Shared versus derived characters in the pore-system of *Loxoconcha* (Ostracoda,Crustacea)

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ABSTRACT

Ontogenetic development of the pore-systems of two species of *Loxoconcha*, phytal *L. japonica* and bottom-dwelling *L. uranouchiensis*, were examined. Adult pore-systems differ between the two species in number and distribution of "smooth"-type bristles, the basal structure of "twisted"-type bristles and the existence of microhairs. These specific features start to differentiate after the A-2 or A-3 juvenile stage, a fairly late moulting stage, and continue to differentiate until the adult stage. These characters are identified as lower phylogenetic ones based on the ontogeny-phylogeny relationship. The result is consistent with the estimate that the characters were regarded as adaptive and specialized through the consideration of their function to the respective habitats. The mode of increase of the two types of pore-systems was revealed. The "twisted"-type bristle, whose number is common between the two species at all stages, reaches the final number, except for one, at the A-3 juvenile stage. In contrast, the "smooth"-type bristle continues to increase in number until adult stage, and, as mentioned above, the specific differences become more obvious as the moulting stages advance. This type of pore-system is valuable for specific differentiation. Two types of pore-system that differ from each other in the pattern of increase were recognized in other ostracod taxa. The two types of pore-systems have different significance in ostracod taxonomy and the recognition of the type is indispensable for future taxonomy. *J. Micropalaeontol.*, **11** (2), 159-166, December 1992.

INTRODUCTION

The utility of "pore-systems" (pores with/without bristles) in ostracod taxonomy has been pointed out in several works (Hanai 1970, Benson 1972; Puri 1974; Tsukagoshi & Ikeya 1987; Kamiya 1989; Hanai and Ikeya 1991). Recently Tsukagoshi (1989, 1990) refined the significance of pore-patterns in ostracod phylogeny by using the ontogenetic development of the pore patterns. He found that fourteen species of *Cythere*, which were different in pore-pattern from each other at the adult stage, were classified into eight groups by the commonness of pore-pattern at the penultimate juvenile stage. Further, the eight groups of A-1 juveniles could be classified into four groups by the common pore-pattern at the A-2 juvenile stage. He indicated that such groupings reflected the phylogeny of *Cythere*.

The pore-systems of adults of a phytal and a bottom-dwelling *Loxoconcha* species were studied by Kamiya (1989). In that work, most differences between the two species were interpreted as adaptive differences to microhabitats based on the functional morphology. The common features were, on the other hand, thought to be higher phylogenetic characters. In the present work, ontogenetic changes in morphology and in the number and distribution pattern of pore-systems were studied for the two species of *Loxoconcha*, *L. japonica* and *L. uranouchiensis*. This study aimed to reveal the developmental process of the distinct and the shared characters in *Loxoconcha* pore-systems through comparison of the ontogeny of the two species. If the previous interpretation that the distinct characters were adaptive and specialized by functional aspect is true, then, such differences are expected to differentiate at a late stage. The consistency of the results between the functional analysis and the analysis based on ontogeny-phylogeny relationship is presented. The similarity and the difference of the pore system development between this genus and other taxa studied by previous workers is also presented. The utility of the pore-system in ostracod lower and higher taxonomy is shown. Finally, some characteristics in the mode of pore-system development in *Loxoconcha* are discussed.

GENERAL DESCRIPTION OF THE PORE-SYSTEMS.

The phytal species, *Loxoconcha japonica* Ishizaki, 1968 lives mainly on the eel grass *Zostera marina*. *Loxoconcha uranouchiensis* Ishizaki, 1968 is a bottom-dwelling species living in and around the *Zostera* beds. Both adults have two types of pore-systems on the carapace. One type, a "smooth"-type bristle is associated with a sieve-pore. This bristle is smooth, tapers slightly and has a bellows-like structure at the base of the bristle. Its function is assumed to be a mechanoreceptor. The other is a "twisted"-type bristle that comes from the same type of sieve-pore. This bristle is often twisted, bent, or is flattened except for the swollen base that is made up of rugged bellows-like structure. Its function is possibly as a chemoreceptor.

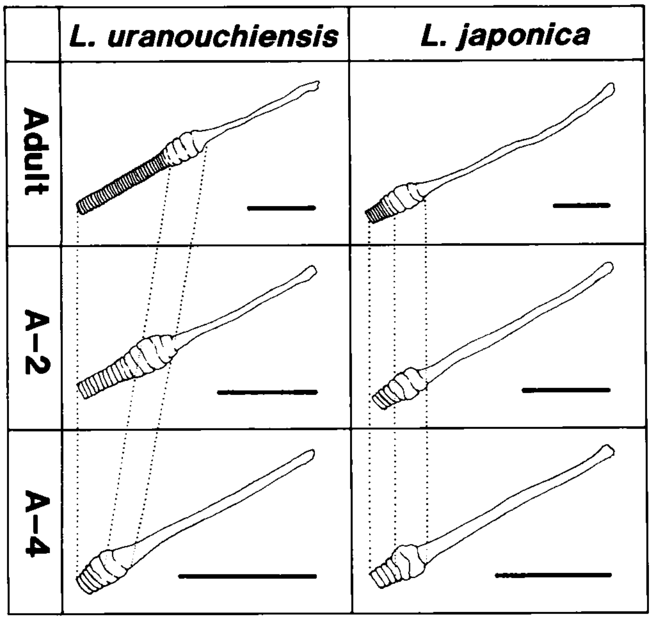

Fig. 1. Morphology of 'twisted' type bristles. Dotted lines show the comparable units of the bellows like structures. Note the development of the fine bellows-like structure in the later stages of *L. uranouchiensis*. Scale bars indicate 5μm.

