The British Silurian ostracod genus Octonaria Jones, 1887: its revision and phylogeny

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ABSTRACT-The ostracod genus *Octonaria* Jones, 1887 has been grossly misunderstood because of misleading illustrations of the type-species, *O. octoformis* Jones, 1887. The type species is considered to be the only member of the genus presently known. All other of the nearly four dozen species and varieties which have been placed in the genus are considered to be junior synonyms of *O. octoformis* or members of other genera. *Octonaria* is presently known only from late Wenlock to early Ludlow strata of the Welsh Borderland area. It was probably derived from a "*Bairdiocypris*" gotlandica – like ancestor and is ancestral to the Late Silurian – Early Devonian North American genus *Thlipsorothella* Lundin & Petersen, 1974.

INTRODUCTION

A recent count taken from the Ellis & Messina Catalogue of Ostracoda (1942–) shows that 43 species (three with question) and varieties have been placed in the genus *Octonaria* Jones, 1887. Probably other forms have been assigned to the genus which have not yet been entered into the Catalogue of Ostracoda (1942–). The variety of forms which have been included in the genus makes it apparent that the genus is poorly understood. Indeed, *Octonaria* has been a "dustbin taxon" for many ovate, subovate to subrectangular ostracods with relatively coarse ridges and/or pits on the lateral surfaces. Many of the species which have been placed in the genus are thlipsuraceans but some are not even members of the Podocopida (*sensu* Scott, 1961, p. Q86).

During our investigation of the biostratigraphic potential of podocope and platycope ostracods from the Wenlock strata of the Welsh Borderland, we found that even the species and varieties originally placed in Octonaria by Jones (1887) represented, in some cases, synonymous minor variants based on poorly preserved specimens and, in other cases, species which belong to other genera. Furthermore, we found that the Wenlock distribution of Octonaria in the Welsh Borderland is restricted to the Homerian (specifically upper lundgreni to upper nassa graptolite zones), although Siveter (1978) and Aldridge et al. (1979) have recorded it from basal Ludlow strata in the same region. The genus has biostratigraphic value in its type area and, in view of the general misunderstanding of the genus, the purpose of this paper is to redescribe and illustrate the type-species, which we believe is the only presently known member of the genus. In addition, we clarify the taxonomic status of Jones' (1887) types, reillustrate the holotype of *Octonaria octoformis* Jones, 1887 and consider ancestor-descendant relationships for *Octonaria*.

PREVIOUS WORK

The ostracod genus Octonaria was erected by Jones (1887) on the basis of material from what is now called the Farley Member of the Coalbrookdale Formation at Shropshire, England. Initially, Jones placed three species, O. octoformis, O, undosa, and O? paradoxa, in the genus. In addition, Jones described six varieties of O. octoformis. O. octoformis is the type-species.

The placement of a wide variety of forms in the genus Octonaria since 1887 can be traced, primarily, to a history of misleading illustrations in Jones' (1887) work as well as in primary articles specifically on the Thlipsuridae and standard references on ostracods in general. Jones' (1887, pl. 12, fig. 2a) original illustration of a left lateral view of a carapace is misleading in that it shows that the ridges on the lateral surface close to form a figure eight. Furthermore, the central node is shown to be a loop which closes on itself to form a swelling with a depression within it. Pl. 1, fig. 11, a photograph of the specimen Jones (1887) illustrated, shows that the ridges do not close and that the central swelling is actually a simple node. Jones' illustration has led many workers to interpret Octonaria as having a complex of coarse ridges separated by depressions or pits. The misleading illustration of Jones (1887) was perpetuated by Ulrich & Bassler (1923, fig. 23-1) whose illustration was a close, but not exact, representation of Jones' (1887) illustration. Swartz (1932, pl.

11, fig. 5) and Bassler & Kellett (1934, fig. 16-1) reproduced Ulrich & Bassler's (1923) illustration. The errors of illustration were accentuated in the American Treatise by Kesling (1961, fig. 304-1d) who further complicated the problem by labelling what is a left valve as a right valve. The illustration in the Russian Treatise (Polenova & Zanina, 1960, fig. 849a) is a faithful reproduction of Jones' (1887) illustration and Krandijevsky's (1968, fig. 7) illustration is very similar to that of Kesling (1961).

