

## THE DOUBLE CARDINAL PROCESS IN THE OLDEST STROPHOMENIDS

BY

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**Abstract:** Some of the oldest Strophomenidae with bifid cardinal processes are described. It is suggested that at least in some of them, the bifid cardinal processes were formed by partial neoteny. The "chilidal plates" of the Sowerbyellinae are regarded as analogous with the socket plates of the Strophomenidae. Further ontogenetical studies are necessary to tell if the family Strophomenidae is monophyletic.

### Introduction

The classification of the strophomenid brachiopods is based mainly on the development of the cardinal processes (cf. WILLIAMS 1953a). The Plectambonitidae have simple, orthoid, cardinal processes, the Leptestiidae have complex ones, and the Strophomenacea have bifid cardinal processes.

The author's studies of Norwegian Middle Ordovician Strophomenids seemed to indicate the possibility that the development of the bifid cardinal processes in the Strophomenacea was not monophyletic. (cf. SPJELDNÆS 1957, pp. 194—196). It seemed therefore desirable to study the development of the cardinal processes in the oldest members of the Strophomenacea, in order to see if these species might throw some light on this important problem. A review of the literature showed that relatively few Lower Ordovician Strophomenidae are known (the Christianiidae were described by SPJELDNÆS 1957). The genus *Kirkina* SALMON 1942, with the only species *K. milliardensis*

SALMON is among the oldest known, but it is not well known, and no material of this species was at the author's disposal. *Rafinesquina*(?) *macallumi* REED 1917 is present in the author's collections, but the age of this species is not definitely known. The present note is therefore mainly based on some specimens of *Rafinesquina*(?) *llandeiloensis* (DAVIDSON), from Llan Mill, near Narberth. All the specimens are found in one slab, which was borrowed from the Geological Survey and Museum, London.

This note is an appendix to the author's studies on the Middle Ordovician Strophomenids of the Oslo Region (SPJELDNÆS, 1957). He is deeply indebted to prof. L. Størmer and prof. Alwyn Williams, Belfast, for inspiring discussions in connection with the problems dealt with in this paper. Furthermore, the author wishes to express his thanks to the Faculty Photographer, Miss B. Mauritz, who has taken the photographs.

### The oldest Strophomenacea

Genus *Kirkina* SALMON 1942.

*Type species*: *K. milliardensis* SALMON 1942 (pp. 599—600, text-fig. 7, pl. 87, figs. 34—35. Cf. also COOPER 1956, pp. 866, 160.)

*Remarks*: This genus is not well known. The only species is reported to have undifferentiated sculpture and very small pseudopunctae, which was supposed to separate it from *Rafinesquina*. Only the dorsal interior is known from the type species, and it does not differ from that of *Rafinesquina* in any important features. Until more material has been studied, it is difficult to estimate the validity of this genus, it might be only a subgenus of *Rafinesquina*, such as *Kjaerina* and *Hedstroemina*.

The stratigraphical range of the type species was unknown to SALMON, but according to HINTZE (1952, pp. 22—23) it is found in several localities in zone "N" in Utah and Nevada. ROSS (1951, p. 33) records *Didymograptus bifidus* from zone "M" in the same area. COOPER (1956, pp. 160, 866) includes these beds in the Lehman formation of the Whiterock Stage. The upper part of this stage probably corresponds to the upper part of the Llandvirn, or the lowest Llandeilo of Europe.

*Rafinesquina(?) macallumi* REED 1917.

Pl. 1, figs. 8—9.

1917 *Rafinesquina expansa* (Sow.) var. nov. *macallumi* —

REED, pp. 865—866, pl. 11, figs. 17—20.

*Age and distribution:* REED recorded this species from a number of localities in the Girvan District, all from the Stinchar Limestone (s. l.). Only the exteriors were known to him. The present material comes from Minuntion, in the *confinis*-grits, and probably at the same horizon at Bougang. The age of the beds are not known exactly, but they are below the Stinchar Limestone proper, which is succeeded by the Didymograptus Shale, with graptolites possibly belonging to the *Nemagraptus gracilis* zone. (According to PRINGLE 1948, pp. 18—20, this graptolite fauna perhaps has a high position in the Glenkiln Shales. The presence of *Didymograptus superstes* and *Glossograptus hincksi* indicate, however, that the fauna is intermediate between the *gracilis* and the *teretiusculus* zones.).

