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VALIDATION OF THE GENUS *ROWLEYELLA* WELLER, 1911, AND DESCRIPTION OF A NEW GENUS (BRACHIOPODA: ATHYRIDIDA)

JOHN L. CARTER Curator, Section of Invertebrate Paleontology

Abstract

The small Lower Carboniferous camarophorellid genus *Rowleyella* Weller, 1911, was placed in subjective synonomy with the Middle Devonian genus *Camarospira* Hall and Clarke, 1893, by Boucot *et al.* (1965). Transverse serial sections of a silicified chert-filled specimen reveal that the genus is internally distinctive and more similar to *Camarophorella* than to *Camarospira*. In *Rowleyella* the dorsal adductor platform is abbreviated and modified to form two chambers just below the cardinal plate. Thus, *Rowleyella* is morphologically distinct from both *Camarospira* and *Camarophorella* and represents a valid genus.

A new genus is proposed for the athyridid species *Athyris crassicardinalis* White, 1860, from the late Kinderhookian (Lower Carboniferous) of Iowa and Missouri. This genus differs from another Kinderhookian athyridid with which it is sometimes associated, *Planalvus* Carter, 1971, mainly in having reversed valve inflation.

INTRODUCTION

When I studied the late Kinderhookian and early Osagean brachiopod faunas of Iowa and Missouri (Carter, 1968, 1971, 1972), I accumulated specimens of poorly known genera and species, but did not deem it useful to redescribe them at that time. However, the prospect of a revised edition of the *Treatise on Invertebrate Paleontology* makes it prudent to present new generic information that is pertinent to the revised *Treatise*. Therefore, description of these specimens now assumes greater urgency. The present paper consists of two disparate parts. The first part comprises a redescription, reillustration and validation of the genus *Rowleyella*, which was misdiagnosed in the original *Treatise*. The second part consists of the description of a new athyridid genus.

THE GENUS ROWLEYELLA WELLER, 1911

This genus was described by Weller (1911:447) as follows: "Shell terebratuliform, with the valves subequally convex. The beak of the pedicle valve perforated by a subcircular foramen which encroaches wholly upon the umbonal region, the delthyrium broadly triangular and wholly closed. Internally each valve is supplied with a strong median septum which, in the pedicle valve, reaches nearly to the center of the valve, that of the brachial valve being somewhat shorter." This brief description was not accompanied by illustrations or genus comparisons *per se*, although Weller took care to discuss possible relationships of his new genus with the terebratulids, pentamerids, and camarophorellins. He concluded that it was most similar to the genus *Camarophorella* Hall and Clarke, 1893, noting that it differed in showing no evidence of a "brachial platform" (dorsal adductor platform or dorsal shoe-lifter process).

Weller (1914) essentially repeated this description but added that he had detected laterally directed spiralia, consisting of about four whorls each. He repeated his assertion that *Rowleyella* was closely related to *Camarophorella*, differing mainly in lacking the dorsal adductor platform on the floor of the valve. He suggested that "If a platform of this sort is present, its margins are entirely free."

This monotypic genus is known only from silicified specimens from the Burlington Limestone (lower white chert beds) in and near Louisiana, Pike County, Missouri. Rowley's two syntypes are illustrated herein (Fig. 1A–D). These specimens have not been photographically illustrated before. Rowley (1900: pl. 5, fig. 51–53) provided crude drawings of one of them and Weller (1914: pl. 82, fig. 64– 69) used non-type specimens for his photographs.

Although all of these specimens are silicified and usually filled with coarse quartz crystals, some specimens retain the internal structures as soft white chert that contrasts well with the nearly clear quartz matrix. A medium-sized specimen was successfully sectioned, providing additional details of the internal morphology. A jugum has still never been observed but enough new information was obtained by sectioning to allow a more complete diagnosis, and to confirm its close relationship with the genus *Camarophorella*, not *Camarospira*.

Family Meristellidae Waagen, 1883 Subfamily Camarophorellinae Schuchert, 1929 Genus *Rowleyella* Weller, 1911 Fig. 1A–Q, 2

Rowleyella Weller, 1911:447. Rowleyella: Weller, 1914:462. Rowleyella: Schuchert, 1929:109. Rowleyella: Likharev, 1960:284. Camarospira Hall & Clarke, 1893 (part): Boucot, Johnson, and Staton, 1965:H658.

