

Differences between the sensory organs of phytal and bottom-dwelling *Loxoconcha* (Ostracoda, Crustacea)

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ABSTRACT—The morphology and distribution patterns of pores with a bristle were studied on two *Loxoconcha* species living in adjacent but different habitats: the phytal species *L. japonica* and the bottom-dwelling species *L. uranouchiensis*. Both species have only one kind of pore – sieve-pore – from which either of two kinds of bristles emerges. The two types of bristles are here called the “smooth”- and the “twisted”-type according to their morphological features. The sieve-pore orifice of the phytal *Loxoconcha* remains completely open, whereas that of the bottom-dwelling species has a special morphology both in the sieve-plate and the basal part of the bristle to cope with the adhesion of dirt. The number and distribution pattern of “twisted”-type bristles (chemo-receptors?) are the same in both species. The “smooth”-type bristles (mechano-receptors?), however, are distributed more densely in the ventral area of the bottom-dwelling species compared with those of the phytal species. This difference seems to be related to the mode of life, specifically the difference in the manner of ventral contact with substrata. Some adaptive characters of ostracod pores are clarified and their significance to ostracod taxonomy and palaeoecology is discussed.

INTRODUCTION

Successive improvements to and popularization of the SEM (scanning electron microscope) have made it possible to observe clearly and easily carapace microstructures of Ostracoda, of which the first SEM photographs were taken about 20 years ago (Sandberg & Plusquellec, 1969). Pores (small holes penetrating the carapace perpendicularly), one of the common microstructures of the ostracod carapace, have been studied for various purposes in palaeontology; e.g. pores and phylogeny (Puri & Dickau, 1969, Puri 1974), pores and environments (Rosenfeld & Vesper, 1977, Hanai *et al.*, 1985) and the evolution of pores (Puri, 1974, Liebau, 1978).

The biological meaning of carapace microstructures was recently elucidated based on the results of studies of insect sensilla and the adoption of TEM (transmission electron microscope) techniques: pores with a bristle (= sensory seta) and reticulate ornament correspond to sensory organs and the arrangement of epidermal cells respectively (Okada, 1981, 1982a, b, 1983, Keyser, 1982, 1983); effectively, the ostracod carapace can be regarded as “calcified skin”.

Only a few studies, however, have described how the different pores and bristles, which may store both ecological and physiological information in abundance, are related to the difference of individual mode of life or behaviour (e.g. Hanai *et al.*, 1985). This is partly due to the fact that there are a few species, even Recent ones, whose habitat and mode of life are adequately understood.

Since the summer in 1983 the Ostracoda in Recent *Zostera* beds have been studied, in particular the phytal *Loxoconcha japonica* and bottom-dwelling *L. uranouchiensis*. These two species are well adapted to their own habitats at individual level (morphological and ethological adaptation: Kamiya, 1988a) as well as at population level (adaptation in mating system: Kamiya (1988c), adaptation in other aspects of population ecology: Kamiya (1988b). Such two related species whose mode of life differs dramatically from each other would be the ideal material to evaluate the relation between pores with a bristle and the mode of life, i.e. adaptation to habitat at sensory organ level. The successful recognition of adaptive characters in the sensory organ would be a useful contribution to palaeontology, facilitating the reconstruction of the palaeoenvironment and/or palaeoecology of fossil species. Some palaeoenvironments can be inferred by functional morphology of pores, independent of the ecological distribution data of living species (Hanai *et al.*, 1985). If we understand the degree to which the pores genetically change in number and distribution pattern through an adaptation to the habitat environment, we can define the taxonomic significance of the pore. Because pores are possessed by every species and are clearly recognisable, they are potentially useful in the taxonomy of species without any distinct carapace ornament.

As a first step towards the recognition of adaptive characters, the morphology and distribution pattern of

pores and bristles are here compared between adults of phytal and bottom-dwelling *Loxoconcha*, and the recognised differences are considered in terms of their mode of life and habitat environments. The ontogenetical change of pores and bristles in the two *Loxoconcha* species, and analyses of other genera will be reported in a separate paper.

MATERIAL AND METHODS

Living specimens were collected from *Zostera* beds in Aburatsubo Cove, on the Pacific coast of central Japan (lat. N 35° 9' 20", long. E 139° 37' 00"). Collected specimens were fixed in 5% formaldehyde or glutaraldehyde (pH, 7.3) solution before being dipped in 60% ethanol. The dipped specimens were then dehydrated in ethanol series, treated in amyl acetate and dried by the critical-point method to observe bristles and the epicuticle. Distribution of pores and bristles was examined for more than 15 specimens of each species.

GENERAL DESCRIPTION

Loxoconcha japonica Ishizaki, 1968 (Pl. 1, figs. 1, 2) is a phytal species living on the leaves of the eel-grass *Zostera marina* which grows in a relatively open marine environment. *L. uranouchiensis* Ishizaki, 1968 (Pl. 1, figs. 3, 4) is a bottom-dwelling species living on the sand bottom surface in and around the *Zostera* beds. Both species grow up through seven ecdyses to the adult, and closely resemble each other in the carapace shape at the earliest (A-7) juvenile stage. However, the shape of the ventral part gradually differs as they grow, and becomes distinctly different (cf. Pl. 1, figs. 1, 2 and figs. 3, 4). The difference in shape reflects the difference in mode of life, especially the mode of copulation. *L. japonica* spends its whole life on the *Zostera* leaves which stand perpendicular to the bottom, clinging to the leaf-surface with its legs so as not to slip down to the bottom, and copulating on the leaves. Their legs are of importance to hold the body so that this species has robust hooks at the tip of the legs. The posteriorly swollen carapace of this species accommodates its relatively huge sexual organs and provides a

convenient form for its copulatory position (ventral to lateral). On the contrary, *L. uranouchiensis* lives on and in the thin organic detritus covering the sand bottom. Its flat ventral surface (see Pl. 1, fig. 4) is usually in contact with this soupy substrate, and may play a role in keeping the body stable. Their carapace shape is suited to copulating in the ventral to ventral position. (In details, see Kamiya, 1988a).

