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Growth in early species of the conodont *Ancyrodella* and implications for correlation of the Middle–Upper Devonian boundary

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The first occurrence of the conodont *Ancyrodella rotundiloba* has been used extensively for correlating the Middle–Upper Devonian (Givetian–Frasnian) boundary in sections worldwide despite many arguments as to its precise taxonomic definition. These arguments are summarised herein and three ontogenetic series illustrated from three samples across the Givetian–Frasnian boundary within the Vorota Formation of the Kozhym River section, Sub-Polar Urals, Russia. General trends within the three ontogenetic series suggest that the ratio of basal pit width to platform width in *Ancyrodella pristina*, and *Ancyrodella recta* increases through ontogeny but the morphology of lateral secondary keel extensions to the basal pit remains constant and is a useful taxonomic feature. Folds and collars on the basal surface occur only in the later stages of development. The outline of the platform within species is variable and controlled by the formation of incipient nodes in juveniles; gerontic specimens can also have very variable platform outlines. Measurements of platform width to basal pit width ratios and platform shape outlines may not therefore be a good way to compare between species. The three ontogenetic series provide typical late Givetian and early Frasnian examples and increase the potential for correlation of the Middle–Upper Devonian boundary particularly using juvenile *Ancyrodella* specimens.

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INTRODUCTION

Conodonts have been used extensively to correlate rocks of Frasnian age throughout the world since Ziegler (1962) first established a zonation. Since then there have been many refinements to the original, but now, two zonal schemes are commonly followed for the Frasnian Stage. Klapper (1989) and Klapper and Foster (1993) proposed 13 zones for the Frasnian of Montagne Noire in southern France and defined them using shape analysis of the P_1 element and multielement concepts for *Palmatolepis*, along with the distribution of P_1 elements of other co-occurring genera such as *Ancyrodella*. This zonal scheme has subsequently been applied to sections in America (Kirchgasser, 1994; Kralick, 1994), Canada (McLean and Klapper, 1998), Australia and the Timan–Pechora region of the Russian Platform (Klapper *et al*., 1996). The competing scheme (Ziegler and Sandberg, 1990) is based entirely on identifications of the Pa element of *Palmatolepis* and defined nine conodont zones for the Frasnian. Klapper and Becker (1999) proposed an alignment of the two zonations based on a resampling of the Martenberg reference section in the Rhenish Slate Mountains and a taxonomic analysis.

In 1982 the Subcommission on Devonian Stratigraphy decided that the base of the Frasnian Stage, which is coincident with the base of the Upper Devonian, should coincide with the base of the Lower *asymmetricus* Conodont Zone, which was defined by Ziegler (1962, 1971) as the first appearance of *Ancyrodella rotundiloba* (Bryant, 1921) (Klapper *et al*., 1987). The Subcommission later ratified the proposal of Feist *et al*. (1985) to place the "golden spike" at the base of Bed 42' at the Col du Puech de la Suque section E in the Montagne Noire, France (Klapper *et al*., 1987).

Since 1985 there have been many arguments over taxonomic concepts in early species of *Ancyrodella* and *A. rotundiloba* in particular. This has a profound influence on the potential for the use of the conodont *Ancyrodella* in the definition and correlation of the base of the Frasnian. The Kozhym River section (Fig. 1) through the basal part of the Vorota Formation of the Sub-Polar Urals, former Soviet Union provides an opportunity to study early species of *Ancyrodella* and their distribution across the Givetian–Frasnian boundary in this region. Common, well-pre-

