Structure and evolution of podocopan ostracod hinges

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A new concept of the hinge classification in the Podocopa is established based on a comprehensive description of the hinge ultrastructure. Four new types of structure are defined, according to the relative position of their ligaments and hingements (teeth elements): basic type, exterior type, intermediate type and interior type. The new classification reveals that the adont hinge, which is known as a simple structure, shares the fundamental structure (basic or exterior type) found in the Platycopida, Darwinuloidea and Bairdioidea, and that it develops not only as the fundamental structure, but also as the advanced structure (interior type) in the Cypridoidea and Cytheroidea. Additionally, the high level of morphological diversification of cytheroid hingements is explained in terms of the structural plasticity of the intermediate and interior hinge structure types. Most cytheroid hinges can develop complex arrangements of teeth (hingements) by only small changes of calcification because their hingements can develop independently from the particular restricted location of the ligaments. The evolutionary pathway of hinge structures is also examined based on a study of fossil records. The pathway indicates that the complex hinge structures of the derived taxa arose from simpler ones, but that sometimes this trend can be reversed and derived taxa can evolve simple hinge structures as adaptations to new habitats. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **92**, 41–62.

ADDITIONAL KEYWORDS: hinge structure – hingement – ligament – Ostracoda.

INTRODUCTION

The Ostracoda is a bivalved crustacean. It has a hinge structure, consisting of the uncalcified ligament and the calcified hingement (Yamada, 2007), which develops along the dorsal margin and connects the two valves. The features of the complex morphology exhibited by the hingement in the Podocopida, together with the preservation of specimens as fossils, provide important and useful criteria for studies on their higher taxonomy. Many previous studies on ostracod hinges have developed a classification of the hingements based on the numbers of their teeth elements (Zalányi, 1929; Bold, 1946; Kingma, 1948; Triebel, 1950; Berousek, 1952; Malkin, 1953), whereas a few studies have mentioned the homology of hingements and compared the structure of an attached margin with that of a free margin (Fassbinder, 1912; Pokorný, 1957; Kornicker, 1969; Yamada, 2007).

Classification based on the number of teeth led to a saturation and confusion of terminology, with many authors defining the same terms in their own way and others trying to redefine those terms (Sylvester-Bradley, 1956; How & Laurencich, 1958). Hanai (1961) summarized these classic studies up until 1961 and defined various types of hingement in Cenozoic cytheroid ostracods. He also evaluated the hingement in evolutionary terms and mentioned the limitation of hingement as a taxonomic character. Moore (1961) made a comprehensive systematic survey of cytheroid ostracods based entirely on characteristics of the hingement. Gründel (1974) later divided the hingements of post-Ordovician ostracods into five basic types (subdivided into 24 subtypes). This hinge classification has been considered useful for higher taxonomy (families or genera) in the post-Palaeozoic cytheroid ostracods.

Fassbinder (1912) had suggested that the attached margin (= hinge margin) is a homologous structure of the free margin, and Pokorný (1957) further advanced this concept of Fassbinder (1912) and of Zalányi (1929) and advocated the homology between the hingement and the free margin. He recognized the podocopan and platycopan hingement as being of two types, 'hemiso-

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lenic' and 'holosolenic', respectively, and concluded that the 'hemisolenic' arose from the 'holosolenic.' Kornicker (1969) developed the concept of Harding (1964) proposing that the ostracod carapace is one cuticular sheet. He emphasized that the carapace consists of four parts, namely 'right and left shells', 'ligament', and 'vestment', and concluded that 'ligament' is an independent structure distinct from other parts of the carapace. He also noted the importance of recognizing the hingement as an 'exterior part' or 'interior part' of the valve. The value of this concept was also mentioned by Hanai (1988), but it is accepted by only a few researchers and thus far the taxonomic or palaeontological usefulness of this concept has not been revealed. Yamada (2007) clarified the ultrastructures of the attached and free margins by transmission electron microscopy (TEM), and concluded that the ligament is not an independent structure but an uncalcified cuticular structure consisting of the epicuticle and procuticle.

There have been only a few studies dealing with the evolution of the hinge structure. Sandberg (1964) regarded the ontogenetic change of hingement as representing evolutionary change, and assumed that the entomodont and holomerodont hinges evolved from the antimerodont hinge. The cytheroid hingements are generally thought to have an evolutionary trend from a simple to a complicated one (Sylvester-Bradley, 1948; Hartmann, 1963; Benson, 1966). Those studies suggested that the hinge structures (especially hingements) reflect the phylogeny of the Ostracoda.

On the other hand, Triebel (1954) suggested that the amphidont hinge came about independently in some genera. Sylvester-Bradley (1956) also postulated parallel evolution from the entomodont hinge to the amphidont hinge in some ostracod lineages. Kamiya (1992) and Tsukagoshi (1994) explained the morphological differences of hingements, which appeared to be intraspecific or intrageneric, as the heterochrony of the feature. Tsukagoshi & Kamiya (1996) proposed that all the basic hingement designs had already appeared at least by the Palaeogene, and that the design became modified exclusively by paedomorphosis in the Neogene. Yamaguchi (2003) constructed molecular phylogenetic trees using the 18 s rDNA of 28 cytheroid ostracods representing 16 families. He demonstrated that amphidont basic type hingements emerged independently at least four times in the lineage of cytheroid ostracods, and concluded that the lophodont hinge is plesiomorphic and that various hinge types evolved from the lophodont hinge. These results indicated that hinge structures do not always reflect the ostracod phylogeny. Later studies support this conclusion. Some authors have mentioned the correlation between the complexity of hingement and the increase of mineralization of the carapace. They proposed that the increased complexity of hingement must be associated with the complication of ornamentation or increase of calcification (Pokorný, 1957; Benson, 1966; Hinz, 1993; Hinz-Schallreuter & Schallreuter, 1999). Yamaguchi (2003) assumed that the increased complexity of hingement was caused by the increase of calcification of the carapace, and that the same hingement types emerged independently in the lineage of cytheroid ostracods. The outcome of all of these studies is that not all researchers agree with the phylogenetic usefulness of hinge structures. The present study establishes a new classification of hinge structures based on homology, using observations of the ligament and hingement with TEM and scanning electron microscopy (SEM). The evolutionary pathways of hinge structures are discussed. In the present study, the term 'hinge structure' is defined as the dorsal cuticular structure consisting of 'ligament' and 'hingement'. The terms 'ligament' and 'hingement' correspond to the uncalcified connecting cuticle and calcified sculptures (i.e. teeth, crenulations), respectively.

MATERIAL AND METHODS

The living specimens used in this study are listed in Tables 1, 2. This study investigated 24 families, 35 genera, and 43 species. All of the figured specimens are deposited in the University Museum, Shizuoka University (SUM-CO-number). In preparation for observation by SEM (JEOL JSM-5600LV) specimens were fixed in either 5% formaldehyde or 70% ethanol solution, and treated with sodium hypochlorite solution to dissolve the organic substances. Carapace specimens were then air-dried and ion coated with gold. For observations by TEM (Hitachi H-7500), living specimens were initially fixed in 2% glutaraldehyde and 2% paraformaldehyde in 0.1 M cacodylate sodium buffer (pH 7.4), with 5% sucrose, for 2 h at 4 °C. They were then postfixed in 1% osmium tetroxide in the same buffer, with 5% sucrose, for 2 h at 4 °C, decalcified in 10% ethylenediaminetetraacetic acid in the same buffer with 7% sucrose for 3 days at 4 °C and dehydrated in an acetone series. Finally, they were embedded in Spurr's resin and polymerized. Sections were obtained using the ultramicrotome. Semi-thin sections were stained with 1% toluidine-blue in 1% sodium tetraborate solution. Ultra-thin sections were stained with 1% potassium permanganate solution in distilled water for 2 min, and lead citrate (Reynolds, 1963) for 3 min.

RESULTS

NEW CLASSIFICATION OF PODOCOPAN OSTRACOD HINGE STRUCTURES

In the present study, a new classification of podocopan hinge structures has been established according

Table 1. List of specimens

Species name	Locality	Substrate
Podocopa		
Platycopida		
Cytherelloidea		
Cytherellidae		
Keijcyoidea infralittoralis Tsukagoshi, Okada & Horne, 2006	Shimoda beach (Shizuoka Pref. Japan)	Algae
Podocopida		
Bairdioidea		
Bairdiidae		
Neonesidea oligodentata (Kajiyama, 1913)	Shimoda beach (Shizuoka Pref. Japan)	Algae
Triebelina sp.	Shimoda beach (Shizuoka Pref. Japan)	Algae
Darwinuloidea		
Darwinulidae		
Darwinula stevensoni (Brady & Robertson, 1870)	Lake Yamanaka (Shizuoka Pref. Japan)	Sediments
Vestalenula cornelia Smith, Kamiya & Horne, 2006	Yaku Island (Kagoshima Pref. Japan)	Sediments
Microdarwinula zimmeri Danielopol, 1968	Ofudoson (Shizuoka Pref. Japan)	Sediments
Macrocypridoidea		
Macrocyprididae		
Macrocypris sp.	Shimoda Ebisujima (Shizuoka Pref. Japan)	Sediments
Pontocypridoidea		
Pontocyprididae		
Propontocypris sp.	Shimoda Ebisujima (Shizuoka Pref. Japan)	Sediments
Cypridoidea		
Cyprididae		
Chrissia sp.	Ofudoson (Shizuoka Pref. Japan)	Sediments
Cypridopsis vidua (Müller, 1776)	Oya rice field (Shizuoka Pref. Japan)	Sediments
Candonidae		
Fobaeformiscandona sp.	Lake Yamanaka (Shizuoka Pref. Japan)	Sediments
Cypria reptans Bronstein, 1928	Yaku Island (Kagoshima Pref. Japan)	Sediments
Paracypridinae sp. A	Shimoda Ebisujima (Shizuoka Pref. Japan)	Sediments
Paracypridinae sp. B	Kanna beach (Okinawa Pref. Japan)	Sediments
Ilyocypridae		
Ilyocypris japonica Okubo, 1990	Oya rice field (Shizuoka Pref. Japan)	Sediments
Cytheroidea		
Bythocytheridae		
Bythoceratina sp.	Shimoda beach (Shizuoka Pref. Japan)	Algae
Sclerochilus sp.	Shimoda beach (Shizuoka Pref. Japan)	Algae
Eucytheridae		
Keijia cf. *demissa* (Brady, 1868)	Kanna beach (Okinawa Pref. Japan)	Sediments
Paradoxostomatidae		
Paradoxostoma triangulum Kajiyama, 1913	Shimoda beach (Shizuoka Pref. Japan)	Algae
Cytheruridae		
Hemicytherura kajiyamai Hanai, 1957b	Shimoda beach (Shizuoka Pref. Japan)	Algae
Semicytherura kazahana Yamada, Tsukagoshi & Ikeya, 2005	Shimoda beach (Shizuoka Pref. Japan)	Algae
Semicytherura wakamurasaki Yajima, 1982	Lake Hamana (Shizuoka Pref. Japan)	Sediments
Loxoconchidae		
Loxoconcha pulchra Ishizaki, 1968	Obitsu river (Chiba Pref. Japan)	Sediments
Leptocytheridae		
Callistocythere pumila Hanai, 1957a	Kurose river (Hiroshima Pref. Japan)	Sediments
Ishizakiella miurensis (Hanai, 1957a)	Obitsu river (Chiba Pref. Japan)	Sediments
Xestoleberidae		
Xestoleberis hanaii Ishizaki, 1968	Shimoda beach (Shizuoka Pref. Japan)	Algae