The trilobites found by the author together with *R.(?) macallumi* give no direct information on the stratigraphy. Among the brachiopods, the author found *Sowerbyella* cf. *llandeiloensis*. This species seems to indicate an Upper Llandvirn or Lower Llandeilo age of the beds, but it might easily be confused with young specimens of other species. The age of the *confinis*-grits are therefore not definitively determined, but it is probably below the Caradoc.

*Description:* The size, outline and sculpture of the present specimens are identical with those figured by REED. The sculpture is differentiated, with 3—7 striae between each rib. The new ribs are all formed along the same concentric line, such as in *Oslomena* (cf. SPJELD-NÆS 1957, p. 164). The valves are moderately convex, and without geniculation. In some large specimens, the margin is abruptly deflected.

The dorsal interior is similar to that of *Rafinesquina(?) llandeiloensis*, except that the socket plates are less defined, and that the cardinal processes are longer and thinner. These features might be due to the different size of the specimens.

A young dorsal interior from Bougang showed some other features, having well defined socket plates, no anchor-shaped platform, and semiparallel cardinal processes. Unfortunately the specimen is slightly

distorted, so that it is unsymmetrical. It seems as if the cardinal processes are placed on both sides of a short, deep cavity. This specimen resembles the figured specimens (pl. 1, figs. 2, 3, 5) of the young valves of *R.(?) llandeiloensis*.

The ventral interior is also like that of *R.(?) llandeiloensis*, with bundles of fine septa instead of distinct muscle impressions. The teeth are larger in the present species, possibly because the specimens are larger, and have no marginal thickening.

*Remarks:* As mentioned above, the difference between this species and *R.(?) llandeiloensis* is rather small, only the sculpture is different. It is therefore possible that further studies on more material will show that *macallumi* is only a subspecies of *llandeiloensis*.

*Rafinesquina(?) llandeiloensis* (DAVIDSON 1866—71).

Pl. 1, figs. 1—7.

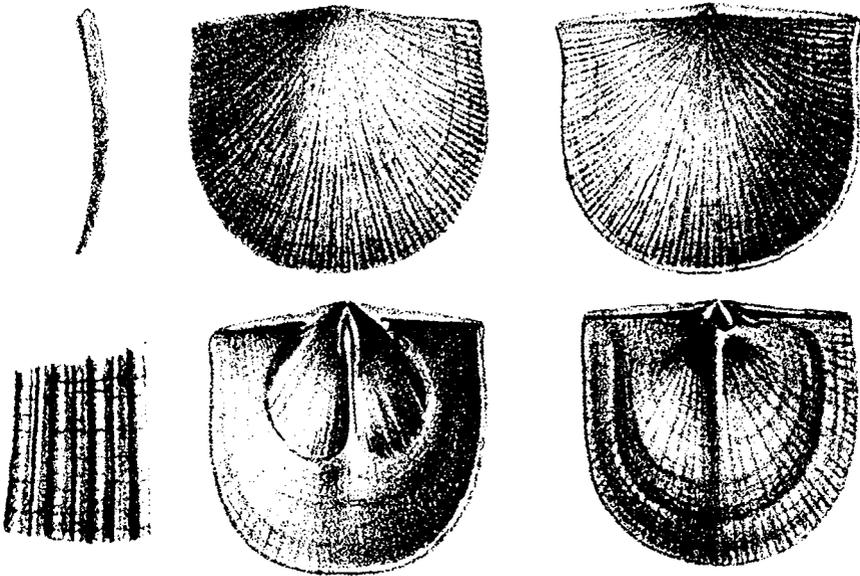
1866—71 *Strophomena compressa* (Sow.) var. *llandeiloensis* —  
DAVIDSON, pp. 316—317, pl. 46, figs. 11—14.

1953 *Rafinesquina llandeiloensis* (DAV.) — WILLIAMS, pp. 184—193  
(not figured).

