FORMATION AND FUNCTION OF PROTEGULAR PITTING IN SOME NORTH AMERICAN ACROTRETID BRACHIOPODS

by PETER H. VON BITTER *and* ROLF LUDVIGSEN

ABSTRACT. SEM examination of well-preserved protegula of acrotretid brachiopods from the Ordovician, Silurian, and Lower and Middle Devonian of Ontario, the Lower Devonian of the Yukon Territory, and the Silurian of Oklahoma, has led to the formulation of a modified selective resorption model for the formation of protegular pits in this group. This model contrasts with the bubble raft model of Biernat and Williams (1970) and proposes that the development of protegular pits is due to resorption by the mantle, with the complexity, degree, and configuration of pitting dependent on the length of the larval stage. Protegular pitting may be terminated at any of a number of stages and is thought to be related to the necessity for the larval stage on one hand to develop a protective rigid shell and on the other to remain buoyant. Thus the resorption of calcium phosphate is probably a weight-controlling mechanism during the planktic stage of the larval acrotretid—a mechanism directly comparable to the use of frets or of a Gitterwerk in airframe construction. The necessity for juvenile acrotretid brachiopods to remain afloat is probably related to unknown environmental factors that made it desirable to postpone settling.

The valve previously considered to be the pedicle valve of *Opsiconidion arcticon* was misassigned. Pedicle valves of species of *Opsiconidion* are now known to be highly conical, to bear well-defined pedicle openings at the apex, and to lack muscle scars. They bear conical protegula with ultrastructure identical to that of the brachial valves.

INARTICULATE brachiopods of the family Acrotretidae bear protegula with a distinctive ultrastructure of minute circular pits (Biernat and Williams 1970; Poulsen 1971; Ludvigsen 1974). Two explanations have been presented for the origin and formation of this ultrastructure. Biernat and Williams (1970) interpreted the pits to be the moulds of a vesicular periostracum (Bubble Raft Model) whereas Ludvigsen (1974) attributed them to resorption by the mantle (Selective Resorption Model). Biernat and Williams (1970, p. 493, pl. 98, figs. 1–3) based their model on the type of protegular ultrastructure shown by *Torynelasma* sp. from the Arenig of Poland, which consists of coarse pits with a size range of 2·0–4·5 μm separated from one another by level areas which bear numerous fine pits about 0·35 μm in diameter. [N.B. In order that our references to the plates of Biernat and Williams (1970) make sense it should be noted that when that publication was printed two of the plate numbers were inadvertently transposed. To correct this: Biernat and Williams plate 98 should read plate 101; Biernat and Williams plate 101 should read plate 98.] Ludvigsen (1974) based his model on the protegular ultrastructure of *Opsiconidion arcticon* Ludvigsen from the Emsian of the Yukon Territory, which consists of shallow, flat-bottomed, and circular pits within a single size range (1·35–3·15 μm). These pits are located at different levels within the protegulum and most show overlapping and cross-cutting relationships to adjoining pits.

Newly acquired material of *O. arcticon* from the Devonian of Ontario displays protegular pitting that appears to be intermediate between the non-cross-cutting

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type described by Biernat and Williams (1970) and the cross-cutting pitting described by Ludvigsen (1974). Such apparent gradation in pitting morphology suggests that a single process may be sufficient to explain the relationship of the pits in the above two models and, in this paper, we present evidence in support of an alternate modified selective resorption model for the formation of protegular pits in acrotretid brachiopods. According to this model, the distinct micromorphology of the protegular surface is not interpreted as a result of discrete types of pit formation, but is attributed to different times of termination of a continuous pitting sequence.

MATERIALS AND METHODS

O. arcticon was recovered from twenty-one samples of Lower and Middle Devonian rocks of Ontario previously studied for conodonts by Telford *et al.* (1977). Eleven additional samples containing *O. arcticon*, also from the Devonian of Ontario, were made available by Dr. T. T. Uyeno of the Geological Survey of Canada. We have also examined topotype material of *O. arcticon* from the Lower Devonian of Yukon Territory; *Opsiconidion* spp. from the Cobourg Formation (Ordovician) at Colborne, Ontario and from the Rochester Formation (Silurian) at Grimsby, Ontario; and *Artiotreta parva* Ireland and *Acrotretella siluriana* Ireland from the Chimney Hill Limestone (Silurian) of Oklahoma.

All illustrated specimens were recovered by standard micropalaeontological acid and heavy liquid techniques used for the recovery of phosphatic microfossils. The inarticulate brachiopod valves were mounted on standard micropalaeontological slides. Selected specimens were washed in a distilled water bath, mounted on aluminium stubs using 'wax W' (Finch 1974), then gold-coated and examined and photographed with a Cambridge Scanning Electron Microscope.

The stratigraphical distribution of specimens studied, together with details of their depository, is indicated in the appendix.

SYSTEMATIC PALAEONTOLOGY

Class INARTICULATA Huxley, 1869
Order ACROTRETIDA Kuhn, 1949
Suborder ACROTRETIDINA Kuhn, 1949
Superfamily ACROTRETACEA Schuchert, 1893
Family ACROTRETIDAE Schuchert, 1893
Subfamily TORYNELASMATINAE Rowell, 1965
Genus OPSICONIDION Ludvigsen, 1974

Type species. Opsiconidion arcticon Ludvigsen, 1974, p. 143, by original designation.

Revised diagnosis. Minute torynelasmatinids with a nearly circular, flat brachial valve which has a very shallow, anteriorly widening furrow. The pedicle valve is highly conical and bears a well-defined pedicle opening at the apex. The dorsal interior is dominated by a triangular, blade-like median septum flanked by a pair of cardinal scars. The dorsal protegulum is large and prominent and carries a U-shaped lateral swelling. The ventral protegulum is similarly large, conical, and has a foramen at its apex. Pedicle valve interiors appear to be smooth and to lack muscle scars. Fine growth lines occur on the exterior of both valves. The protegulum of both valves is ornamented by a characteristic step-like, pitted pattern of one or more size ranges.