Table 1. *Continued*

Species name	Locality	Substrate
Cobanocytheridae		
Paracobanocythere sp.	Shimoda beach (Shizuoka Pref. Japan)	Sediments
Limnocytheridae		
Limnocythere stationis Vavra (1891)	Lake Yamanaka (Shizuoka Pref. Japan)	Sediments
Limnocytherina sanctipatricii (Brady & Robertson, 1869)	Spree river (Berlin Germany)	Sediments
Cytheridae		
Cythere omotenipponica (Hanai, 1959b)	Hayama beach (Kanagawa Pref. Japan)	Algae
Cytherideidae		
Perissocytheridea inabai Okubo (1983)	Obitsu river (Chiba Pref. Japan)	Sediments
Perissocytheridea japonica Ishizaki (1968)	Lake Hamana (Shizuoka Pref. Japan)	Sediments
Cushmanideidae		
Pontocythere miurensis (Hanai, 1959a)	Obitsu river (Chiba Pref. Japan)	Sediments
Pontocythere japonica (Hanai, 1959a)	Lake Hamana (Shizuoka Pref. Japan)	Sediments
Krithidae		
Parakrithella pseudadonta (Hanai, 1959a)	Shimoda beach (Shizuoka Pref. Japan)	Algae
Schizocytheridae		
Schizocythere kishinouyei (Kajiyama, 1913)	Hayama beach (Kanagawa Pref. Japan)	Algae
	Ise Bay (Off Aichi Pref. Japan)	Sediments
Hemicytheridae		
Caudites asiaticus Zhao & Whatley, 1989	Kanna beach (Okinawa Pref. Japan)	Sediments
Trachyleberididae		
Trachyleberis scabroquneata (Brady, 1880)	Aburatsubo Bay (Kanagawa Pref. Japan)	Sediments

to the relative position of ligaments and hingements. It is based on the concept of hinge classification developed by Kornicker (1969) from exhaustive TEM observations and a redefinition of the nomenclature of hinge structures. Using this classification, the basic structures of podocopan hinges can be compared with each other, irrespective of the complexity of hingements, and the morphological evolution of the hinge structures can be discussed. The new classification of hinge structures is described below (Fig. 1).

Basic type
The ligament connects to each of the calcified valves and the hingement is not developed.

Exterior type
The overlap structure of one valve develops over the ligament, and the ligament cannot be observed from the exterior view. The hingement is present on the exterior or lateral position of the ligament.

Intermediate type
The overlap structure of one valve develops over the ligament, and the ligament cannot be observed from the exterior view. In addition, the hingement develops below the ligament.

Interior type
The hingement develops below the ligament without the overlapping valve structure, and the ligament can be observed from the exterior dorsal view.

The results applied to podocopan hinge structures are presented in Table 2. The hinge structures, which have tripartite hingements, are shown for each element (anterior–median–posterior). The details of each podocopan hinge structure are described below.

PLATYCOPIDA

CYTHERELLOIDEA (CYTHERELLIDAE)

Keijcyoidea infralittoralis: basic–interior–basic type (Figs 2A, 3A, B)
The hinge structure of this species, except for the median element (a tooth), conforms to the basic type (Fig. 3A). In the median element, the hinge structure shows the interior type (Fig. 3B). In the cytherelloid species, excluding the genus *Keijcyoidea*, a tooth does not develop in their hingements. Thus, most cytherelloid hinge structures are thought to show the simple basic type of hinge structure.

Table 2. Podocopan hinge structures

Species name	Hinge structure	Hingement
Keijcyoidea infralittoralis Tsukagoshi *et al.* 2006	Basic–interior–basic	A tooth
Neonesidea oligodentata (Kajiyama, 1913)	Exterior	Adont
Triebelina sp.	Exterior	Adont
Darwinula stevensoni (Brady & Robertson, 1870)	Basic	Adont
Vestalenula cornelia Smith *et al.* 2006	Basic	Adont
Microdarwinula zimmeri Danielopol, 1968	Basic	Adont
Propontocypris sp.	Interior	Adont
Chrissia sp.	Basic	Adont
Cypridopsis vidua (Müller, 1776)	Basic	Adont
Fobaeformiscandona sp.	Exterior	Adont
Cypria reptans Bronstein, 1928	Exterior	Adont
Paracypridinae sp. A	Interior	Adont
Paracypridinae sp. B	Interior	Adont
Ilyocypris japonica Okubo, 1990	Basic	Adont
Bythoceratina sp.	Interior–intermediate–interior	Lophodont
Sclerochilus sp.	Exterior	Lophodont
Keijia cf. *demissa* (Brady, 1868)	Interior–interior–interior	Pentodont
Paradoxostoma triangulum Kajiyama, 1913	Exterior	Lohodont
Hemicytherura kajiyamai Hanai, 1957b	Intermediate–intermediate–intermediate	Merodont
Hemicytherura tricarinata Hanai , 1957b	Intermediate–intermediate–intermediate	Merodont
Semicytherura kazahana Yamada *et al.* 2005	Intermediate–intermediate–intermediate	Merodont
Semicytherura wakamurasaki Yajima, 1982	Intermediate–basic–intermediate	Merodont
Loxoconcha pulchra Ishizaki, 1968	Interior–intermediate–interior	Gongylodont
Loxoconcha japonica Ishizaki, 1968	Interior–intermediate–interior	Gongylodont
Callistocythere pumila Hanai, 1957a	Interior–exterior–intermediate	Entomodont
Callistocythere rugosa Hanai, 1957a	Interior–exterior–intermediate	Entomodont
Callistocythere setouchiensis Okubo, 1979	Interior–exterior–intermediate	Entomodont
Ishizakiella miurensis (Hanai, 1957a)	Interior–basic–intermediate	Entomodont
Xestoleberis hanaii Ishizaki, 1968	Intermediate–intermediate–intermediate	Merodont
Paracobanocythere sp.	Basic	Adont
Limnocythere stationis Vavra, 1891	Interior–interior–interior	Lophodont
Cythere omotenipponica (Hanai, 1959b)	Intermediate–intermediate–intermediate	Merodont
Perissocytheridea inabai Okubo, 1983	Interior–intermediate–interior	Merodont
Perissocytheridea japonica Ishizaki, 1968	Interior–intermediate–interior	Merodont
Pontocythere miurensis (Hanai, 1959a)	Basic–exterior–interior	Desmodont
Pontocythere japonica (Hanai, 1959a)	Basic–exterior–interior	Desmodont
Parakrithella pseudadonta (Hanai, 1959a)	Intermediate–intermediate–intermediate	Pseudadont
Schizocythere kishinouyei (Kajiyama, 1913)	Intermediate–intermediate–intermediate	Schizodont
Aurila hataii Ishizaki, 1968	Intermediate–intermediate–intermediate	Amphidont
Caudites asiaticus Zhao & Whatley, 1989)	Intermediate–intermediate–intermediate	Amphidont
Trachyleberis scabroquneata (Brady, 1880)	Interior–interior–interior	Amphidont

PODOCOPIDA

BAIRDIOIDEA (BAIRDIIDAE)

Neonesidea oligodentata: exterior type (Figs 2B, 3C)

Triebelina sp.: exterior type (Figs 2C, 3D)
In previous studies, the bairdioid hinge structure was identified with a simple 'adont'; but the overlap structure develops over the ligament and the bairdioid hinge structure shows the exterior type.

DARWINULOIDEA (DARWINULIDAE)

Darwinula stevensoni: basic type (Figs 2D, 3E)

Vestalenula cornelia: basic type (Figs 2E, 3H)

Microdarwinula zimmeri: basic type (Figs 2F, 3K)
Basic type hinge structures are recognized in these species. The fibres of the long ligament are sparse, especially in *D. stevensoni* (Fig. 3E). In *V. cornelia*, the ligament is elongate and its fibres are low in electron-

carapace close   carapace open

Basic type

Exterior type

Intermediate type

Interior type
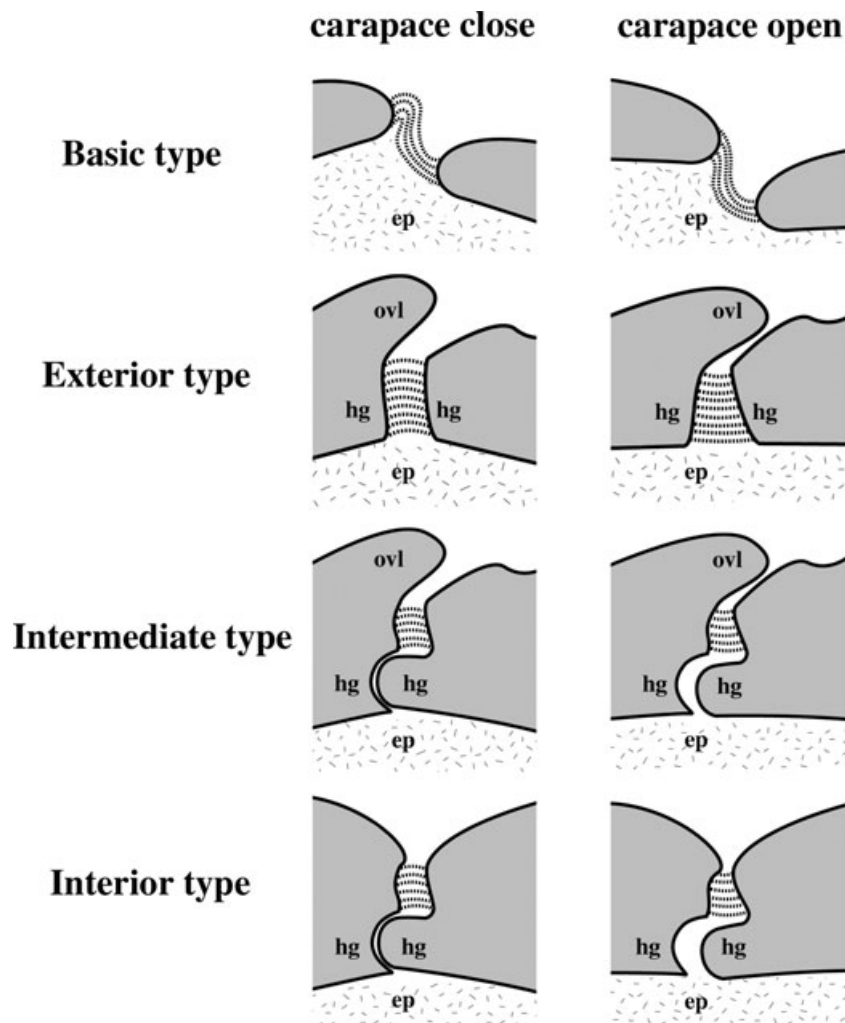
Figure 1. New classification on podocopan hinge structures. Schemes represent the transverse sections of hinge structures. Grey areas indicate the calcified valves and bundles of broken lines reveal the ligament. hg, hingement. ep, epidermis. ovl, overlap structure.

density (Fig. 3H). In *M. zimmeri*, the extreme thin ligament consists of only a few fibres (Fig. 3K).

CYPRIDOIDEA (CYPRIDIDAE)
Chrissia sp.: basic type (Figs 2H, 3F)

Cypridopsis vidua: basic type (Figs 2G, 3G)
Long ligaments develop in these species. In *C. vidua*, the inner part of the left valve has a ridge. However, this ridge does not work as the complementary structure, and this study does not therefore identify the ridge with the hingement (Fig. 3G).

