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REINTERPRETATION OF HINGE STRUCTURES OF TWO DEVONIAN BIVALVIA: *CONGERIOMORPHA* AND *TUSAYANA*

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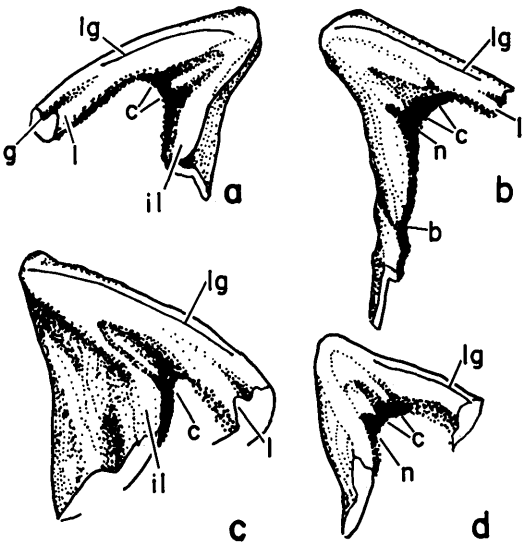
ABSTRACT.—Hinge structures of *Congeriomorpha* are reinterpreted to be primitive cardinal and lateral teeth, and the genus is placed in the order Veneroida, new family Congeriomorphidae.

The left hinge of *Tusayana* is here considered to have two simple cardinal teeth with a bifid socket between them; the right valve then has two cardinals also, with the posterior one bifid. The bifid sockets suggest derivation from an actinodont hinge grade, and the genus is tentatively referred to the family Permophoridae.

IN 1948, Stoyanow described from the singular Late Devonian faunule of the Island Mesa beds, north-central Arizona, two bivalves referred to the new genera *Congeriomorpha* and *Tusayana,* neither of which was assigned to a family. Newell and LaRocque (*in* Moore, 1969, p. N287) placed *Congeriomorpha* in Ambonychiidae, order Pterioida, and LaRocque (ibid., p. N583) placed *Tusayana* in Hippopodiidae, order Veneroida. The external shell shape of *Congeriomorpha* resembles some Ambonychiidae (its shell shape is also similar to some Mytilidae), but its broad nymph and narrow ligamental groove are decidedly atypical for the order Pterioida. *Tusayana,* which has a somewhat *Dosinia*-like shape, does not resemble gibbous *Hippopodium*—the only other genus in the Hippopodiidae—and differs additionally in having two cardinal teeth rather than one in each valve and a well defined lunule.

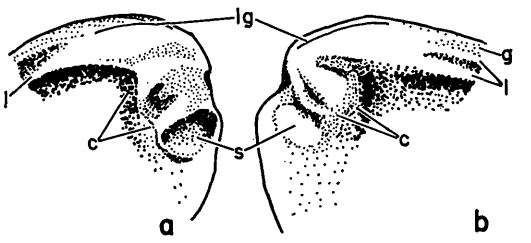
Stoyanow (1948) described *Congeriomorpha* as having in each valve a subumbonal myophoric depression divided by a ridge and suggested that this divided myophoric depression served as two areas of muscle attachment as in *Congeria,* family Dreissenidae. The subumbonal structures can be interpreted to consist of a hinge plate with low, elongate cardinal teeth and sockets. These cardinal teeth have low relief and when the valves are closed a tooth does not occupy as much of its socket as is usual in more modern hinges; conversely the cardinal sockets of *Tusayana* seem too shallow for their teeth. The apparent rude fit of the cardinal teeth and sockets may be due to abrasion before deposition or imperfect silicification, but it is more likely a "normal" grade of hinge development for Devonian heterodonts, in which these teeth probably articulated well enough to inhibit rotational shearing of the valves along the plane of commissure when the valves were completely closed. In both genera the posterior lateral teeth and sockets appear to fit better mechanically and may have been functional when the valves were slightly gaping. In both genera the hinge is massive relative to shell size and the shell is notably thicker in the beak area than toward the ventral margin, features reminiscent of the Megalodontidae; however, the teeth resemble other heterodonts.