MORPHOLOGY OF PORE

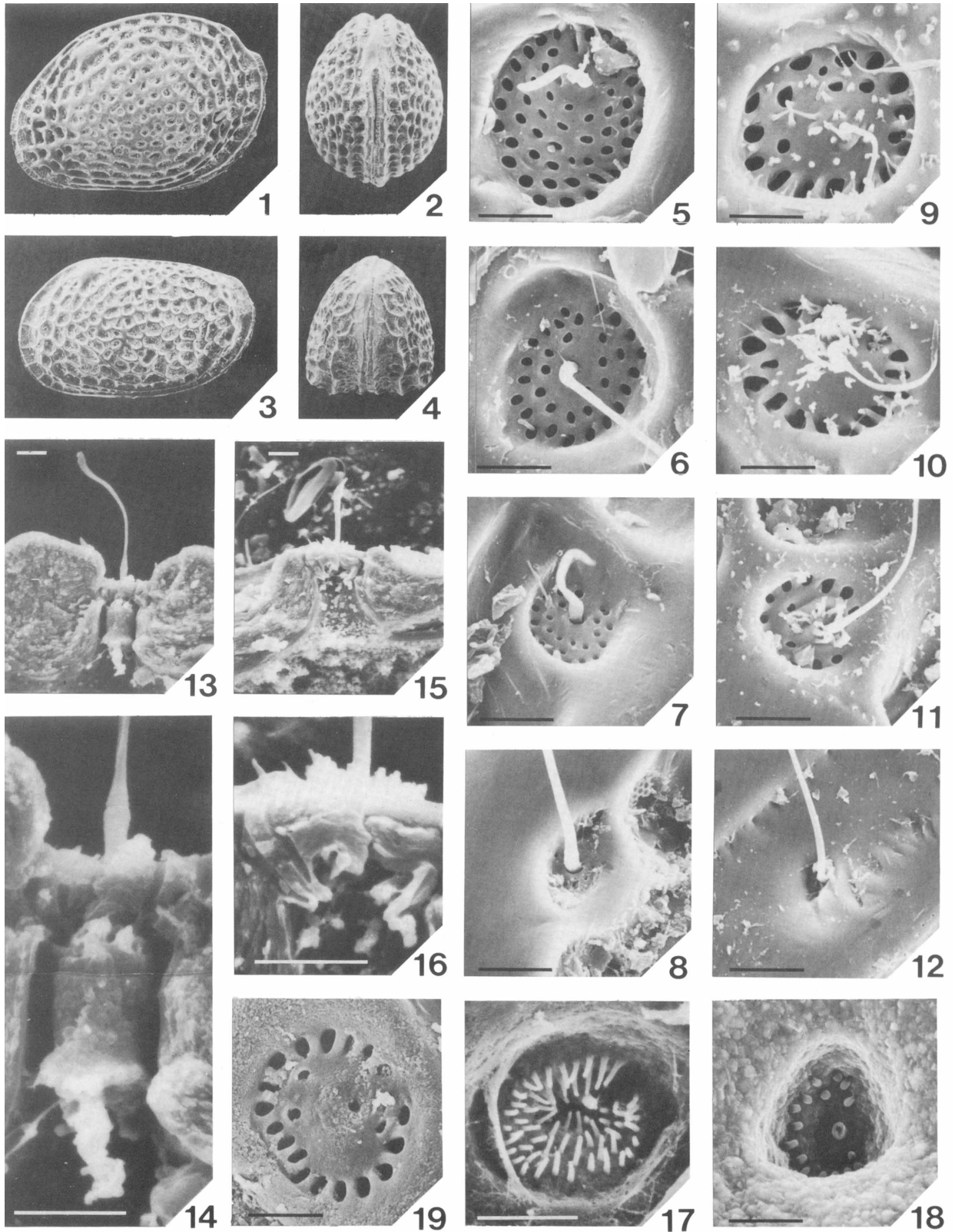
General structure. In general ostracod pores have been morphologically grouped into two types: sieve- and simple-pores. As a result of this investigation it was proved that both *L. japonica* and *L. uranouchiensis* have only sieve-type pores, but the morphology of these pores is different between the two species. The sieve pore of *L. japonica* is composed of a sieve-central-pore projecting a bristle (about 1 μ m in diameter) and sieve-micro-pores without bristles which surround the central-pore subcentrally (e.g. Pl. 1, figs. 5, 6). *L. uranouchiensis* has sieve pores made up of a sieve-central-pore with a bristle surrounded by a single ring of sieve-micro-pores (e.g. Pl. 1, figs. 9, 10).