CYPRIDOIDEA (CANDONIDAE)
Fabaeformiscandona sp.: exterior type (Figs 2J, 3I)

Cypria reptans: exterior type (Figs 2K, 3J)

Paracypridinae sp. A: interior type (Figs 2L, 3M)

Paracypridinae sp. B: interior type (Figs 2M, 3L)
The freshwater and marine species belong to the family Candonidae. In the freshwater species *C. reptans* and *Fabaeformiscandona* sp. their hinge structures show the exterior type, whereas, for the marine species Paracypridinae sp. A and B, their hinge structures exhibit the interior type.

CYPRIDOIDEA (ILYOCYPRIDAE)
Ilyocypris japonica: basic type (Figs 2I, 3N)
This species has prominent ridges on the carapace surface, although it lives in freshwater. The hinge structure is classified as the basic type.
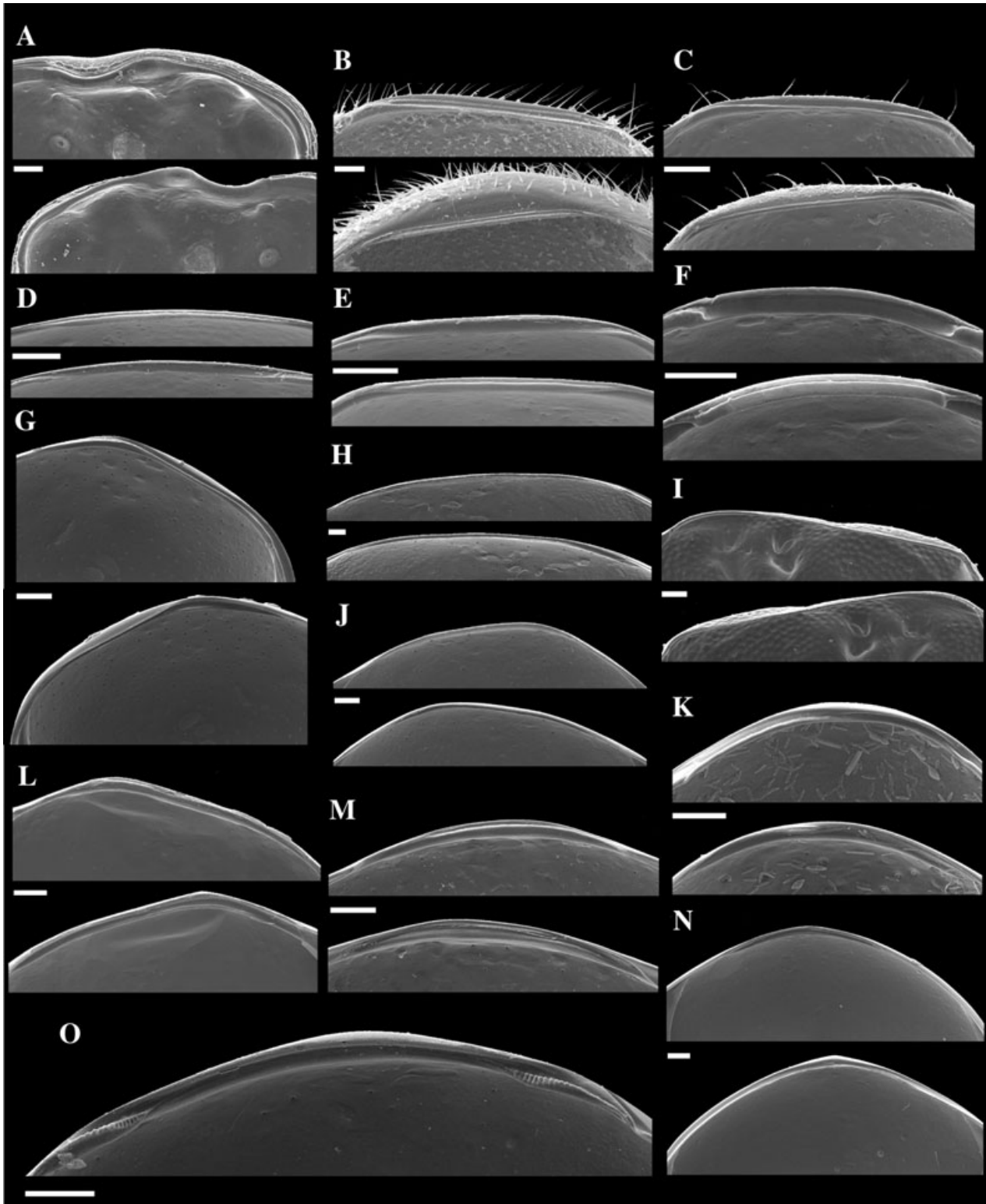
Figure 2. Scanning electron microsocopy photographs of podocopan hingements. A, *Keijcyoidea infralittoralis*. B, *Neonesidea oligodentata*. C, *Triebelina* sp. D, *Darwinula stevensoni*. E, *Vestalenula cornelia*. F, *Microdarwinula zimmeri*. G, *Cypridoides vidua*. H, *Chrissia* sp. I, *Ilyocypris japonica*. J, *Fabaeformiscandona* sp. K, *Cypria reptans*. L, Paracypridinae sp. A. M, Paracypridinae sp. B. N, *Propontocypris* sp. O, *Macrocypris* sp. (left valve only). Right and left valves are shown as the upper and lower images of each pair, respectively. Scale bars = 50 μm.
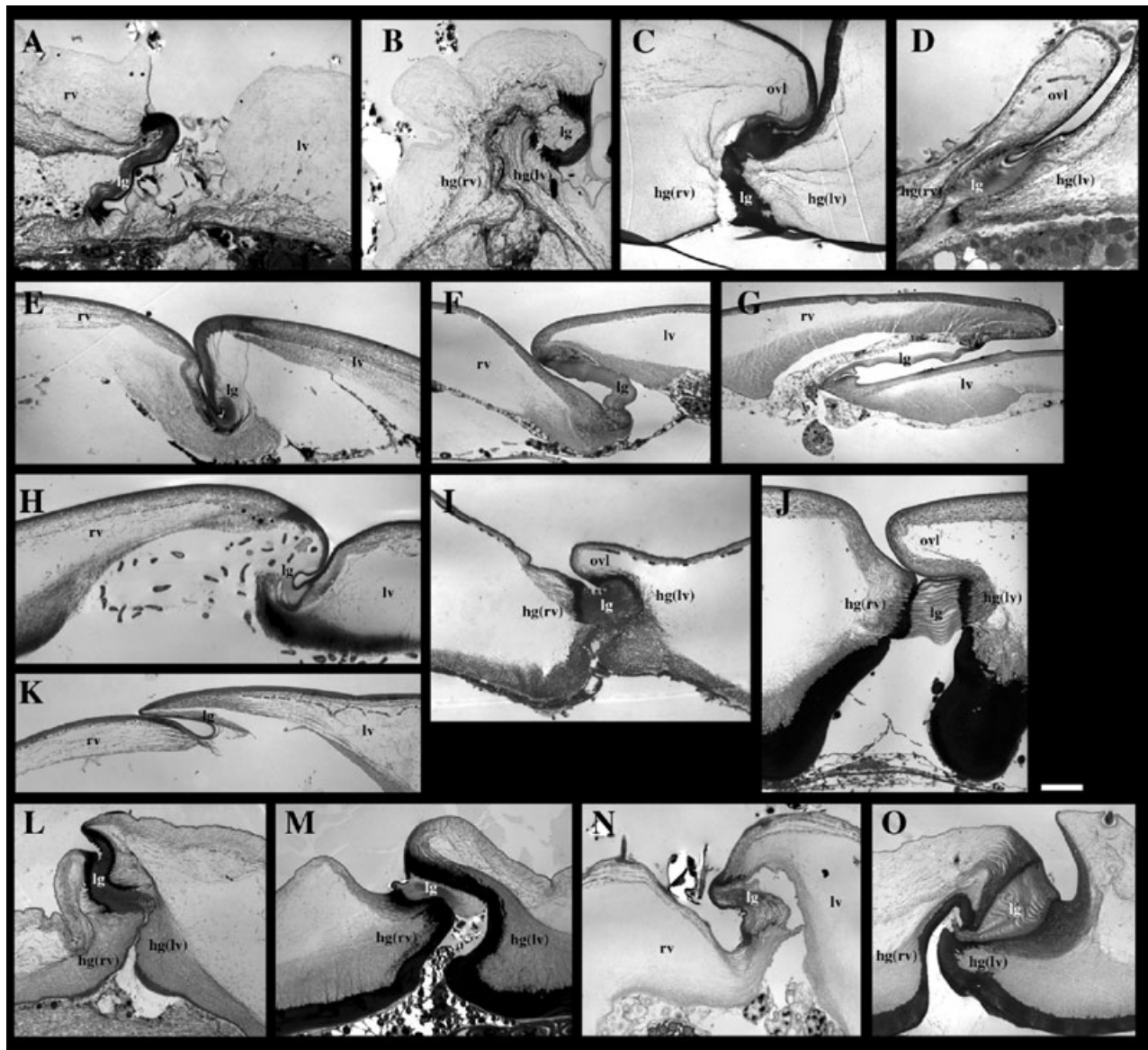
Figure 3. Transmission electron microsocopy photographs of podocopan hinge structures. A, terminal element of hinge structure in *Keijcyoidea inflalittoralis*. B, median element of hinge structure in *Keijcyoidea infralittoralis*. C, *Neonesidea oligodentata*. D, *Triebelina* sp. E, *Darwinula stevensoni*. F, *Chrissia* sp. G, *Cypridoides vidua*. H, *Vestalenula cornelia*. I, *Fabaeformiscandona* sp. J, *Cypria reptans*. K, *Microdarwinula zimmeri*. L, Paracypridinae sp. B. M, Paracypridinae sp. A. N, *Ilyocypris japonica*. O, *Propontocypris* sp. hg(lv), hingement of left valve; hg(rv); hingement of right valve; lg, ligament; lv, left valve; ovl, overlap structure; rv, right valve. Scale bar = 2.5 µm (A, D, K, L, M), 2.9 µm (B, F), 3.2 µm (C, O), 2.0 µm (E, H, J), 5.0 µm (G), 1.3 µm (I) and 1.9 µm (N).

CYPRIDOIDEA (NOTODROMATIDAE)

Notodromas: exterior type (Harding, 1964: fig. 19)
The present study refers to the illustration of this taxon from Harding (1964) because no specimen could be captured. The complementary structure develops over the ligament, so this hinge structure is classified as the exterior type.

PONTOCYPRIDOIODEA (PONTOCYPRIDIDAE)

Propontocypris sp.: interior type (Figs 2N, 3O)
The hinge structure exhibits the interior type. The calcified part of the left valve extends over the ligament but this hinge structure is not included into the intermediate type because the ligament is not wholly covered with the left valve.

CYTHEROIDEA (BYTHOCYTHERIDAE)

Bythoceratina sp.: interior–intermediate–interior type (Figs 4A, 5A, B)

Sclerochilus sp.: exterior type (Figs 4B, 5C)
Bythoceratina sp., which develops prominent ornamentation, has both terminal elements of the interior type and the median element of the intermediate type (Fig. 5A, B). Both terminal elements consist of smaller teeth than those of the other cytheroid species (Fig. 4A, upper), and the median element develops crenulations (Fig. 4A, lower). In *Sclerochilus* sp., which has the smooth bar as the hingement, the hinge structure is the exterior type because of the small overlap structure which develops over the ligament (Fig. 5C).