The type material of *Congeriomorpha andrusovi* Stoyanow consists of nine syntypes, 6 left valves and 3 right valves. Of these the left valve (Text-fig. 1a, 3a) pictured in figures 1–4 (Stoyanow, 1948, pl. 120) is the most complete; the other eight specimens consist of the umbonal region with most of the thinner ventral portion of the shell gone. The partial right valve paired (Stoyanow, ibid., fig. 1) to the nearly complete left valve (UCLA cat. no. 38800) is from a specimen at least a fifth larger than UCLA 38800. Probably as a result of Stoyanow's careful leaching of the silicified fossils, the fine sand matrix was readily removed from this right valve (UCLA cat. no. 38801), and its hinge (Text-fig. 1b, 3b) is like that of Stoyanow's figure 6 (Text-fig. 1d, 3d), but the structures are a little more clearly preserved. A long, arcuate, narrow ligamental groove, beginning beneath the beak, lies behind a broad nymph. The hinge plate margin curves smoothly from the posterior side just dorsal to the lateral socket. The plate margin is notched where it abuts the anterior side of the shell.



TEXT-FIG. *1a–d—Congeriomorpha andrusovi* Stoyanow, syntypes (× 1). *1a*, UCLA 38800, left valve. *1b*, UCLA 38801, right valve. *1c*, UCLA 38807, right valve having cardinal teeth and insertive lunule characteristic of left valve and normal posterior lateral. *1d*, UCLA 38803, right valve. The ventral end of the posterior cardinal appears to have been chipped off and the dorsal end of the ligament groove has been obliterated. *c*, cardinal tooth; *l*, lateral tooth; *il*, insertive lunule; *b*, byssal notch; *n*, notch for lunule; *lg*, ligament groove; *g*, groove for posterior shell margin of opposite valve.

This notch is the socket for the margin of the lunule or "scute" of the left valve. (Because the original internal shell structure was obliterated by silicification there is an argument for using Stoyanow's term scute, but I prefer lunule for this structure as this structure functions, at least partially, as a hinge element and may have been made up of the same shell layer as the hinge (Carter, 1967). The lunular margins project like lateral teeth, and the right lunular margin overlaps that of the left. Two low ridges radiating from the beak on the hinge plate are here interpreted as cardinal teeth which fit into sockets in the left valve (the two halves of the myophoric depression of Stoyanow). Between these teeth is a socket for the left valve's cardinal tooth (Stoyanow's vertical ridge). Posterior to the ligamental groove is a lateral tooth whose length can not be determined, as all valves are broken. Marginward from the lateral is the socket for the posterior lateral of the left valve. The dorsal margin of the right valve fits into a groove on the margin of the left. Because of the insertive lunule in the left valve the right valve hinge appears broader than the left.



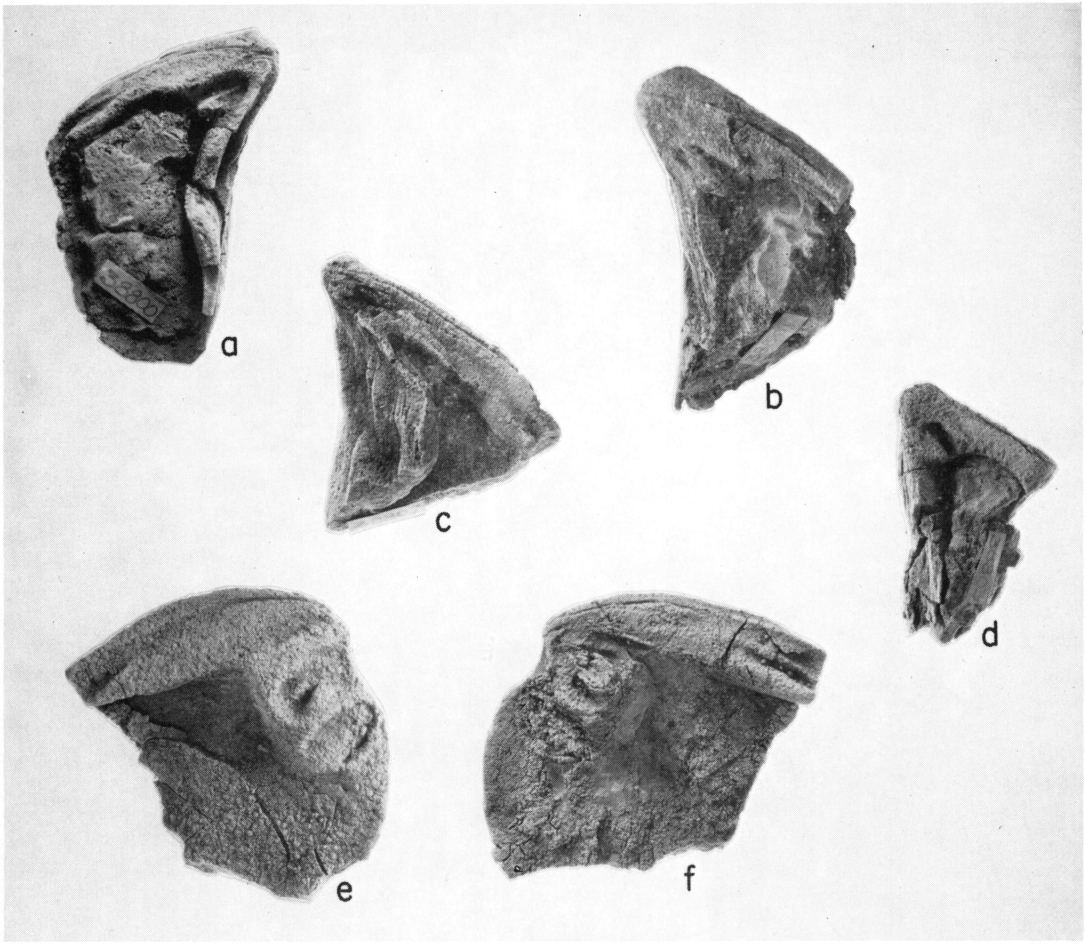
TEXT-FIG. *2a–b—Tusayana cibola* Stoyanow (× 1). *2a*, Holotype, UCLA 38809. *2b*, Paratype, UCLA 38810. *c*, cardinal tooth; *g*, groove for posterior shell margin; *l*, lateral tooth; *lg*, ligament groove; *s*, muscle scar.