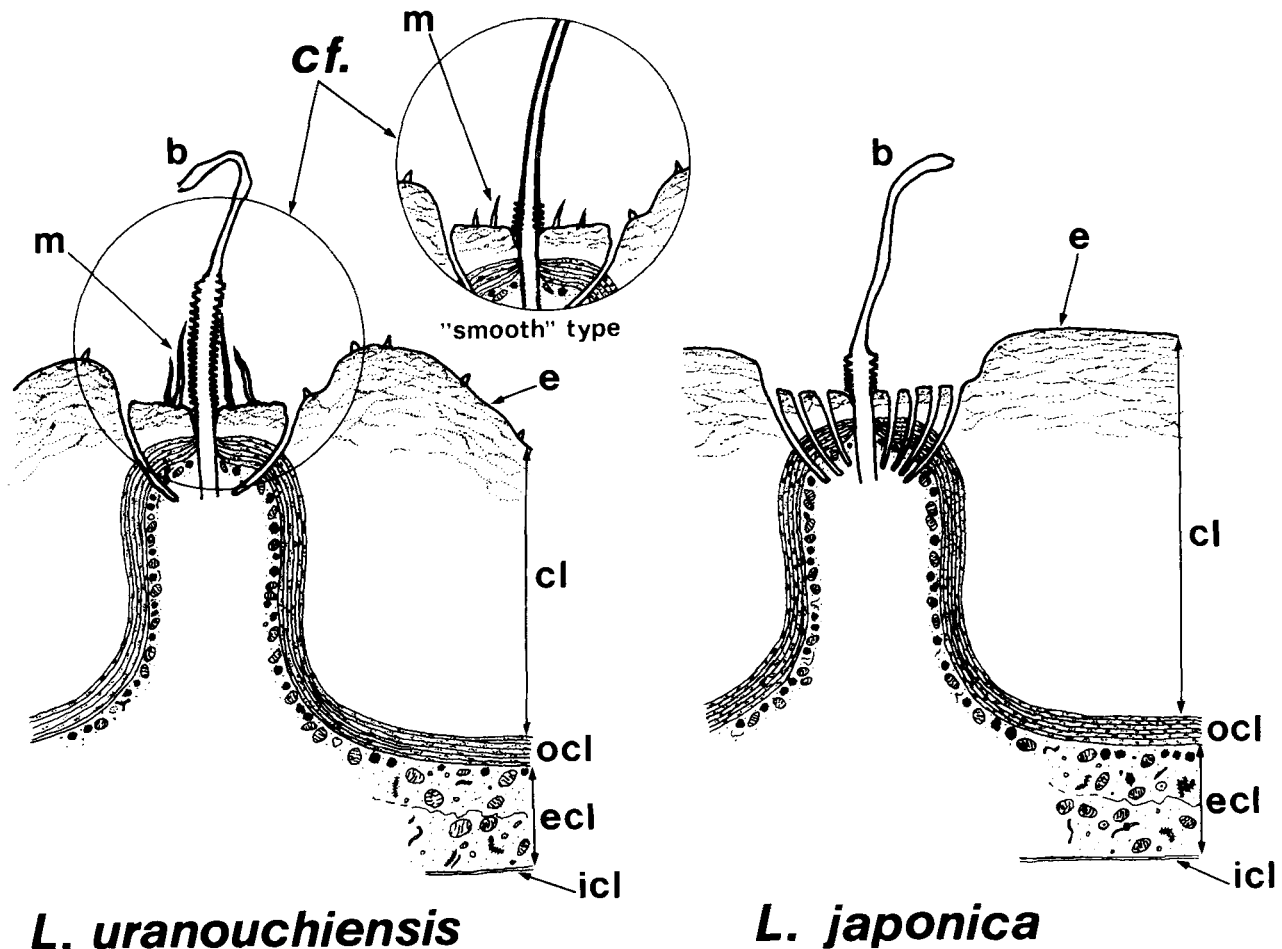
In both species, pores are situated centrally on muri ("intramural pore": Sylvester-Bradley & Benson, 1971) in the dorsal and lateral centre of the carapace, and on the slope of muri or on the solum adjacent to muri (similar to "celate pore with apophysis": Sylvester-Bradley & Benson, 1971) near the free margin where muri become narrow.

Fractured surfaces of pores perpendicular to the carapace surface were examined in both species (Pl. 1, figs. 13–16). The carapace of both species consists of (from inner to outer surface): an inner cuticular layer, epidermal cell layers, a chitinous layer, a calcareous layer and an epicuticle. The wall surface of sieve-micro-pores is covered by epicuticle and the micro-pores penetrate the calcareous layer, intruding into the epidermal cell layers (Fig. 1, Pl. 1, figs. 13–18), as Okada (1983) pointed out as "multiple pouch structures" in cytheracean species.

Explanation of Plate 1

- Figs. 1–4. Carapace shape (female) ($\times 80$): fig. 1. *Loxoconcha japonica*, lateral view (L-valve); fig. 2. *L. japonica*, posterior view; fig. 3. *L. uranouchiensis*, lateral view (L-valve); fig. 4. *L. uranouchiensis*, posterior view.
- Figs. 5–12. Pores (with "smooth"-type bristle) along a line transverse to the longitudinal axis of a carapace ($\times 2450$): figs. 5–8: *L. japonica*, 9–12: *L. uranouchiensis*; figs. 5 & 9. Near hingement; figs. 6 & 10. At lateral centre; figs. 7 & 11. At ventral centre; figs. 8 & 12. Near ventral margin.
- Figs. 13–16. Fractured surface of a pore (with "twisted"-type bristle) perpendicular to the carapace surface; fig. 13. *L. japonica* ($\times 980$); fig. 14. Magnified pore orifice in fig. 13 ($\times 3700$); fig. 15. *L. uranouchiensis* ($\times 970$); fig. 16. Magnified pore orifice in fig. 15 ($\times 3700$).
- Figs. 17, 18. Pores from interior view: fig. 17. *L. japonica*, epidermal cell layers were stripped off (cf. Pl. 1, fig. 14, Fig. 1) ($\times 3300$); fig. 18. *L. uranouchiensis*. Epidermal cell layers and outer cuticular layer were stripped off (cf. fig. 16, Fig. 1) ($\times 2450$).
- Fig. 19. Pore in sub-fossil specimen of *L. uranouchiensis* ($\times 2450$). Scale bars indicate 5 μ m.





L. uranouchiensis

L. japonica

Fig. 1. General structure of pores with "twisted" type of bristle in two species of *Loxoconcha*. On *L. uranouchiensis*, showing morphological differences in bristle bases and micro-hairs between "twisted" and "smooth" types of bristles (see text on "transformation of epicuticle"). Detailed carapace structure, particularly the soft tissue, was drawn by reference to TEM photographs (Kamiya, In preparation). b: bristle, m: micro-hair, e: epicuticle, cl: calcareous layer, ocl: outer cuticular layer, ecl: epidermal cell layers, icl: inner cuticular layer.