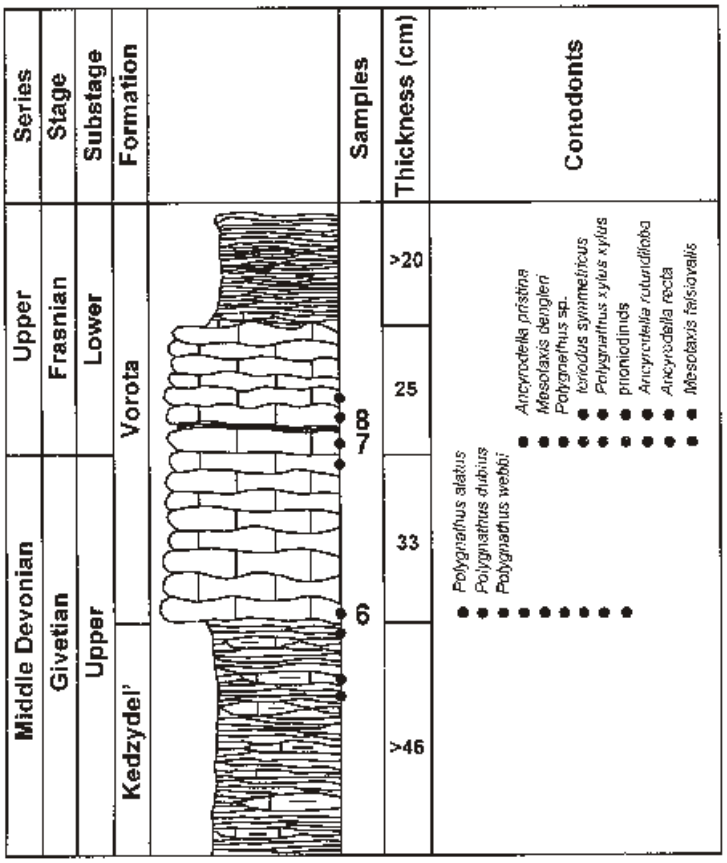

Fig. 1. Conodont ranges and the position of the studied samples (6–8) in the Givetian–Frasnian section through the Vorota Formation at the Kozhym River, Sub-Polar Urals, 65° 40' 58.7"N 59° 46' 14.3"E (after Tsyganko, 2000, 2002)

Black circles on the section represent the beds sampled by Tsyganko (2000, 2002) for conodonts; the lithologies shown are black shale with limestone intercalations and well-bedded organic rich limestone in the middle part of the section

served P_1 elements of early *Ancyrodella* forms are present in three closely spaced samples that appear to have undergone very little post mortem sorting as a wide range of element sizes are present in ontogenetic series. Previous taxonomic studies have often attempted to illustrate the evolution of *Ancyrodella* in a stratophenetic context (e.g., Klapper, 1985; Garcia-Lopez, 1986; Sandberg *et al*., 1989; Kralick, 1994; Iudina, 1995) with relatively few contributions documenting ontogenetic series of *Ancyrodella* (e.g., Bultynck and Jacobs, 1981; Bultynck, 1983). Documentation of ontogenetic series on a sample by sample basis could provide useful information to answer some of the questions posed by the arguments on early *Ancyrodell*a taxonomic concepts. This paper aims to provide a summary of these arguments, present some ontogenetic series of *Ancyrodella* and use these to test the potential for the use of *Ancyrodella* in the definition of the base of the Frasnian (Middle–Upper Devonian boundary). This paper is not intended as a complete taxonomic review of early *Ancyrodella* species but as a guide to future studies and a possible aid to identification of *Ancyrodella* species using juvenile specimens.