This reinterpretation of the hinge structures places *Congeriomorpha* as an early heterodont. Using the notation of Boyd and Newell (1968, and *in* Moore, 1969, p. N909), its hinge would be

posterior RV v 0 1 . n (0) 1 0 1 . 0 anterior
LV 0 1 . n (1) 0 1 0 . il

(v for the insertive posterior valve margin and il for the insertive lunular margin are additions to the notation of Boyd and Newell). Noted above is a very obscure posterior cardinal in the left valve which opposes an obscure depression of the right valve.

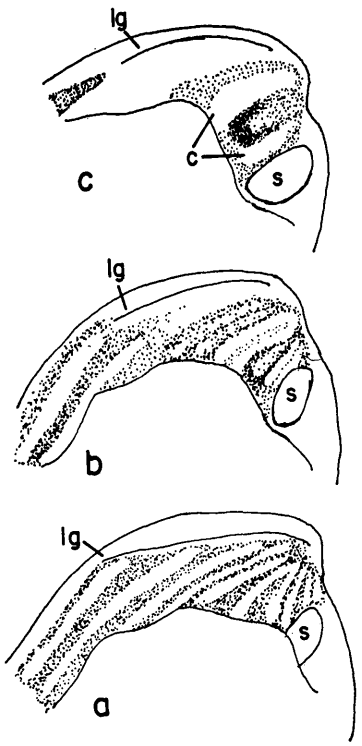
Stoyanow's material included three right valves. The now exposed hinge of UCLA 38801 agrees with that of his figure 6 but not of his figure 10, plate 120. This later specimen (UCLA 38807), refigured in Text-figures 1c, 3c, is a remnant of a large individual, perhaps the largest individual in the type lot. Its anomalous hinge may have had the structures partially obliterated by wear, solution, or breakage before silicification. The cavities about the beak suggest incomplete silicification and thus incomplete replication of the hinge structures. The narrow distorted hinge area may have resulted from a crowded, bysally attached life habit similar to *Mytilus*. But its hinge does fit the above description if the anterior portions are transposed. That is, the posterior lateral and insertive posterior hinge margin are normal for a right valve, but the low cardinal between well developed sockets and insertive lunular margin are normal for a left valve. Similar partial transpositions were originally discussed by Popenoe and Findlay (1933) and have been found in Permian heterodonts by Boyd and Newell (1968). Cox (*in* Moore,



TEXT-FIG. *3a–f*—Hinges of *Congeriomorpha andrusovi* Stoyanow and *Tusayana cibola* Stoyanow (all × 1). *3a–d, C. andrusovi* Stoyanow, syntypes. *3a,* UCLA 38800 (=IMB.1*), left valve, the most complete specimen. *3b,* UCLA 38801 (=IMB.1), right valve. *3c,* UCLA 38807 (=IMB.7), umbonal portion of right valve of large "gerontic" individual which, in part because of its narrow hinge line, is interpreted as having cardinal teeth and insertive lunule characteristic of a left valve and normal posterior lateral. *3d,* UCLA 38803 (=IMB.3) right valve. The chipping of the ventral end of the posterior cardinal is more apparent in the photograph than on the actual specimen in which silicification has produced a rough surface that obscures such details. This specimen can be roughly paired with UCLA 38808 (=IMB.8). *3e, T. cibola* Stoyanow, holotype, UCLA 38809 (=IMB.9). *3f, T. cibola* Stoyanow, paratype, UCLA 38810 (=IMB.9). *IMB for Island Mesa Beds? (Photographs by Takeo Susuki.)