Intra-individual variation. Sieve pores in a carapace show a tendency for the diameter of the sieve-plate, as well as the number and the diameter of each sieve-micro-pore, to gradually decrease from the hinge line toward the free margin (Pl. 1, figs. 5–12). Large sieve pores are observed along the dorsal hinge line in *L. japonica* (Pl. 1, fig. 5). These pores have a whole diameter of about $15\ \mu\text{m}$ and are composed of approximately 55–65 sieve-micro-pores. The number of the micro-pores declines to about 35–55 laterally (Pl. 1, fig. 6), 20–30 ventrally (Pl. 1, fig. 7) and 5–15 along the ventral margin (Pl. 1, fig. 8). In the pores along the ventral margin the diameter of sieve-plates decreases to about $5\ \mu\text{m}$ and the micro-pores become very small (Pl. 1, fig. 8). The same tendency is recognized from the anterocentral region towards the anterior margin and the posterocentral region to the posterior margin.

The bottom-dwelling *L. uranouchiensis* has a similar trend: dorsally about 20 sieve-micro-pores in a pore

(Pl. 1, fig. 9), decreasing to 15–18 laterally (Pl. 1, fig. 10), 12–15 ventrally (Pl. 1, fig. 11), and finally the sieve-micro-pores disappear near the ventral margin (Pl. 1, fig. 12) (These pores without micro-pores might be discriminated from sieve pores and called simple pores, as has been usually done. However, they are treated indiscriminately in this paper, being regarded as the same pores in essence).

MORPHOLOGY OF BRISTLES

Both *L. japonica* and *L. uranouchiensis* have two types of bristles, "smooth" and "twisted"-type, compared schematically in Fig. 2. The "smooth" type of bristle in *L. japonica* extends smoothly and tapers slightly (Pl. 2, fig. 1). A bundle of finger-like structures is seen at the tip of this bristle (Pl. 2, fig. 2). At the base a fine bellows-like structure of annular thickenings ("circular reinforcement" in Puri, 1974, "circular fold" in Okada, 1982) is regularly developed. The "twisted"

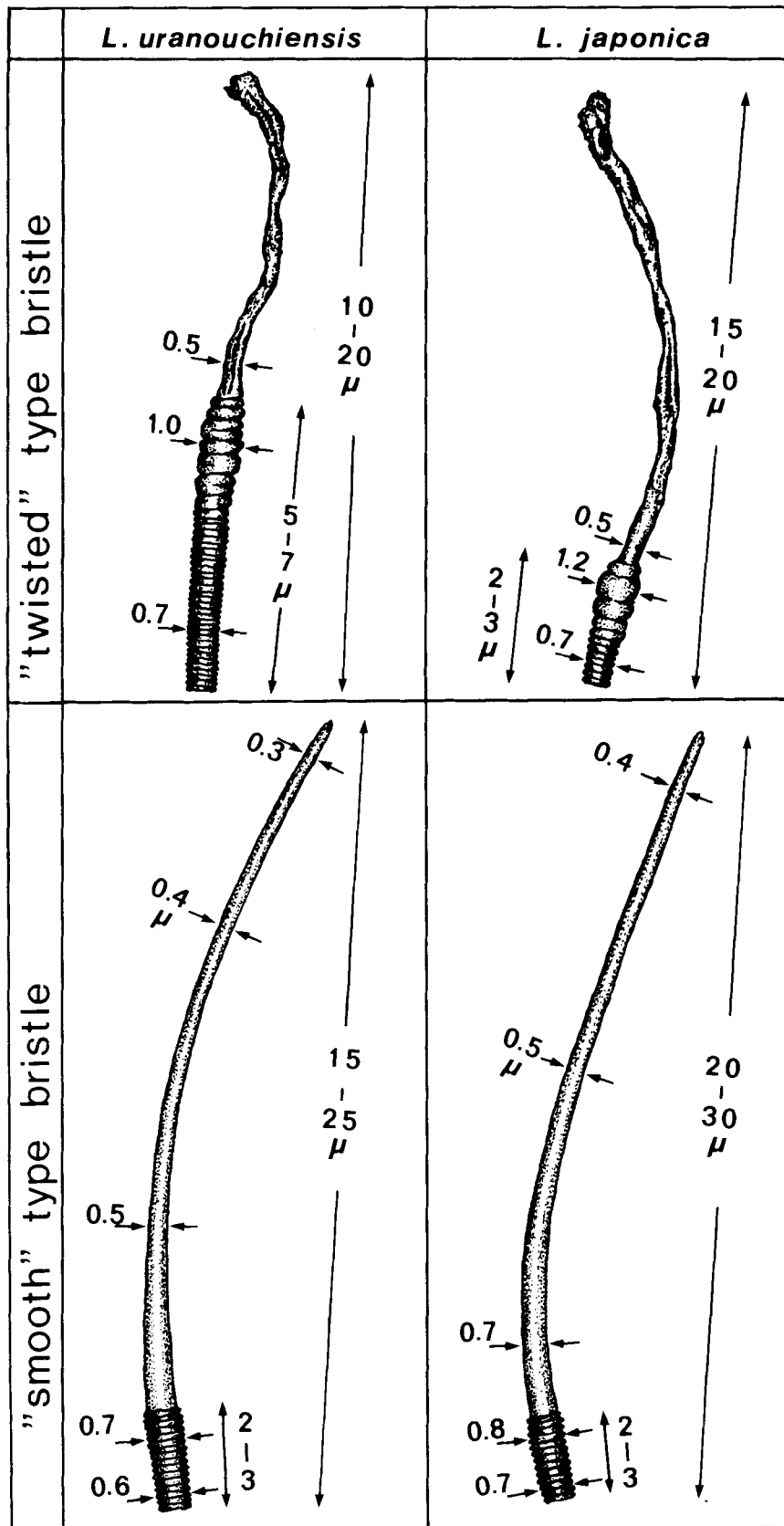


Fig. 2. Morphology of two types of bristles in two species of *Loxoconcha*.

type of bristle in *L. japonica* twists, bends or flattens except at the base where it shows a coarse bellows-like structure (Pl. 2, fig. 3). This may suggest that the cuticular wall of the twisted part is thin so that the inside of the bristle is largely hollow, while the cuticular wall of the "smooth"-type bristle is rather thick. The tip of "twisted"-type bristle, which is still broad, ends abruptly. The twisted part above the bellows, especially around the tip, is usually fouled, adhered to by fine dirt.