Remarks. The reassignment of this genus to the subfamily Torynelasmatinae is based on the discovery that the single specimen identified by Ludvigsen (1974) as the pedicle valve of *O. arcticon* does not belong to this species nor to this genus. On re-examination of the Yukon residues, a number of high, conical valves bearing protegular pitting were found, identical to that on the brachial valves, and these are now identified as the pedicle valves of *O. arcticon*. Because the pedicle valves were not noted previously a brief description of these valves from the Lower Devonian of the Yukon Territory is provided here:

Pedicle valve acutely conical, exterior growth rings well developed, spaced at approximately 20–40 μm (Pl. 91, figs. 10, 11). Foramen small (approximately 120 μm in one well-preserved specimen (Pl. 91, fig. 11)) and surrounded by an unequally conical protegulum (Pl. 91, figs. 10, 11) which has an inner height of 130 μm and an outer height of 200 μm. Protegular ultrastructure consists of shallow, circular cross-cutting pits of a single general size (Pl. 91, fig. 12) identical to those shown for the brachial valve by Ludvigsen (1974). Interior of available pedicle valves smooth and lacking any internal structures.

Opsiconidion arcticon Ludvigsen, 1974

Plate 90, figs. 1–12; Plate 91, figs. 1–12

1974 *Opsiconidion arcticon* Ludvigsen, p. 133, fig. 4-1, 2, 3, fig. 5-1, 2, 3, 4, 8 (only).

Remarks. The Ontario specimens of this species differ from those from the Yukon Territory primarily in possessing two rather than a single set of cross-cutting protegular pits in both dorsal and brachial valves, and in having a dorsal protegulum that is most commonly 180 μm in diameter. The Yukon material has a dorsal protegulum that is usually slightly smaller (170 μm) but attains a larger maximum size (205 μm) than in Ontario material (195 μm) (text-fig. 1). Similarly the conical ventral protegulum, like the dorsal protegulum, appears to be slightly larger than that found on the Yukon specimens. Finally, the dorsal valves of *O. arcticon* from Ontario are generally smaller than those studied by Ludvigsen (1974) from the Yukon Territory (text-fig. 2).

Material. Figured specimens ROM 37373 to ROM 37381 inclusive; unfigured specimens ROM 37388 to ROM 37406 inclusive, ROM 37411, ROM 37412, ROM 37417, ROM 37418, ROM 37419; GSC 32055 to GSC 32058 inclusive, GSC 32060; GSC 59034 to GSC 59043 inclusive.

Distribution. Lower to Middle Devonian of Ontario, Canada; Lower Devonian of the Yukon Territory, Canada.

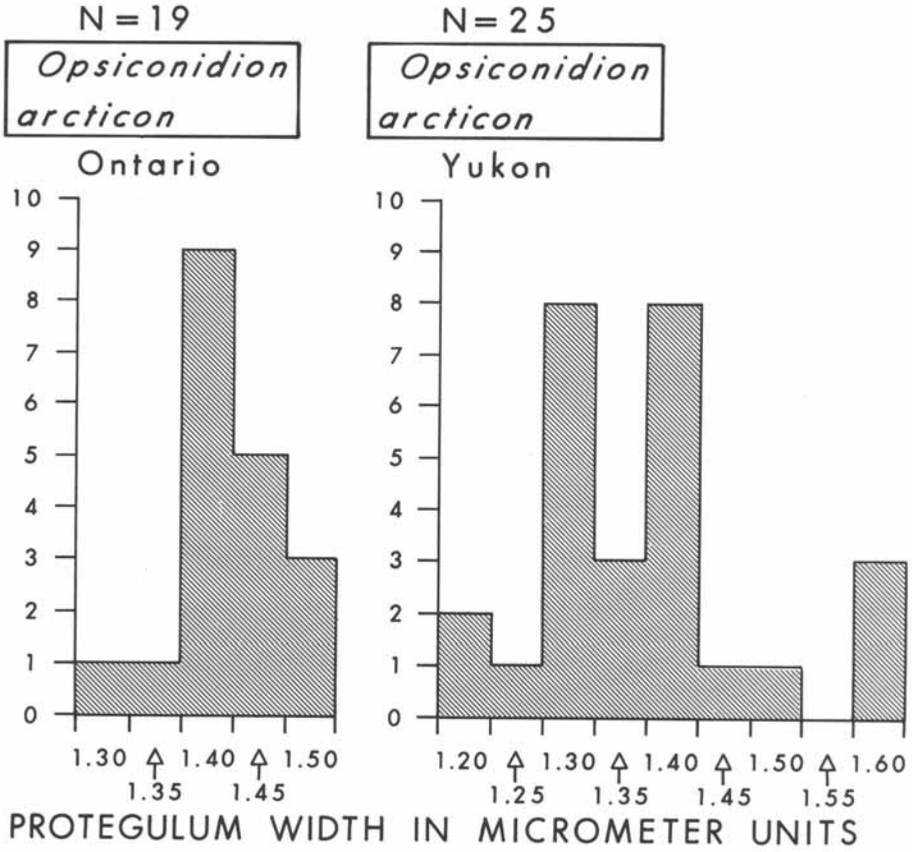
Opsiconidion spp.

Plate 92, figs. 1–6

Remarks. Lack of abundant, well-preserved material precludes a more definite assignment for specimens recovered from strata of Ordovician and Silurian age.

Material. Upper Ordovician figured specimens ROM 37382 and ROM 37383; unfigured specimens ROM 37409. Middle Silurian figured specimen ROM 37384; unfigured specimen ROM 37408.

Distribution. Early Upper Ordovician and Middle Silurian of Ontario, Canada.