Differences in the adult pore-systems between the two species are as follows: the bottom-dwelling *Loxoconcha uranouchiensis* has; 1) longer bellows-like structures at the base of the "twisted"-type bristles; 2) unique micro-hairs that come from sieve-plate surface and surround the base of the bristles; 3) an arrangement of sieve micro-pores in a sieve-plate that is not subconcentric but of a single-ring type, and; 4) greater numbers of "smooth"-type bristles, the distribution of which is especially dense in the ventral area. These characters were considered to be adaptations to the mode of life on a sandy bottom, and therefore, useful for ecological as well as phylogenetic work with other related species (Kamiya, 1989).

The "twisted"-type bristle is, on the other hand, identical in number between the two species. This character may be stable among congeneric species and useful in phylogenetic studies of genera and families (Kamiya, 1989).

MATERIALS AND METHODS

The specimens used in the present study were living when collected at Aburatsubo Cove (lat. N35°9' 20", long. E139°37'00") on the Pacific coast of central Japan. The specimens were fixed in 5% formaldehyde (pH 7) solution before being dipped in 60% ethanol. They were dried by the critical-point method and observed using a SEM. The A-7, A-6 and some other young juveniles, which were too small to prepare for the critical-point method, were observed after natural drying. At least five specimens of each moulting stage were examined for the distribution of pores and bristles.

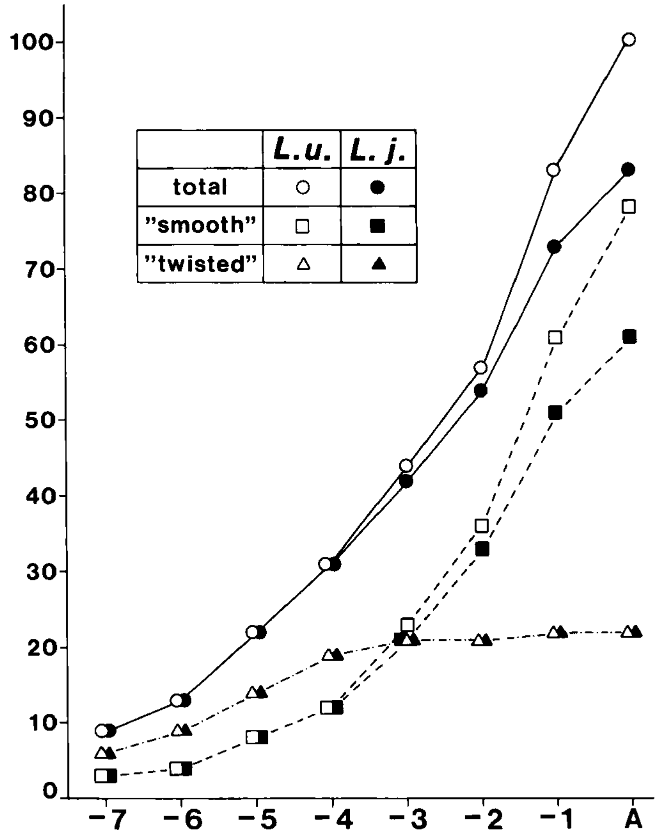

Fig. 2. Number of bristles on the valve (vertical axis) for each state (horizontal axis). Open and solid symbols represent the number for *L. Uranouchiensis* and *L. japonica*, respectively.

ONTOGENETIC CHANGE IN MORPHOLOGY

Bristles (Fig. 1, Pls 1, 2)

Two types of bristles — with either regularly-developed fine bellows-like structure or rough and swollen bellows-like structure — are recognized in the earliest juvenile stage of the phytal species, and these are also seen in the earliest juvenile stage of the bottom-dwelling species. The bristles seem to be differentiated as "smooth" and "twisted" types in the earliest stage in both species. The size of the bristles increases through ontogeny. Taking *L. japonica* as an example, the maximum length of the "smooth"-type bristles is about 15μm for A-7 and -6, 20-25μm for A-5, -4, -3 and -2, and 30μm for A-1 and the adult. The maximum length of the "twisted"-type bristles is about 13μm for A-7 and -6, 14-18μm for A-5, -4, -3 and -2, and 25μm for A-1 and the adult. Therefore, the size of the bristles in the adult stage doubles after seven moultings. The rate is slightly lower for *L. uranouchiensis*. These rates of increase are lower than those of such characters as carapace size and the sieve-plate diameter (it quadruples, for example). The morphology of the "smooth"-type bristle of both species and the "twisted"-type of *L. japonica* changes little through ontogeny. On the other hand, a remarkable change occurs in the "twisted"-type bristles of *L. uranouchiensis*. The rough and swollen