The "smooth" type of bristle in *L. uranouchiensis* is similar to that of *L. japonica* but slightly shorter and slenderer (Pl. 2, fig. 4). On the contrary, the "twisted" type shows a noticeable difference: although the distal part of the bristle is similar, the bellows-like structure of this bottom-dwelling species is conspicuously long, occupying almost half length of the bristle (Pl. 2, figs. 5, 6).

Unlike the pores, the bristles showed no tendency to intra-individual variation.

TRANSFORMATION OF EPICUTICLE

On the carapace of *L. uranouchiensis* the epicuticle, which thinly covers the outer surface of the calcareous layer, is transformed into hair-like or wart-like structures (similar to "moulting trichoids" in Keyser, 1982, "processes" and "papillae" in Siveter, 1982). The hair-like structures, here called "micro-hairs", stand upright from sieve plates and surround the base of the bristle (Pl. 1, figs. 9–11, Pl. 2, figs. 5–7). This is particularly remarkable around the base of "twisted"-type bristles compared with "smooth"-type ones, as if the prolonged bellows-like structure of the former is protected by these micro-hairs (Fig. 1, e.g. cf. Pl. 1, fig. 9 and Pl. 2, fig. 6). The whole surface of the carapace is covered by numerous small wart-like projections derived from the epicuticle (Pl. 2, figs. 8, 9). Neither micro-hairs nor wart-like projections were recognized on the carapace of *L. japonica* except along the hinge area. Small hair-like structures were here found in the enfolded area of the hinge as if avoiding exposure (Pl. 2, fig. 10). The transformed epicuticle leaves no trace on the carapace of fossil and sub-fossil specimens (e.g. Pl. 1, fig. 19).

NUMBER AND DISTRIBUTION PATTERN OF BRISTLES/PORES

The number and the distribution pattern of the bristle/pores are shown in Figs. 3 and 4 which illustrate all the bristles/pores possessed by the two species. The number and distribution pattern are genetically controlled and fixed, so that very few variations were recognized in them.

One carapace of *L. japonica* has usually 166 bristles/pores whereas that of *L. uranouchiensis* has 202, although the former has a larger carapace than the latter (female's mean length is about 550 μm in *L. japonica* and about 500 μm in *L. uranouchiensis*: Kamiya (1988c). The difference in number comes from the difference of pores projecting the "smooth" type of bristle. Both *L. japonica* and *L. uranouchiensis* possess 44 "twisted"-type bristles, equal in number and distribution pattern (Fig. 3). Conversely, *L. japonica* has 122 (166–44) "smooth"-type bristles, while *L. uranouchiensis* has 158 (202–44). This is mainly because the ventral area, especially along the margin, of bottom-dwelling *L. uranouchiensis* has a higher density of "smooth"-type bristles, and most of these bristles can be referred to as specific characters of this species when compared with *L. japonica* (Figs. 4–8).

DISCUSSION

Hanai *et al.* (1985) pointed out that while species living in a high energy open marine environment have wide pore-opening (e.g. sieve pores of *Cythere omotenipponica*, *Aurila* sp. and *Loxococoncha japonica*), the pore of mud-dwellers, regardless of living on the deep-sea or inner bay mud bottom, have developed narrow pore-orifices in various ways to keep off dirt. One example is that the orifice is depressed below the carapace surface, transforming it into a sunken sieve pore (e.g. sunken-sieve pores of *Bicornucythere bisanensis* and *Bradleya* sp.), and another is that the finger-like projections from the opening wall, composed of epicuticle and procuticle, cover the openings of pores without bristles, like a dome (e.g. Ben-type pore [= exocrine pore; Okada, 1983] of *Bicornucythere bisanensis*). The present work not only supports the