Camarospira Hall & Clarke, 1893 (part): Grunt, 1986:42.

Type species (by original designation). – Terebratula fabulites Rowley, 1900:265.

Diagnosis.—Small, elongate, subequally biconvex, with slightly flattened venter and weakly uniplicate anterior commissure but lacking fold and sulcus; foramen circular to ovate; delthyrium closed by dorsal umbo and narrow deltidial plates; ornament lacking except for very-fine growth lines and coarser, irregularly spaced growth varices; interior of ventral valve with spondylium supported by strong high median septum and short mystrochial plates; dorsal interior with concave or shallow V-shaped cardinal plate supported by strong short median septum; dorsal adductor platform originates at dorsal beak; sides of dorsal adductor platform extending to floor of valve extremely short; ventral portions of adductor platform attached to dorsal surfaces of inner socket ridges, forming two short subtriangular chambers directly under cardinal plate; spiralia directed laterally, composed of four whorls each; jugum unknown; shell substance impunctate; inner shell surfaces of both valves finely and densely papillose as in *Camarophorella*.

Development of the dorsal muscle platform. – The Camarophorellinae is a small group of three genera of meristelloid athyridids endemic to North America. They are characterized by having a ventral spondylium, a dorsal median septum, and a complex jugal structure that includes a ventral process that splits ventrally, forming two posteriorly recurved loops, the distal ends of which fuse with the jugum dorsally. The earliest genus *Camarospira*, of Middle Devonian age, lacks a dorsal muscle platform and its jugum is unknown. Hence this genus is not included in the following discussion.

In the late Famennian the earliest species of Camarophorella appears, Camarophorella buckleyi (Rowley, 1908) from the Louisiana Limestone of Missouri. This



Fig. 1.—*Rowleyella fabulites* (Rowley). A–D, the two syntypes from the Burlington Limestone (lower white chert) at Louisiana, Pike County, Missouri. A, B, ventral and dorsal views of the largest syntype, University of Illinois RX-165B. This specimen is probably the one illustrated by Rowley (1900: pl. 5, fig. 51–53). It is a juvenile *Cranaena* sp., $\times 5$. C, D, ventral and dorsal views of the lectoholotype, University of Illinois RX-165A, selected herein, a small, spalled silicified specimen (most of the shell of the ventral valve is removed clearly showing the ventral median septum), $\times 5$. E–Q, four specimens from the Burlington Limestone (lower white chert) at the City Quarry, Louisiana, Pike County, Missouri. E, posterior view of a silicified natural internal mold showing the mystrochial plates and very short dorsal shoe-lifter process, CM 34945, $\times 8$. F–Q, ventral, dorsal, anterior and lateral views of three well-preserved, complete specimens, CM 34946–34948, $\times 3$.

species ranges into the earliest Carboniferous Glen Park Formation in Missouri and Illinois (Carter, 1988). Other early Carboniferous species are: *Camarophorella lenticularis* (White and Whitfield, 1862), the type species, from the Prospect Hill Sandstone of southeastern Iowa and possibly the Chouteau Limestone of Missouri; *C. dorsata* Carter, 1967, from the Chappel Limestone of central Texas; and *C. mutabilis* Hyde, 1908, from the Logan Formation of Ohio. *Camarophorella buckleyi* differs from the early Carboniferous species in one important respect, namely, the dorsal muscle platform originates well in front of the cardinal plate. Because the interior of this species has not been illustrated serial sections of it are shown in Fig. 3. Weller (1914: pl. 82, fig. 63) illustrated one of the syntypes of *C. lenticularis* which shows the dorsal adductor platform originating anteriorly, probably just in front of the cardinal plate, but not as far forward as in *C. buckleyi*. Carter's (1967: fig. 17) illustration of *C. dorsata* showed the dorsal adductor



Fig. 2. – Transverse serial sections of a small silicified specimen of *Rowleyella fabulites* (Rowley), CM 34949, Burlington Limestone (lower white chert), from the City Quarry, Louisiana, Pike County, Missouri. Numbers refer to distance in mm from ventral beak. $\times 6$.

platform placed posteriorly and dorsal to the cardinal plate, but not at the beak. Hyde (1908: pl. 6, 8, 9) showed specimens of *C. mutabilis* in which the dorsal adductor platform seemingly originates at or very near the dorsal beak.