CYTHEROIDEA (EUCYTHERIDAE)

Keijia sp. cf. K. demissa: interior–interior–interior type (Figs 4C, 5D, E)
The terminal elements consist of large teeth (Fig. 4C, upper) and exhibit the interior type (Fig. 5D, E). The crenulations develop in the median element (Fig. 4C, lower). The hinge structure of the median element shows the interior type, although the crenulations become smaller towards the middle part (Fig. 4C).

CYTHEROIDEA (PARADOXOSTOMATIDAE)

Paradoxostoma triangulum: exterior type (Figs 4D, 5F, G)
The hingement appears as the smooth bar (Fig. 4D, lower), although the terminal elements appear as vestiges (Fig. 4D, upper). The hinge structure of all elements shows the exterior type, but the appearance differs between the terminal and median element. In the terminal elements, the cuticular layers of both valves extend over the ligament and form the overlap structure (Fig. 5F). In the median element, the membranous layer of the right valve overlaps the ligament (Fig. 5G).
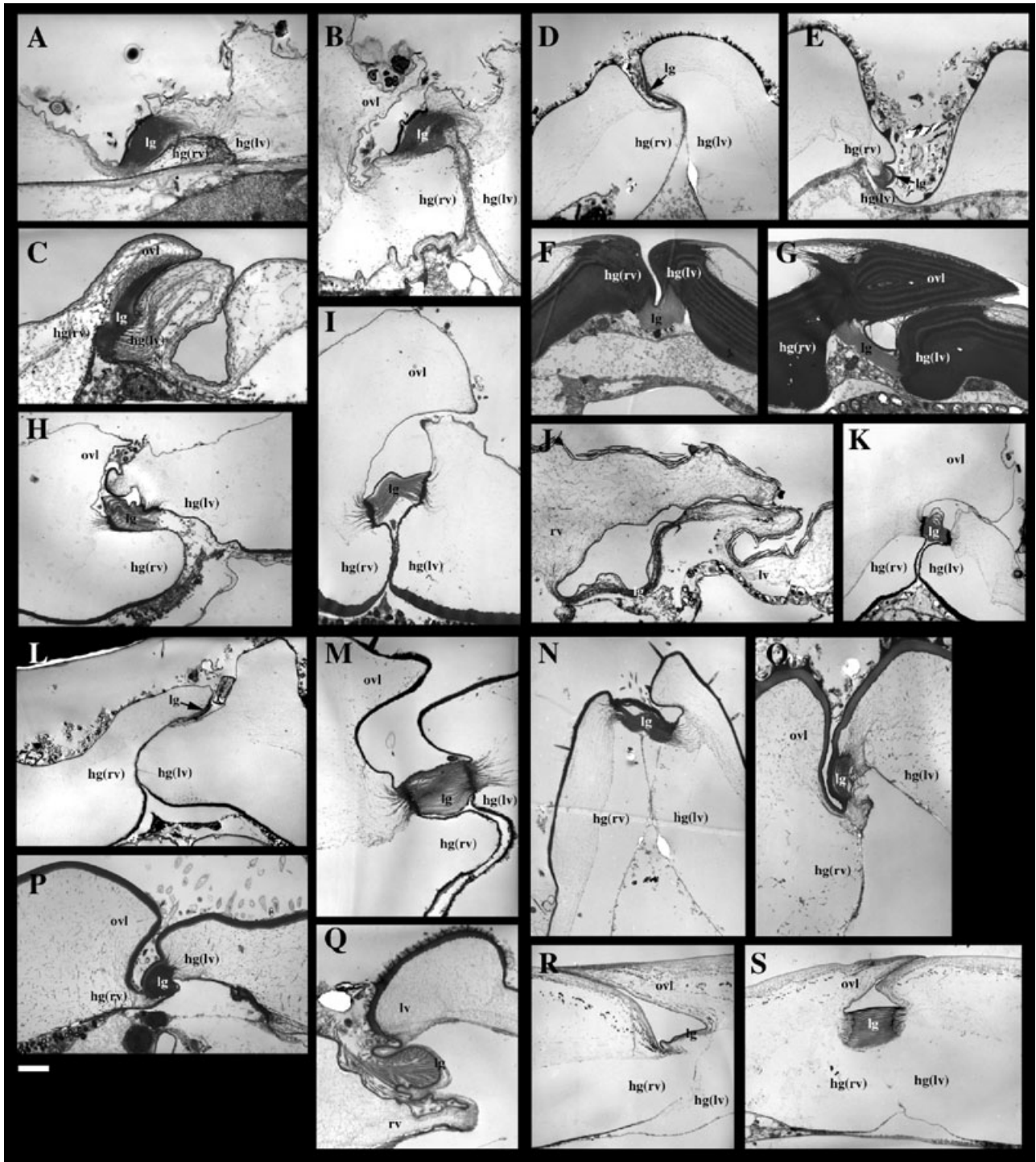
CYTHEROIDEA (CYTHERURIDAE)

Hemicytherura kajiyamai: intermediate–intermediate–intermediate type (Figs 5H, 6B)

Hemicytherura tricarinata: intermediate–intermediate–intermediate type (Fig. 5I)
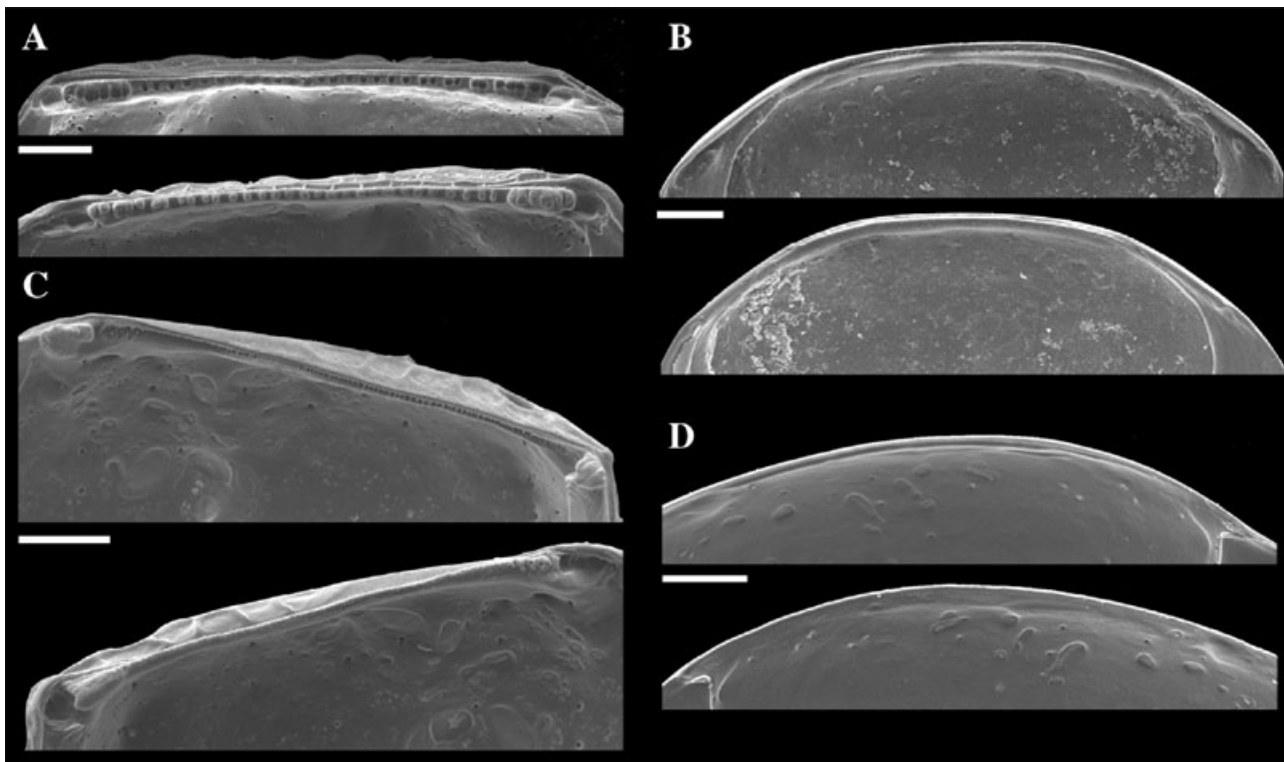
Figure 4. Scanning electron microsocopy photographs of podocopan hingements. A, *Bythoceratina* sp. B, *Sclerochilus* sp. C, *Keijia* sp. cf. *K. demissa*. D, *Paradoxostoma triangulum*. Right and left valves are shown as the upper and lower images of each pair, respectively. Scale bars = 50 μm.

Semicytherura kazahana: intermediate–intermediate–intermediate type (Figs 5K, 6C)

Semicytherura wakamurasaki: intermediate–basic–intermediate type (Figs 5J, 6A)
In *H. kajiyamai* and *H. tricarinata*, the crenulations develop as the terminal elements and at both ends of the median elements. The middle part of the median element appears as the smooth bar (Fig. 6B, lower). The hinge structure of all elements develops as the intermediate type (Fig. 5H, I). In *S. kazahana*, which has a thick carapace, the crenulations develop in all elements (Fig. 6C). In *S. wakamurasaki*, which has a thin carapace, the teeth develop in the terminal