*Age and distribution:* This species is recorded from several horizons and localities in the Llandeilo District by WILLIAMS (1953, pp. 184—193), ranging from the Ffairfach Group (Upper Llandvirn) to the Lower Llandeilo. Judging from the associated fauna (*Marrolithus inflatus incipiens* WILLIAMS, *Flexicalymene cambrensis*, *Horderleyella* sp., *Dalmanella* cf. *parva*, *Tallinnella complicata* and other ostracods, *Sowerbyella antiquata llandeiloensis* and bryozoans) the present material comes from the zone of *Marrolithus inflatus incipiens*, the uppermost part of the Llandvirn. The material comes from Llan Mill, near Narberth, Carmarthenshire, which is the type locality for *R.(?) llandeiloensis*. The specimens are all found on one slab, which belongs to the Geological Survey and Museum, London. About 20 interiors are found on the slab, more or less fragmentary.

*Description:* The sculpture is variably differentiated. In some specimens only every second or third rib is slightly stronger than the others, and in others there are from two to eight striae between each rib.

The valves are moderately convex, the dorsal one geniculating



Textfig. 1. *Rafinesquina* (?) *llandeiloensis* (DAVIDSON). The original figures from DAVIDSON (1866—71) pl. 46, figs. 11, 13, 14. The specimens are from Llan Mill, Carmarthenshire. About  $1\frac{1}{2}$  times the original size.

dorsally in large specimens. The ventral valves are generally somewhat more convex than the dorsal ones, and have a marginal thickening. The areas are narrow, the delthyrium and notothyrium wide. A small, strongly curved, thin pseudodeltidium is present in large specimens, and a low chilidium is always present even in the larval valves.

The ventral interior shows slightly developed muscle impressions which seem to consist of bundles of fine septa, resembling those of *Gorudia* and *Paleostrophomena*. Only in one of the specimens present are the muscle impressions complete, such as in that figured by DAVIDSON (textfig. 1.). The teeth plates are strong, and continuous with the elevated edges of the delthyrium (*e*, pl. 1, fig. 1). Even small valves are generally very thick, and the marginal deposits of calcareous tissue are conspicuous (*mt.*, pl. 1, fig. 1).

The dorsal interior of adult specimens shows two long, diverging cardinal processes resting on a high, anchor-shaped platform. The muscle attachment surfaces are inclined steeply towards the noto-

thyrium. The socket plates, forming the lateral branches of the "anchor", are strongly developed. The sockets are very shallow, scarcely discernable except in young specimens (pl. 1, fig. 2, *sc*).

On the anterior side of the socket plates, there are in some cases a number (3—4) of crenulations, resembling those found in the earliest Stropheodontids. They are, however, not found in all specimens, and might in some cases be casts of the coarse-grained matrix. In the figured specimen (pl. 1, fig. 4, *cr*) they are very strong. Such "pseudocrenulations" of the teeth and socket plates are known from a number of Strophomenid species (SPJELDNÆS 1957, pp. 20—32, 190—191), and do not necessarily mean that this species belongs to the Stropheodontidae, even if the resemblance with *Stropheodonta* (*Eostropheodonta*) *williamsi* SPJELDNÆS (1957, pl. 12, figs. 3—5), the oldest real Stropheodontid known at present, is striking.

The chilidium is low, but the chilidal plates (pl. 1, fig. 2 *ch*) are high, thin and sharply delimited from the socket plates. In younger Strophomenid species, it is generally ancylosed to the socket plates and can only be distinguished by its histological structure. (cf. SPJELDNÆS 1957, textfig. 40—41).

The young dorsal interiors show additional features (pl. 1, figs. 2, 3, 5). The notothyrial platform is absent, the cardinal processes are resting directly on the notothyrial floor, and the muscle attachment surfaces are parallel with the interior surface of the valves. A distinct, horizontal slit is found between the cardinal processes (*sl*, pl. 1, fig. 2). The socket plates are distinctly developed, and the cardinal processes are fused to their proximal ends. In the smallest specimens, (pl. 1, fig. 5) they can scarcely be discriminated from them. The chilidium is comparatively better developed in the small specimens.

The trend outlined in the larval development of the valves of *R.* (?) *llandeiloensis* seems to be the same as that found in *Christiania holtedahli* and *Kjerulfina foliovalve* described from the Middle Ordovician of the Oslo Region (SPJELDNÆS 1957, pp. 51—52, 117—120, 155—156).

