Miocene to the present [19, 75, 76]. This remarkable morphological difference in the anterior hingement element, between the sexes and the A-1 juvenile stage within the same species from one family, was first reported by [16].

This is likely why few publications include clear illustrations of ostracod hingements of male and female forms together with the A-1 juvenile stage, especially for ostracod taxa with a complex, rather than simple, hingement morphology; *e.g.*, adont and lophodont hingement types. We know of only one example of a detailed comparison of the number of teeth per gongyodont hingement in adult male and female forms with the A-1 juvenile of *Loxoconcha uranouchiensis* [9]. Further examples of the sexual dimorphism and paedomorphosis of the complicated hingement type will likely be found in other species or families of podocopid ostracods if hingements of male, female, and A-1 juveniles are precisely examined using SEM.

With regard to copulatory behaviour in *Loxoconcha kamiyai* and *L. mutsuense*, hingement sexual dimorphism does not appear to be directly related to functional morphology [16]. The anterior hingement element is located on the inner area of the carapace at the anterodorsal margin. This is farthest from the copulatory organ, which stretches out from the postero-ventral area between the two valves during mating (Figure 21) [16] [77]. Therefore, as yet there are no reasonable interpretations of the actual function of this kind of sexually dimorphic morphology.

Therefore, the mating and reproductive behaviours of the living species *Loxoconcha mutsuense* must be observed in detail by video recording, because the other species, *L. kamiyai*, has been extinct since the middle Pleistocene [16]. Such detailed observations will for the first time allow clarification of the actual function and significance of this dimorphism in their life-history. The significance for this dimorphism in the life-history or mating behaviour of the two species will facilitate elucidation of the evolutionary

processes of the ecology and reproductive modes of shallow marine podocopids during the Cenozoic.

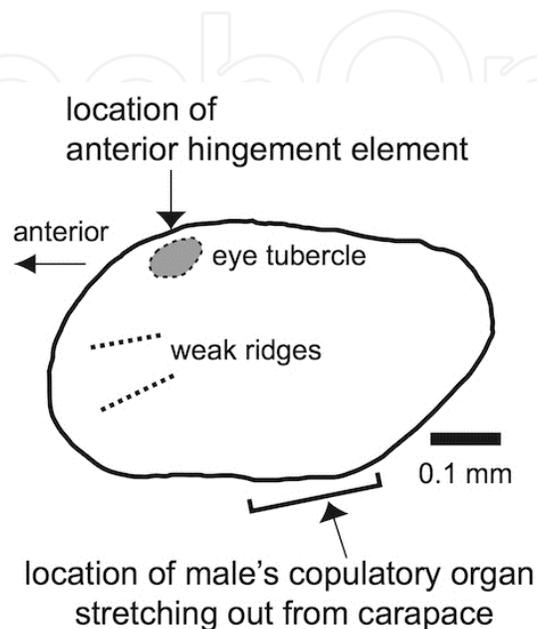


Figure 21. Schematic profile for location of anterior hingement element and inferred location of copulatory organ stretching out from inner carapace for *Loxoconcha kamiyai* and *Loxoconcha mutsuense* (= *Loxocorniculum mutsuense*; Podocopida) in lateral view for left valve of male, based on observations for mating behaviour of other living *Loxoconcha* species (*L. japonica* and *L. uranouchiensis*) in Kamiya (1988b).

4.2. Example of the inner carapace with implications for the historical origin of the ostracod male

A type of sexual dimorphism with paedomorphosis in the inner marginal area of ostracod carapaces has been reported in the freshwater podocopid *Vestalenula cornelia*, of the family Darwinulidae [17], although this dimorphism was not found on the hingement (Figures 6 and 22). According to [17], the sexual dimorphism in *V. cornelia* is found along the ventral edge of the valve (Figure 22). The male has two internal tooth-shaped structures on the left valve, whereas the female has a single internal tooth on the left valve. Furthermore, the female has a keel-shaped structure on the right valve, which is absent from the male form (Figure 22). It is interesting that the A-1 juvenile has a similar arrangement to that of the adult male, in terms of carapace length–height and lateral outline [17]. Therefore, the male form of this species also exhibits paedomorphic morphology.

A speculative hypothesis to explain this interesting observation of pedomorphosis was proposed by [16], who suggested that the adult male forms of marine podocopid ostracods may have originated from adult female forms by pedomorphosis in ancient times; *i.e.*, the early Palaeozoic. The gongylodont hingement, characteristic of the family Loxoconchidae, is generally considered to be one of the most complex-shaped and derived hingements among all podocopid ostracod families since the late Cretaceous [7] [52]. Thus, the most derived hingement in loxoconchid ostracods would have by chance exhibited atavistic features. These may have been common in ancient and primitive ancestors of marine ostracods, although most podocopid species had already lost these characteristics by the early Cenozoic. Identification of this kind of sexual dimorphism in more complicated hingement shapes may be easier than in simpler and more primitive hingements, such as the adont or lophodont types.