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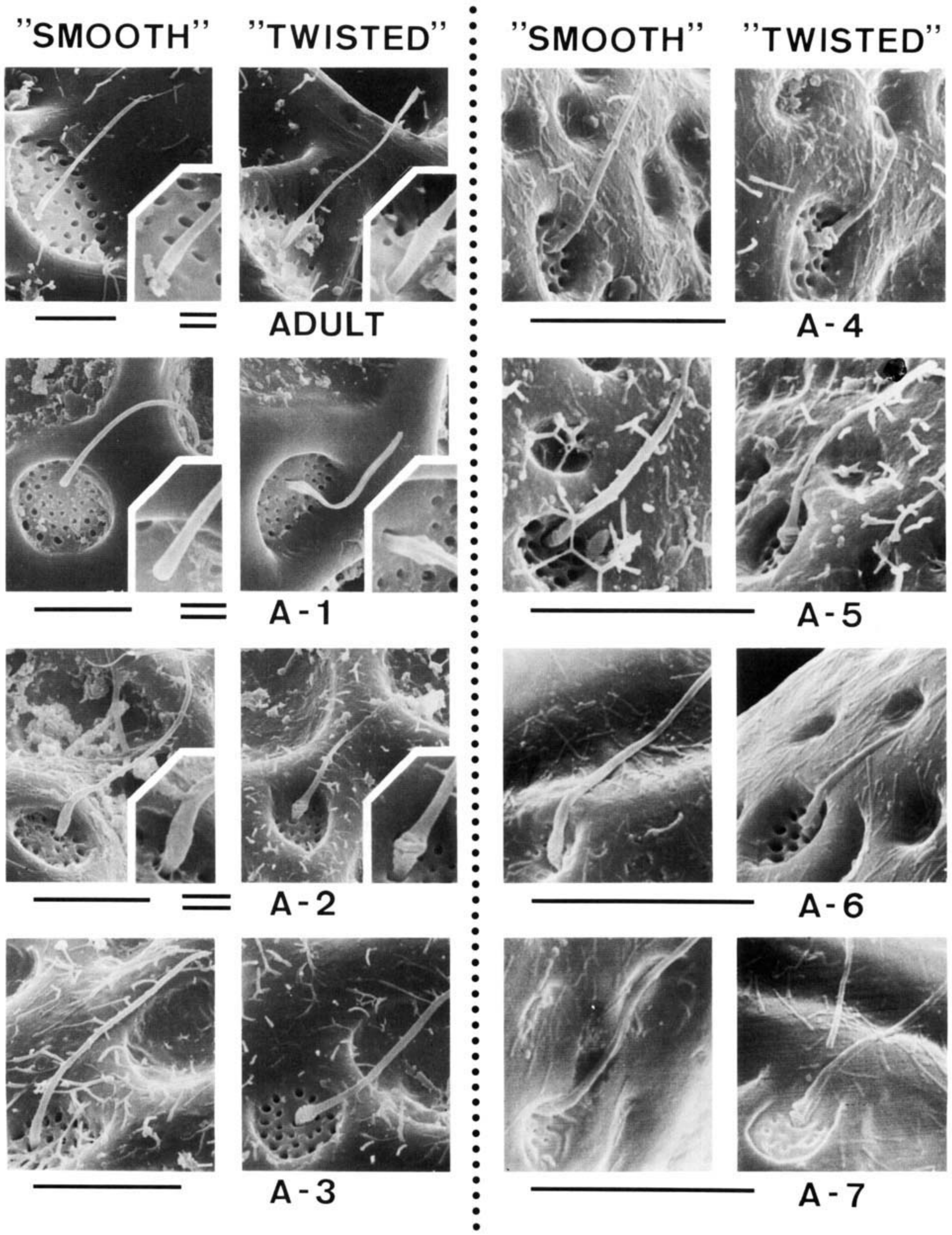
Explanation of Plate 1

Morphology of bristles in eight stages of the phytal *L. japonica*. Magnification x 1380 for Adult, (x3120 in enlargement), x1660 for A-1 (x3900 in enlargement), x1980 for A-2 (x4160 in enlargement), x2600 for A-3, x3380 for A-4, x3900 for A-5, A-6 and A-7. Single scale bar 10μm, double scale bar 2μm (for enlargements).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"TWISTED"
"SMOOTH"
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ADULT
A-1
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A-7