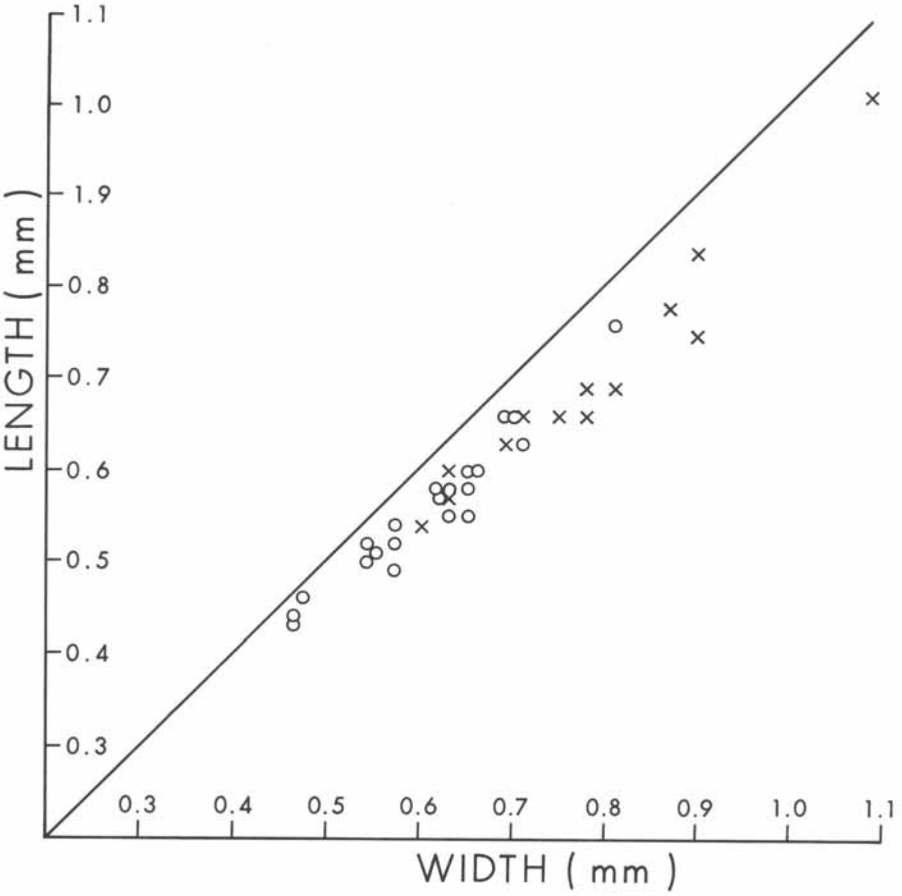


TEXT-FIG. 1. Bar graph of protegular width (diameter) of brachial valves of *Opsiconidion arcticon* Ludvigsen from the Devonian of southern Ontario and the Yukon Territory, Canada. 1 micrometer unit = 130 μm.

FORMATION OF PROTEGULAR PITS

The protegular ultrastructure of the Ordovician, Silurian, and Devonian acrotretids examined for the present study is similar and consists of shallow, circular, flat-bottomed pits with a size range of about 0·30 μm to 10·0 μm in diameter. The specific pattern produced by the protegular pitting and the depth, size range, and contact relationship of individual pits, however, show considerable variation. Three basic patterns may be recognized:

1. Pitting pattern consists of a coarse set of protegular pits with a size range of about 3 to 8 μm in diameter separated from one another by level areas that bear numerous fine pits approximately 0·30 μm in diameter. The pits of the coarse set may touch one another along the circumference, but never display



TEXT-FIG. 2. Length–width diagram of brachial valves of *Opsiconidion arcticon* Ludvigsen from the Devonian of southern Ontario (O) and the Yukon Territory (X), Canada. Data on Yukon Territory specimens from Ludvigsen (1974).

cross-cutting relationships. This pattern is seen in *Artiotreta parva* Ireland (Pl. 92, fig. 9), *Torynelasma* sp. (Biernat and Williams 1970, pl. 98, figs. 1–2), and *Rhysotreta corrugata* Cooper (Biernat and Williams 1970, pl. 98, fig. 4).

2. Pitting consists of a coarse set of protegular pits with a size range of 5–10 μm whose edges either touch or cut across the margin of their neighbours. The periphery of each pit of this set is accentuated by a ring of smaller and deeper pits with a size range of 1–3 μm that must be younger than the coarse set because they cut across that set. This pattern is seen in *Opsiconidion arcticon* (Pl. 90, figs. 3, 12) from the Devonian of Ontario.

3. Pitting consists of single size range of pits 1-3 μm (rarely up to 8 μm) in diameter. Nearly all of the pits show cross-cutting relationships to adjoining pits. This pattern is seen in *O. arcticon* (Pl. 91, figs. 9, 12) and *O.* spp. (Pl. 92, figs. 2, 4, 6).

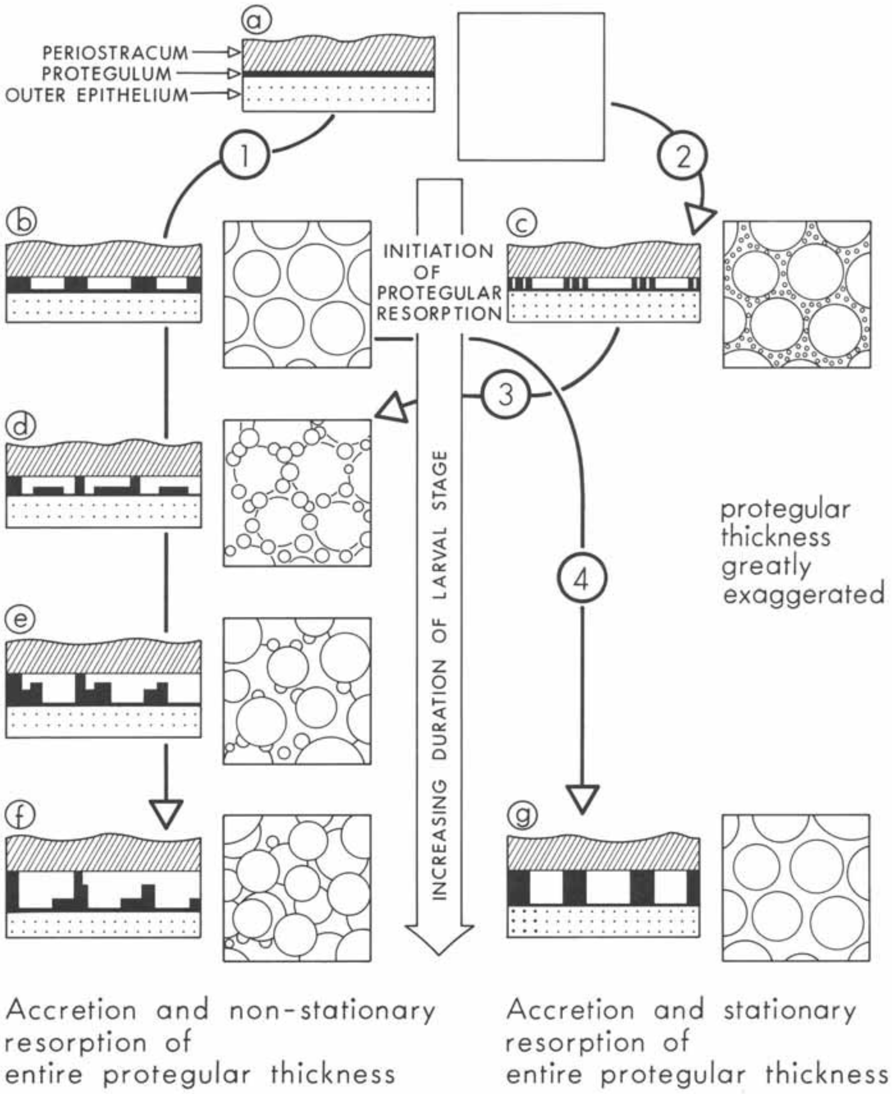
The first pattern provided the basis for Biernat and Williams's 'Bubble Raft Model' (1970), the third for Ludvigsen's 'Selective Resorption Model' (1974), and the second pattern now serves as a morphological intermediate. This gradation in micromorphology of acrotretid protegula suggests that a single mechanism of pit formation is responsible for the pitting patterns observed by both Biernat and Williams and by Ludvigsen. Because the micromorphology includes cross-cutting relationships of pits, we conclude that resorption must be the process responsible for the pitting, and because the mantle is the only part of these brachiopods capable of resorption, we attribute the resorption to the epithelium; that is, from the valve interior.