GEOLOGICAL SETTING

Frasnian conodont faunas of the Urals region have been well studied and attempts have been made to correlate the Frasnian of the region with the two global zonal schemes (see Klapper *et al*., 1996 and Ovnatanova *et al*., 1999 for summaries). Reviews of Devonian conodont studies from the Kozhym River region of the Sub-Polar Urals have been presented by Savage and Yudina (1999, 2001) and P_1 elements from the genera *Palmatolepis*, *Polygnathus*, *Ancyrodella*, *Ancyrognathus*, *Icriodus* and *Mesotaxis* have been illustrated. The three samples studied herein are from the Givetian–Frasnian Vorota Formation of the Kozhym River section of the Sub-Polar Urals (Fig. 1; Tsyganko, 2000, 2002, outcrop 108). The Middle–Upper Devonian boundary has presumably been based on the first occurrence of the conodonts *Ancyrodella rotundiloba* and *Mesotaxis falsiovalis* in the section as indicated by the range charts in Tsyganko (2002, fig. 4.3). The short section (Fig. 1) also shows the boundary between the underlying Kedzydel' Formation which consists of bituminous shales with thin limestone intercalations. However, there are some disagreements as to the position of the base of the Vorota Formation in the region with Yudina *et al*. (2002) preferring to include the dark grey organic rich limestones of the Syv'yu River section within the basal Vorota Formation. The basal part of the Vorota Formation at the Kozhym River section (*sensu* Tsyganko, 2000, 2002) consists of 78 cm of dark bituminous limestones and black shales rich in the bivalve *Buchiola* with rare associated brachiopods and nautiloids. The three samples for this study were taken from the base of the Vorota Formation and one either side of the interpreted Middle–Upper Devonian boundary (Fig. 1). The field sample numbers (6, 7 and 8) have been retained as the faunas from the other samples collected on the same trip may be published at a later date. Several species of *Polygnathus* are present in the section as well as species of *Icriodus* and *Mesotaxis* (Fig. 1). The conodont elements are almost all complete and show a range of sizes indicating that little or no sorting of element types has taken place. This is consistent with the Vorota Formation being deposited at a time when conditions were relatively stagnant within a relatively deep-water intra shelf basin (Yudina *et al*., 2002).

ANCYRODELLA AND THE MIDDLE–UPPER DEVONIAN BOUNDARY

In 1985, Klapper revised the taxonomy of *Ancyrodella* and this changed the concepts of ranges of species within the Lower *asymmetrica* Zone. Based on six sections in the Montagne Noire in France (Klapper, 1985; Feist and Klapper, 1985), Klapper (1989) defined four zones within the Lower

asymmetrica Zone of the standard zonation with the base of the lowest zone corresponding to the first occurrence of the early form of *Ancyrodella rotundiloba*. However, Sandberg *et al*. (1989) argued that the expansion of the concept of *Ancyrodella rotundiloba* by Klapper (1985) had included more primitive forms that occur much earlier than *Ancyrodella rotundiloba sensu stricto*. They argued that the Middle–Upper Devonian boundary had therefore been fixed, not at the base of the Lower *asymmetrica* Conodont Zone, but at a point within the preceding zone. To account for these more primitive forms, Sandberg *et al*. (1989) erected a new species *Ancyrodella soluta* and recognised a previously overlooked species *Ancyrodella pristina* arguing that it could be used, with difficulty, to correlate the Middle–Upper Devonian boundary. Sandberg *et al.* (1989) also erected three new conodont zones based on pelagic species including the *falsiovalis* Zone that spans the Middle–Upper Devonian boundary. Racki and Wrzolek (1989) suggested that the first occurrence of *A. rotundiloba sensu stricto* and the change from early *A. rotundiloba* (*sensu* Klapper, 1985) should be used to recognise the base of the Upper Devonian as the concept of *A. rotundiloba s.s*. was already well established (Bultynck and Jacobs, 1981; Bultynck, 1982, 1983; Klapper, 1985). The boundary could then be recognised by an evolutionary change rather than the sudden occurrence of a taxon that could be representing a facies change. Sandberg *et al*. (1989) emphasised the importance of biofacies to the zonal scheme and placed *Ancyrodella* in a neritic setting in a polygnathid-ancyrodellid biofacies away from the outer pelagic belt biofacies. They suggested that this could have accounted for difficulties of earlier workers recognising and naming species of *Ancyrodella* from shallower water biofacies.

