A lingulate brachiopod *Acrotretella*: New data from Ordovician of Poland

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A new record of the phosphate microbrachiopod genus *Acrotretella* Ireland, 1961 from the Lower Ordovician of the Baltic syneclise, in north-east Poland is the oldest known species of the genus. *Acrotretella goldapiensis* sp. n. co-occurs with conodonts in shallow-water facies of Late Llanvirn age. The new data from Poland extend the stratigraphical range of the genus from the Llanvirn to the middle Silurian (Ludlow); during the later Ordovician and Early Silurian *Acrotretella* apparently migrated westwards to sequentially occupy shallow-water facies on the palaeocontinents of Baltoscandia (Poland and Sweden), Avalonia (England), Laurentia (North America) and Australasia (Australia) with relatively little morphological change.

Key words: Brachiopoda, Lingulata, Ordovician, Silurian, Baltic Syneclise, Poland, palaeogeography.

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Introduction

The phosphate microbrachiopod *Acrotretella* has long been known as a distinctive, monospecific and short-lived genus confined to the Silurian. It was originally described by Ireland (1961) from the Chimney Hill Limestone of the Hunton Formation in Oklahoma, USA. More recently, however, Satterfield & Thomas (1969) retrieved the genus from residues of the basal limestone of the Bainbridge Formation of Missouri and Illinois, further extending its geographical range on the Laurentian palaeoplate. An additional Silurian record from Europe (Wenlock Limestone, Woolhop Inlier, England) is less confident as the material is extremely badly fragmented and apparently represented only by the dorsal valves of the acrotretellide genus (Ireland 1958, 1961). This record was noted by Rowell (1965) with a question

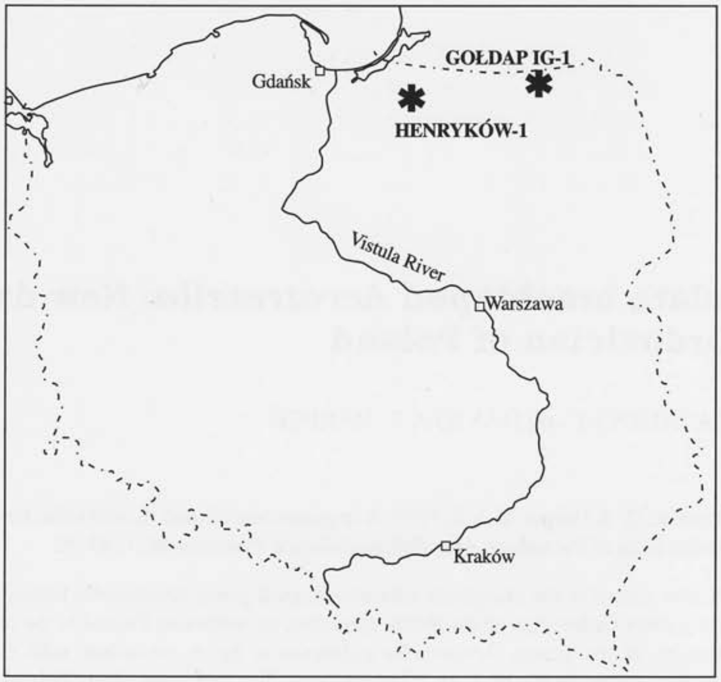

Fig. 1. Sketch-map of the Gołdap IG-1 and Henryków IG-1 localities from where *Acrotretella* was retrieved.

mark and reiterated by Satterfield & Thomas (1969). To date, no further details on the latter sample have been published. More noteworthy, however, is the perfectly preserved and morphologically variable *Acrotretella* from the Silurian, Panuara Group of western New South Wales, Australia described and figured by Dean-Jones (an unpublished M. Sc. Thesis 1979). Dean-Jones, in fact, erected three new species of *Acrotretella*, but as his thesis is unpublished, these names are currently unavailable. Another occurrence of the genus from Silurian carbonates in the Tamworth Belt, Australia, is also noted (Dr. Glenn A. Brock written communication). The two last decades have provided a few further records of the genus. Valuable new data based on scarce and poorly preserved material from the Ordovician (Caradoc, Ashgill) of Sweden (Holmer 1986, 1989) and of Poland (?late Arenig, Bednarczyk 1989, archival data; Llanvirn, Biernat & Bednarczyk 1990, and this paper) have been recorded. The specimens described here are housed in the Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, abbreviated ZPAL.