Thus, the dorsal muscle platform in the genus *Camarophorella* migrates posteriorly through time, from well in front of the cardinalia, ultimately originating near the dorsal beak. In the genus *Rowleyella* this posterior migration is carried one step farther and culminates with the almost complete loss of the dorsal shoelifter process and development of a double chamber under the cardinal plate, fused to the dorsal surfaces of the inner socket ridges. The sides of the original shoe-lifter process are extremely short and are lost posteriorly, very near the dorsal beak. The large transverse plate seen in Fig. 2, sections 1.05–1.8, is homologous to the roof of the original shoe-lifter process and is analogous to the camarophorium in the stenoscismatoideans. In this manner the length of the adductors is greatly shortened.

Discussion. – Rowley (1900: pl. 5, fig. 51–53) illustrated only one of his two very small syntypes (University of Illinois, RX-165A, B) of Terebratula fabulites,



Fig. 3.—Transverse serial sections of *Camarophorella buckleyi* (Rowley), CM 34950, from the Louisiana Limestone, Louisiana, Pike County, Missouri. Note the anterior development of the dorsal shoe-lifter process, well in front of the cardinalia. Numbers refer to distance in mm from the ventral beak. $\times 4$.

using three very small, crude line drawings at natural size. Weller (1914:464) studied Rowley's types and stated that the specimen illustrated by Rowley (University of Illinois, RX-165B) "has been carefully examined, and although the shell itself is intact, the presence of a median septum in each valve seems to be clearly indicated." I have also studied this specimen and conclude that the specimen Rowley illustrated appears to be a small specimen of Cranaena, a terebratulid. I find no evidence of the existence of a median septum in either valve, but the specimen has a labiate foramen and is obviously punctate (Fig. 1). However, the remaining syntype (University of Illinois RX-165A) is indeed a small, possibly juvenile, example of this small camarophorellid genus and is herein designated the lectoholotype. It is illustrated on Fig. 1C, D. Because Rowley's original name and description could apply equally well to either syntype, one could justifiably restrict the name Terebratula fabulites to the small terebratulid syntype. However, Weller's interpretation of this species is entrenched in the literature. Conservation of his concept of the species by designating the other syntype as lectotype is the most logical choice.

The number of known specimens of this genus is very small. At the time Rowley (1900) described this species he had only the two syntypes. He subsequently collected several more specimens which are now in the collections of the University of Illinois-Urbana. Weller (1914:464) described and illustrated two specimens which are now housed in the Field Museum of Natural History. Six specimens are in the collections of The Carnegie Museum of Natural History, four of which are illustrated here.

Neither Rowley (1900) nor Weller (1911, 1914) observed the presence of mystrochial plates in the pedicle valve of *Rowlevella fabulites*. These plates are easily seen in Fig. 1E and 2 (0.2–0.75). Their development and placement is comparable to that of the genus *Camarophorella*. These authors failed to observe the very short shoe-lifter process, or dorsal adductor platform, in the dorsal umbo. These plates are best observed in transverse sections (Fig. 2 [0.60–0.70]). The extremely short shoe-lifter process is fused with two nearly vertical plates attached to the dorsal surfaces of the inner socket ridges, forming a pair of subtrigonal chambers. The purpose of these chambers is not known but they probably functioned in much the same manner as the shoe-lifter process, that is, as a means of shortening the adductor muscles. Rudwick (1970:65) speculated that brachiopods with nontendinous muscles might achieve greater muscular efficiency by means of shortening muscle length with various kinds of platforms. In this interpretation strongly biconvex brachiopods with non-tendinous muscles tend to develop muscle platforms. Once tendinous muscles appeared in a given stock, muscle platforms would tend to disappear.

Description of a New Genus

Family Athyrididae Davidson, 1881 Subfamily Athyridinae Davidson, 1881 Genus **Densalvus**, new genus Fig. 4

Type species.—*Athyris crassicardinalis* White, 1860:229 (Lectoholotype designated herein, University of Michigan, Museum of Paleontology 66073).

Species assigned. – Monotypic.

Stratigraphic range.-Early Carboniferous (late Kinderhookian) of Iowa and Missouri.