SYSTEMATIC DESCRIPTION

Specimens figured herein are deposited in the Department of Palaeontology of the British Museum (Natural History) (B.M.N.H.), the Department of Geology at Arizona State University (A.S.U.) and the United States National Museum of Natural History (U.S.N.M.). Sample number prefixes (R.F.L.) refer to samples collected by the junior author.

Order Podocopida Müller, 1894 Superfamily Thlipsuracea, Ulrich, 1894 Family Thlipsuridae Ulrich, 1894 Genus Octonaria Jones, 1887

Type-species. Octonaria octoformis Jones, 1887.

Diagnosis. Thlipsuridae with ovate to subreniform lateral outline. Valves sculptured with a coarse anterior ridge which approximately parallels the anterodorsal, anterior and anteroventral borders of the valve, and with a coarse posterior ridge which approximately parallels the posterodorsal, posterior and posteroventral borders of the valve. Anterior and posterior ridges fuse variably in ventral position but do not fuse dorsally. Variably developed node slightly anterior of central position on each valve may fuse ventrally with anterior and posterior ridges. Hinge straight, inclined to longitudinal axis of valve, with list on left valve. Hinge elements of right valve poorly known. Contact groove along posterior and ventral margin of left valve, absent along anterior margin. Position of adductor muscle marked interiorly by large circular depression corresponding to exterior node. Left valve larger than right and overreach of right valve by left valve pronounced along dorsal border.

Remarks. External sculpturing, hinge structure and orientation, valve relationships and contact margin morphology are important in defining the genus. Unfortunately, we do not have well preserved single valves which illustrate all of these features. The hinge apparently is like that of *Thlipsura* Jones, 1869 (Lundin & Petersen, 1975) but we have no adequate single right valves to verify the existence of a hinge groove. Because of inadequate preservation, transverse thin sections through the hinge of carapaces are not

definitive with regard to details of the right valve hinge. Study of two such thin sections, however, indicate that the right valve hinge may also be a simple list. It appears, in this case, that the ventral bevelled surface of the left valve hinge contacts a dorsal bevelled surface of the right valve hinge. The hinge and contact margin features of the left valve (Fig. 1B) have been interpreted from several single left valves and thin sections of carapaces. At best, the contact groove is poorly developed.

As discussed above, Jones' original illustration and subsequent illustrations by other authors mislead authors into supposing *Octonaria* is ornamented by a series of depressions and ridges. Illustrations of all species, except the type-species, which have been placed in *Octonaria* indicate significant differences in shape, surface sculpture and/or valve relationships. Therefore, we presently restrict the composition of the genus to the type-species.

Octonaria octoformis Jones, 1887 (Pl. 1, figs. 3-17; Fig. 1)

- 1887 Octonaria octoformis sp. nov. Jones: 404, pl. 12, fig. 2.
- 1887 Octonaria octoformis var. intorta var. nov. Jones: 404, pl. 12, fig. 3.
- 1887 Octonaria octoformis var. simplex var. nov. Jones: 405, pl. 12, fig. 4.
- non 1887 Octonaria octoformis var. informis var. nov. Jones: 405, pl. 12, fig. 5.
- 1887 Octonaria octoformis var. bipartita var. nov. Jones: 405, pl. 12, fig. 6.
- 1887 Octonaria octoformis var. persona var. nov. Jones: 405, pl. 12, fig. 7.
- 1887 Octonaria octoformis var. monticulata var. nov. Jones: 406, pl. 12, fig. 8.
- 1887 Octonaria undosa sp. nov. Jones: 406, pl. 12, fig. 1.
- 1923 Octonaria octoformis Jones; Ulrich & Bassler: fig. 23-1.
- 1932 Octonaria octoformis Jones; Swartz: 52, pl. 11, fig. 5.
- 1934 Octonaria octoformis Jones; Bassler & Kellett: fig. 16-1.
- 1960 Octonaria octoformis Jones; Polenova & Zanina: fig. 849.
- 1961 Octonaria octoformis Jones; Kesling: fig. 304-1d.
- 1965 Octonaria octoformis Jones; Pokorny: fig. 855.
- 1968 Octonaria octoformis Jones; Krandijevsky: fig. 7, pl. 11, fig. 27.
- 1978 Octonaria octoformis Jones; Siveter: 78, pl. 5, figs. 9, 10.
- 1984 Octonaria octoformis Jones; Siveter: pl. 1, fig. 15.



