ORNAMENTATION AS A CHARACTER IN SPECIFIC DIFFERENTIATION OF OSTRACODS

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UNIVERSITY OF MICHIGAN PRESS
ANN ARBOR
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INTRODUCTION

The ornamentation of ostracods, important for specific differentiation, is in need of further study because of its variation within the species, a variation that is due to several causes. Ornamentation differs from instar to instar, between sexual dimorphs, and among individuals, and it is affected by the mode of preservation. Unless such influences are taken into consideration, ornamental features cannot be used accurately for taxonomic work. In this paper variations of such nature in Paleozoic forms are described and illustrated.

In any group, as more species are investigated, it becomes increasingly important to evaluate how well the specific characters fulfill their function as criteria of relationships. To say that true relationships can be established may, perhaps, be presumptuous, particularly in regard to fossil assemblages, but to retain without question an existing framework for setting up species is to be perfunctory. Application of dubious criteria only continues to create unreliable, fallible species. The analysis of specific characters, therefore, deserves at least as much attention as the discrimination and description of new species. Classification of fossil organisms, especially, depends not only upon additional faunas to fill in the geologic record but upon a keen appraisal of the characters by which one specimen is taxonomically different from another. Specific characters, as interpreted, not only influence classification, they control it.

Unless the range of variation of a diagnostic character within a species is known and recognized, descriptions involving it are apt to be vague or incomplete. The original description of a species should define precisely
the limits of form of whatever fossils the author considers to be conspecific. A species is valid, once published, although it may be ill-defined and have little more to recommend it than a unique combination of letters and a type specimen. Revision of our nomenclatural inheritance is difficult, as most of us are well aware. But this is all the more reason for a critical evaluation of specific characters. Species can have no better standing than that of the characters on which they are based. Reliable characters are a prerequisite for reliable species.

Ornamentation is one of the characters used for specific determinations in many Paleozoic and in some Mesozoic and Cenozoic ostracods. Spines, punctae, reticulation, tubercles, and denticles have been used in definitions of species. The logical sequence for study in ostracods, or in any other group of organisms for that matter, is first to note the constancy and validity of the characters regarded as specific, then examine their occurrence, and finally divide the organisms into species according to the range of development of the characters that have been found reliable. The present investigation revealed that, unless the factors that control ornamentation are clearly understood, such features as papillae, punctae, and reticulation may prove uncertain and unreliable. On the other hand, whenever the factors can be weighed, ornamentation is a valuable character in the erection of species.

Four factors that affect the size, number, and distribution of the features of ornamentation can readily be distinguished. Others may exist, but so far none have been detected. The ascertained factors, which have been previously listed (Kesling, 1953b, p. 1444), are the instar, sexual dimorphism, individual variation, and preservation. Each of these is considered independently below, although two or more may affect the specimens of one species.

All specimens illustrated are catalogued and deposited in the Museum of Paleontology of the University of Michigan.

The author is grateful to Dr. Lewis B. Kellum, Dr. George M. Ehlers, and Dr. Chester A. Arnold for their criticism of the manuscript of this paper.
nodes, denticulations, and other ornamentation in two species of *Cythereis*. Cooper (1945, pp. 368–75) studied the changes occurring in instars of the kirkbyid *Ectodemites plummeri* Cooper. Sohn (1950, pp. 33–39) described ornamentation in adult and immature ostracods of the Kirkbyidae and Miltonellidae. Spjeldnaes (1951, pp. 745–55) wrote on immature instars of *Beyrichia jonesi* Boll. Kesling investigated the ontogeny of a hollinid species (1952, pp. 249–55) and a beyrichiid species (1953a, pp. 19–24). Authors other than those mentioned have also noted the ontogenetic changes that take place in ornamentation.

In this study two species from the Middle Devonian Wanakah shale are illustrated to show the variation in ornamentation of their instars. The one is a beyrichiid ostracod, *Hibbardia lacrimosa* (Swartz and Oriel), that has been redescribed by Kesling (1953a, pp. 19–24). In its first instar (Pl. I, Figs. 1–2) the tip of L3 in each valve is a smooth knob projecting outward from the dorsal part of the lobe. In successive immature instars (Pl. I, Figs. 3–14) the tip assumes the form of a low pyramid and, as seen in dorsal view, migrates from the lateral outline in toward the hinge line. The size of the meshes of the reticulation does not appear to increase regularly with ontogeny, but the meshes in the two youngest instars are much smaller than those in the third (Pl. I, Figs. 5–6). The other, a kirkbyid ostracod, *Amphisoma asetia* Kesling and Copeland, has several features in the older instars that are not found in the younger. The second and third instars (Pl. I, Figs. 21–22, 29) give no indication of a horizontal central ridge, but the fourth instar (Pl. I, Figs. 23–24, 30) has a faint crest just above the central pit, and each of the successive older instars (Pl. I, Figs. 25–28, 31–36) has a ridge in this position. The adult (Pl. I, Figs. 28, 33, 35), furthermore, has a short vertical ridge along the top of the low node that lies in front of the central pit, which all the immature specimens lack; and the adult has another feature not found in the younger forms, a crest between the dorsal ridge and the hinge line (compare Pl. I, Figs. 34 and 36).