Fig. 4.—*Densalvus crassicardinalis* (White, 1860). A–L, three syntypes from the White Collection, University of Michigan, all from the Wassonville Dolomite at Burlington, Des Moines County, Iowa; A–D, dorsal, ventral, posterior and lateral views of a large dorsal valve, University of Michigan 66074; E–H, dorsal, ventral, posterior and lateral views of a silicified shell with a well-preserved dorsal valve but spalled ventral valve, University of Michigan 66075; I–L, ventral, dorsal, posterior and lateral views of the lectotype (selected herein, University of Michigan 66073), a small pedicle valve with dorsal cardinalia attached; M–P, three of Weller's illustrated specimens, including a large dorsal valve exterior, a large dorsal valve interior, and two views of a small ventral valve, respectively, from the Chouteau Limestone at Sedalia, Pettis County, Missouri, Field Museum of Natural History, Weller Collection UC 9817; Q–T, two views each of silicified dorsal and ventral valves, CM 34951 and CM 34952, from the Hampton Formation (Eagle City Limestone Member), near Legrand, Marshall County, Iowa; all × 3.

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Etymology.-From the Latin densus-thick, and alvus-belly (feminine); referring to the thick ventral valve.

Diagnosis.—Small, unequally biconvex athyridids with strongly inflated ventral valve and weakly convex dorsal valve; dorsum flattened and venter well rounded; dental plates lacking; cardinal plate large, athyridid, not perforate; macro-ornament apparently simple but possibly weakly lamellose anteriorly; micro-ornament very finely and weakly capillate.

Description.—Small for the subfamily; outline variable, usually transversely subovate to subpentagonal; ventral valve much more inflated than dorsal valve; greatest width attained slightly posterior to midlength; lateral profile lenticular to guttate; hingeline short, curved; lateral extremities well rounded; dorsal fold and ventral sulcus lacking, dorsum flattened and venter well rounded instead; growth varices irregularly spaced; surface very weakly and finely capillate; growth lines very fine and almost evenly spaced, tending to be slightly lamellose anteriorly; other ornamentation not observed.

Ventral valve well inflated, thicker than opposite valve, with greatest convexity on venter in anterior view or anteriorly in lateral view; flanks weakly convex, sloping steeply to lateral margins; beak inconspicuous, not differentiated from umbo; foramen small, subcircular, mesothyridid; delthyrium filled by dorsal umbo and cardinal plate; beak ridges not present; interior with stout blunt teeth; dental plates lacking; muscle field large, moderately impressed, with low myophragm.

Dorsal valve weakly convex in both anterior and lateral views of most specimens, becoming thicker anteriorly in some gerontic shells, but usually much thinner than ventral valve; dorsum usually markedly flattened; dorsal umbonal region slightly inflated; beak sharply triangular, projecting into delthyrium, fused with cardinal plate; interior with flattened, subquadrate, imperforate cardinal plate fused to high stout socket ridges; brachidium unknown; dorsal adductor scars narrow, laterally depressed, medially raised, separated by low myophragm that extends from cardinal plate past midlength; ovarian pits present posterolaterally; shell substance impunctate.

Comparisons. — This new genus commonly occurs with another athyridid genus that is similar in size and general appearance, the genus *Planalvus* Carter, 1971. It differs from *Planalvus* mainly in having reversed valve convexity. In *Densalvus* the dorsal valve is thin and the ventral valve is thick; whereas in *Planalvus* the opposite is true, the dorsal valve is thick and ventral valve is thin. *Densalvus* seems to lack the spiny lamellae that occur in *Planalvus*, but I have not observed any well-preserved exteriors in *Densalvus crassicardinalis*. The unusual reversed valve inflation and lack of dental plates internally serve to distinguish this new genus from other members of the order.

Remarks.—Weller (1914:472) noted that *Athyris crassicardinalis* "is not a true member of the genus *Athyris*, neither can it be placed in another genus with any more certainty. It is not unlikely a representative of an undescribed genus...." He hesitated to propose a new genus without definitive knowledge of its brachidium. I agree that the nature of the brachidium is important for systematic placement of this genus within a family. However, the unusual external and internal morphology of these shells is ample justification for proposing a new genus. Determination of its precise relationships to other genera in this group awaits discovery and description of the brachidium.

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