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THE BRACHIOPOD GENUS *MAORISTROPHIA* ALLAN (LOWER DEVONIAN, STROPHOMENACEA) REDESCRIBED

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Abstract

Maoristrophia was formerly assigned to the Strophomenacean family Stropheodontidae, but a review of the internal morphology based on well preserved specimens from Reefton, New Zealand and from Victoria, Australia, indicates a possible assignment to the family Strophomenidae, but it is emphasized that the direct ancestor of *Maoristrophia* is unknown. *Maoristrophia* is recognized beyond the New Zealand, south-eastern Australia-Tasmania region for the first time. It represented in Kazakhstan by the species *Maoristrophia* (formerly *Leptostrophia*) *carinata* (Borisyak).

Introduction

The writers have had a keen interest in the genus *Maoristrophia* Allan 1947 because it appears to be a Lower Devonian brachiopod restricted geographically and having relatively unusual morphology. It has been known for a number of years from the New Zealand-Australia region and we had regarded it as an endemic form.

During a trip to the United States in late 1965 by Gill, we were afforded the opportunity to compare Australian specimens gathered by Gill with collections made from the Reefton beds of New Zealand by Boucot with the aid of Professor Robin Allan, Christchurch.

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Systematic Palaeontology

Phylum BRACHIOPODA

Superfamily Strophomenacea King

Genus **Maoristrophia** Allan 1947

(Pl. 39, fig. 1-15)

Type Species: *M. neozelanica* Allan 1947, p. 440, Pl. 61, fig. 1, 4, 8.

Diagnosis: Strophomenaceans with ventral fold and dorsal sulcus; ventral diductor scars bounded by muscle bounding ridges; dorsal cardinalia with small disjunct cardinal process lobes and broadly divergent inner socket ridges situated on ponderous brachiophore ridges.

Shell Shape: Small specimens are typically plano-convex in lateral profile. The pedicle valve is uniformally convex and very gently so throughout its length. Large specimens have brachial valves that are more convex anteriorly, maintaining a moderately thick body cavity. In outline the valves are subquadrate to shield-shaped and commonly are slightly wider than long until late growth stages. The hinge line is long and straight and is the point of maximum width in most specimens, but some larger specimens broaden out and attain a maximum width in the anterior half of the shell. Cardinal angles commonly are near 90° and are not known to develop mucronations. The pedicle valve bears a broad, low fold that widens appreciably anteriorly. Although low, it commonly is well marked by the presence of shallow, divergent furrows bounding it on either side and the medial structures commonly are developed even on small specimens where length is a centimetre or less. The brachiel valve bears a corresponding shallow median sulcus set off by a pair of radial elevations corresponding to the pair of ventral furrows.

EXTERNAL ORNAMENT: The radial ornament is costellate—the costellae increasing in number anteriorly principally by intercalation. Intercalation is more clear-cut on specimens of the pedicle valve, but in the brachial valve new costellae arise along the sides of interspaces. The costellae are especially well marked due to their elevation above the adjoining interspaces, giving them a somewhat angular appearance, but in cross-section they appear to be cusp-like elevations, rounded on their tops and separated by U-shaped interspaces. In the type species there are commonly 8 to 10 costellae in a space of 5 mm, 10 mm anterior to the hinge line, measured in the middle portion of a brachial valve.

The concentric ornament consists of a few well-marked growth lines at distant irregular intervals on some species, but these may not develop on others. Numerous very fine filae that give a reticulate pattern to the exterior are present on the type species.

POSTERIOR STRUCTURES: The ventral interarea is broad, low, flat and apsacline. The delthyrium is broad and apparently was mostly open, but there is a nearly flat, plate-like cover apically. The interarea of the brachial valve is long, ribbon-like, flat, and steeply hypercline.