Other changes, beside the increase in complexity and number of ornamental structures, have been found to accompany ontogeny. Older instars may have larger posterior lobes and forward shift of all lobes (hollinids); anterior migration of the large central pit (kirkbyids); greater number of marginal pore canals, larger lateral expansions, and more complex hinges (cythereids); and forward movement of the muscle scar (all forms).

Usually, new species are established on adult specimens and the immature instars are worked out later. We can expect, on the basis of known species, that all younger instars will have simpler, less ornate valves than the older ones.
SEXUAL DIMORPHISM

Living ostracods, in which the internal organs have been studied, are known to have two kinds of reproduction. Some species have only females in the adult stage and reproduce parthenogenetically. In these there can be, of course, no dimorphism in the valves. Others have both males and females and reproduce syngamically. Not all of this second group, however, have dimorphic valves. Some do, but the rest have dimorphism only in the gonads, genitalia, and/or appendages, with the valves appearing to be the same in both male and female.

Fossil ostracods, in which the internal organs are not preserved, have dimorphic valves in some species but not in others. In species with dimorphic valves reproduction is supposed to have been syngamic. In those in which no dimorphism can be detected, reproduction may have been either syngamic or parthenogenetic. In the fossil species that are dimorphic the males and females differ in ornamentation; in the shape of the postero-dorsal part of the valves (cyprids); or in having one dimorph (assumed to be the female) with anteroventral or ventral pouches (beyrichiids), posterior inflations (kloedenellids), anteroventral enlargements of the carinae (sigmoopsids), or incurved frills or loculi (hollinids).

The two examples that follow illustrate some of the small differences in ornamentation that may occur in the two dimorphs of a species. In most species, however, no such significant distinction can be made between the ornamentation of the male and that of the female.

In *Hibbardia lacrimosa* (Swartz and Oriel), a beyrichiid, the female has a type of ornamentation in the anteroventral part of each valve (Pl. I, Fig. 20) that is not found either in the male or in the immature instars (Pl. I, Fig. 18). Immediately in front of the female's pouch the velate ridge is interrupted and the reticulation that extends onto the lateral surface is much finer than that of the rest of the valve. In the corresponding region in the male the ridge is complete and the reticulation like that of the rest of the surface.

In *Ctenobolbina megalia* Kesling and Tabor, a hollinid, the channel between the frill and marginal ridge in the female (Pl. II, Fig. 2) is smooth. In some species it is difficult to decide whether a difference should be attributed to ornamentation or lobation. For example, in *Ctenoloculina acanthina* Kesling the ornamentation on L1, L2, and L3 (Pl. I, Fig. 39) extends ventrally onto the spurs in the male; but in the female (Pl. I, Fig. 41) it stops at the juncture of the lobes and the smooth side of the frill. But did this dimorphism result because the ornamentation in the female
was confined to the dorsal two-thirds of the lobes or because the lobation of the female was interrupted by the frill? I believe it was the latter. The distinction is a technical one.

**INDIVIDUAL VARIATION**

In some species the specimens that belong to the same instar and sex exhibit a gradation from almost smooth valves to highly ornamented ones. Since, according to the experiments of Fassbinder (1912, p. 563), protuberances can develop through a change of diet, it may be that some of the variations in ornamentation in fossil ostracods were caused by the response of the animal to food or other ecological factor. If so, it cannot now be verified. It may also be possible that some variable specimens collected from a single outcrop represent individuals which lived in widely different environments and were swept together after death by waves and currents into an entirely foreign environment. At this time there is no way to prove or disprove these speculations. Hence, all such variations, as those below, are classed as individual.

In *Octonaria laevilitata* Kesling and Kilgore (Pl. II, Figs. 6–10, 12) there is a great disparity in left valves. In about 90 per cent of the specimens this valve is completely smooth, but in the rest it has one or two furrows with a variable number of pits. *Ctenoloculina thliberilobota* Kesling (Pl. II, Figs. 17–23) has marked differences in the ornamented areas on L2 and L3. In L2 the ornamentation may be a curved strip with parallel sides (Pl. II, Fig. 19), a panduriform area (Pl. II, Figs. 20, 22), separate dorsal and ventral areas (Pl. II, Figs. 17, 23), or a ventral area only (Pl. II, Fig. 21). In L3 it may be continuous (Pl. II, Figs. 20, 22), interrupted (Pl. II, Fig. 21), or limited to the dorsal half of the lobe (Pl. II, Fig. 17). *Hollinella devoniana* Van Pelt has some valves with very few papillae (Pl. II, Fig. 13) and others with many (Pl. II, Figs. 15–16).

Almost every species with strong ornamentation shows some individual variation, but in a few there are such marked differences that certain of their specimens may be classified incorrectly.