Locality

The Ordovician of the Baltic Syneclise in the north-eastern part of Poland is recorded in more than a hundred boreholes, mainly in carbonate and clay lithofacies. The *Acrotretella* specimens, studied here, are from shallow-water deposits, at a borehole depth of about 1869.8 m of the Gołdap IG 1 borehole, in the north-eastern part of

Poland, about 230 km NNE of Warsaw (Fig. 1). It was drilled by the State Geological Institute, Warsaw and sampled for conodonts by K. Małkowski (Mannik & Małkowski 1998). These deposits comprise Llanvirn and partly Caradoc rocks and overly Arenig rocks at a depth of 1879.4 m (Modliński 1974, 1991). Generally, the lowermost Llanvirn deposits are organodetrital limestones, which pass upwards into brown-cherry limestones interbedded with marly grey organodetrital limestones, sometimes containing a few small ferrugineous ooliths (Biernat 1973; Modliński 1974). Much of the same lithology characterizes the uppermost Llanvirn. Of the other co-occurring actotretide brachiopods (generally rare and poorly diverse), *Biernatia rara* (Biernat, 1973), *Ephippelasma spinosum* (Biernat, 1973) and rare specimens of *Numericoma* sp. are present in association with conodonts such as *Baltoniodus prevariabilis* Fåhraeus, 1966, *Dapsilodus mutatus* (Branson & Mehl, 1933), *Microsacordina* sp., *Propanderodus rectus* Lindström, 1955; together these suggest a late Llanvirn age. Both the microbrachiopod and conodont biofacies suggest shallow-water conditions (Harper & Rasmussen 1997). Specimens of *Acrotretella goldapiensis* sp. n. obtained by etching are similarly few in number like those in collection from Sweden (Holmer 1986, 1989).

Systematic palaeontology

Order Acrotretida Kuhn, 1949
Family Torynelasmatidae Rowell, 1965

Nomen translatum (in Popov & Holmer 1994) ex Torynelasmatinae Rowell, 1965: p. H279.

Remarks. — The family Torynelasmatidae comprises, up to now, seven genera of which only *Acrotretella* is from the Ordovician–Silurian; the remaining are Ordovician taxa. The genera are as follows: *Torynelasma* Cooper, 1956, *Acrotretella* Ireland, 1961, *Issedonia* Popov, 1980 in Nazarov & Popov 1980, *Polylasma* Popov, 1980 in Nazarov & Popov 1980, *Mylloconotreta* Williams & Curry, 1985, *Cristocoma* Popov & Holmer, 1994, *Sasyksoria* Popov & Holmer, 1994. Controversial seems to be the inclusion of *Issedonia* and *Cristocoma*; both genera have a high conical ventral valve and dorsal septum much like that of e.g. *Opsiconidion* Bitter & Ludvigsen, 1974. Biernat (1984) assigned this genus to the family Biernatidae Holmer, 1989. In addition, *Sasyksoria* has a simple dorsal septum lacking a surmounting plate. Nevertheless, some of the Ordovician torynelasmatid genera like: *Cristocoma*, *Mylloconotreta, Sasyksoria* possess spinous and/or spiky dorsal septa much like those of the Silurian *Acrotretella* (Dean-Jones 1979).

Genus *Acrotretella* Ireland, 1961

Type species: *Acrotretella siluriana* Ireland, 1961: p. 1139, pl. 137: 13–18; Chimney Hill Limestone, Oklahoma (Arbuckle Mountains), USA.

Diagnosis (after Holmer 1986: p. 119, emended). — Ventral valve broadly conical with well developed, undivided, procline to catacline pseudointerarea; apical process and pedicle tube absent; dorsal valve with indistinct, undivided pseudointerarea; median septum low to high, spinous/?spiky, variably extended forward, with concave surmounting plate; larval shell on both valves usually distinct, bulbous on dorsal valve.

Species assigned. — *Acrotretella siluriana* Ireland, 1961, middle Silurian (Wenlock), Oklahoma, Illinois, Missouri, USA; *Acrotretella* sp. in Holmer 1986, upper Ordovician (Caradoc–Ashgill) Sweden; *A.* sp. in Holmer 1989, upper Ordovician (Caradoc), Sweden; *Acrotretella goldapiensis* sp. n., lower Ordovician (Llanvirn), Poland, and three named, but unpublished *Acrotretella* species from lower-middle Silurian (Llandovery–Ludlow) of New South Wales, Australia.