Fig. 1. Octonaria octoformis Jones, 1887. Dorsal (A), ventral (C), right lateral (D), left lateral (E) views of carapace (X67, based on specimen illustrated on Pl. 1, figs. 12–15) and interior view (B) of adult left valve (X67, based primarily on specimen ASU X-88, sample RFL 24a, Farley Member, Coalbrookdale Formation, Harley Hill, Welsh Borderland).

Diagnosis. As for the genus.

Holotype. Carapace, B.M.N.H. IN 52416. Jones (1887) stated that his material consisted of one specimen. We have no doubts that the indicated specimen is the one illustrated by Jones. It is further illustrated herein on Pl. 1, figs. 9–11.

Material. Approximately 130 specimens, mainly carapaces, but some isolated valves, Department of Geology, Arizona State University.

Description. The carapace is subovate to subreniform in lateral view, subrectangular in dorsal and ventral views and subquadrate in end view. The anterior and posterior margins are variably rounded, the dorsum is gently convex and the venter is slightly convex to sinuate. Maximum height is at or slightly behind midlength, maximum length is at or slightly below midheight and maximum width is distinctly posterior. The valves are unequal, the left overlapping the right along the free margin. Overlap is reduced along the anterior margin. The left valve strongly overreaches the right along the dorsum. The valves are sculptured by massive arcuate ridges. The anterior one approximately parallels the anterodorsal, anterior and anteroventral borders. The posterior one approximately parallels the posterodorsal, posterior and posteroventral borders. The ridges connect ventrally just below a variably developed node which is slightly anterior of the centre of each valve. The ridges do not connect dorsally but on most specimens they fuse with the ventral side of the node. The depressions which are partially surrounded



Fig. 2. Size dispersion diagram for 21 carapaces and left valves of *Octonaria octoformis* from sample RFL 24a.

by the ridges and node are subcircular to oval to somewhat comma-shaped. The anteriormost surface of the right valve is developed into a weak admarginal ridge on some specimens. The hinge is straight, inclined to the longitudinal axis of the valves and consists of a simple list, at least on the left valve (see Remarks under generic diagnosis). The exterior node is reflected interiorly as a circular depression which marks the position of the adductor muscle attachment. The exterior ridges are reflected interiorly as depressions but are primarily developed by thickening of the shell. A poorly-developed contact groove is present along the posterior, posteroventral, and posterior twothirds of the ventral margin of the left valve.

Dimensions. See Fig. 2.

Remarks. Immature specimens which are available for study represent only the last two preadult instars. Except for smaller size and a general reduction in the

Explanation of Plate 1

All figures are $\times 40$

- Fig. 1. "Thlipsurella" v-scripta (Jones), B.M.N.H. In 52483, right lateral view of carapace Jones (1887) illustrated as Octonaria octoformis var. informis.
- Fig. 2. Parulrichia paradoxa (Jones), B.M.N.H. In 52434, lateral view of left valve Jones (1887) illustrated as O? paradoxa.
- Fig. 3. O. octoformis Jones, B.M.N.H. In 53482, left lateral view of carapace Jones (1887) illustrated as O. octoformis var. simplex.
- Fig. 4. O. octoformis Jones, B.M.N.H. In 2431, right lateral view of carapace Jones (1887) illustrated as O. octoformis var. intorta.
- Fig. 5. O. octoformis Jones, B.M.N.H. In 52414, left lateral view of carapace Jones (1887) illustrated as O. octoformis var. monticulata.
- Fig. 6. O. octoformis Jones, B.M.N.H. In 1960, right lateral view of carapace Jones (1887) illustrated as O. octoformis var. persona..
- Fig. 7. O. octoformis Jones, B.M.N.H. In 52600, lateral view of right valve Jones (1887) illustrated as O. undosa.
- Fig. 8. O. octoformis Jones, B.M.N.H. In 52446, right lateral view of carapace Jones (1887) illustrated as O. octoformis var. bipartita.
- Figs. 9-11. O. octoformis Jones, B.M.N.H. In 52416, holotype, dorsal, right lateral and left lateral views of carapace.
- Figs. 12-15. O. octoformis Jones, ASU X-86, sample RFL 24a, Farley Member, Coalbrookdale Formation, Harley Hill, Welsh Borderland, right lateral, ventral, dorsal and left lateral views of adult carapace.
- Fig. 16. O. octoformis Jones, ASU X-87, sample RFL 24a (specimen lost), right lateral view of adult carapace.
- Fig. 17. O. octoformis Jones, U.S.N.M. 83021, left lateral view of adult carapace from "Shales over Wenlock Limestone" catalogued by U.S.N.M. as O. octoformis var. simplex.



which may be absent)Distribution. The presently known distribution of the
species is late Wenlock to early Ludlow strata of the
Welsh Borderland.ost notable variationWelsh Borderland.