In text-fig. 3 we interpret the basic pitting patterns as having ontogenetic and possibly ecological significance rather than strict taxonomic significance, and further suggest that the pitting sequence may be developed along a few related pathways. Such analysis implies that the distinct protegular ultrastructure evident in various species of acrotretid brachiopods records the cessation of pitting and the termination of larval ontogeny or, in other words, the settlement of a previously planktic larval brachiopod. A delay in settling and, therefore, extension of larval ontogeny results in continuation of shell resorption and a further alteration of protegular ultrastructure.

Thus, in the larval ontogeny of an acrotretid brachiopod we see an initial secretion of a thin protegulum on the interior surface of the periostracum. Through this protegular sheet are resorbed a number of relatively large circular pits which are separated by level areas that may either be solid or perforated by very small pits. The pits are then sealed off from the epithelial layer by the secretion of another thin protegular sheet. If the larval stage ceases at this point, the protegular ultrastructure shown by *Dictyonites perforata* Cooper (Biernat and Williams 1970, pl. 101, fig. 2), *Torynelasma* sp. (Biernat and Williams 1970, pl. 98, figs. 1, 2), or *A. parva* Ireland (Pl. 92, figs. 9, 11) results. If, however, the larval stage is extended and the planktic brachiopod is required to cope with a continuously accreting protegulum, then protegular resorption continues. Initially, small pits are resorbed along the margins of the

TEXT-FIG. 3. Model relating protegular micromorphology and length of larval stage of acrotretid brachiopods. Each stage (*a*–*g*) is shown as a schematic cross-section and a protegular map. Protegular resorption is developed along four related pathways (1–4). Each stage records the cessation of pitting and termination of larval ontogeny and corresponds to the micromorphology seen in the following protegula:

stage *a.* Protegulum prior to resorption.
stage *b.* *Dictyonites perforata*; Biernat and Williams 1970, pl. 101, fig. 2.
stage *c.* *Artiotreta parva*; Pl. 92, fig. 9. *Torynelasma* sp.; Biernat and Williams 1970, pl. 98, figs. 1, 2. *Rhysotreta corrugata*; Biernat and Williams 1970, pl. 98, fig. 4.
stage *d.* *Opsiconidion arcticon*; Pl. 90, fig. 12.
stage *e.* *O. arcticon*; Pl. 91, fig. 5.
stage *f.* *O. arcticon*; Pl. 91, fig. 9. *Opsiconidion* spp.; Pl. 92, figs. 2, 6.
stage *g.* *Curticia minuta*; Biernat and Williams 1970, pl. 100, figs. 1, 2.


ⓐ
PERIOSTRACUM
PROTEGULUM
OUTER EPITHELIUM
①
②
ⓑ
ⓒ
INITIATION OF PROTEGULAR RESORPTION
③
ⓓ
ⓔ
ⓕ
INCREASING DURATION OF LARVAL STAGE
④
protegular thickness greatly exaggerated
ⓖ
Accretion and non-stationary resorption of entire protegular thickness
Accretion and stationary resorption of entire protegular thickness

earlier-produced and larger pits to produce the ultrastructure seen in Plate 90, figs. 3, 4, and 12. The locus of second-stage pitting ensures that the maximum volume of shell material is removed by resorbing through the thickest portion of the protegular shell. As protegular accretion continues, random resorption of pits through the protegulum plus the previously formed microcaverns produce the ultrastructure seen in Plate 91, figs. 4, 5 and, finally, that seen in Plate 91, figs. 9, 12 and Plate 92, figs. 2, 6. During the last stage of resorption, the initial pitting patterns become almost completely obscured and their former presence can only be surmised on the basis of 'younger' larval shells of other acrotretid brachiopods.

The protegular ultrastructure displayed by *Curticia minuta* Bell (Biernat and Williams 1970, pl. 100, figs. 1, 2) possibly records an alternate strategy of larval resorption. In this species (and possibly also in the acrotretid illustrated by Poulsen 1971, pl. 1, figs. 1B, C, 2B), the non-cross-cutting protegular pits are exceedingly deep; i.e. the ultrastructure is one would expect if the locus of resorption was concisely confined to the same points during protegular accretion.

FUNCTIONAL ASPECTS OF PROTEGULAR PITTING IN ACROTRETIDS

The discussion above suggests that the protegulum has a history that begins with the secretion of the first thin protegular sheet and terminates with the settlement of the larval brachiopod. This history cannot be read on a single specimen, as is generally the case with organisms with accretionary skeletons, because only the last event is clearly recorded on the larval shell. Some idea of the sequence of events required to produce the variety of protegular features may be gained from examination of shells whose larval ontogenies terminated at different stages. We have attempted to do this in text-fig. 3.