Remarks. — *Acrotretella* is currently assigned to the family Torynelasmatidae Rowell, 1965 (Popov & Holmer 1994). Obvious is its similarity, in particular, to the genus *Torynelasma* Cooper, 1956 *sensu* Holmer (1986, 1989) with type species *T. toryniferum* Cooper (see Cooper 1956: pl. 9C: 28–30, 35–38; pl. 28E: 13–16).

All species of *Acrotretella* are of small size (sagittal lengths range from about 0.5 to ca 1 mm) and are closely similar to the type species figured by Ireland (1961), with only subtle differences separating species (Ireland 1961; Satterfield & Thomas 1969; Dean-Jones 1979; Holmer 1986, 1989: fig.76; this paper: Fig. 2).

Acrotretella goldapiensis sp. n.

Figs 1–3.

Holotype: Ventral valve ZPAL Bp.XXIXa/l, Fig. 2A, C. Other material: three figured dorsal valves (two incomplete): ZPAL Bp.XXIXa/2 Fig. 2B; ZPAL Bp.XXIXa/3, Fig. 2D, F, G; ZPAL Bp.XXIXa /4, Fig. 2E, H.

Type locality: Gołdap, Baltic Syneclise, NW Poland.

Type horizon: Ordovician, Llanvirn (*Pygopus serus* Zone).

Etymology: 'goldapiensis' – from the locality Gołdap.

Diagnosis. — Small (sagittal length of dorsal valves ca 0.5 mm) *Acrotretella* species with larval shell finely pitted, ventral valve broadly conical, medially depressed, dorsal valve rounded, post-larval concentric ridges rare, 4 per 0.1 mm at 0.25 mm from posterior margin on dorsal valve, regularly arranged and distinctly thickened marginally; inter-spaces wide. Like *A. siluriana,* but with less convex larval stage, a lower and wider ventral valve, a more concave pseudointerarea and better developed swellings bounding the pedicle foramen.

Description. — Ventral valve is broadly conical, pseudointerarea evenly concave in its median part, delimited laterally, slightly catacline to procline. Pedicle foramen comparatively large, as wide as long, circular and flanked by low swellings (Fig. 2A, C). The finely pitted larval valve nearly circular (ca 9.17 μm), well marked, distinctly delineated from the post-larval shell (Figs 2A, C, 3). Interior unknown.

Dorsal valve rounded in outline, somewhat transverse, a little convex posteriorly, bulbous, and flattened to weakly concave anteriorly; posterior margin straight, larval valve bulbous with subcircular outline, well delineated and delimited from the post-larval valve similar to that of the ventral valve (Fig. 2B).

Interior (Fig. 2B–H) with relatively wide and long pseudointerarea medially grooved with anacline propareas, all bearing fine growth lines; its anterior margin is somewhat elevated above the valve floor; faintly marked traces of posterior cardinal muscle scars of subcircular outline are slightly elevated; near the centre a pair of small elliptical muscles, separated by vascula media, are discernible. The relatively high median septum extends from 0.3 to 0.7 of the valve length (i.e. into the anterior third of valve) being highest in its anterior half; it arises near the centre of valve (from ca