INTERIOR OF PEDICLE VALVE: The interarea is extended dorsally along its medial portion as a pair of denticulate plates on either side of the hinge line. No dental lamellae are present, nor is there any supporting shell-thickening beneath the denticulate plates. In the apex of large specimens there is a low triangular or rounded elevation reminiscent of the ventral process in stropheodontids, but much less ponderous. The muscle field is broadly divergent and widens anterolaterally. Posterolaterally it is bounded by a pair of strong plate-like muscle bounding ridges that are commonly either slightly arcuate, convex posterolaterally, or are more or less straight posteriorly and bend inward somewhere near their midlength. The diductor scars are open anteriorly and merge imperceptibly with the interior of the valve. Most of the length of the diductor field on large specimens is bisected by a very faint, low myophragm which also bisects very poorly impressed adductor scars. Small specimens are pustulose, but large ones are relatively smooth on the interior.

INTERIOR OF BRACHIAL VALVE: The cardinal process consists of a small pair of lobes, cleft ventrally and directed posteriorly. The posterior face is V-shaped with the two lobes meeting at the apex of the valve. The areas lateral and anterior to the cardinal process lobes are thickened and extended posteriorly as a pair of thin, plate-like inner socket ridges enclosing the distal ends of broad, denticulate sockets that diverge anterolaterally and are shallow basally. Anteriorly the socket ridges merge with a pair of ponderous rounded brachiophore ridges in small specimens and triangular plate-like brachiophore ridges in larger ones. These bound the posterior adductors and extend along the inner edge of the sockets. The anterior edges of the sockets are elevated on large specimens forming step-like ridges on each.

In the larger specimens the anterior terminations of the thickened plates are drawn out into point-like processes. In small and medium sized specimens there commonly is a thick myophragm dividing the area of attachment of the adductor muscles, but the muscle impressions themselves are not differentiated. Also in most small and medium sized specimens the major portion of the internal surface is crenulated by the costellae and exhibits a papillose surface.

SHELL STRUCTURE: The shell is pseudopunctate.

GERONTIC FEATURES: Large specimens of both valves invariably develop a peripheral ridge slightly inside the valve margins and parallel to them. The remainder of the shell interior is also thickened and is not corrugated by the impress of the costellae. The margin of the valves outside of the peripheral ridge is radially grooved in an even pattern. Additional gerontic features appear in the brachial valve which develops a single pair of brachial plates that originate adjacent to the myophragm posteriorly and diverge for about ⅗ of their length anterolaterally, then bend to converge again toward the midline anteriorly. In their initial development, the brachial plates are low ridges, but are most elevated at their points of deflection. In their fullest development, they become elevated thickened areas on their medial sides. The largest specimens show some differentiation of the adductor muscle impressions with what appears to be a relatively large posterior adductor area laterally outside the brachial plates and small anterior adductors medially within the brachial plates, along their posterior third. The external sulcus which forms a medial ridge or fold internally is, on some shells, accentuated by the development of a myophragm that extends from the base of the cardinal process lobes into a median ridge-like elevation that persists to the peripheral ridge anteriorly.

Relations of the Genus *Maoristrophia*

MORPHOLOGIC IMPLICATIONS: *Maoristrophia* has previously been regarded as a stropheodontid (Allan 1947, p. 440; Williams 1953, p. 32; 1965, p. H 398) yet there are good grounds on which to challenge an assignment to the Stropheodontidae. The shape of the valves is not particularly diagnostic and would be no more incongruous for a stropheodontid than a strophomenid or a leptaenid, and a fold and sulcus is not particularly suggestive of any group. The type of ribbing is somewhat suggestive of that developed on *Holtedahlina* and perhaps more so than of a stropheodontid. The fine concentric growth lines are not unlike those seen on schuchertellids and on certain strophomenids such as *Rhipidomena* (Cooper 1956, Pl. 250, fig. 10).