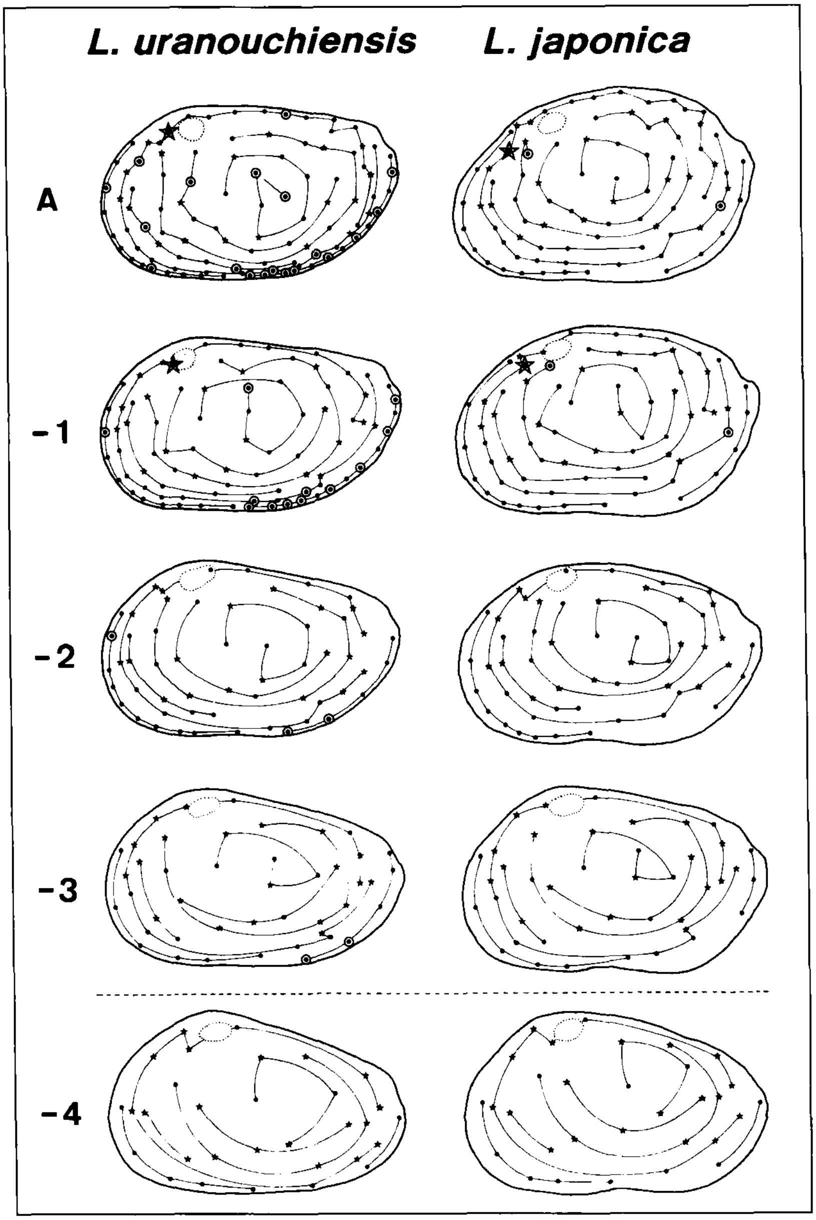

Fig. 3. Differences in bristle-distribution betwen the two species. Dots and solid stars correspond to "smooth" and "twisted"-type bristles, respectively. Bordered dots mean the "smooth"-type bristles specific to one species. Until the A-4 juvenile stage, there is no difference between the two species. Lines connecting the symbols were drawn for convenience to allow easy comparison between species as well as stages, but basically followed the reticulation pattern.

bellows-like structure remains near the base of the bristle during the A-7 to A-3 juvenile stages. In these stages, the structure is identical to *L. japonica*. The rough and swollen part starts to shift from the base to the middle of the bristle after the A-2 juvenile stage (Fig. 1). The part between the base and the swollen structure is occupied by a regularly developed fine bellows-like structure. The whole bellows-like structure, which is swollen at the distal end, occupies the proximal half of the bristle in the A-1 and adult stages.

Micro-hairs (Pls 1, 2).

Micro-hairs, which are similar to the "moulting trichoids" of Keyser (1982), and "processes" and "papillae" of Siveter (1982), cover the surface of the carapace of both species in the same manner from the earliest stage to the A-2 stage (for details see Kamiya, 1989). However, they disappear on the carapace of the A-1 and the adult in *L. japonica*. In contrast, besides the general micro-hairs on the carapace, unique long micro-hairs appear on the sieve plate of *L. uranouchiensis* after the A-2 juvenile stage. The micro-hairs surround the base of the "twisted"-type bristle densely, but are comparatively sparse around the base of the "smooth"-type bristle. The long micro-hairs are almost completely developed at the A-1 stage.

Pores (Pls. 1, 2)

The differences between the two species — the arrangement of sieve micro-pores is either subconcentric or a single-ring — can be traced back to the A-7 juveniles. This character differentiates the two species from the earliest stage. The maximum diameter of the sieve-plate increases from 4µm (A-7) to 15µm (adult) in both species. The size of the plate quadruples through seven moultings. This rate of increase is similar to that of carapace size.

Ontogenetic change in number and distribution pattern (Table 1, Figs 2-5).

Here, the number of the pores means the number of pores in a single valve. The "smooth"-type bristles increase in number at every moulting. The total number is identical in both species in the first four instars. They are 3, 4, 7, 12 for A-7, A-6, A-5, and A-4 stages, respectively. The *Loxoconcha japonica* bristles then increase to 21, 33, 51, 61 for A-3, A-2,. A-1, and the adult. In *L. uranouchiensis* the numbers are 23, 36, 61, 78 for the same juvenile

Table 1. Number of bristles on the valve in eight stages. Number in parentheses indicates new bristles in the stage after moulting.