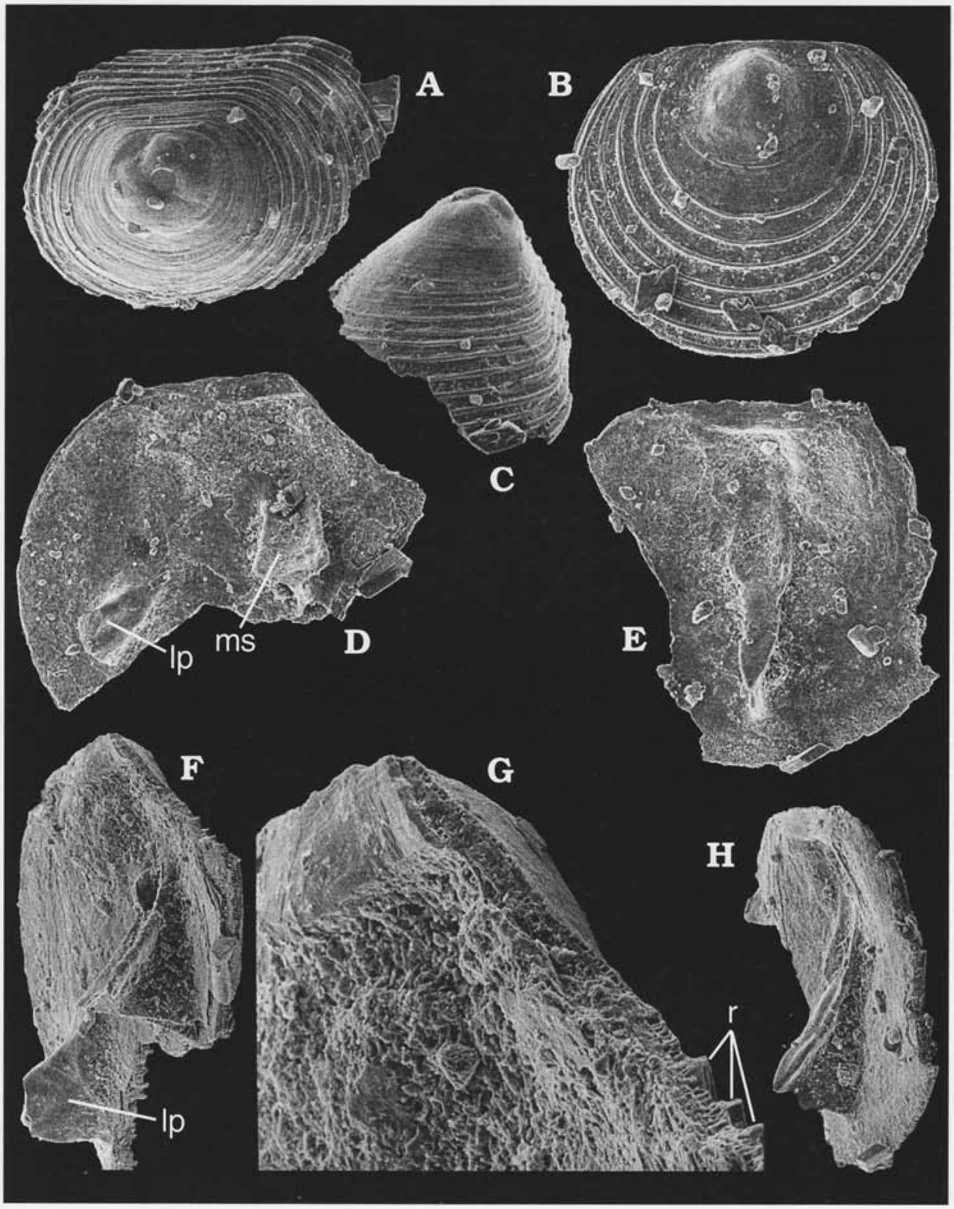

Fig. 2. **A–H.** *Acrotretella goldapiensis* sp. n. Gołdap IG-1. Llanvirn. **A**, **C**. Apical and side views of a ventral valve (ZPAL Bp.XXIXa/1, holotype; × 100. **B**. Exterior of a dorsal valve (ZPAL Bp.XXIXa/2), × 100. **D**, **F**, **G**. Internal view of an incomplete dorsal valve (ZPAL Bp.XXIXa/3), showing: **D** – partly preserved pseudointerarea, fragmentary median septum (ms) with concave surmounting plate and lateral process (lp) × 107; **F** – side view to show posterior half of median septum and a complete lateral process; × 107; **G** – enlarged **F** showing partly fractured posterior valve edge; exposed are three external surface concentric ridges (r) and lamellar-columnar camerate structure of the secondary layer, × 270. **E**. Interior of the dorsal valve (ZPAL Bp.XXIXa/4) laterally damaged but preserving a complete median septum. **H**. Side view of **E**, × 107.