Both Biernat and Williams (1970) and Ludvigsen (1974) suggested that acrotretid protegular pitting was an original feature of these larval brachiopods and that protegular pitting was a means to increase buoyancy. Ludvigsen (1974) further suggested

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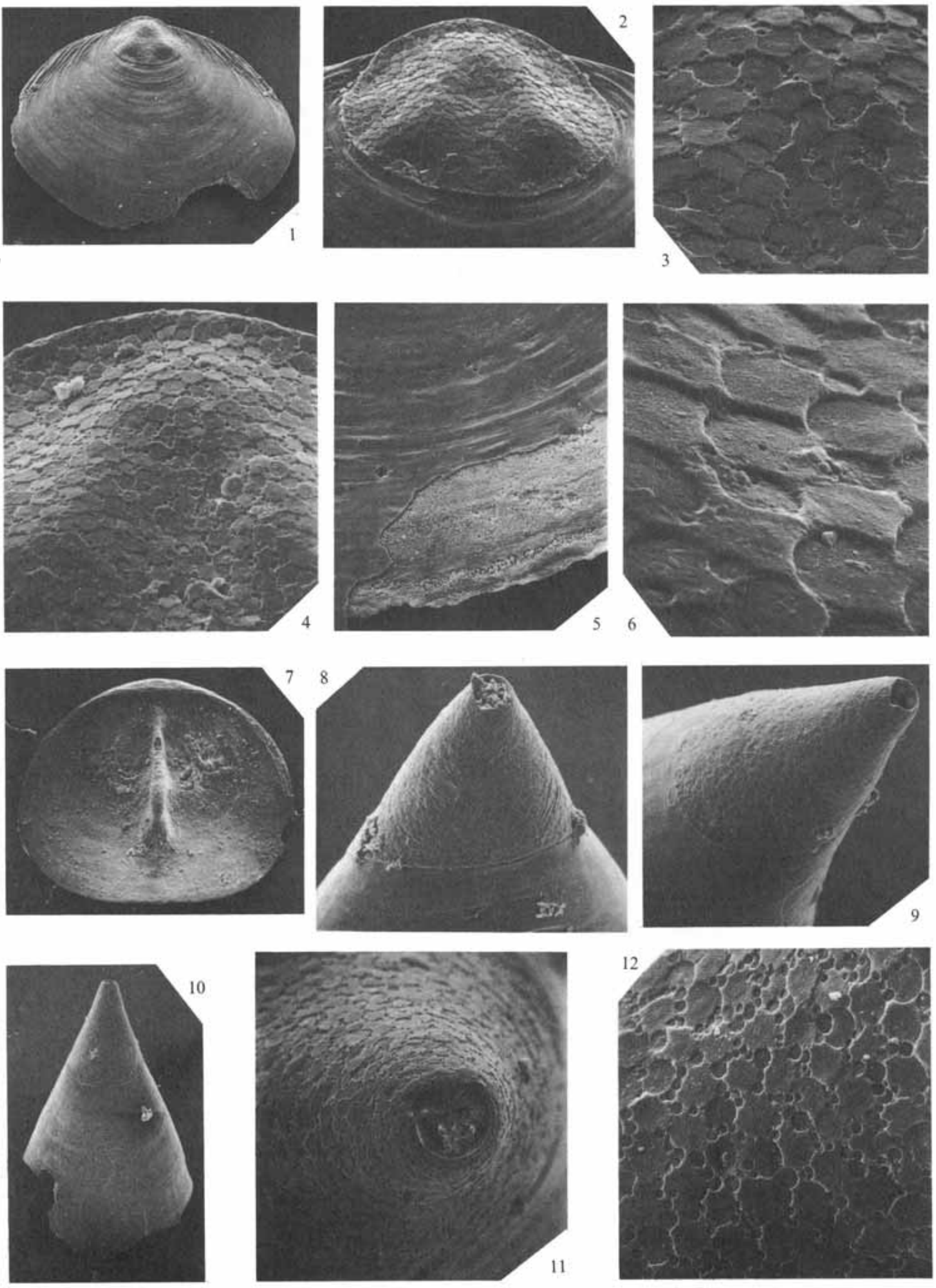
EXPLANATION OF PLATE 90

Scanning electron micrographs of *Opsiconidion arcticon* Ludvigsen, Middle Devonian Onondaga Formation; all except fig. 7 from Walpole Township, Ontario, Canada.

Fig. 1. Brachial valve exterior, sample 42, ROM 37373, ×88.
Fig. 2. Brachial protegulum, sample 42, ROM 37373, ×325.
Fig. 3. Detail, brachial protegulum, sample 42, ROM 37373, ×1300.
Fig. 4. Detail, brachial protegulum, sample 42, ROM 37374, ×650.
Fig. 5. Detail, exterior shell layer of brachial valves, sample 42, ROM 37374, ×330.
Fig. 6. Detail, brachial protegulum, sample 42, ROM 37375, ×3250.
Fig. 7. Brachial valve interior, sample 501, Bertie Township, Ontario, Canada, ROM 37376, ×77.
Fig. 8. Pedicle protegulum, sample 2902, ROM 37378, ×252.
Fig. 9. Pedicle protegulum, sample 2902, ROM 37377, ×224.
Fig. 10. Pedicle valve exterior, sample 2902, ROM 37377, ×78.
Fig. 11. Detail, pedicle protegulum, sample 2902, ROM 37377, ×560.
Fig. 12. Detail, pedicle protegulum, sample 2902, ROM 37377, ×1120.



VON BITTER and LUDVIGSEN, *Opsiconidion arcticon* that the protegular morphology of *O. arcticon* indicated a prolonged free-swimming larval stage and that the larva was essentially a miniature adult. Here we suggest that the particular type of protegular morphology is a key to the longevity of the larval brachiopod. Short larval periods, and therefore short pelagic stages, are indicated for species such as *A. parva* and *D. perforata* with simple non-cross-cutting protegular pits, whereas long larval periods and long pelagic stages are indicated for *O. arcticon* and, perhaps, *C. minuta* with complex cross-cutting (or deep) protegular pits. The dispersal capability of an acrotretid brachiopod should, therefore, increase with increasing complexity of protegular pitting.

The necessity to limit weight relative to the density of the supporting medium is shared by floating and swimming organisms as well as by flying objects. The method of decreasing larval shell weight on the one hand while building a protective housing on the other as developed by acrotretid brachiopods, seems directly comparable to the use of 'frets' or lightening holes (German = Gitterwerk) used in the wing ribs, etc., of some aircraft.

Opsiconidion has a wide geographical range in North America, and *O. arcticon* seemingly ignores the high degree of endemicity evident in the distribution of other brachiopods during the Emsian/Eifelian (Johnson 1971). The genus also has a long stratigraphical range from early Upper Ordovician to early Middle Devonian. Perhaps these distributional characteristics are related to the attributes that we associate with the peculiar protegular microsculpture.