	L. uranouchiensis			*L. japonica*		
	smooth	twisted	total	smooth	twisted	total
Adult	78 (17)	22 (0)	100 (17)	61 (10)	22 (0)	83 (10)
A-1	61 (25)	22 (1)	83 (26)	51 (18)	22 (1)	73 (19)
A-2	36 (13)	21 (0)	57 (13)	33 (12)	21 (0)	54 (12)
A-3	23 (11)	21 (2)	44 (13)	21 (9)	21 (2)	42 (11)
A-4	12 (5)	19 (4)	31 (9)	12 (5)	19 (4)	31 (9)
A-5	7 (3)	15 (6)	22 (9)	7 (3)	15 (6)	22 (9)
A-6	4 (1)	9 (3)	13 (4)	4 (1)	9 (3)	13 (4)
A-7	3	6	9	3	6	9

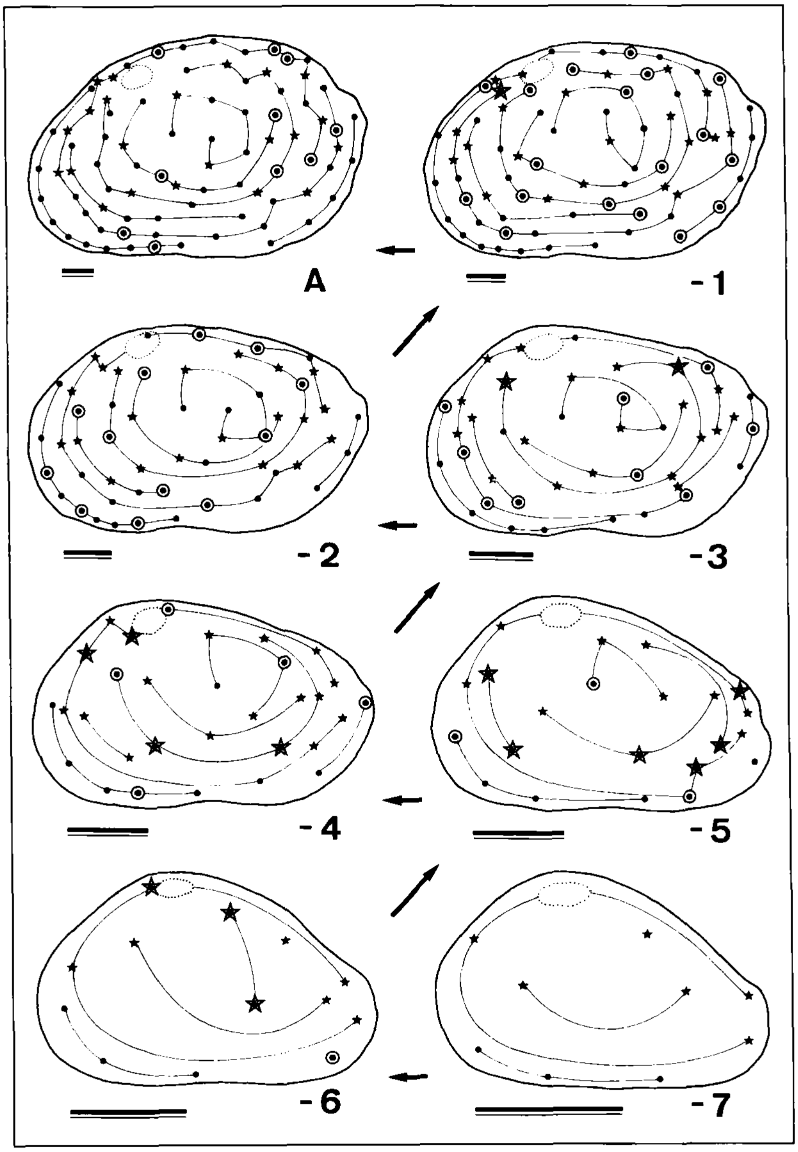

Fig. 4. Distribution of bristles in eight stages in the phytal *L. japonica*. Dots and solid stars represent "smooth" and "twisted"-type bristles, respectively. Bordered dots and stars indicate bristles that are new to the stage after moulting. Lines connecting the suymbols were drawn for convenience to allow easy comparison among stages, but basically followed the reticulation pattern. Scale bar indicates 50μm.

stages and the adult (Table 1). Therefore, the difference in number between the two species is 2, 3, 10, 17 for A-3, A-2, A-1 and the adult (Fig. 3). The number of bristles/pores increases most drastically at the A-2/A-1 moulting, 18 for *L. japonica* and 25 for *L. uranouchiensis* (Table 1).

The ontogenetic increase of the "twisted"-type bristles is similar between the two species. The increase of the number is greater in the earlier half of the moulting series than the latter half. The bristles number, 6, 9, 15 and 19 for A-7, A-6, A-5 and the A-4 stage respectively. The two new bristles are added at the A-4/A-3 moulting and one at the A-2/A-1 moulting, reaching 22 at the A-1 stage. There is no increase in number at the A-1/A and A-3/A-2 moultings. The A-6/A-5 moulting is the most active moulting for the numerical increase of this type of bristle, which adds six new bristles (Table 1).