In the pedicle valve the denticulation, lack of dental lamellae, configuration of the muscle field bounded by muscle bounding ridges at once suggests stropheodontid affinities for *Maoristrophia*. The principal differences of the ventral muscle scar of *Maoristrophia* from that of strophomenids are absence of flabellation, a tendency of the muscle bounding ridges to enclose the adductors anteriorly, and dental lamellae. Otherwise the ventral scar of strophomenids, such as *Öpikina* and *Strophomena* and others illustrated by Cooper (1956, Pl. 230-265) is not especially different.

In the brachial valve, on the other hand, the structures are not at all of the stropheodontid sort. The cardinal process is a small, cleft, V-shaped structure very much like that which is common in leptaenids and in strophomenids (Cooper 1956, Pl. 241, fig. 13; Pl. 243, fig. 25). Sockets are present in *Maoristrophia* as in strophomenids and leptaenids, but they are not developed in stropheodontids. The denticulate hinge line, which might suggest stropheodontid affinity, is seen in the brachial valve to be restricted to the sockets—a feature not uncommon outside the Stropheodontidae. It appears that the combination of inner socket ridges and brachiophore ridges that bound the sockets in *Maoristrophia* are constructed in a similar way to those developed in the Ordovician strophomenid *Öpikina* (see Cooper 1956, Pl. 236-245 and particularly fig. 30-32 of Pl. 244). Large specimens of *Maoristrophia* develop an inner pair of brachial plates similar to those found in strophomenids (Cooper 1956, Pl. 243, fig. 24-26) and in leptaenids (Cooper 1956, Pl. 225, fig. 4). On the other hand, both strophomenids and leptaenids bear two pairs of brachial ridges, both inner and outer, although the outer pair may be almost indiscernible. In the latter case the resulting configuration of the brachial plates is similar to that found in *Maoristrophia* (Cooper 1956, Pl. 245, fig. 26). The peripheral ridge of *Maoristrophia* is not particularly instructive since it occurs indiscriminably in leptaenids, strophomenids, and stropheodontids.

SUMMARY: It appears that we are faced with a paradoxical association of morphologic features. On the one hand, the pedicle valve of *Maoristrophia* fairly consistently indicates similarities to the stropheodontid brachiopods, while on the other hand the structure of the brachial valve is equally consistent in suggesting strophomenoid or leptaenoid affinities. It appears to the writers that among the two choices, the relations suggested by the morphology of the brachial valve are more likely to be meaningful for the origin of the genus. The brachial structures are more complicated; they show more similarities with strophomenids. Relationship with the strophomenids is more likely than with the leptaenids because the muscle field in the former is generally broad and open, while the muscle field of the latter appears to be more specialized in that it is confined commonly by muscle bounding ridges of a diagnostic pattern. Comparison of brachial valve structures supports this since the closest comparisons are with the strophomenid genus *Öpikina*.

Since the morphology of the two valves is inconsistent in suggesting relations, we cannot give *Maoristrophia* a firm family assignment; however, from the above discussion it appears that an assignment to the family Strophomenidae is more likely.

Assignment to the Strophomenidae creates problems because there is no obvious Silurian strophomenid to serve as the immediate ancestor of the genus; there is an obvious gap between *Maoristrophia* and morphologically similar Ordovician genera. On the other hand, leptaenids and stropheodontids are plentiful in Silurian horizons, but to date these families lack genera which could be accepted as ancestors.

Species assigned to *Maoristrophia*

Maoristrophia neozelanica Allan 1947, p. 440.

Maoristrophia banksi Gill 1952, p. 180, Pl. 36, fig. 1-8.

Gill proposed a second species, *M. careyi*, from the same locality and horizon as *M. banksi*. The differences in shape, which were thought to distinguish the two species, probably are due to deformation (Talent 1964), but the Tasmanian material was not re-studied by the writers.

Maoristrophia keblei Gill 1952, p. 182, Pl. 36, fig. 9-11.

Leptostrophia (?) *carinata* Borisyak 1955, p. 34, Pl. 3, fig. 7, 8.

This species was re-described by Kaplum and his illustrations (1961, Pl. 9, fig. 1-6) portray the generic features.