Figure 5. Transmission electron microsocopy photographs of podocopan hinge structures. A, terminal element of hinge structure in *Bythoceratina* sp. B, median element of hinge structure in *Bythoceratina* sp. C, *Sclerochilus* sp. D, terminal element of hinge structure in *Keijia* sp. cf. *K. demissa*. E, median element of hinge structure in *Keijia* sp. cf. *K. demissa*. F, terminal area of hinge structure in *Paradoxostoma triangulum*. G, median area of hinge structure in *Paradoxostoma triangulum*. H, terminal element of hinge structure in *Hemicytherura kajiyamai*. I, median element of hinge structure in *Hemicytherura tricarinata*. J, median element of hinge structure in *Semicytherura wakamurasaki*. K, median element of hinge structure in *Semicytherura kazahana*. L, terminal element of hinge structure in *Loxoconcha pulchra*. M, median element of hinge structure in *Loxoconcha pulchra*. N, anterior element of hinge structure in *Ishizakiella miurensis*. O, posterior element of hinge structure in *Callistocythere pumila*. P, median element of hinge structure in *Callistocythere pumila*. Q, median element of hinge structure in *Ishizakiella miurensis*. R, terminal element of hinge structure in *Xestoleberis hanaii*. S, median element of hinge structure in *Xestoleberis hanaii*. hg(lv), hingement of left valve; hg(rv), hingement of right valve; lg, ligament; lv, left valve; ovl, overlap structure; rv, right valve. Scale bar = 1.4 μm (A, B, C, F, G, J, M), 4.0 μm (H), 2.5 μm (E, K, P), 2.0 μm (I, O), 6.7 μm (L, N), 3.3 μm (Q, S) and 2.9 μm (R).
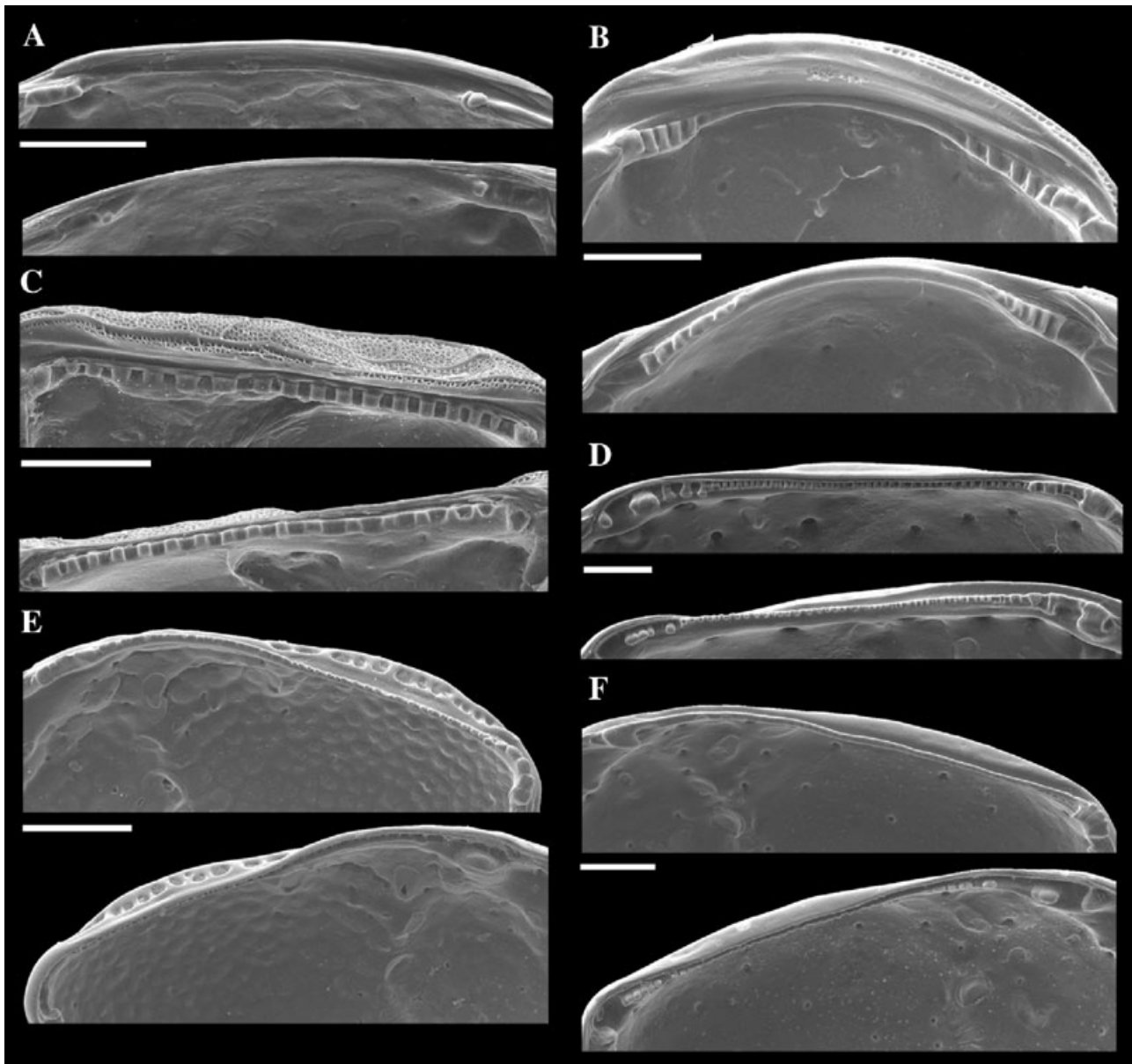
Figure 6. Scanning electron microsocopy photographs of podocopan hingements. A, *Semicytherura wakamurasaki*. B, *Hemicytherura kajiyamai*. C, *Semicytherura kazahana*. D, *Loxoconcha pulchra*. E, *Ishizakiella miurensis*. F, *Callistocythere pumila*. Right and left valves are shown as the upper and lower images of each pair, respectively. Scale bars = 50 μm.

elements (Fig. 6A, upper) and the smooth bar appears as the median element (Fig. 6A, lower). The difference of hinge structure is recognized in the genus *Semicytherura*. The terminal elements of these species show the intermediate type, but the median elements in *S. kazahana* and *S. wakamurasaki* develop as intermediate type and basic types, respectively (Fig. 5J, K).

CYTHEROIDEA (LOXOCONCHIDAE)

Loxoconcha pulchra: interior–intermediate–interior type (Figs 5L, M, 6D)

Loxoconcha japonica: interior–intermediate–interior type
The terminal elements of genus *Loxoconcha* develop large biramous teeth, and the median element exhibits crenulations (Fig. 6D). The hinge structures in the terminal elements and median element exhibit the interior and intermediate types, respectively (Fig. 5L, M).

CYTHEROIDEA (LEPTOCYTHERIDAE)

Callistocythere pumila: interior–exterior–intermediate type (Figs 5O. P, 6F)

Callistocythere rugosa: interior–exterior–intermediate type

Callistocythere setouchiensis: interior–exterior–intermediate type

Ishizakiella miurensis: interior–basic–intermediate type (Figs 5N, Q, 6E)
Different hinge structures can be recognized in the family Leptocytheridae. In the right valve of *Callistocythere* sp., the large teeth of the terminal elements connect via the median bar (Fig. 6F, upper), but in *I. miurensis* the median element develops as crenulations (Fig. 6E, upper). In the left valve of *Callistocythere* sp., the crenulations develop as the median element and are reduced towards the middle part (Fig. 6F, lower) but, in *I. miurensis*, these crenulations do not develop (Fig. 6E, lower). The hinge structures of these species in the anterior and posterior element show the interior type and intermediate types, respectively (Fig. 5N, O). The hinge structures of the median elements in the genus *Callistocythere* and *Ishizakiella* are classified into the exterior type and basic types, respectively (Fig. 5P, Q).

CYTHEROIDEA (XESTOLEBERIDAE)

Xestoleberis hanaii: intermediate–intermediate–intermediate type (Figs 5R, S, 7A)
The hingement of this species consists of the terminal elements as distinct crenulations, and the median ele-

ment as slight crenulations (Fig. 7A). The tripartite overlap structure develops over the hingement. The hinge structures of all elements in this species are classified as the intermediate type (Fig. 5R, S).

CYTHEROIDEA (COBANOCYTHERIDAE)

Paracobanocythere sp.: basic type (Figs 7B, 8A)
Paracobanocythere sp., which has an extremely thin carapace and lives in the interstitial pore water of sediments, develops a hingement containing the smooth bar (Fig. 7B, upper), and its hinge structure exhibits the basic type.

CYTHEROIDEA (LIMNOCYTHERIDAE)

Limnocythere stationis: interior–interior–interior type (Figs 7D, 8B, C)
This species is the only nonmarine cytheroid species examined in the present study. Its hingement is much weaker than that of European species of *Limnocythere*. The European species *Limnocytherina sanctipatricii* develops prominent terminal elements (Fig. 7C, upper), but those of *L. stationis* are poor (Fig. 7D, upper). Thus, the hingement of this species seems to consist mainly of the smooth bar (Fig. 7D, lower). The hinge structures in all elements show the interior type (Fig. 8B, C).

CYTHEROIDEA (ENTOCYTHERIDAE)

Entocythere: basic type (Harding, 1964: fig. 14a, b, c)
This species is a nonmarine parasitic taxon. The illustration referred to here for this taxon is from Harding (1964) because no specimen could be found. The hinge structure is classified into the basic type.

CYTHEROIDEA (CYTHERIDAE)

Cythere omotenipponica: intermediate–intermediate–intermediate type (Figs 7E, 8D, E)
The hingement consists of crenulations (Fig. 7E), and the tripartite overlap structure develops over the ligament. The hinge structures in all elements are recognized as the intermediate type (Fig. 8D, E).
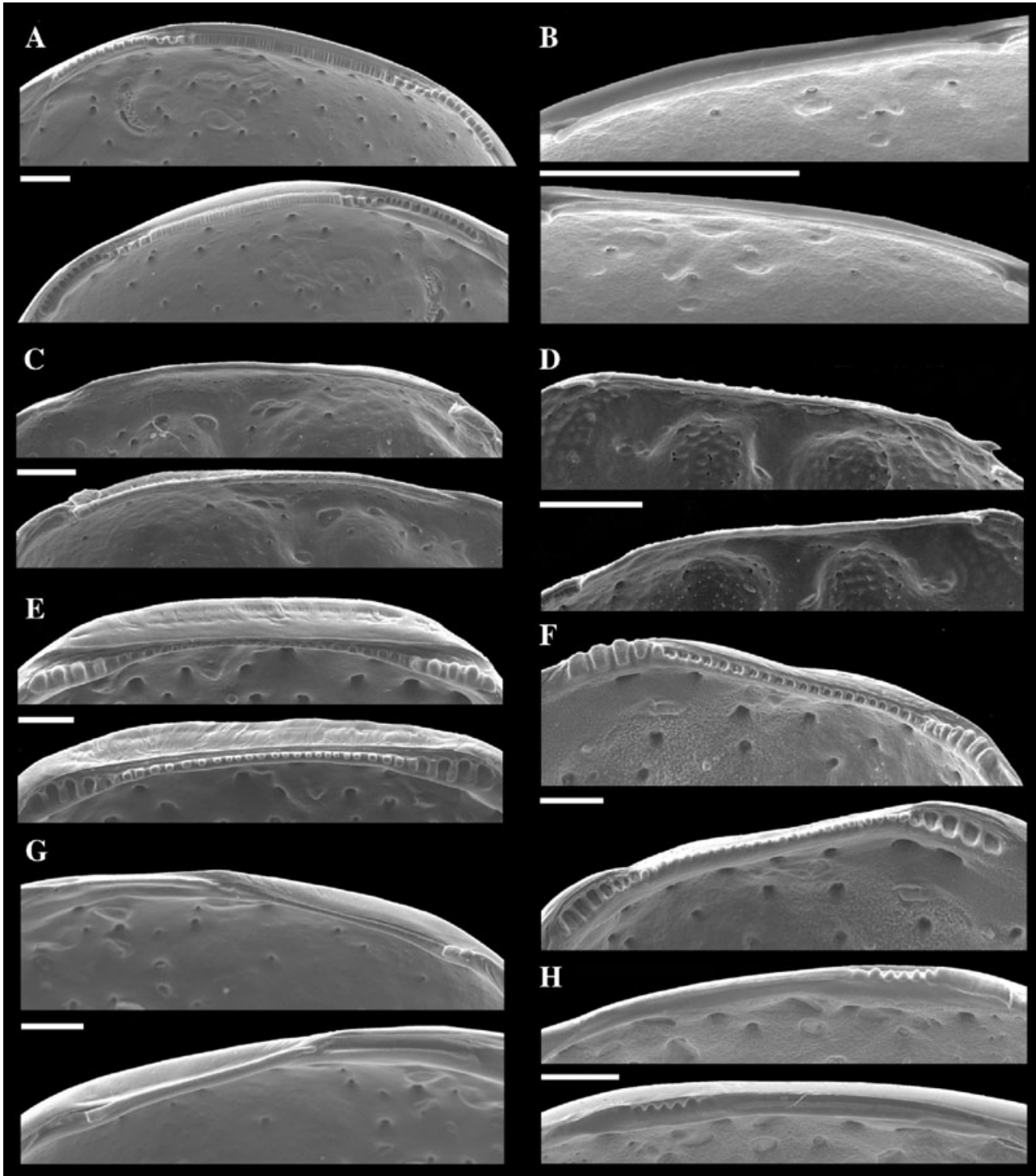
CYTHEROIDEA (CYTHERIDEIDAE)

*Perissocytheridea japonica: interior–intermediate–interior type (Figs 7F, 8F)*

Perissocytheridea inabai: interior–intermediate–interior type (Fig. 8G)
The hingements of these species are composed of large crenulations in the terminal elements and the small