The distribution of pore-systems in the valve is illustrated in Figs. 4 and 5 for *L. japonica* and *L. uranouchiensis* for all stages. At the earliest stage, all three "smooth"type bristles are distributed along the ventral margin. Six "twisted"-type bristles are distributed over the rest of the valve. The "smooth"type bristle appears in the lateral central area after the A-6/A-5 moulting. The "smooth"-type bristles then rapidly increase in number and surpass the "twist" after the A-4/A-3 moulting (Fig. 2). New "smooth"-type bristles along the postero-ventral free margin are mainly produced by the moultings at A-4/A-3 and A-2/A-1 (Figs. 4, 5; right row). Conversely, many new bristles along the antero-ventral free margin appear by the moultings at A-5/A-4, A-3/A-2 and A-1/A (Figs. 4, 5; left row).

DISCUSSION AND CONCLUSIONS

Based on the relationship between ontogeny and phylogeny, the following standards may be used for a discussion of higher-lower phylogenetic characters. Among congeneric species, 1) characters that are common and identical through all stages correspond to phylogenetic characters at a high taxonomic level, such as genus and family, 2) characters that are different at early juvenile stages have less phylogenetic meaning, 3) characters that start to differentiate at a late juvenile stage are the lowest phylogenetic characters; in other words, these are highly adaptive or specialized characters at the species level.

If the above criteria are applied, the number of "twisted"-type bristle corresponds to the type 1 character, and is regarded as a higher phylogenetic character. The fact that the greatest numbers of the bristles of this type are acquired before the A-3 stage indicates that the bristles must play an important basic role in the life of the ostracod. Similar modes of increase have been found in the pore-systems of other ostracod taxa, for example, the constant-type pore of *Xestoleberis hanaii* (see Hanai and Ikeya, 1991), the bristle type 3 of the Cythere group (Tsukagoshi, 1990), and the exocrine pore of *Bicornucythere bisanensis* (Okada, 1983). *Cythere* and *Bicornucythere* acquire the final number at the A-3 moulting stage. The final number is 12 of *Xestoleberis hanaii*, 13 for *Cythere*, which is shared by all 14 species of *Cythere*, and 16 for *Bicornucythere*. This compares to 22 in *Loxoconcha*. Although the mode of increase and the distribution on the carapace are similar, the "twisted'-type bristle, bristle type 3 and the exocrine pore are different from each other in morphology. The bristle type 3 of *Cythere* tapers to a point (Tsukagoshi, 1990) and the exocrine pore of *Bicornucythere bisanensis* does not have a bristle (Okada, 1983). Further, histological and physi-

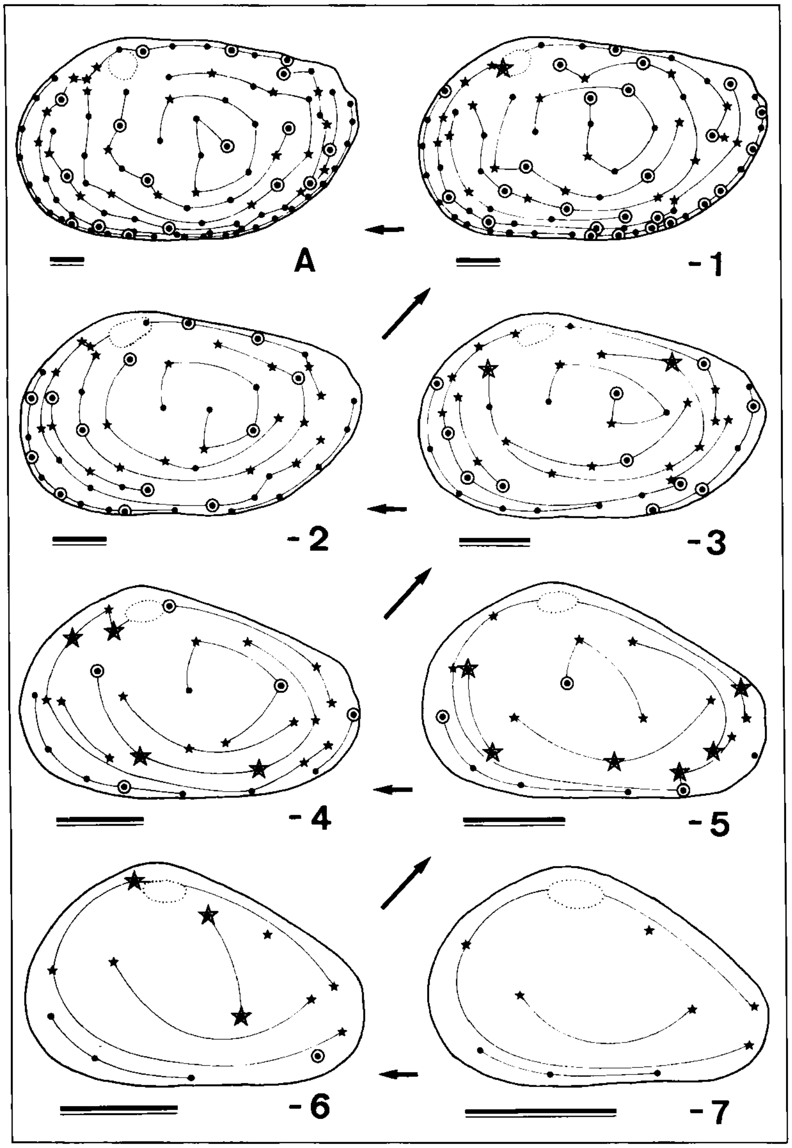

Fig. 5. Distribution of bristles in eight stages in the bottom-dwelling *L. uranouchiensis*. Symbols are the same as in Fig. 4.