Occurrence of *Maoristrophia* in New Zealand

LOCALITY: *Maoristrophia* is found in the Reefton beds at Lankey Ck, Reefton, South I., New Zealand (Allan 1947, p. 436; Suggate 1957).

AGE: The presence of *Acrospirifer coxi* Allan (1947, p. 447; 1935, Pl. 2, fig. 1-3, Pl. 3, fig. 1, 2) is good evidence of Early Emsian age for the Reefton beds because it is very close to the widely distributed Lower Emsian fossil *Acrospirifer hercyniae*. The presence of *Pleurothyrella venusta* Boucot, Caster, Ives, & Talent (1963, p. 100) is in line with a Lower Emsian assignment since *Pleurothyrella* is known only in beds that appear to be Lower Emsian elsewhere. *Reeftonia* is known from beds thought to be of Early Emsian age in Victoria represented by the species *Reeftonia alpha* (Gill); see Talent 1963, p. 57. *Maoristrophia*, as outlined below is known elsewhere only from rocks of Early Devonian age.

Occurrence of *Maoristrophia* in Victoria

LILYDALE DISTRICT: The Lower Devonian marine strata of the Lilydale district are the youngest in the sequence of Palaeozoic rocks forming the bedrock and occupy the core of the synclinorium. All the Yering Group is Lower Devonian and comprises the following formations in stratigraphic order (Gill 1965):

Cave Hill Conglomerate	100 ft thick
Lilydale Limestone	700 ft thick
Ruddock Siltstone	8,000 ft thick

Maoristrophia has been found only in the Ruddock Siltstone and is confined to the upper part of it, viz. (1) N. of Lilydale, (2) Hull Rd, Lilydale, and (3) Hull Rd, Mooroolbark. The third locality is the youngest, and the first is probably the oldest. The localities have been mapped (Gill 1940) and all are Upper Yeringian (Gill 1945a). *M. keblei* is the species recorded (Gill 1949, 1950, 1952).

North of Lilydale is a quarry exposing mostly siltstone, but also some bands of sandstone in which most of the fossils occur. *'Chonetes'* of the *cresswelli-robustus* group occur at that locality as does *Acrospirifer lilydalensis*. There are also strophomenids characteristic of the Upper Yeringian. The same fossils occur at the other two localities which are almost entirely in the silt facies. The same species occur at Mooroolbark as at Lilydale but appear to be slightly younger.

The strata at Hull Rd, Lilydale, occur a few hundred feet stratigraphically under the Lilydale Limestone, while those at Hull Rd, Mooroolbark, occur on about the same strike as the limestone. The latter are therefore definitely younger.

Megakozlowskiella cooperi occurs in the Lilydale Limestone, and *'Hipparionyx'* aff. *minor* occurs at the two Hull Rd localities. *Trimerus* is the commonest trilobite, but *Scutellum* (*Scabriscutellum*) sp. also occurs. This subgenus was described from the Bohemian sequence and is previously unreported in Victoria. The beds are considered to be Siegenian in age, but the highest of the strata could be Early Emsian. This, however, is just an estimate.

KILLARA DISTRICT: The Yering Group is repeated E. of Lilydale in the Killara district. Syme's Quarry, Syme's Tunnel, and Syme's Homestead are three highly fossiliferous sites ranged from S. to N. along the strike of a formation of siltstone. The localities have been mapped (Gill 1945b).

Many index fossils found in the Upper Yeringian at Lilydale are found at Killara, including *Acrospirifer lilydalensis, 'Chonetes'* of the *cresswelli-robustus* group, and *Megakozlowskiella cooperi*. As at Hull Rd, Lilydale, some land plants have been included in the marine sequence. At Killara, pelagic forms such as *Acanthopyge australis* are found among the trilobites (Gill 1939, 1951). Fragments of the carpoid *Rutroclypeus* (limited elsewhere to the Lower Devonian of Australia and Germany) occur at Syme's Homestead (see Gill & Caster 1960). An unusual occurrence is the graptolite *Desmograptus*. The containing siltstone is Lower

Devonian, and of the same age as the strata referred to in the Upper Yeringian at Lilydale.