Figure 7. Scanning electron microsocopy photographs of podocopan hingements. A, *Xestoleberis hanaii*. B, *Paracobanocythere* sp. C, *Limnocytherina sanctipatricii*. D, *Limnocythere stationis*. E, *Cythere omotenipponica*. F, *Perissocytheridea japonica*. G, *Pontocythere miurensis*. H, *Parakrithella pseudadonta*. Right and left valves are shown as the upper and lower images of each pair, respectively. Scale bars = 50 μm.
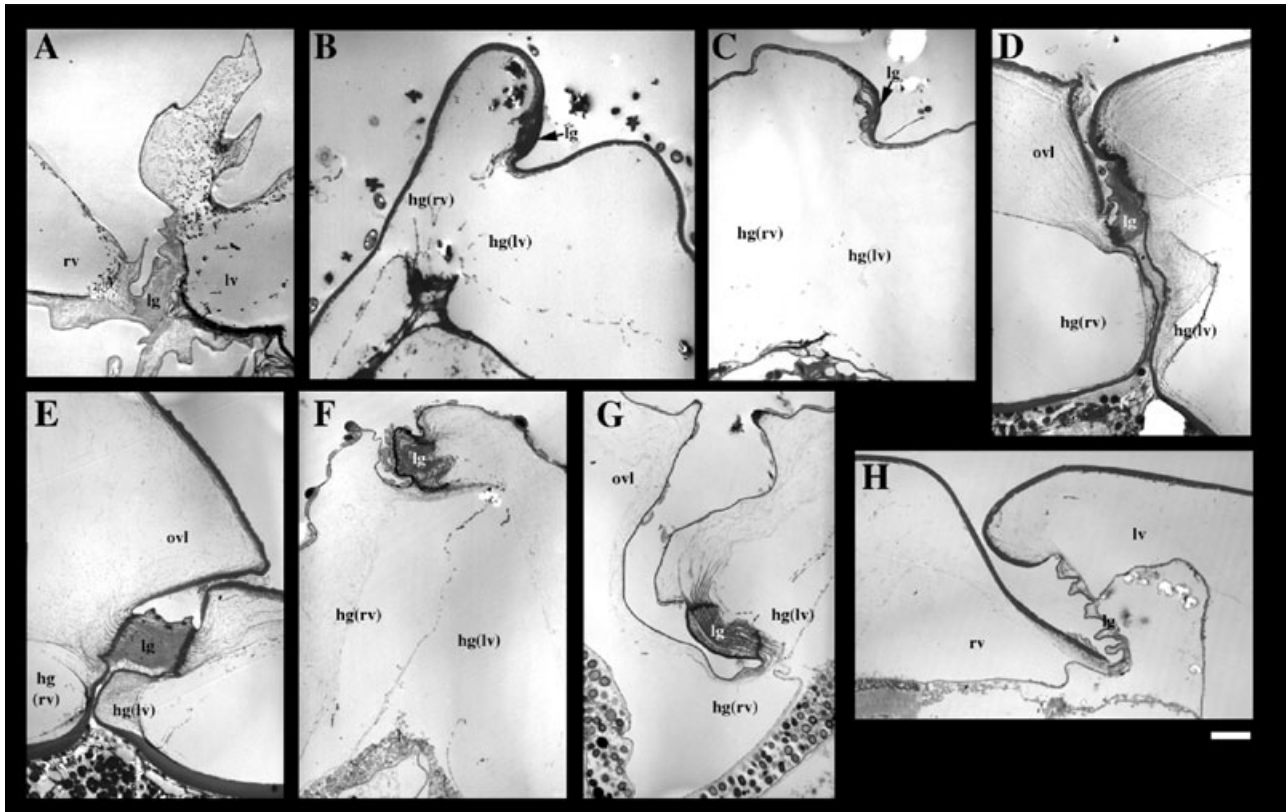
Figure 8. Transmission electron microsocopy photographs of podocopan hinge structures. A, *Paracobanocythere* sp. B, terminal element of hinge structure in *Limnocythere stationis*. C, median element of hinge structure in *Limnocythere stationis*. D, terminal element of hinge structure in *Cythere omotenipponica*. E, median element of hinge structure in *Cythere omotenipponica*. F, terminal element of hinge structure in *Perissocytheridea japonica*. G, median element of hinge structure in *Perissocytheridea inabai*. H, anterior element of hinge structure in *Pontocythere miurensis*. hg(lv), hingement of left valve; hg(rv), hingement of right valve; lg, ligament; lv, left valve; ovl, overlap structure; rv, right valve. Scale bar = 1.7 μm (A, B), 1.0 μm (C), 4.0 μm (D), 2.9 μm (E, F), 1.3 μm (G) and 3.3 μm (H).

crenulations in the median elements (Fig. 7F). The hinge structures in the terminal elements and median element develop into the interior and intermediate types, respectively (Fig. 8F, G).

CYTHEROIDEA (CUSHMANIDEIDAE)

Pontocythere miurensis: basic–exterior–interior type (Figs 7G, 8H, 9B)

Pontocythere japonica: basic–exterior–interior type (Fig. 9A)
The hingement of the genus *Pontocythere* consists of the smooth bar (Fig. 7G, lower) as the median element and the crenulations as the posterior element (Fig. 7G, upper). The hinge structure of the anterior element is classified as the basic type because the anterior element does not form a complementary structure, and the elongate ligament connects to each valve (Fig. 8H). In the median element the hinge structure exhibits the exterior type, with a poor ligament developing

below the overlap structure (Fig. 9A). In the posterior element, small short crenulations develop below the ligament and the hinge structure shows the interior type (Fig. 9B).

CYTHEROIDEA (KRITHIDAE)

Parakrithella pseudadonta: intermediate–intermediate–intermediate type (Figs 7H, 9E, F)
The hingement is composed of the smooth bars and short crenulations (Fig. 7H, upper). The hinge structures of all elements are classified into the intermediate type consisting of a small overlap structure and a large hingement (Fig. 9E, F).

CYTHEROIDEA (SCHIZOCYTHERIDAE)

Schizocythere kishinouyei: intermediate–intermediate–intermediate type (Figs 9C, D, G, 10A)
The anterior and posterior elements consist of a large biramous and small tooth, respectively (Fig. 10A,
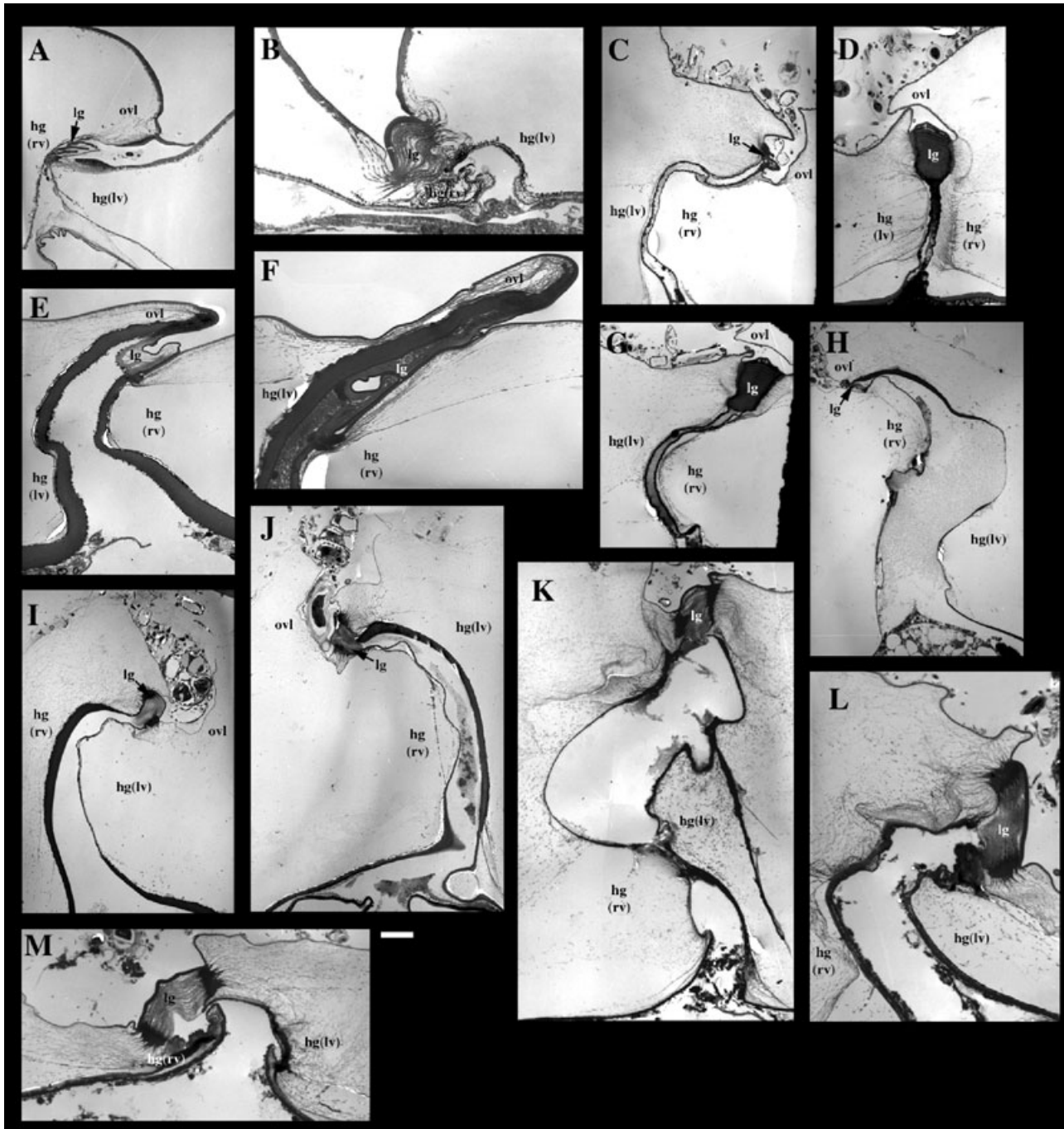
Figure 9. Transmission electron microsocopy photographs of podocopan hinge structures. A, median element of hinge structure in *Pontocythere japonica*. B, posterior element of hinge structure in *Pontocythere miurensis*. C, anterior element of hinge structure in *Schizocythere kishinouyei*. D, median element of hinge structure in *Schizocythere kishinouyei*. E, median element of hinge structure in *Parakrithella pseudadonta*. F, terminal element of hinge structure in *Parakrithella pseudadonta*. G, posterior element of hinge structure in *Schizocythere kishinouyei*. H, anterior element of hinge structure in *Caudites asiaticus*. I, median element of hinge structure in *Caudites asiaticus*. J, posterior element of hinge structure in *Caudites asiaticus*. K, anterior element of hinge structure in *Trachyleberis scabrocuneata*. L, median element of hinge structure in *Trachyleberis scabrocuneata*. M, posterior element of hinge structure in *Trachyleberis scabrocuneata*. hg(lv), hingement of left valve. hg(rv), hingement of right valve; lg, ligament; lv, left valve; ovl, overlap structure; rv, right valve. Scale bar = 2.9 µm (A), 2.0 µm (B, I), 1.7 µm (E), 1.4 µm (F, M), 5.6 µm (C), 2.7 µm (D, J, K), 4.5 µm (G), 3.6 µm (H) and 1.0 µm (L).
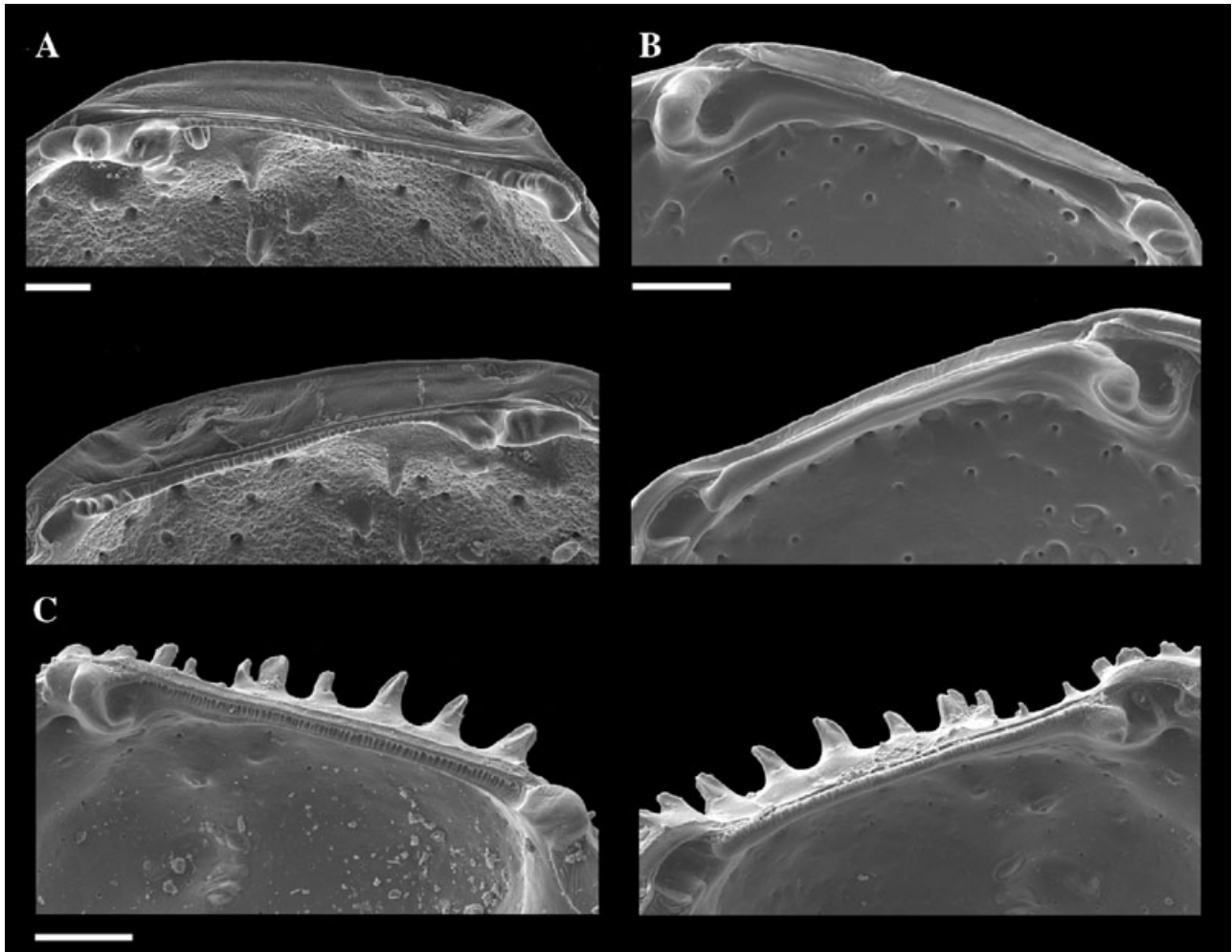
Figure 10. Scanning electron microsocopy photographs of podocopan hingements. A, *Schizocythere kishinouyei*. B, *Caudites asiaticus*. C, *Trachyleberis scabrocuneata* (RV, left image; LV, right image). Right and left valves are shown as the upper and lower images of each pair, respectively. Scale bars = 50 μm.