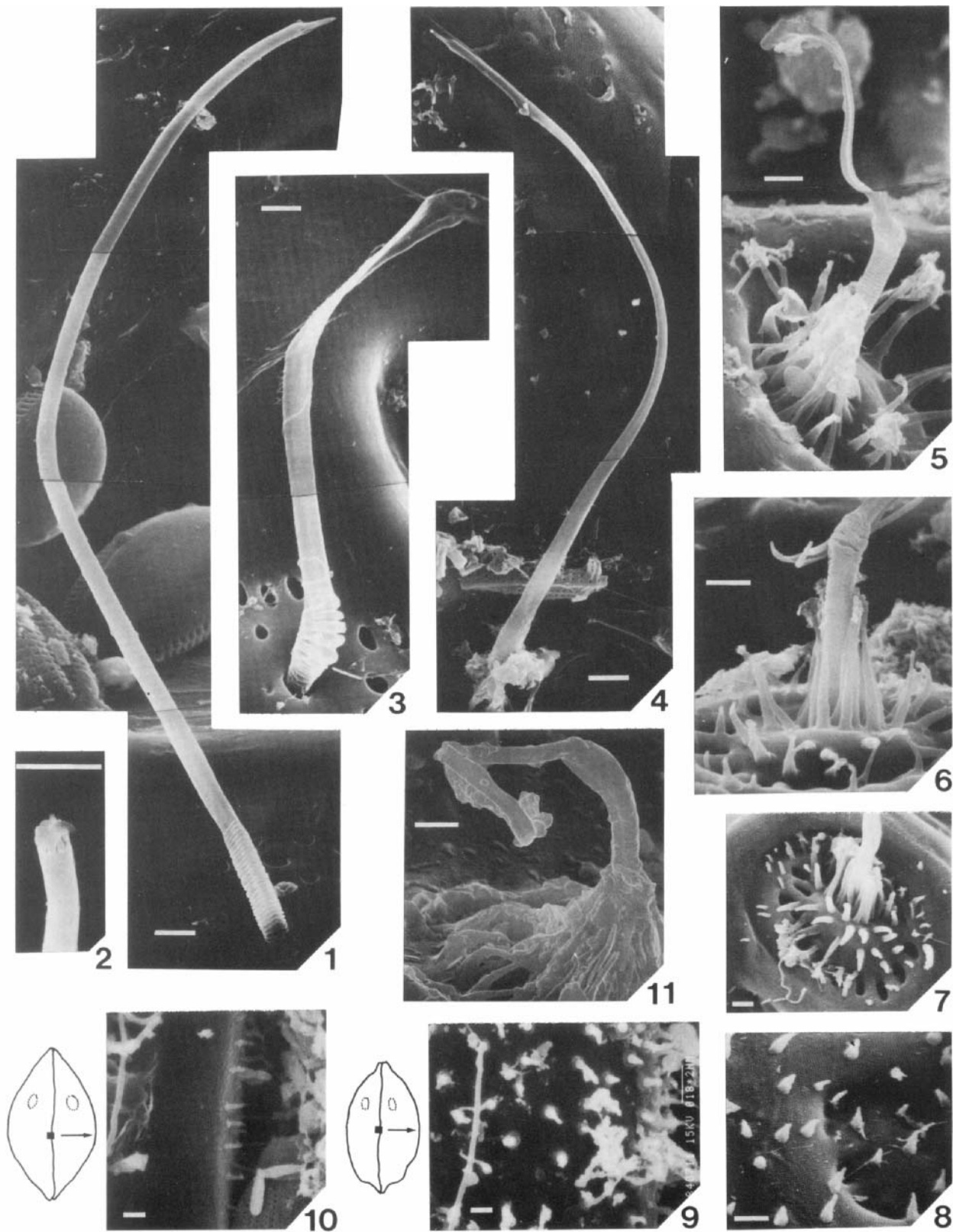
Explanation of Plate 2

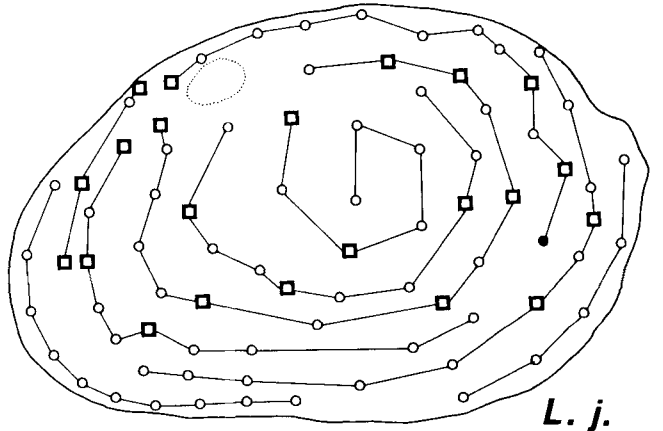
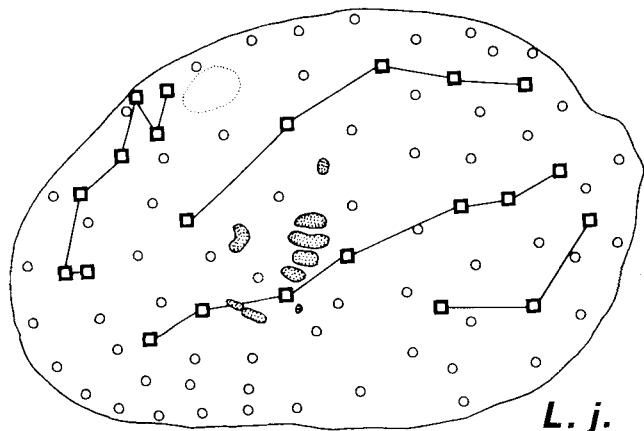
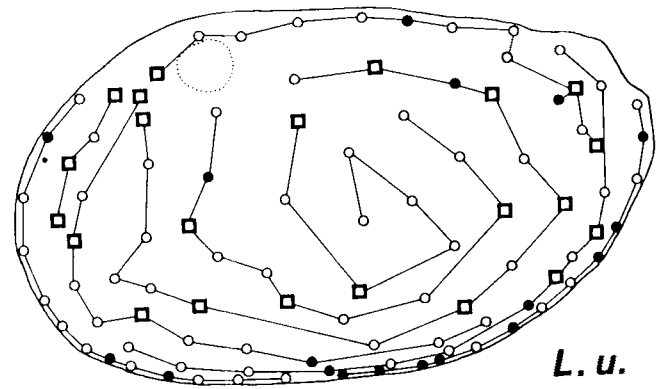
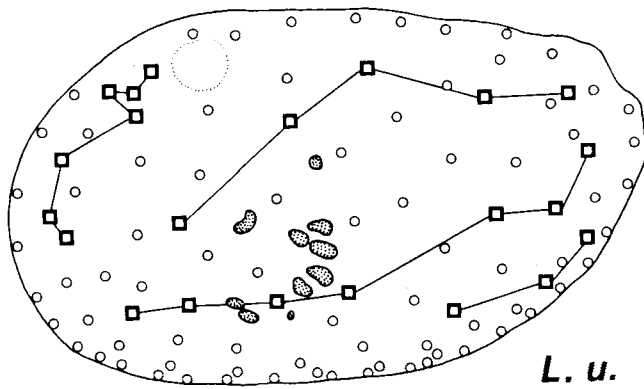
Figs. 1–5. Shape of bristles: fig. 1. "Smooth"-type bristle of *L. japonica* ($\times 6700$); fig. 2. Tip of the "smooth"-type bristle of *L. japonica* ($\times 14600$); fig. 3. "Twisted"-type bristle of *L. japonica* ($\times 6600$); fig. 4. "Smooth"-type bristle of *L. uranouchiensis* ($\times 6600$); fig. 5. "Twisted"-type bristle of *L. uranouchiensis* ($\times 6400$).

Figs. 6, 7. Well-developed long "micro-hairs" around the "twisted"-type bristles of *L. uranouchiensis*: fig. 6. Base of the bristle ($\times 7400$); fig. 7. Whole view of the pore ($\times 3700$).

Figs. 8–10. Wart-like or hair-like small projections on carapace surface: fig. 8. Wart-like projections of *L. uranouchiensis* at lateral centre ($\times 5800$); fig. 9. Wart-like projections of *L. uranouchiensis* along hingement ($\times 3700$); fig. 10. Hair-like projections of *L. japonica* at enfolded area along hingement ($\times 3700$).