The sockets and the area just outside them are covered with tissue with very large pseudopuncta (in the adult specimens). In old specimens this tissue is concentrated at the socket plates and perhaps the "pseudocrenulations" originated from these coarse pseudopuncta. This concentration of large pseudopuncta is found also in the

*Rafinesquina sardesoni*-group of SALMON (1942, p. 572, textfig. 5 b). In *Oepikina*, the pseudopuncta are considerably larger in the central part of the valve, near the hinge line, than in the marginal parts. In this case, however, the large pseudopuncta are not restricted to the sockets and the area just outside them, such as in the *Rafinesquina*-species in question.

Neither in the adults nor in the larval valves are there any traces of a medial cardinal process.

*Oslomena* (?) sp.

Pl. 1, fig. 10.

1917 *Rafinesquina (Playfairia) semiglobosina* (DAVIDSON) parte. — REED, pp. 869—870, non pl. 12, figs. 13—20.

In the material from Minuntion, Girvan District, Scotland, there is a ventral interior belonging to this species. The valve is strongly convex, with a very slight geniculation, and with flat cardinal angles.

The interior has small, but well defined muscle impressions, which resemble those found in the genus *Oslomena* SPJELDNÆS (1957, pp. 161, 164, textfig. 34, p. 141.), and is different from those of *Rafinesquina* both in size and shape.

This species is mentioned here because it shows that the *Oslomena*-type of Strophomenids occurs together with the *Rafinesquina*-type in beds of this age.

TAXONOMY

It is outside the scope of this paper to discuss the taxonomy of the earliest Strophomenidae, and therefore it is only pointed out that the earliest species (*llandeiloensis* and *macallumi*) probably do not belong to *Rafinesquina* as it is defined now (SALMON 1942, COOPER 1956). It is restricted to the Upper Ordovician and the uppermost part of the Middle Ordovician, and the species described here are from the lowest part of the Middle Ordovician. According to BANCROFT (1929, p. 41—42) a similar species from the Hoar Edge Grit in Shropshire belongs to *Rafinesquina*, and not to *Kjaerina* or *Hedstroemina*. The genus *Kirkina* SALMON is unfortunately not well known, and further studies might show that the present species can be referred to it.

*Macrocoelia plebeia* COOPER (1956, p. 899, pl. 121G, 233B) is also similar in some respects, but both *plebeia* and the species described here differ considerably from the rest of the species in that genus. At present it seems convenient to refer all these species to *Rafinesquina* (?).

### The cardinal processes

From what is described above, and from the results obtained by SPJELD NÆS (1957, pp. 23—26, 50—52, 194—196) the following conclusions might be summarized:

1) No signs of a trifid, Sowerbyellin cardinal process is observed in the ontogeny of the typical Strophomenidae.

2) In *Oepikina* and some species of *Christiania*, a modification of the Sowerbyellin cardinal process is found in the adults.

3) In all larval specimens belonging to the Strophomenidae there is a distinct groove between the cardinal processes. This groove is supposed to be the pedicle groove.

4) A striking difference is found between the ontogenetic and the phylogenetic development of the cardinal processes in *Christiania*.

The ontogenetic development of all known protrematous brachiopods seems to indicate that the pedicle was impressed in both valves in the youngest larval stages, and was later transferred to the ventral valve only. In most brachiopod groups (Orthids, Clitambonitids, Plectambonitids) the cardinal processes developed after the pedicle was transferred to the ventral valve, or after it was reduced or lost. In the Strophomenidae, the bifid cardinal processes were probably formed when the pedicle was still impressed in the dorsal valve also, and a median cardinal process could not be formed.

This type of development seems to be an example of partial neoteny (merostasis), since one larval feature (the pedicle impressed in the dorsal valve) is retained until a comparatively late stage in ontogeny. STØRMER (1942, pp. 152—157) used this principle in his studies of the phylogeny of the trilobites, and De BEER (1940) indicated that

it is genotypical changes of this kind which are responsible for the formation of higher taxonomic units (above genus).