upper). The median element reveals a crenulated bar with the anterior biramous tooth (Fig. 10A, lower). The hinge structures of all elements are classified as intermediate types, which have a rather small overlap structure (Fig. 9C, D, G).

CYTHEROIDEA (HEMICYTHERIDAE)

Caudites asiaticus: intermediate–intermediate–intermediate type (Figs 9H, I, J, 10B)

Aurila hataii: intermediate–intermediate–intermediate type

The hingements of these species are composed of large teeth in the terminal elements (Fig. 10B, upper), and a median bar comprising the anteromedian large tooth with dorsal crenulations (Fig. 10B, lower). The hinge structure exhibits the intermediate type, which has an extremely small overlap structure and a major hingement below the ligament in all elements (Fig. 9H, I, J).

CYTHEROIDEA (TRACHYLEBERIDIDAE)

Trachyleberis scabrocuneata: interior–interior–interior type (Figs 9K, L, M, 10C)

The hingement of the Trachyleberididae consists of large teeth in the terminal elements (Fig. 10C, left), and a median bar comprising the anteromedian large tooth with lateral crenulations (Fig. 10C, right). The hinge structures in all elements are classified as the interior type (Fig. 9K, L, M).

DISCUSSION

STRUCTURAL DIVERSITY OF PODOCOPAN HINGES

Previous morphological studies on podocopan hinges have mainly concentrated on a classification based on the number of teeth elements (Sylvester-Bradley, 1956; Hanai, 1961), and these classifications were applied to higher levels of taxonomy (family or super-

family level). It was known, however, that the simplest hingement, 'adont', consisting of bar and groove, is found in several lineages.

In Platycopida, Bairdioidea, and Darwinuloidea, which appeared in the Early Palaeozoic and retain the primitive features to the present day, their hinge structures are classified into the simple types (basic type or exterior) in the present study (Table 2). By contrast, the hinge structures in the Cytheroidea and Cypridoidea, which contain numerous species and which show many diversified characters, have a much higher level of morphological diversity than in the primitive taxa mentioned above. The hinge structures especially of Cypridoidea, most species of which are mainly found in nonmarine aquatic habitats, have been exclusively classified into the simplest hinge 'adont' in previous studies. They can be reclassified as simple and advanced types (basic, exterior, and interior), although they all develop the simplest hingement consisting of the bar and groove.

Consequently, the hinge structures of the primitive taxa (Platycopida, Bairdioidea, Darwinuloidea) have diversified to a low level, but those of derived taxa (Cytheroidea, Cypridoidea) are highly diversified irrespective of the complexity of the hingement.

PLASTICITY OF CYTHEROID HINGE STRUCTURES

The hingements of the Cytheroidea represent various morphologies and have been classified into almost 20 types even amongst the extant species (Hinz-Schallreuter & Schallreuter, 1999). Two characteristics of cytheroid hinge structures are considered to underlie the various morphologies of their hingements. One is that most cytheroid ostracods develop advanced hinge structures (intermediate and interior types), and the other is that most cytheroid hingements are composed of three teeth elements.

The advanced hinge structure provides for the high morphological plasticity of the hingement due to the separation of ligament and hingement in the intermediate and interior types. The hinge structure of the basic type does not provide for the hingement. The hinge structure of the exterior type develops a simple hingement, consisting of the bar and groove at the ligament joint area. It is ascertained that these simple hinge structures (basic and exterior types) have no space for the development of a hingement beneath the ligament. In addition, the hingement of the exterior type cannot involve complex morphologies because numerous organic fibres aggregate in the ligament joint area, and these fibres inhibit morphological changes to the hingement through quantitative change of calcification. By contrast, the intermediate

and interior types have enough space to develop the hingement beneath the ligament, and they can develop complex hingements through small changes of calcification.

The latter process is conspicuous in the Cytheroidea, and their hingement morphologies have diversified remarkably, by tripartition into anterior, median, and posterior elements and subdivisions. Most cytheroid species develop tripartite hingements because it is assumed that they are benthonic and crawl on or dig into the sediment surface and use their terminal elements for resistance to the distortional force of the heavy sediment particles. The tripartite hingements are also observed in the other marine ostracods; *Keijcyoidea infralittoralis* (Fig. 2A) and *Macrocypris* sp. (Fig. 2O), which live on or in the sediments (coarse sand). On the other hand, the tripartite hingements do not develop in the interstitial species (crawling on the surface of sediment particles without digging) *Paracobanocythere* sp. (Fig. 7B), the phytal species *Sclerochilus* sp. (Fig. 4B), *Paradoxostoma triangulum* (Fig. 4D), and the parasitic species *Entocythere* (Harding, 1964: fig. 14), even though they belong to the Cytheroidea. These facts support the hypothesis that the development of the tripartite hingement increases the resistance of the carapaces constituent values to the distortional force of heavy sediment particles in an infaunal mode of life.

It is concluded that the two characteristics described above ensure the morphological plasticity of the cytheroid hingement, and promote diversification.

WHAT ARE HINGE STRUCTURES AFFECTED BY?

Previous studies have discussed the relationship between the complexity of hingements and the degree of calcification (Pokorný, 1957; Benson, 1966), but they did not discuss other factors such as salinity, locomotion, and habitat in relation to the complexity of hingements.

Most cypridoid ostracods are found in nonmarine aquatic habitats and their hinge structures are composed of simple basic and exterior types. The minor cypridoid marine species (e.g. Paracypridinae), however, have advanced hinge structures (i.e. the interior type; Fig. 3L, M). In the Cypridoidea, the benthic (e.g. *Chrissia* sp., *Fabaeformiscandona* sp., and Paracypridinae sp. B) and nekto-benthic species (e.g. *Cypridopsis vidua*, *Cypria reptans*, and Paracypridinae sp. A) develop the same hinge structures in each of the families.

On the other hand, most cytheroid ostracods live in marine and brackish environments, and their hinge structures are highly complicated. The nonmarine species *Limnocythere stationis* has advanced hinge

structure (interior type) and a tripartite hingement (Figs 7C, D, 8B, C), but the nonmarine taxon *Entocythere* has a simple hinge structure (basic type) and a nontripartite hingement (Harding, 1964: fig. 14). The genus *Entocythere* is an unusual taxon that parasitizes the gills of crayfish, whereas the interstitial species *Paracobanocythere* sp. (Fig. 7B), the phytal species *Sclerochilus* sp. (Fig. 4B), and *Paradoxostoma triangulum* (Fig. 4D) also have simple hinge structures (basic and exterior) and nontripartite hingements, although they are found in marine environments.

The nonmarine and marine cypridoid ostracods are therefore equipped with simple (basic, exterior) and advanced (interior) hinge structures, respectively. In the Cytheroidea, only the interstitial, phytal, and parasitic cytheroid species have simple hinge structures (basic and exterior types), although most cytheroid species develop advanced hinge structures (intermediate and interior types) irrespective of their saline environments. These facts lead us to conclude that the cypridoid hinge structures exhibit distinct differences relative to their habitats (freshwater or marine; mineral environment), and that the cytheroid hinge structures are affected by the modification of the carapace features in connection with the difference of their habitats rather than to the salinity of their environments.

EVOLUTIONARY PATHWAYS OF PODOCOPAN
HINGE STRUCTURES

Only a few studies have discussed the evolution of ostracod hingements. Hingements have been generally thought to reflect ostracod phylogeny and to have an evolutionary trend from simple to complex (Sylvester-Bradley, 1948; Hartmann, 1963; Sandberg, 1964; Benson, 1966). On the other hand, studies on hingements, which reported parallel evolution (Triebel, 1954; Sylvester-Bradley, 1956; Yamaguchi, 2003) and discussed pseudomorphosis (Kamiya, 1992; Tsukagoshi, 1994; Tsukagoshi & Kamiya, 1996), ascertained that hingements do not have exactly regular evolutionary trends and concluded that they do not always reflect ostracod phylogeny. The present study surveys the fossil records of major taxa in Podocopa from the literature (Fig. 11). The presumed evolutionary pathway of the podocopan hinge structures is oulined below.