Fig. 11. "Twisted"-type bristle of *L. uranouchiensis* in general conditions (not just after final moulting) ($\times 7200$). Scale bars indicate 1 μm .





□ "twisted" type bristle
○ "smooth" type bristle

□ "twisted" type bristle
○ "smooth" type bristle common to both species
● "smooth" type bristle specific to one species

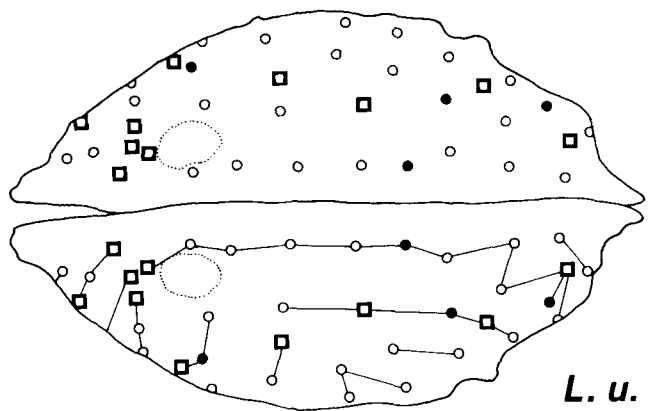
Fig. 3. Distribution of "twisted" type of bristles/pores in the left valves of two species of *Loxoconcha*. Distribution was compared utilizing muscle scars (dotted area) and eye node as standard markers; (the zigzag lines are merely lines of convenience to allow easy recognition of the correspondence between the two species). *L.u.*: *Loxoconcha uranouchiensis*, *L. j.*: *L. japonica*.

Fig. 4. Distribution of bristles/pores in the left valves of two species of *Loxoconcha*. Distribution of "smooth" type of bristle was compared utilizing "twisted" type of bristles as standard markers. The zigzag lines were drawn for convenience but basically followed the reticulation arrangement. *L.u.*: *Loxoconcha uranouchiensis*, *L.j.*: *L. japonica*.

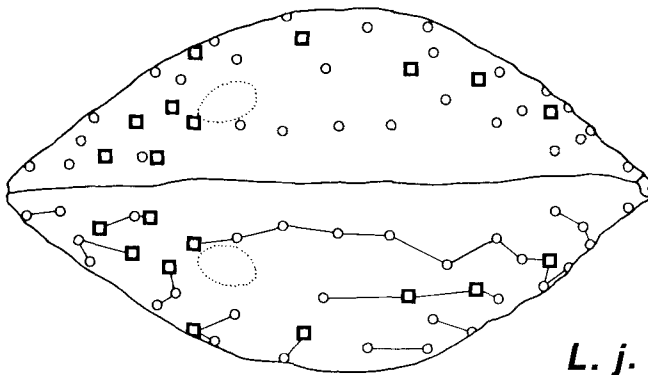
conclusion of Hanai *et al.* (1985) but also shows the existence of another countermeasure to the adhesion of dirt through transformation of bristle and epicuticle. Although bottom-dwelling *L. uranouchiensis* has essentially wide sieve pores, projections of epicuticle from the sieve-plate prevent the direct adhesion of dirt to the bristle base and the micro-pore orifices. The "twisted"-type bristles of this species with the remarkably developed bellows-like structure are protected in their lower to middle parts by long micro-hairs producing the same effect as if the bristles project from a "tubercle". In fact, the carapace surface of this species, including the bristle base, is densely adhered to by dirt (Pl. 2, fig. 11) except in specimens examined just after ecdysis. On the other hand, the congeneric phytal

species, *L. japonica*, leaves its pore-orifice completely open, but the orifice remains relatively clean even in the old individuals. The morphology of pore openings and bristles, especially that of the basal part, can be concluded to be closely related to the habitat environments.

The distribution pattern of bristles/pores in a carapace seems related to the mode of life of the ostracod. In the ventral area of the carapace, the bristles/pores are distributed densely in the bottom-dwelling species but sparsely in the phytal species. This can be attributed to the difference in ventral contact with substrata. The bristles distributed densely on the bottom dweller's ventre are the "smooth"-type, and, according to study of insect sensilla (e.g. Tominaga, 1980), their

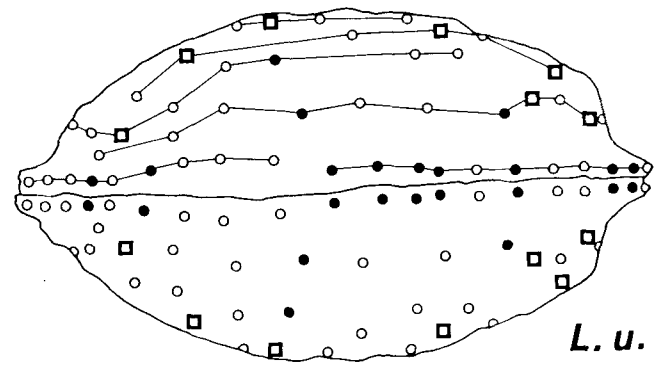


L. u.

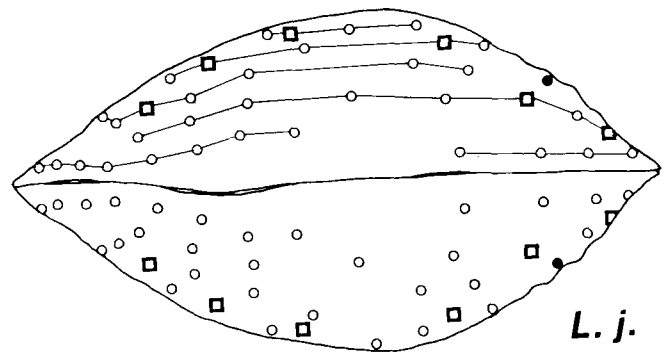


L. j.

Fig. 5. Distribution of bristles/pores observed in dorsal view. The form of zigzag lines, legend and abbreviations are same as in Fig. 4.