ological studies are required to determine whether these morphological features are homologous. Even if the function may vary among higher taxa, this type of pore-system will possibly be a standard that measures the relationship between genera and family group taxa.

The type of arrangement of the sieve-micropores is a type 2 character, a phylogenetic character at an intermediate level. It may serve as a criterion to divide the genus *Loxoconcha* into sub-groups. Schallreuter (1983) found the subconcentric arrangement of sieve-micropores in *Klimphores* and the single-ring-type arrangement in *Miehikella*, both of which are Ordovician species. He implied that the species with subconcentric arrangement might have lived in darker environments by referring to the work of Mueller (1894), who considered the sieve-micropores to be a light sensory organ. Present work, however, shows that the darkness is not related to the type of sieve-micropore.

The structure of the bristle base (length of the bellows-like structure), the existence of microhairs, and the number and distribution pattern of "smooth"-type bristles are the type 3 character, characters at the lowest level in phylogeny. These are regarded as highly adaptive or specialized. The "smooth"-type bristle is similar to the variable-type pore of *Xestoleberis*, the type 2 and type 5 of *Cythere*, and the sensilum pore of *Bicornucythere* in terms of the mode of increase on the carapace and their assumed function. This type of pore-system has been significant in species level taxonomy. It is certainly this pore-system that made the fourteen species of *Cythere* distinguishable by the pore-distribution comparison (Tsukagoshi, 1990). The different distribution pattern often appears first at the adult stage between related species (*e.g.* Tsukagoshi, 1990). However, there is an example where a pore-distribution difference does not occur between two closely related species of *Loxoconcha* (Kamiya, 1992).

The analyses of the pore-system characters through the ontogeny-phylogeny relationship showed three levels of taxonomic characters in the pore-systems. These results are consistent with the previous estimate of the level of the taxonomic characters of the pore-systems based on the functional aspects (Kamiya, 1989), except for the sieve-micropore arrangement. As already indicated (Kamiya, 1989), Ostracoda have at least two types of pore-systems whose taxonomic significance is different; one is usable for species level taxonomy and the other is important at the genus and/or family level. The determination of the pore-system type is essential for ostracod taxonomy.

The following are the most noteworthy characteristics in the mode of development of the pore-systems of *Loxoconcha*: 1) Most species differences, between the two species studied, begin to appear after the A-4/A-3 moulting. This is true for the morphology of the bristles and microhairs as well as their distributional pattern. 2) A-6/A-5, A-4/A-3 and A-2/A-1 moultings bring new "smooth"-type bristles/pores to the postero-ventral margin and lateral centre of the valves. On the other hand, A-5/A-4, A-3/A-2 and A-1/A moultings mainly introduce new bristles at the antero-ventral margin and the lateral centre. Thus, seven moultings are divided into two groups in terms of the area on the valves where the differentiation of the "smooth"-type bristle hap-