It is suggested that the basic type has the most simple hinge structure in the Podocopa (Platycopida, Darwinuloidea) by the Early Ordovician (Fig. 12). By the Late Ordovician, the marginal infold was developed due to the increase of calcification in the podocopan free margin, whereas the hinge structure with a simple exterior type of hingement appeared (Fig. 12A; Bairdioidea).

The hinge structures mentioned above do not have complicated hingements because their hingements do not develop or locate in the ligament joint area, but the intermediate and interior type of hinge structures, which equip the ligament and hingement independently, appeared by the Silurian (Fig. 12B; Bythocytheridae, Macrocypridoidea?). Additionally, due to the development of the tripartite hingement, the cytheroid lineage had acquired high plasticity of hinge structures by the Early Palaeozoic. In the Mesozoic, species diversity of the Cytheroidea exploded at the family level, and many kinds of hingement morphologies emerged (Fig. 12C). Leading up to the present time, they have adapted to various aquatic habitats, and some of them (Paradoxostomatidae, Cobanocytheridae, Entocytheridae, and *Sclereochilus*) have reduced their advanced hinge structures to simple ones through a process of adaptation to their habitats (Fig. 12D).

The superfamily Cypridoidea developed by the Late Palaeozoic (Fig. 12E), and most cypridoid species have retained simple hinge structures (basic and exterior types) up to the present, as a result of adaptation to nonmarine aquatic habitats (Fig. 12F). Some candonid species (Candonidae: Paracypridinae), which appeared by the Early Cenozoic, adapted to a marine environment and became equipped with the advanced interior type of hinge structure (Fig. 12F). They do not have tripartite hingements, a feature shared with cytheroid species, in spite of the marine habitat. It is suggested that they do not need the intensification of resistance to the distortional force of heavy sediment particles for their nekto-benthic or interstitial ecology. The macrocypridoid and pontocypridoid hinge structures are assumed to have evolved from the cypridoid hinge structures in the Early Cenozoic and Middle Mesozoic, respectively, based on their strong fossil records (Fig. 12G). On the other hand, the cypridoid hinge structures may have evolved from the macrocypridoid hinge structures as an adaptation to the nonmarine habitats by the Late Palaeozoic (Fig. 12E) because the macrocypridoid species retain primitive features and their uncertain fossil records are reported from the Early Palaeozoic. These two evolutionary pathways of macrocypridoid hinge structures are alternatives.

Bivalved arthropods that have their body encased in a carapace, as in the Ostracoda and Conchostraca, have been reported from the Early Palaeozoic. Some of them (i.e. *Leperditia*, *Kummingella*) have two strongly calcified valves that are often preserved in fossils. It is assumed that these bivalved arthropods developed a flexible cuticle between the two calcified valves that enables the mobility of the valves. The Ostracoda are the only living arthropods equipped with the hinge structure mentioned above. Thus, the evolutionary
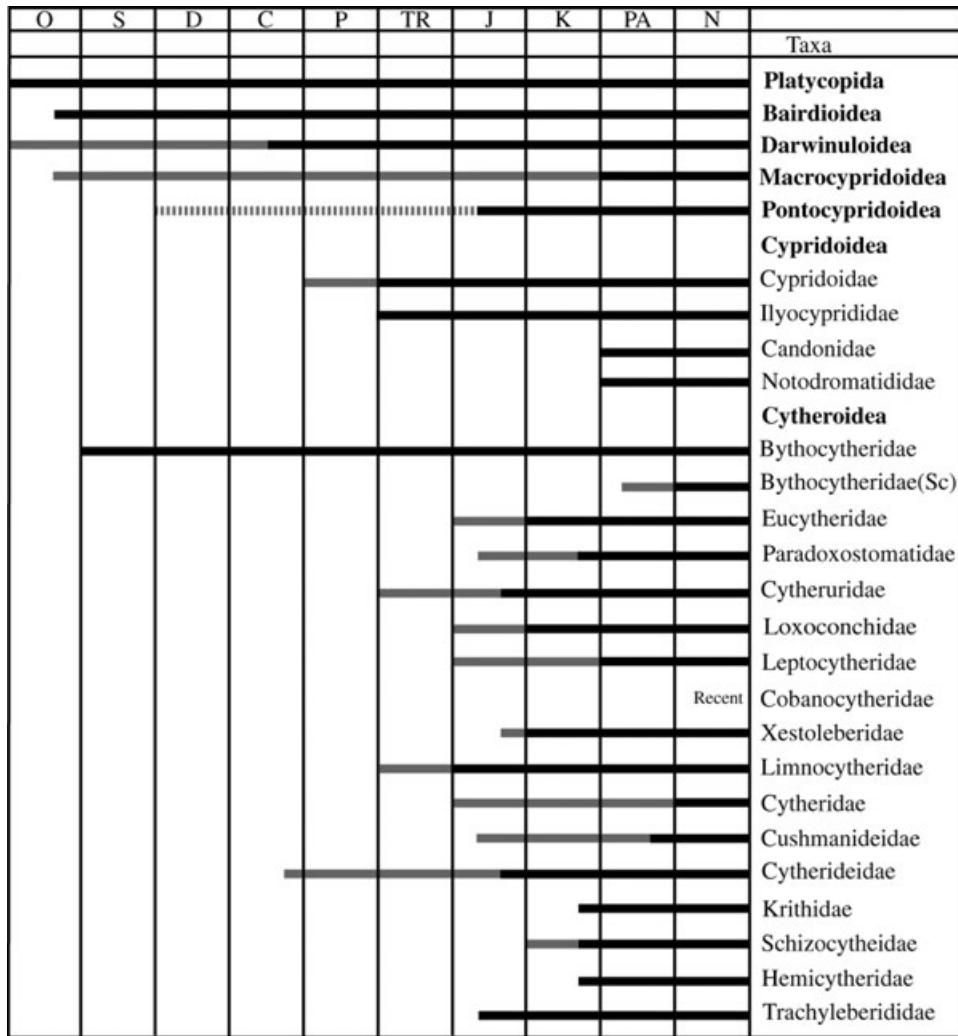
Figure 11. Fossil records of podocopan ostracods. O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; TR, Triassic; J, Jurassic; K, Cretaceous; PA, Palaeogene; NG, Neogene; Sc, genus *Sclerochilus*. Fossil data are complied mainly from Moore (1961) and Schram (1986). Grey bars indicate uncertain fossil records. A broken bar shows the fossil record which could not be confirmed as a figured data.

pathway of ostracod hinge structures is the sole model that can represent the evolution of the bivalved arthropod exoskeleton. The diversity of hinge structures in ostracods proposed by this investigation is only seen in one lineage, namely the Podocopa, which can develop strongly calcified valves. This diversity of structure arises from the evolution of the strength of the valve juncture, as a consequence of adaptive radiation to the various habitats involved with miniaturization of podocopan body size.

CONCLUSION

The podocopan ostracod hinge structures are classified into four types: basic, exterior, intermediate and interior based on the relative position of ligaments and hingements. This classification implies that the derived taxa share all four types, although the primitive taxa have the two simple types (basic and exterior) exclusively.

The morphological diversity of hingements in the Cytheroidea, which has the highest species diversity, is caused by the plasticity of the advanced hinge structures (intermediate and interior types) and the tripartite hingements.

The podocopan hinge structures must reflect the influences of habitat, ecology, and other environmental variables, rather than the phylogeny of the animals. Hinge structures are therefore important features for the elucidation of ostracod evolution.
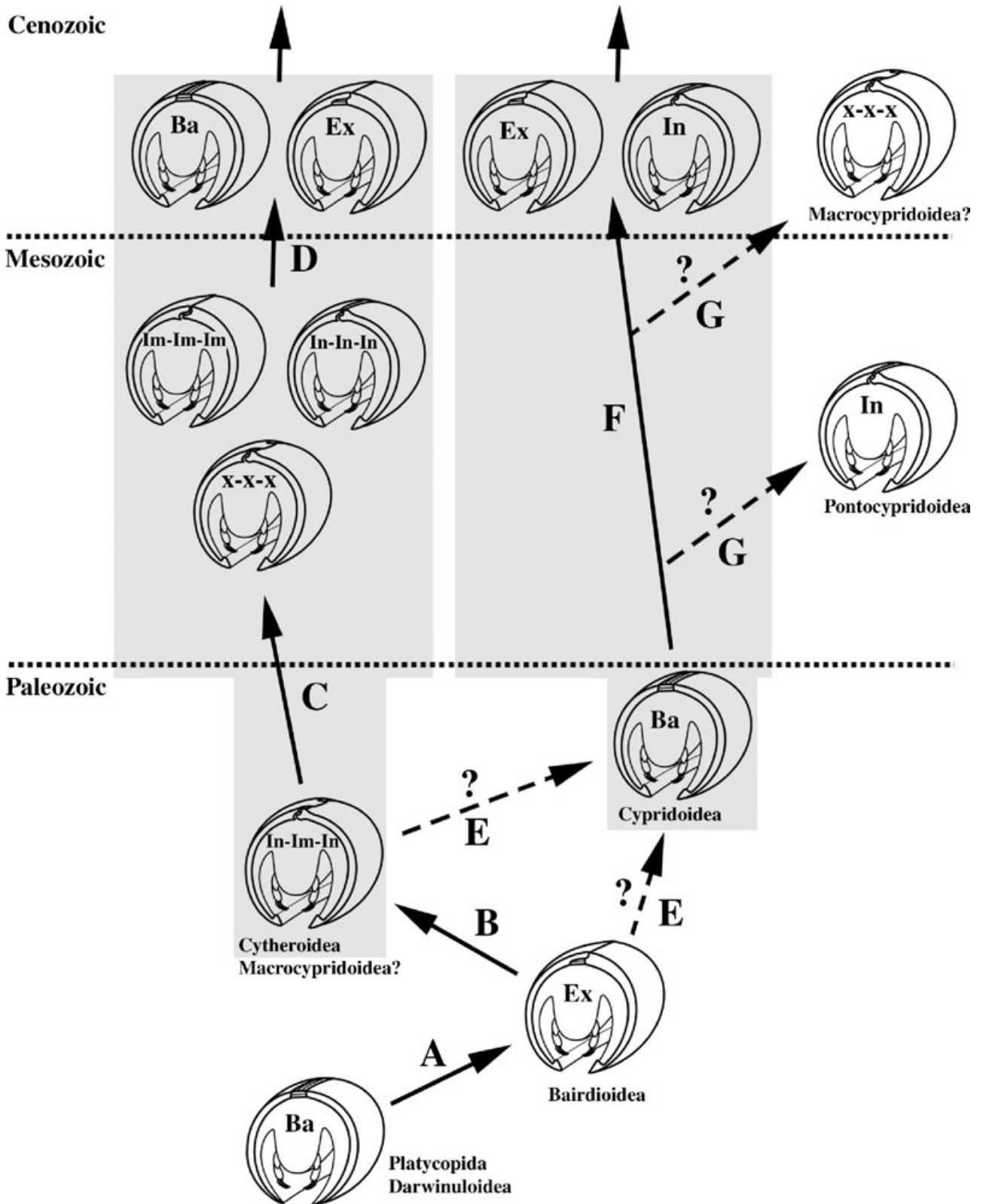
Figure 12. Evolutionary pathways of podocopan hinge structures. Ba, basic type; Ex, exterior type; Im, intermediate type; In, interior type; x-x-x, various combinations of tripartite hinge structure.

ACKNOWLEDGEMENTS

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