In a recent provocative paper, Scheltema (1977, p. 106) suggested that species with a high larval dispersal capability not only have a wide geographical range but also show a low tendency to form allopatric species and tend to show low rates of phyletic change and extinction. In such species, the potential for gene flow between

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EXPLANATION OF PLATE 91

Scanning electron micrographs of *Opsiconidion arcticon* Ludvigsen, Middle Devonian Onondaga Formation, Ontario (figs. 1–6) and Lower Devonian Michelle Formation, Yukon Territory (figs. 7–12), Canada.

Fig. 1. Pedicle valve exterior, sample 902, Wainfleet Township, ROM 37379, ×133.

Fig. 2. Detail, pedicle protegulum, part of protegulum broken away exposing smooth adult shell, ROM 37379, ×336.

Fig. 3. Cross-section, pedicle protegulum, ROM 37379, ×3050.

Fig. 4. Brachial protegulum, sample 42, Walpole Township, ROM 37380, ×340.

Fig. 5. Detail, brachial protegulum, part of protegulum broken away exposing smooth adult shell, ROM 37380, ×675.

Fig. 6. Cross-section, brachial protegulum, ROM 37380, ×3600.

Fig. 7. Brachial valve exterior, locality A of Ludvigsen (1974), holotype GSC 32055, ×60.

Fig. 8. Brachial protegulum, holotype GSC 32055, ×226.

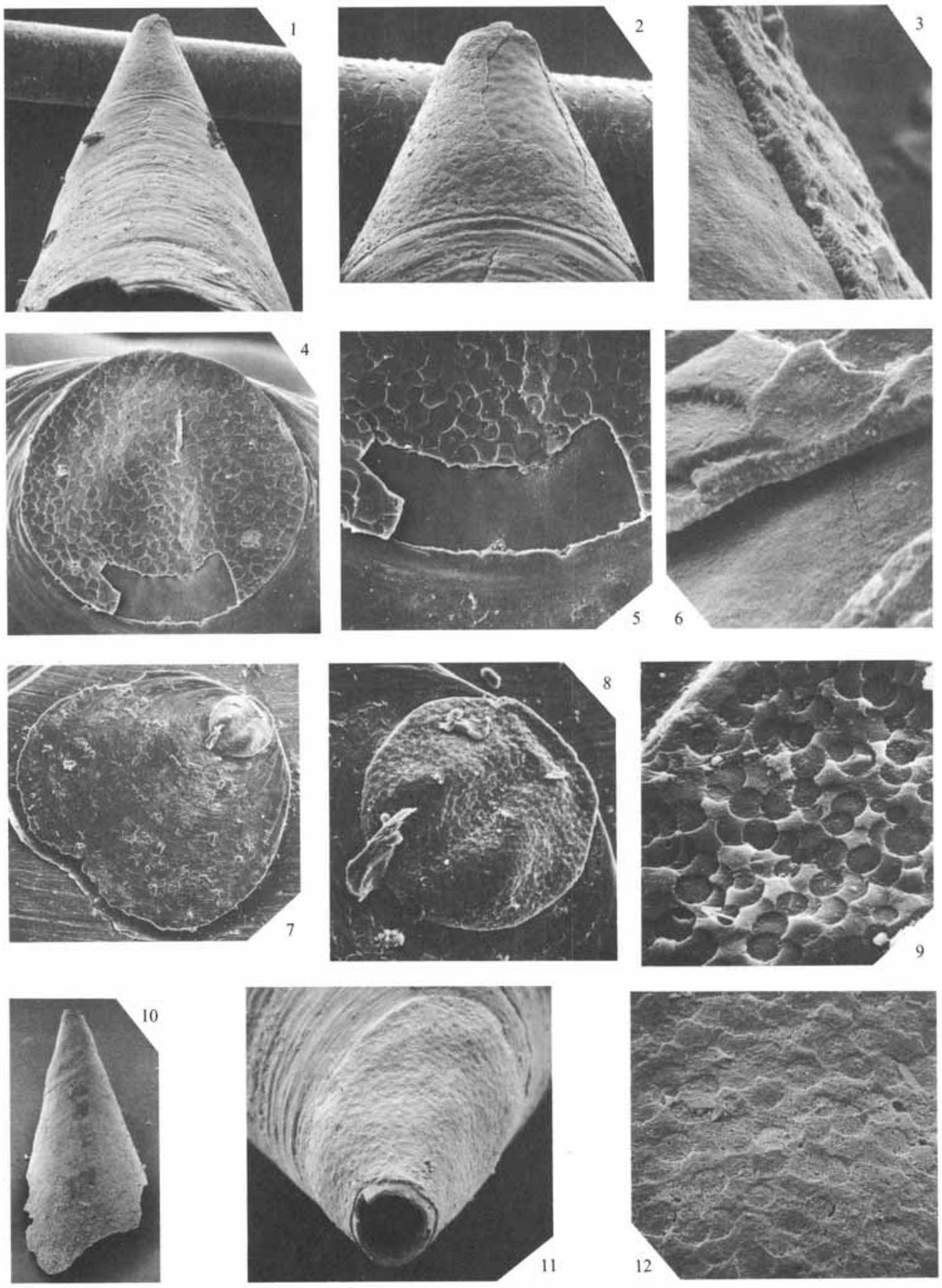
Fig. 9. Detail, brachial protegulum showing undercutting of protegulum (arrow), holotype GSC 32055, ×2030.

Fig. 10. Pedicle valve exterior, locality C of Ludvigsen (1974), ROM 37381, ×67.

Fig. 11. Detail, pedicle opening and protegulum, ROM 37381, ×260.

Fig. 12. Detail, pedicle protegulum, ROM 37381, ×1300.

PLATE 91



VON BITTER and LUDVIGSEN, *Opsiconidion arcticon* isolated populations is great. Thus, geographical speciation is unlikely to occur and, because the species live in a variety of environments, they tend to be genetically heterogeneous. Scheltema (1977) used extant and Tertiary marine gastropods and bivalves as bases for his discussion, but his conclusions may be equally applicable to Palaeozoic brachiopods. We suggest that the developmental and distributional features of *O. arcticon* may be explained in a similar fashion.

The effect of local environment may be considerable in influencing the timing of settlement. The larvae may choose to delay settling if the immediate environment is inhospitable. *O. arcticon* from the Yukon Territory occurs in dark argillaceous carbonates and shows more advanced protegular resorption than does the same species from Ontario, where it occurs in clean, non-argillaceous carbonates. Possibly the local environment in southern Ontario was more favourable to larval settling than that in the Yukon Territory.