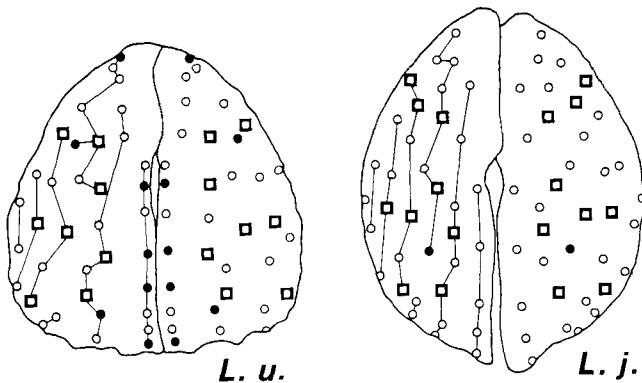


L. u.



L. j.

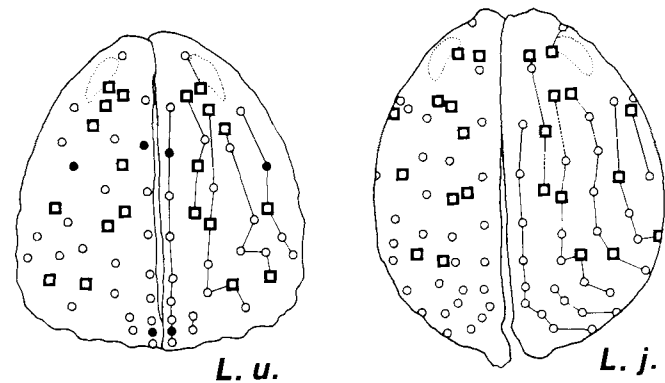
Fig. 6. Distribution of bristles/pores observed in ventral view. The form of zigzag lines, legend and abbreviations are same as in Fig. 4.



L. u.

L. j.

Fig. 7. Distribution of bristles/pores observed in anterior view. The form of zigzag lines, legend and abbreviations are same as in Fig. 4.



L. u.

L. j.

Fig. 8. Distribution of bristles/pores observed in posterior view. The form of zigzag lines, legend and abbreviations are same as in Fig. 4.

smoothly tapered form implies that they are mechano-receptors. The distribution patterns of pores can be preserved in fossils, so that these observations are worthy of attention both from palaeoecological and palaeobiological viewpoints. The morphological features around pore orifices and the distribution of (mechano-receptor) pores may be highly adaptive characters which vary among congeneric species through speciation in response to the habitat environment.

Okada (1982) stated that *Bicornucythere bisanensis* has not only sensory pores with bristles but also exocrine pores without bristles; in contrast to the sensory pores, the final number (32/one carapace) of the exocrine pores is acquired at the A-3 moulting stage juvenile and do not change at the later three moultings. The "twisted"-type bristle of *Loxoconcha* has not been investigated histologically, but it can be expected not to function as an exocrine bristle. This is because the tip of the bristle is so thin and the opening of the tip is so

small for an exocrine tube that the extremely high pressure would be needed behind the bristle to press any substance out of such a small tube. Considering the thin cuticle which might easily allow some molecules to pass through inside the bristle, the bristle might be a type of chemo-receptor. Another possibility is that it can sense different osmotic properties or different temperature. The function of "twisted"-type bristle seems, whatever it is, significant, as is implied by the related double transformation of cuticle (prolongation of bellows-like structure and development of micro-hairs) in *L. uranouchiensis*. It is significant that the number and distribution of this type of bristle are stable phylogenetically (44/one carapace of *Loxoconcha*). As an additional example, a preliminary study by Hanai, Abe, Kamiya and Tabuki (unpublished) and independent intensive research by A. Tsukagoshi (personal communication) recognized that *Cythere omotenipponica* has also two kinds of bristles, one numerous and increasing in the final ecdyses, and the other "twisted", and its final number is small and already acquired at the A-3 moulting stage. Keyser (1980) and Liebau (1971) investigated the differentiation of bristles/pores in podocopid ostracods and discussed its taxonomic significance among close taxa. In general, it is likely that ostracods have on its carapace many mechano-receptor pores with bristles, whose number is fixed within species but flexible within genera, besides comparatively few (chemo-receptor?) pores (with/without bristles) whose number is definite within genera or families. Mechano-receptor pores may be able to multiply easily in response to ecological requirements, both in ontogeny and in phylogeny. Using the distribution of "flexible" pores (mechano-receptors), the ecological and probably the phylogenetic relationships among species can be compared, while the distribution of "stable" pores (chemo-receptors?) would be useful in studies of the phylogenetic relationships among genera and/or families. The analysis of bristles/pore types and understanding of their function will thus be indispensable in phylogenetic taxonomy, even though any causal relation between the function of bristle and pore-morphology has not been clarified.

Of the sieve pores, the sieve-central-pore projecting a bristle, functions to support the bristle; but the function of sieve-micro-pores around a bristle has been debated (e.g. Müller, 1897, Puri, 1974, Keyser, 1983). Müller (1897) considered them as a light sensory organ. In recent work using the TEM, Keyser (1983) inferred them to supply a protective substance for the new bristle during moulting or to play a part in the cuticle-formation of bristle. Rosenfeld & Vesper (1978) showed a relationship between the shape of sieve-plate (arrangement of the micro-pores) and the salinity of the environment. Investigating the phylogenetic trend of pores, Puri (1974) indicated that in the genus *Cush-*

manidea, simple pores with bristle and sieve-plates with sieve-micro-pores which are distinctly separate in the Eocene species, are fused into one kind of sieve pore in the Recent species. The present study reveals that the number and the size of sieve-micro-pores in one sieve pore decreases from the pores along the hinge toward those along the free margin. Present work also shows that entirely similar micro-pores developed around two types of bristles that are different morphologically and probably functionally. These observations indicate that the role of sieve-micro-pores is independent of the function of the associated bristle but dependent on their position in a carapace.

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