**PRESERVATION**

In fossil ostracods of the same species, instar, and sex the process of preservation can greatly affect the ornamentation of individuals. In certain species the thin outer layer of the shell has one sort of ornamentation and the layer below has another and completely different kind. Some of the specimens have this outer layer completely preserved, some only partly, and others not at all. As a result two specimens of the same species may each have a different ornamentation or one specimen may show both types.
The shell of living ostracods consists of a thin outer layer of chitin, a thick middle layer of calcite, and a thin inner layer of chitin. In fossil ostracod valves having two distinct layers of shell material, the thin outer layer may be the replacement of the original chitin by calcium carbonate during fossilization. The outer layer is fragile and could easily have been removed by corrosion or abrasion. It is possible that this layer was present in many species, but has disappeared from all specimens before their collection.

In *Ctenoloculina acenthina* Kesling the outer layer has a fine reticulation on the lobes (Pl. I, Figs. 39, 41). But one specimen (Pl. I, Fig. 37) had lost part of the outer layer on L3, revealing the small papillae in the layer below. Another (Pl. I, Fig. 38) had lost nearly all of the outer layer, so that the ornamentation on the lobes consisted only of the small, discrete, acuminate papillae. In size of valves, shape of lobes, and arrangement of the large papillae around the lobes, all specimens are alike. They are, therefore, classified as one species.

Some specimens of *Ctenoloculina thiberilobota* Kesling have the thin outer layer, which is somewhat granular with numerous very small punctae, nearly complete on L4 (Pl. II, Figs. 17, 21). Others have this layer partly broken away (Pl. II, Figs. 18–20, 22) or almost completely absent (Pl. II, Fig. 23), showing the papillose layer beneath. The thin outer layer can be chipped off with a fine needle and the ornamentation of the lobes changed at will from finely punctate to rather coarsely papillose. Ornamentation of the species thus includes both types and either or both may occur in a selected specimen.

One specimen of *Falsipollex valgus* Kesling (Pl. II, Fig. 24) has two small areas on the posterodorsal and posteroventral parts of the valve in which the outer layer is preserved. The outer layer is reticulate and this is the only specimen found which shows any part of it. In all others just the large rounded papillae of the inner layer have been preserved. The existence of the thin reticulate layer was not even suspected until this specimen was examined.

In some specimens of *Ctenobolbina megalia* Kesling and Tabor (Pl. II, Figs. 1, 4) there are abraded areas in the posteroventral part of the valves which apparently show that the underlying layer, with two sizes of papillae, duplicates the outer layer. If this interpretation is correct, it indicates that some species have the ornamentation of the two layers identical.

In addition to the changes incident to abrasion, corrosion of the shell material may alter the form of ornamental structures in either layer. Specimens of highly ornamented species from one locality may show
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gradations from those with coarse papillae to those with thin, small spines. These variations may logically be attributed to differing amounts of corrosion.

LITERATURE CITED


Submitted for publication January 29, 1954
EXPLANATION OF PLATE I

(All figures × 24)

_Hibbardia lacrimosa_ (Swartz and Oriel)

Figs. 1–14. Dorsal and right lateral views of immature carapaces in the first through seventh instars. Hypotypes Nos. 28515, 28512, 28502, 28492, 28481, 28472, and 28461.

Figs. 15–16. Dorsal and right lateral views of adult female carapace. Hypotype No. 28455.


_Amphizona asceta_ Kesling and Copeland

Figs. 21–27. Lateral views of left valves in second, third, fourth (2 valves), fifth, and sixth (2 valves) instars. Paratypes Nos. 30539, 30656, 30644, 30628, 30625, 30608, and 30604.

Fig. 28. Left lateral view of adult carapace. Paratype No. 30590.

Figs. 29–32. Lateral views of right valves in second, fourth, fifth, and sixth instars. Paratypes Nos. 30659, 30638, 30614, and 30605.

Fig. 33. Right lateral view of adult carapace. Paratype No. 30589.

Figs. 34–35. Dorsal and left lateral views of adult carapace. Holotype No. 30587.

Fig. 36. Dorsal view of carapace in sixth instar. Paratype No. 30532.

_Ctenoloculina acaenthina_ Kesling


Figs. 39–42. Right lateral and ventral views of male and female carapaces. Paratypes No. 28942 and Holotype No. 28940.
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EXPLANATION OF PLATE II

(All figures × 24 except as noted)

*Ctenoboibina megalia* Kesling and Tabor

*Fig*. 1–2. Right lateral and ventral views of male carapace. Allotype No. 27782.

*Fig*. 3. Ventral view of female carapace. Holotype No. 27783.

*Fig*. 4. Left lateral view of male carapace. Hypotype No. 28906.

*Octonaria laevilatata* Kesling and Kilgore

*Figs*. 5–6, 11–12. Right and left lateral views of two carapaces. Paratypes Nos. 27994 and 28000.


*Hollinella devoniana* (Van Pelt)


*Ctenoculina thliberilobota* Kesling


*Falsipollex valgus* Kesling

*Fig*. 24. Lateral view of female left valve. Hypotype No. 28994. × 50.