In comparing the bifid and the trifid cardinal processes, there is also another problem which can be pointed out. In the Sowerbyellinae the lateral elements of the cardinal processes are regarded to be a reduced chilidium ("chilidal plates"). If this was true, these elements can not be analogous with the bifid cardinal processes. In all Strophomenidae sectioned by the author, the chilidium is histologically different from the rest of the valve (cf. SPJELDØES 1957, textfigs. 40—41), and this histological difference is not found in *Sowerbyella*. This indicates that the so called "chilidal plates" are analogous with the socket plates, and that the real chilidium is completely or almost completely reduced in *Sowerbyella*. This is also supported by the fact that a trifid cardinal process is found in at least one Leptestiniid with a chilidium (cf. *Ptychoglyptus valdari* SPJELDØES 1957, textfig. 17).

In this species there is no connection between the chilidium and the trifid cardinal process. Since it is highly unlikely that two different types of trifid cardinal processes occur in the Leptestiniids, it seems natural to conclude that the "chilidal plates" in the Sowerbyellinae (and some Leptestiniinae) are analogous with the cardinal processes in the Strophomenidae, both being formed from the proximal ends of the socket plates.

In many highly developed Strophomenids, it is difficult to discriminate between the socket plates and the chilidium without a thin section because they are ancylosed. In the primitive species, such as *Rafinesquina*(?) *llandeiloensis*, the two different elements are clearly discernible (Pl. 1, figs. 2, 4, 5).

The question of the origin of the family Strophomenidae is still unsolved. *Rafinesquina*(?) *llandeiloensis* belongs to the *Kjaerina-Hedstroemina-Rafinesquina-Stropheodonta*-lineage (cf. SPJELDØES 1957, pp. 194—196, textfig. 42). In the other Strophomenid lineage, that of *Oepikina*, the Sowerbyellin cardinal process is still present, but the lateral elements are much larger than the medial one. This might be interpreted in two ways.

1) The retention of the passage of the pedicle to the ventral valve might have been less prominent in this lineage, leaving time for the development of a central cardinal process also. In this case the family

Strophomenidae might be monophyletic, since both lineages have the same feature (retention of the pedicle movement), even if it is of different degree in each of them.

2) The *Oepikina*-lineage of development of the cardinal process might also be interpreted as a simple development from the Sowerbyellin type, by more rapid growth of the lateral elements of the cardinal processes. In this case the two lineages are not at all related, and might have their origin in two different Plectambonitid groups.

In order to solve this problem, it is necessary to study a large number of larval valves of *Oepikina* and related forms. Until this is done, it is not possible to tell definitely if the family Strophomenidae is monophyletic, or if it is polyphyletic.

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## EXPLANATION TO PLATE 1

- Figs. 1—7. *Rafinesquina*(?) *llandeiloensis* (DAV.). All specimens from the zone of *Marrolithus inflatus incipiens* at Llan Mill, near Narberth, Carmarthenshire. *Fig. 1.* Ventral interior, 5x. *Figs. 2, 3, 5.* Larval dorsal valves. (*Figs. 2, 5,* 20x, *fig. 3,* 12x.) *Fig. 6.* Small, but well calcified ventral interior. Note absence of distinct muscle impressions, and marginal thickening. 3.5x. *Fig. 7.* Complete dorsal interior showing geniculation. 1.7x.
- Figs. 8—9. *Rafinesquina* (?) *macallumi* REED. From the *confinis*-grits at Minuntion, Stinchar Valley, Girvan District, Scotland. *Fig. 8.* Fragmentary ventral interior. 3x, *Fig. 9.* Fragmentary dorsal interior. 3x.
- Fig. 10.* *Oslomena* (?) sp. Cast of ventral interior, 1.7x. Loc. and hor. as in figs. 8—9.

All figs. except 10. are from latex impressions of casts. Figs. 1, 2, 3, 6, 7, 10 are whitened with ammonium chloride.

The specimens figured on figs. 1—7 belong to Geological Survey and Museum, London, no. 85415, the others belong to Paleontological Museum, Oslo.

Abbreviations: *Ch* = Chilidial plates, *Cp* = Cardinal processes, *Cr* = Pseudocrenulations on the socket plates. *E* = Elevated ridges of socket plates. *Mt* = Marginal thickening of the valves. *Pd* = Pseudodeltidium. *Sc* = Sockets. *Sl* = Slit between the cardinal processes. *Sp.* = Socket plates.