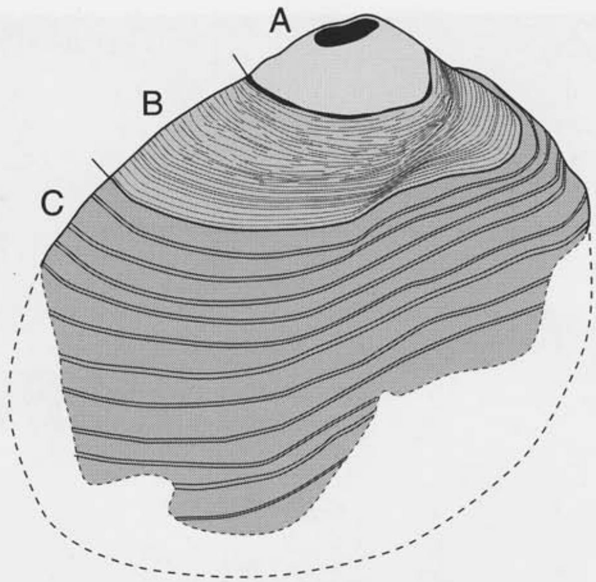

Fig. 3. Interpretation of three growth stages of *Acrotretella goldapiensis* sp. n. in the aspect of the surface ornamentation. A – larval shell, B – early post-larval shell, C – adult shell.

0.3 of valve length) in the form of two parallel, incipiently low but steeply rising ridges, merging into a spoon-like surmounting plate supported by a high median blade similar to that in *Acrotretella* sp. (Holmer 1989: figs 76C, D, F; Fig. 2F, H). From near the valve centre, elongate lateral processes (two or more?) diverge anteriorly (Fig. 2D) as low, rounded swellings very much like those in *Acrotretella* species figured from the Silurian of New South Wales by Dean-Jones (1979).

Surface ornamentation. — Ornamentation of adults consists of distinct concentric ridges, thickened marginally and regularly arranged in contrast to those of the early post-larval shell (Fig. 2A–C). Three growth stages: larval, early post-larval and adult are clearly evident on the available ventral valve (Fig. 3) and preserve some traces connected with a change of the mode of life from the free swimming larva to the fixed benthic adult shell. (1) The pitted disc-like larval shell (Bitter & Ludvigsen 1979), devoid of concentric lines, comparatively large (ca 1/5 of the whole shell length) is markedly delineated in places by unevenly thick marginal edges (Fig. 3A). This marked irregularity may express some disturbance in the shell secretion of the larva when attempting to settle on the substratum and to start adaptation to new conditions. (2) Early post-larval stage (Fig. 3B), transitional to the adult one, constitutes about 1/4 of the whole post-larval valve length (Figs 2A–C, 3) and appears as a relatively narrow belt. Concentric fila, generally discontinuous and of chaotic pattern and slightly varying in thickness, are densely arranged and, in places, disrupted. This may be suggestive of a comparatively short but, generally, very difficult period of adaptation of the animal to the new, sedentary, life style. (3) Late post-larval (adult) shell (Fig. 3C) consists of prominently sharp concentric ridges almost of uniform appearance and arrangement, widely and regularly spaced all over the shell surface (12 on ventral and six on dorsal valves). These strong ridges have greatly thickened and somewhat outwardly deflected marginal edges with slightly raised crests and possibly forming something like overlapping lamellae. Their surfaces bear much finer fila usually anastomozing. Such irregularity in the appearance of the concentric ridges may signal much more stable environmental conditions.

Remarks. — As noted above, *Acrotretella goldapiensis* sp. n. is similar externally to *A. siluriana* Ireland, 1961 in, for example, shell shape and outline of both valves, and also in the style of the surface concentric lines in the adult stage. Differences are slight and few (see diagnosis). Similar too are the Australian acrotretellides as demonstrated by the excellent illustrations in Dean-Jones (1979). Three species have been described from the Australian sections in New South Wales. The oldest species, from the Boree Creek Formation (Upper Llandovery–Wenlock), is very similar to both *A. goldapiensis* and *A. siluriana* but differs in having a slightly more transversely elliptical outline, larger valves (mean sagittal length of 0.7 mm for 39 dorsal valves compared with an average of 0.64 for two dorsal valves of *A. siluriana* and 0.4 mm for a well preserved specimen of *A. goldapiensis*) and a more circular larval shell. *A. goldapiensis* sp. n. has a simple blade in the dorsal valve like the Boree Creek species; one of the two younger Australian species from the Borenore Limestone (Ludlow) has anterior margins of the median blade with convolute, digitate or spinous to spiky terminations (Dean-Jones 1979: pl. 39: 2a–c; pl. 42) much like those of *Ephippelasma* species. But like *A. goldapiensis* sp. n., all the Australian forms have two well developed, simple and thick prongs on both sides of dorsal septum (Fig. 2D–lp), strongly divergent laterally, and additional short ones (Dean-Jones 1979: pl. 40: 2a–c; pl. 42: 1a, b). *Acrotretella* sp. from the Ordovician Dalby Limestone (Caradoc), Dalarna, Sweden, known from the only the dorsal valve (Holmer 1989), possesses a nearly circular and weakly delineated larval shell with a bulbous central node; accentuated concentric lines are more widely arranged (2 per mm at 2.5 mm from the posterior margin) than in the Polish species; whereas *A.* sp. a from the Bestorp Limestone (Ashgill), Västergötland, Sweden (Holmer 1986) is similar to the Dalby form, but has more accentuated concentric growth lines (4 per mm at 2.5 mm from posterior margin). In this respect it is similar to *A. goldapiensis.* A few ventral valves of the unpublished ?*Acrotretella* sp. from the ?late Arenig (Billingsenian) rocks (Henrykowo borehole, Poland, Fig. 1) and recorded by Bednarczyk (1989: pl. 3: 7–9) are considered to be conspecific with *A. goldapiensis* sp. n.