1969, p. N57) records, as the earliest known transposed hinges, some of Permian age discussed by Newell; but if the above interpretation is correct, this specimen of *Congeriomorpha andrusovi* Stoyanow of Late Devonian age is an earlier example of hinge transposition.

The number and placement of teeth in *Congeriomorpha* is similar to *Mecynodon,* family Mecynodontidae, but the more massive hinge plate, insertive lunular and posterior valve margins, and byssal attachment suggest that *Mecynodon* and *Congeriomorpha* are not closely enough related to be included in the same family. The family Congeriomorphidae is therefore proposed for the latter. The shape of *Congeriomorpha* suggests a mode of life similar to living *Mytilus* (Mytilidae, Mytiloida) or *Mytilopsis* (Dreissenidae, Veneroida); and it may be this adaptation, uncommon for later heterodonts, that causes *Congeriomorpha* to resemble only the family Dreissenidae among Veneroida. Both *Congeriomorpha* and *Mytilopsis* have an insertive lunular margin, but the former has heterodont dentition which



TEXT-FIG. *4a–c*—Hypothetical derivation of heterodont *Tusayana* hinge from actinodont. *4a*, Hinge of *Tanaodon-Neoactinodonta* type. *4b*, Hypothetical intermediate stage with teeth grouped into more and less prominent elements and dorsal ends of long posterior teeth suppressed. *4c*, *Tusayana* hinge with posterior laterals separated from cardinals by edentulous interval. Relict actinodont tooth makes central cardinal socket bifid.

Dreissenidae have lost. Unfortunately the muscle scars of *Congeriomorpha* are unknown, probably obscured by silicification; but they can not have been placed as in *Congeria.*

Tusayana cibola Stoyanow has previously been illustrated with the beaks pointing straight up. Hinges of *T. cibola* Stoyanow are shown in Text-figures 2a–b, 3e–f rotated approximately 90° so that the lunular margin is nearly vertical rather than horizontal. There is only one left valve, and in it I am unable to recognize the bifid cardinal mentioned by Stoyanow (1948, p. 788) and LaRocque (*in* Moore, 1969, p. N583). Instead there appears to be a short anterior cardinal and a longer lower posterior cardinal with a bifid socket between them. Conversely the large posterior cardinal of the right valve is obscurely bifid. The anterior muscle scar is on a thickened buttress that, in the holotype and two paratypes, is dorsally depressed and ventrally raised above the adjacent hinge plate (Text-fig. 2a, 3e) while in the specimen for Text-figures 2b, 3f the muscle scar is completely raised. None of the right valves articulate even partially with the single left valve. The hinge of *Tusayana* may be diagrammed as

posterior RV 0 1 0 1 . n 0 1 0 1 . anterior
LV v 0 1 . n 1 0 1 (0) .

If the heterodont hinge is indeed derived from actinodont (e.g. Cox *in* Moore, 1969, p. N111; Nevesskaya et al., 1971, p. 146), the peculiar bifid socket of the left valve of *Tusayana* and the slight longitudinal division of the posterior cardinal socket of the right valve suggest an early heterodont hinge stage in which the actinodont radiating teeth and sockets beneath the beaks have been grouped into raised and sunken elements making fewer but compound teeth and sockets. Bruce Runnegar (1974, written communication) has suggested a comparison of Late Devonian *Tusayana* to Middle Devonian *Tanaodon* (?=*Neoactinodonta*). These middle Devonian forms have a form of actinodont dentition from which the heterodont dentition of *Tusayana* could be derived by bundling of the radiating teeth adjacent to the umboes, suppression of the elongate teeth beneath the nymphs, and retention of posterior laterals posterior to the ligament (Text-fig. 4a–c). It is unlikely that *Tusayana* was a descendant of *Tanaodon* or *Neoactinodonta* as *Tusayana* was apparently discoidal in shape and *Tanaodon* and *Neoactinodonta* were elongate with a posterior angulation, and although *Tanaodon* and *Neoactinodonta* are geologically older they do not seem enough so to me to allow time for their hinge teeth to evolve into those of *Tusayana.*

The dentition and anterior muscle scars of *Tusayana* resemble those of several genera in the family Permophoridae, and *Tusayana* can at present most plausibly be placed in that family.

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