PHYLOGENETIC RELATIONSHIPS Ancestor

The details of valve relationships, hinge morphology (as presently known) and orientation, contact margin features and stratigraphic occurrence indicate that a form like "Bairdiocypris" gotlandica (Jones, 1889) is ancestral to Octonaria. These forms are similar in all regards except that the former has no surface sculpturing of the valves. We propose that the "B." gotlandica – "B." phillipsiana (Jones & Holl, 1869) (see Abushik, 1971, p. 117) lineage is a lineage from which Octonaria was derived. This lineage spans the late Llandovery to late Wenlock interval. The presently known lowest occurrence of Octonaria is in the upper half of the Wenlock.

Descendant

The Ludlow and Pridoli history of this group of ostracods is poorly known. On a morphological basis, however, it is clear that the Late Silurian - Early Devonian genus Thlipsorothella Lundin & Petersen, 1974, is a descendant of Octonaria. The hinge structure, valve relationships and basic plan of shell sculpture are the same. Octonaria differs from Thlipsorothella in possessing strong L/R overreach along the dorsum and in having the hinge distinctly inclined to the longitudinal axis of the valve (Fig. 1B). In Thlipsorothella dorsal overreach of the right valve by the left is reduced or absent (Lundin, 1968, pl. 19, fig. 2a; pl. 20 fig. 1b) and the hinge is essentially parallel to the longitudinal axis of the valve (Fig. 3). Adamczak (1966) pointed out that the inclination of the hinge is reduced through time among platycope ostracods like Nyhamnella, Gotlandella, Cavellina and Cytherella. Our data indicate a similar trend in the "Bairdiocypris" -Octonaria - Thlipsorothella complex.

The indicated phylogenetic relationship between *Octonaria* and *Thlipsorothella* is significant because the geographic distribution of *Octonaria* is east of the remnant Iapetus Ocean whereas that of *Thlipsorothella* is west of it (specifically the North American midcontinent). This adds additional evidence to the, thus far, weakly established link between ostracod faunas of the British-Baltic area and the North American midcontinent referred to by Lundin and Siveter (1985).

CONCLUSIONS

- 1) Octonaria Jones, 1887 is a monotypic genus. The only presently known representative is O. octoformis Jones, 1887.
- 2) Octonaria has a geological range of late Wenlock to early Ludlow.
- 3) Octonaria is known only from the Welsh Borderland area.

development of the central node (which may be absent) and ridges, the immature specimens are like the adults. Among the adult specimens the most notable variation involves lateral and dorsal outline (which on some specimens has been affected by post-depositional processes), development of the ridges and central node, and degree of fusion of the central node with the anterior and posterior ridges. Substantial variation in these parameters occurs among specimens from our collections as well as those of Jones in the B.M.N.H.

Jones (1887) described six varieties of O. octoformis and two additional species of Octonaria, O. undosa (Pl. 1, fig. 7) and O? paradoxa (Pl. 1, fig. 2). O. octoformis var. informis (Pl. 1, fig. 1) is a junior synonym of Thlipsura v-scripta Jones & Holl, 1869, a species which has commonly been referred to Thlipsurella Swartz, 1932. O? paradoxa belongs to Parulrichia Schmidt, 1941 and is probably synonymous with P. diversa (Jones & Holl, 1886). O. undosa and the remaining five varieties of O. octoformis (Pl 1, figs. 3-6, 8) are based on abraded and/or deformed specimens and we consider them to be synonymous with O. octoformis.



4) Octonaria probably descended from a "Bairdiocypris" gotlandica – like form and is ancestral to the North American genus *Thlipsorothella*.

ACKNOWLEDGEMENTS

We wish to thank D. J. Siveter for assistance with the collection of samples used in this study. This study is part of a project supported by a grant to the junior author by the National Science Foundation (Grant No. EAR-8200816).

Manuscript received July 1986 Revised manuscript accepted December 1986

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