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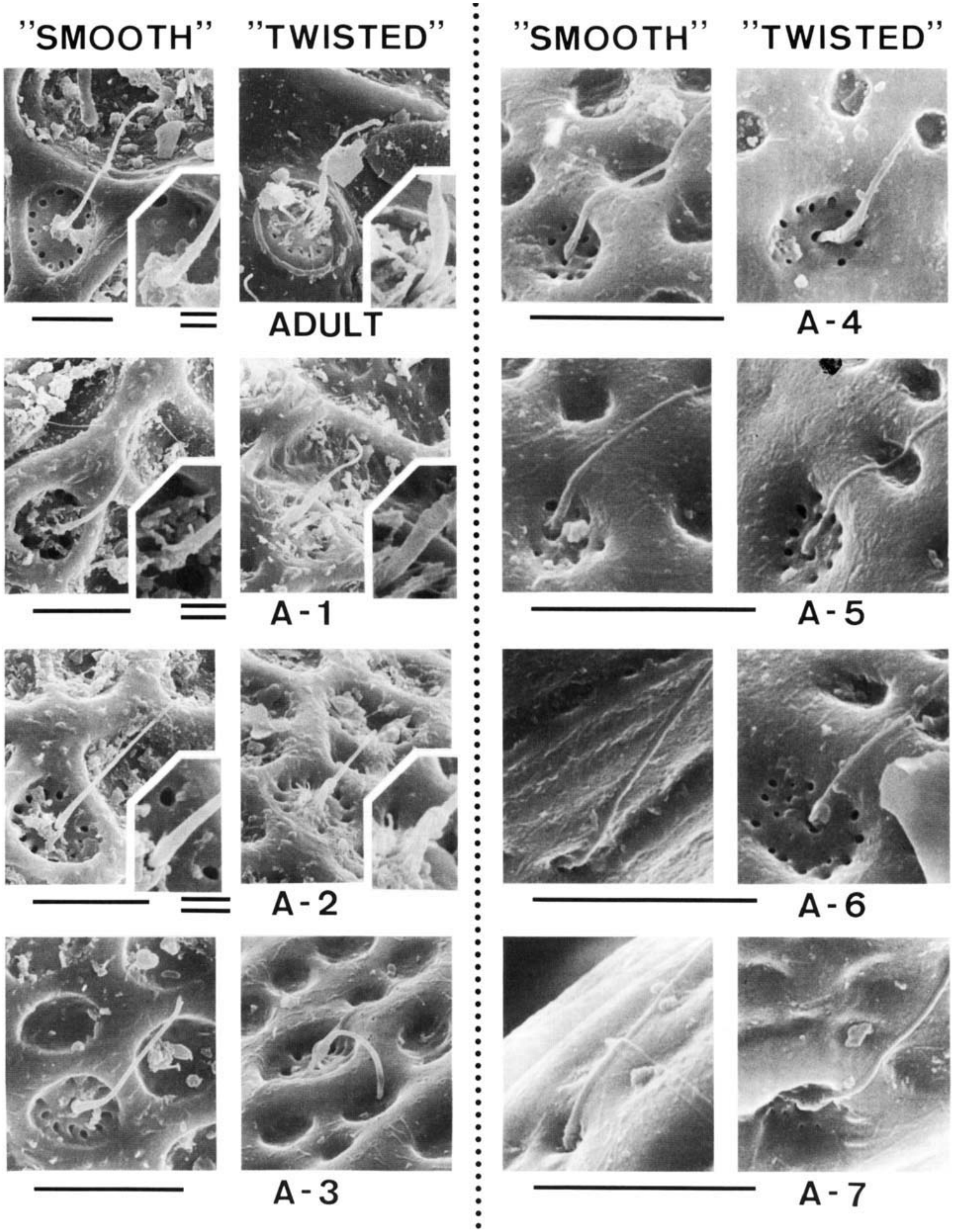
Explanation of Plate 2

Morphology of bristles in eight stages in the bottom-dwelling *L. uranouchiensis*. Magnification x 1380 for Adult (x3120 in enlargement), x1660 for A-1 (x3900 in enlargement), x1980 for A-2 (x4160 in enlargement), x2600 for A-3, x3380 for A-4, x3900 for A-5, A-6 and A-7. Single scale bar 10μm, double scale bar 2μm (for enlargements).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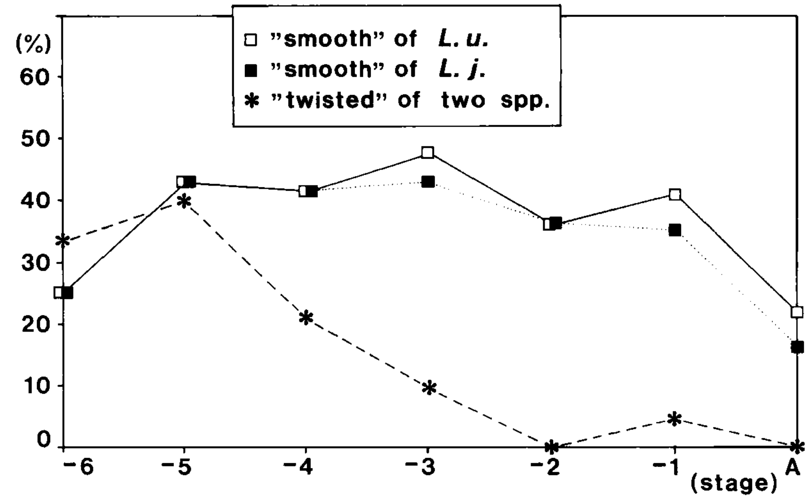

Fig. 6 (Left). Ratio of new bristles produced through moultings. The ratio is shown for two types of bristles, respectively, by (No. of new bristles) / (No. of new and existing bristles) for each stage. Note the zigzag line that shows the ratio of the "smooth"-type bristle.

pens. 3) The stages in the ontogeny when more "smooth"-type bristles are produced divide the moultings into the same two groups as in 2) (Fig. 6). A-6/A-5, A-4/A-3 and A-2/A-1 moultings are the active ones, and A-5/A-4, A-3/A-2 and A-1/A are the non-active ones. These results indicate that the sensory organ system has a cyclic mode of development, and one cycle is composed of two stages. The A-7 and A-6 juvenile stages for the first cycle, A-5 and A-4 stages for the second cycle, and so on. 4) The greatest increase in the numbers of bristles/pores of the "smooth"-type is found between the A-1 and A-2 stages. A postero-ventral area dense with bristles is one of the main specific characters of the bottom-dwelling species; it is formed by the A-2/A-1 moulting. The pore-system is almost mature morphologically in the A-1 juvenile stage. It is not the final moulting stage but the penultimate one that is critical in producing specific-level characteristics in these two *Loxoconcha*.

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