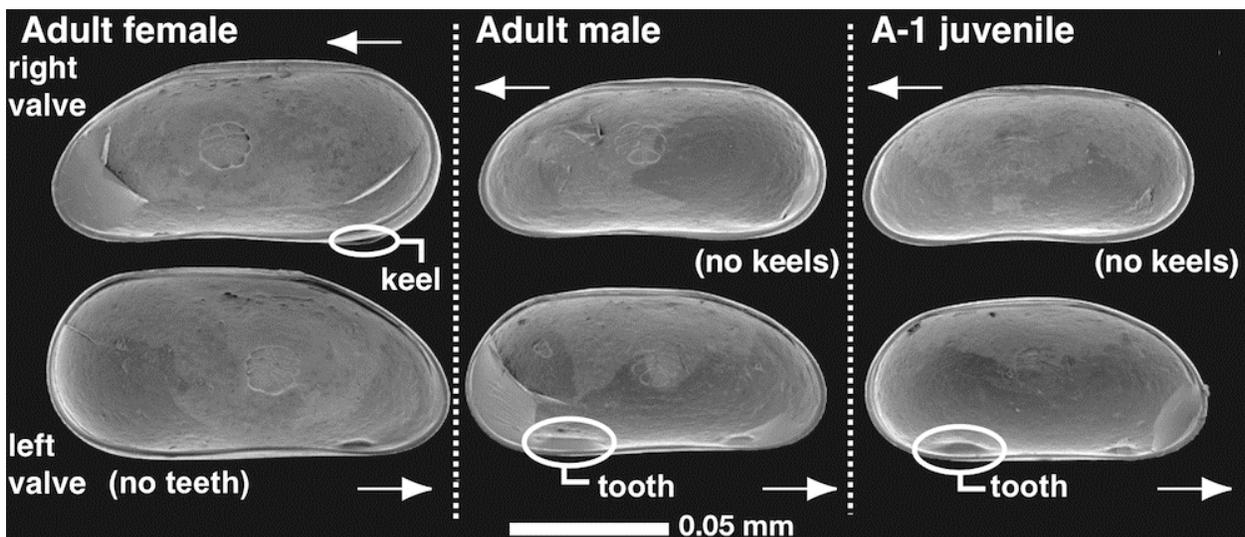


Figure 22. Comparison of SEM images of internal lateral view (adult female, adult male, A-1 juvenile) for right and left valves of *Vestalenula cornelia* (Podocopida) from modern springs in Yaku-shima Island of southwestern Japan, modified from Smith *et al.* (2006). Left column: adult female, central column: adult male, right column: A-1 juvenile, upper row: right valve, lower row: left valve. Arrows indicate anterior.

Non-marine ostracods are considered to have originated and diversified from marine ostracods multiple times, mainly during the Palaeozoic and Mesozoic [7]. Therefore, sexual dimorphism with pedomorphosis in the hingement of a marine species (*Loxoconcha kamiyai*)

and in structures on the internal ventral margin of a freshwater species (*Vestalenula cornelia*) may provide insight into the origin of the ostracod male and the post-Palaeozoic history of ostracod sexual dimorphism with paedomorphosis [16]. Therefore, more data regarding the sexually dimorphic characteristics of ostracod carapaces (or appendages as much as possible) of many taxonomic groups, accompanied by heterochronic morphology since the early Palaeozoic, should be collected. Additionally, the excellent marine and non-marine ostracod fossil records since the Ordovician that are extant worldwide should be further researched.

5. Summary and future work

1. Many ostracod species have the ability to reproduce sexually, and are relatively easily fossilised because due to their highly calcified carapaces. Ostracods are abundant in sediments ranging from the Palaeozoic Ordovician (since ca. 490 million years ago) to the Cenozoic Holocene, in modern deposits. Considering these unique characteristics, ostracods represent useful tools for investigation of the history of sexual dimorphism of organisms on earth since the Ordovician. Many examples of ostracod sexual dimorphism, in terms of both shape and size, are evident on carapaces and appendages from the Palaeozoic to Recent.
2. Two podocopid species of the family Loxoconchidae (e.g., *Loxoconch kamiyai*) show a unique sexual dimorphism in the adult stage on the anterior hingement element. Pore distribution patterns on their carapaces strongly suggest close phylogenetic affinities for these two species. Taking the female hingement morphology as a standard, male hingement can be explained in terms of a type of heterochrony; i.e., paedomorphosis. Sexual dimorphism on the hingement accompanied by paedomorphosis occurs in only one phylogenetic group in this family, which is distinguished by the ontogenetic pore pattern distribution. This unique morphological feature may represent relict primitive characteristics of ancient ostracods, and could be important for evaluation of the history of sexual dimorphism and the origin of sex in ostracods since the early Palaeozoic. To clarify the long-term history of evolutionary processes in terms of their ecology and reproductive modes since the Ordovician, more data on sexual dimorphism of ostracod carapaces with appendages of many taxa that exhibit heterochronic morphology should be collected.
3. Many examples of ostracod sexual dimorphism are found in various taxonomic groups, including both living and extinct species. However, the actual functions of most of the dimorphic characteristics remain unclear, even for many living species, although many hypotheses have been put forward. Many of these sexually dimorphic characteristics are likely strongly related to the ecology of reproductive modes, such as mating behaviour and brood care. To clarify the actual functions in living species, ostracod behaviour, especially mating and brood care under breeding conditions, should be observed using video recordings. The lack of such observations is the primary reason why the ecological behaviour of most living ostracod species is unclear.

4. To elucidate the functions of sexually dimorphic characteristics in extinct groups; *e.g.*, the brood pouch of Palaeocopida in the Palaeozoic, fossil eggs or juvenile carapaces in the inner part of the adult carapaces from Palaeozoic sediments must be identified. For Palaeocopida, we must attempt to find fossils resting their appendages, despite their rarity. Furthermore, detailed observation of the ecological behaviour of living species will facilitate understanding of the actual functions of sexually dimorphic morphology in both living and extinct species [31]. Due to the excellent ostracod fossil record from Palaeozoic to Cenozoic, the living ostracod sexual dimorphism data can be applied to extinct species. Combined studies of the ecology and functional morphology of both living and fossil ostracod species will clarify the history of the evolutionary ecology and reproductive modes of organisms during the last ca. 500 million years.

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