Acknowledgements. For the loan of specimens we thank Dr. T. T. Uyeno (Geological Survey of Canada, Calgary). We are indebted to Dr. Gordon Winder (University of Western Ontario) for noting the similarities between Ordovician acrotretids recovered by him and our Devonian specimens, and for donating this important material to the Royal Ontario Museum. Dr. Richard Grant (U.S. National Museum) generously had SEM micrographs taken of the holotype of *Acrotretella siluriana* for comparison.

We have had much aid from ROM personnel. It is a pleasure to acknowledge the able assistance in the preparation of plates and text-figures of Ms Lynda Nakamoto and Ms Maureen Wehnde. Messrs. Brian Boyle and Alan McColl aided considerably in photographic aspects, and Mr. Eric Lin (University of Toronto) is responsible for the fine SEM photography. Miss Joan Burke typed numerous drafts and did much editorial work. Use of the scanning electron microscope was possible through a grant from the National Research Council to the Department of Zoology, University of Toronto, for the development of a programme in systematic and evolutionary zoology.

REFERENCES

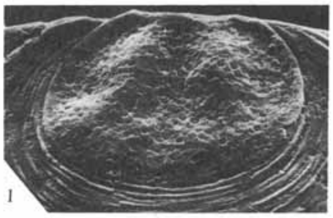
BIERNAT, G. and WILLIAMS, A. 1970. Ultrastructure of the protegulum of some acrotretide brachiopods. *Palaeontology*, **13**, 491-502, pls. 98-101.

FINCH, E. M. 1974. An improved method of mounting palaeontological specimens for SEM examination. Ibid. **17**, 431-434, pl. 59.

EXPLANATION OF PLATE 92

Scanning electron micrographs of *Opsiconidion* spp., Ordovician and Silurian, Ontario, Canada (figs. 1-6), and *Artiotreta parva* Ireland, Lower Silurian, Chimney Hill Member, Oklahoma, U.S.A. (figs. 7-12).

Fig. 1. Brachial protegulum, Silurian, Rochester Formation, Grimsby, Ontario, ROM 37384, ×374.
Fig. 2. Detail, brachial protegulum, ROM 37384, ×1168.
Fig. 3. Pedicle valve exterior, Ordovician, Cobourg Formation, Colborne, Ontario, ROM 37382, ×98.
Fig. 4. Detail, pedicle protegulum, ROM 37382, ×700.
Fig. 5. Brachial valve exterior, Ordovician, Cobourg Formation, Colborne, Ontario, ROM 37383, ×157.
Fig. 6. Detail, brachial protegulum, ROM 37383, ×1572.
Fig. 7. Conjoined brachial and pedicle valve exterior, ROM 37385, ×104.
Fig. 8. Brachial valve exterior showing bulbous brachial protegulum, ROM 37386, ×163.
Fig. 9. Detail of brachial protegulum, ROM 37386, ×2205.
Fig. 10. Detail of pedicle protegulum, ROM 37387, ×206.
Fig. 11. Detail of pedicle protegulum, ROM 37387, ×1024.
Fig. 12. Pedicle valve exterior showing pedicle opening and pedicle protegulum, ROM 37387, ×104.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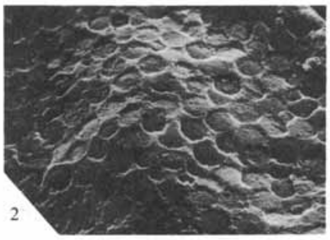
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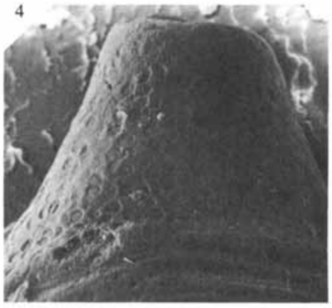
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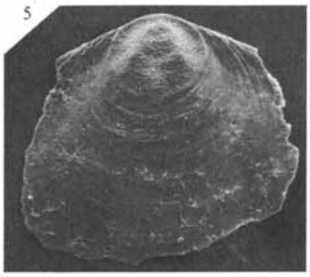
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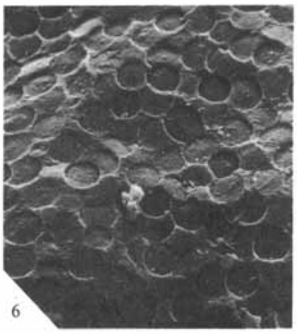
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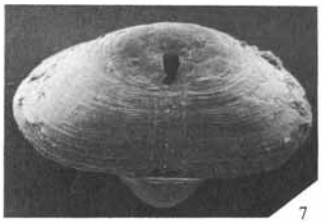
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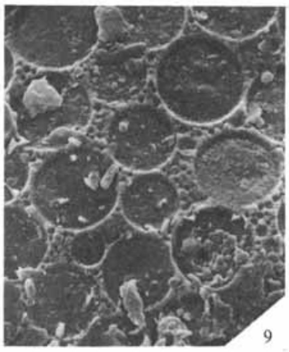
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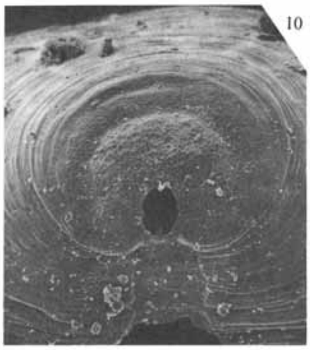
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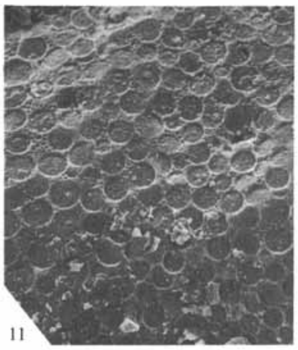
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12

VON BITTER and LUDVIGSEN, *Opsiconidion* spp.

JOHNSON, J. G. 1971. A quantitative approach to faunal province analysis. *Am. J. Sci.* **270,** 257–280.

LUDVIGSEN, R. 1974. A new Devonian acrotretid (Brachiopoda, Inarticulata) with unique protegular ultrastructure. *Neues Jb. Geol. Paläont. Mh.* **3,** 133–148.

POULSEN, V. 1971. Notes on an Ordovician acrotretacean brachiopod from the Oslo region. *Bull. geol. Soc. Denm.* **20,** 265–278.