HEATHCOTE DISTRICT: *Maoristrophia keblei* Gill (1952) has been recognized in the Mt Ida formation (but see Talent 1964) in the Heathcote district of Victoria, Australia (Thomas 1937, 1941). The site is Geological Survey of Victoria locality 54, Parish of Redcastle, and has been published by the Survey in a map of the parish. Talent (1964) has recorded *Maoristrophia* from the Mt Ida Formation (Pl. 7, fig. 3-4; Pl. 13, fig. 7; p. 30) and the McIvor Formation (p. 30). According to Talent (1965) the Mt Ida Formation is of Late Gedinnian age. N. W. Schleiger and J. A. Talent (pers. comm.) have collected an undescribed species of *Maoristrophia* from beds equivalent to the base of the McIvor Formation from an horizon judged by them to be probably of late Ludlow age.

Occurrence of *Maoristrophia* in Tasmania

Gill (1952) described *M. careyi* and *M. banksi* from locality 16, a trench on the right bank of the Little Henty R. at Zeehan in W. Tasmania. The locality has been mapped and the co-ordinates given by Gill and Banks (1950, Pl. 2 and Appendix B). The formation is the Lower Devonian Bell Shale with a fauna equivalent to that of the Lower Yeringian in the Lilydale district of central Victoria.

Occurrence of *Maoristrophia* in Kazakhstan

LOCALITY AND AGE: The terrigenous facies of the Kazakhstan Devonian has been summarized by N. L. Bublitschenko (1960). According to Bublitschenko, Lower Devonian beds are exposed N. of L. Balkhash in the Dshungaro-Balkhash region. Bublitschenko (1960, p. 434) reports the presence of *Maoristrophia carinata* (as *Leptostrophia carinata*) in the Lower Sardshal beds with *Acrospirifer* of the *murchisoni* type and *Leptocoelia*. The writers would assign the Lower Sardshal beds to the Siegenian.

Appendix of Localities

USNM 11002: Lankeys Ck; loose block with *Reeftonia* about ¾ mile N. of Highway No. 7. Also loose blocks on E. slope of valley, Reefton Subdivision, New Zealand.

USNM 11725: Weathered argillite from creek bed, white patch samples from another argillite boulder in Lankeys Ck above the junction with Stony Ck also presumably from the argillites which outcrop just upstream from the main limestone; Reefton Subdivision, New Zealand.

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Explanation of Plate

PLATE 39

Fig. 1-6—*Maoristrophia neozelanica* Allan, Reefton beds, Lankey Ck, New Zealand. 1-2—Internal mould of brachial valve and rubber impressions × 1·25, USNM 153135, USNM loc. 1102. 3—Rubber impression of external mould of brachial valve × 1·25, USNM 153136, rubber impression of counterpart of specimen in fig. 1, USNM loc. 11002. 4—Internal mould of pedicle valve × 1·5, USNM 153137, USNM loc. 11725. 5-6—Internal mould of brachial valve and rubber impression × 2, USNM 153138, USNM loc. 11002.

Fig. 7-15—*Maoristrophia keblei* Gill, Ruddock Siltstone, Hull Rd, Mooroolbark, Lilydale district, Victoria. 7—Internal mould of pedicle valve × 3, NMV No. P24662. 8, 9—Internal mould of brachial valve and rubber impression × 3, NMV No. P24663. 11—Internal mould of pedicle valve × 2, NMV No. P24664; rubber impression in fig. 10 is from the counterpart of this specimen, NMV No. P24665. 12—Internal mould of pedicle valve × 3, NMV No. P24666. 13-14—Internal mould of brachial valve and rubber impression × 4, NMV No. P24667. 15—External mould of brachial valve × 3, NMV No. P24668.