Discussion

The available data indicate an European origin for the genus. The stratigraphically oldest *Acrotretella* is noted with certainty from the Llanvirn strata of the Baltic Syneclise in Poland and, in turn, from Caradoc and Ashgill strata in Sweden (Viru and Harju series of Västergötland, Östergötland and Dalarna; Holmer 1986, 1989). Very likely, the larvae of these microbrachiopods had a prolonged planktonic phase, judging from the relatively large size of the larval shell in comparison with that of the adult one, allowing migration during the Late Ordovician/Early Silurian westward via the seaway of the narrowing Iapetus Ocean (Sheehan 1975; Cocks & Fortey 1982; Harper *et al.* 1996; Harper & Rasmussen 1997). These animals entered North American seas and commenced successive colonization much like other European invaders, probably during the early Silurian. The known records of *Acrotretella siluriana* in Oklahoma are late Llandovery–Wenlock in age similar to those in Illinois and Missouri (located close to the Llandovery–Wenlock boundary). In Australia the distribution of the genus is more extended, ranging from the late Llandovery to Ludlow.

These minute brachiopods were clearly tolerant of changing environments, since the genus survived the ecological crises associated with the end Ordovician extinctions (Sheehan 1975; Cocks 1988; Biernat & Bednarczyk 1990; Harper & Rong 1995; Robertson *et al.* 1991; Wright & McClean 1991). Moreover, the apparent stasis in the *Acrotretella* lineage may be related to its persistence in shallow-water environments where wide fluctuations in physical conditions promoted *plus ça change* strategies (Sheldon 1996).

Conclusions

The comparatively wide stratigraphical range from the Ordovician (?Arenig) to the Silurian (Ludlow) and extended palaeogeographical distribution (Baltoscandia, Avalonia, Laurentia, Australasia) of *Acrotretella* suggest a step-wise westward expansion with time of the genus during the later Ordovician and early Silurian.

The genus survived the end Ordovician extinction events to establish a widespread distribution during the mid-Silurian in shallow water environments.

The morphological stability of the genus, however, suggests a slow radiation, incorporating few, rather small structural modifications against a background of stasis.

Acknowledgements

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Ramienionóg *Acrotretella*: nowe dane z ordowiku Polski

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Streszczenie

Ramienionóg *Acrotretella* Ireland, 1961 nie jest, jak to przez długi okres przypuszczano, monospecyficznym rodzajem ograniczonym do późnego syluru Ameryki Północnej, i ewentualnie Europy (Wielka Brytania: Ireland 1961; Satterfield & Thomas 1969; Rowell 1965). Ma on znacznie szerszy zasięg paleogeograficzno-stratygraficzny. Rodzaj ten został znaleziony również w górnosylurskich osadach Zachodniej Australii (Dean-Jones 1975) oraz w ordowickich osadach Szwecji (Holmer 1986, 1989) i Polski (obecna praca). Jak dotąd, rodzaj ten obejmuje cztery udokumentowane gatunki, w tym trzy ordowickie. Nowy gatunek *Acrotretella goldapiensis* z ordowiku Polski (Synekliza Bałtycka – wiercenie Gołdap-IG, opisany w niniejszej pracy jest, jak dotąd, najstarszym przedstawicielem rodzaju *Acrotretella*. Współwystępujące konodonty określają wiek gatunku na późny lanwirn.