SCHELTEMA, R. S. 1977. Dispersal of marine invertebrate organisms: paleobiogeographic and biostratigraphic implications. Pp. 73–108. *In* KAUFFMAN, E. G. and HAZEL, J. E. (eds.). *Concepts and methods of biostratigraphy*. xiii+658 pp., Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania.

TELFORD, P. G., VON BITTER, P. H. and TARRANT, G. A. 1977. Lower–Middle Devonian conodont biostratigraphy and palaeoecology, Niagara Peninsula, Ontario. *Life Sci. Occ. Pap. R. Ont. Mus.* **30,** 1–16.

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APPENDIX

Distribution and abundance of acrotretid brachiopods examined

A. *Opsiconidion arcticon* Ludvigsen from collections of Telford *et al.* (1977). (For geographical and stratigraphical information refer to that paper.)

Sample no.	ROM no.	Brachial valves	Pedicle valves	Formation and age
501	37388, 37376	4	—	Onondaga Formation, Middle Devonian
T112	37389	—	1	Onondaga Formation, Middle Devonian
T114	37390	—	2	Onondaga Formation, Middle Devonian
T401	37391	—	1	Onondaga Formation, Middle Devonian
T403	37392	—	1	Onondaga Formation, Middle Devonian
T404	37393	—	3	Onondaga Formation, Middle Devonian
T405	37394	—	1	Onondaga Formation, Middle Devonian
T507	37395	—	2	Onondaga Formation, Middle Devonian
902	37379	—	1	Onondaga Formation, Middle Devonian
1002	37396	—	2	Onondaga Formation, Middle Devonian
1003	37397	4	2	Onondaga Formation, Middle Devonian
1004	37398	—	3	Onondaga Formation, Middle Devonian
41	37399	—	3	Bois Blanc Formation, Lower Devonian
2902	37377, 37378	—	2	Onondaga Formation, Middle Devonian
2904	37400	—	1	Onondaga Formation, Middle Devonian
42	37401, 37380, 37373–37375 incl.	9	53	Onondaga Formation, Middle Devonian
43	37402	—	1	Onondaga Formation, Middle Devonian
9006	37403	—	1	Onondaga Formation, Middle Devonian
9009	37404	—	2	Onondaga Formation, Middle Devonian
9201	37405	1	4	Bois Blanc Formation, Lower Devonian
9401	37406	—	1	Bois Blanc Formation, Lower Devonian

B. *Opsiconidion arcticon* Ludvigsen from Geological Survey of Canada collections.

GSC collection and locality nos.	GSC type no.	Brachial valves	Pedicle valves	Formation, age, and locality
1UA 72-2 C38807	59035	1	—	Onondaga Formation, Middle Devonian, Canada Cement Quarry, 3·5 km W. of Port Colborne, and 1·2 km S. of Highway 3
4UA 72-11 C38835	59040	1	—	Onondaga Formation, Middle Devonian, Ridgemount Quarries Ltd., 1·2 km N. of Highway 3, and 6·4 km W. of Fort Erie
38UA 72-3 C38986	59041	1	—	Dundee Formation, Middle Devonian, abandoned quarry located 0·8 km E. of Selkirk, and 0·3 km N. of road, on property of Mr. H. Hoover
8UA 72-1 C38844	59042	1	—	Dundee Formation, Middle Devonian, section along Dry Creek, on W. side of road, located 1·3 km N. of Cheapside, on property of Mr. K. Schweyer
8UA 72-2 C38845	59043	2	—	Dundee Formation, Middle Devonian, section along Dry Creek, on W. side of road, located 1·3 km N. of Cheapside, on property of Mr. K. Schweyer
2UA 72-7 C38821	59036	1	—	Onondaga Formation, Middle Devonian, R. E. Law Crushed Stone Ltd. Quarry, 3·4 km W. of Port Colborne, on N. side of Highway 3
2UA 72-9 C38823	59037	2	—	Onondaga Formation, Middle Devonian, R. E. Law Crushed Stone Ltd. Quarry, 3·4 km W. of Port Colborne, on N. side of Highway 3
4UA 72-8 C38832	59038	4	—	Onondaga Formation, Middle Devonian, Ridgemount Quarries Ltd., 1·2 km N. of Highway 3, and 6·4 km W. of Fort Erie
4UA 72-9 C38833	59034	10	1	Onondaga Formation, Middle Devonian, Ridgemount Quarries Ltd., 1·2 km N. of Highway 3, and 6·4 km W. of Fort Erie
4UA 72-10 C38834	59039	1	—	Onondaga Formation, Middle Devonian, Ridgemount Quarries Ltd., 1·2 km N. of Highway 3, and 6·4 km W. of Fort Erie

C. *Opsiconidion arcticon* Ludvigsen from the Lower Devonian of the Yukon Territory, Canada. (For geographical and stratigraphical information refer to Ludvigsen (1974).)

ROM no.	Brachial valves	Pedicle valves	Formation, age, and locality
37417, 37418, 37419	31	2	Michelle Formation, Lower Devonian, locality A of Ludvigsen (1974)
37381, 37411, 37412	3	5	Michelle Formation, Lower Devonian, locality C of Ludvigsen (1974)

D. *Opsiconidion* sp.

ROM no.	Brachial valves	Pedicle valves	Formation, age, and locality
37382, 37383, 37409	5	Numerous	Cobourg Formation, early Upper Ordovician, St. Lawrence Quarry, 2 ft thick unit, sample 44-46 of G. Winder, 15 ft below top of quarry; Colborne, Ontario, Canada
37384, 37408	2	—	Rochester Shale, Middle Silurian, E Bank of Forty Mile Creek S. of Beamer Conservation Area, Grimsby, Ontario, Canada

E. *Artiotreta parva* Ireland

ROM no.	Brachial valves	Pedicle valves	Formation, age, and locality
37385, 37386, 37387, 37410, 37413, 37414, 37827	Numerous some conjoined	Numerous	Chimney Hill Limestone, Lower Silurian, S. side Arbuckle Mountains, Oklahoma, U.S.A.

F. *Acrotretella siluriana* Ireland

USNM no.	Brachial valves	Pedicle valves	Formation, age, and locality
140111	—	Holotype (not figured in this paper)	Chimney Hill Limestone, Lower Silurian, S. side Arbuckle Mountains, Oklahoma, U.S.A.