Kralick (1994) documented *Ancyrodella* species from the Middle Genesee Formation of New York and erected two new taxa *Ancyrodella triangulata* and *Ancyrodella recta* to account for transitional forms between the late form of *A. rotundiloba* and *Ancyrodella alata*. He also suggested that *A. soluta* and *A. pristina* are not sufficiently different from each other to constitute separate species. Stratigraphical changes in *Ancyrodella* faunas were also documented in the Dershor Book section from the northern Chernyshev Swell of the Sub-Polar Urals (Iudina, 1995), where a four step *Ancyrodella* sequence of *A. soluta*, *A. rotundiloba*, *A. alata* and *A. rugosa* was shown. Iudina (1995) suggested that the base of the Frasnian in this section could be placed either at the first appearance of the lowest ancyrodellid *A. soluta* or, using the criteria specified by Racki and Wrzolek (1989), at the first occurrence of *A. rotundiloba s. s*. For a good summary of the taxonomic conundrums involving early and late forms of *A. rotundiloba*, see Kirchgasser (1994).

ONTOGENY OF *ANCYRODELLA*

Across the three samples from the Kozhym River section, Vorota Formation, Sub-Polar Urals, three distinctive ontogenetic series can be seen. Sample 6 contains predominantly *Ancyrodella* specimens from series 1, sample 7 has a few from series 2 and mainly specimens from series 3; sample 8 only from series 3. Each sample may well contain several *Ancyrodella* taxa. However, identifications and taxonomic discussion will be confined to the next section. Each figure represents specimens from a single sample so that ontogenetic series can be compared from sample to sample, and not confused with stratigraphical/evolutionary changes. The specimens have also been illustrated with the largest specimens at the top of the page and a vertical scale bar of 150 microns for each specimen so that gradual size changes during growth can be seen. It is not always possible to see features of the basal pit as some are filled with basal body. On some figures (e.g., Fig. 2C, P, W), the basal view is not shown as sediment or a large fragment of basal body obscures the whole basal pit. All figured specimens are deposited at the Department of Palaeontology, Natural History Museum, London, where additional photographed and non-photographed specimens have also been deposited.

SERIES 1

The most juvenile elements have a relatively chunky free blade with three broad denticles and a large basal pit that extends under the entire element (Fig. 2X, Y). The development of the platform is relatively symmetrical with two prominent nodes present early in ontogeny, close to the central proto-carina (Fig. 2T, V and W). At the point of the first nodes being developed, the platform outline is already becoming v-shaped but tapers rapidly to the posterior (Fig. 2X, Y). The outline of the platform is irregular in early stages of development (Fig. 2W, T), particularly when the third and following nodes are added on the posterior margins, causing the margins to be slightly wider at these points and the margins to take on an irregular wavy outline (Fig. 2Q). In more juvenile specimens, the first added nodes are larger than incipient nodes (Fig. 2Q, N) but through ontogeny nodes take on a more regular size (Fig. 2L and larger specimens). The anterior platform margins on juvenile specimens are straight to slightly angled posteriorly (Fig. 2X, V, T and Q) but as they grow they become more pointed to the anterior and develop denticle-like nodes on the anterior-most point that can be seen even in lower view (Fig. 2B, E, G, M and O). In juvenile specimens, lateral secondary keels from the dominant basal pit extend almost to the platform margin (Fig. 2U, Y) but these keels become less marked and the basal pit less extensive (Fig. 2O) until in more adult specimens the keels do not extend the whole way to the basal margin (Fig. 2B, E, G and J) and the basal pit becomes smaller relative to the total size of the platform (Fig. 2E). The secondary keels extend perpendicular to the axis of the specimen and throughout ontogeny, curve slightly to the anterior on one side of the specimen (Fig. 2E, J, O, R and S). More mature specimens have a slight folding on the lower surface of the lobes (Fig. 2E, G and J). The platform nodes on the most adult specimens are arranged in a single antero-posterior row either side of the carina but on the lobes are more randomly arranged (Fig. 2A, C and D). The margins of adult specimens are irregular, particularly at maximum width of the largest specimens (Fig. 2A) but generally they taper evenly to the posterior (Fig. 2A, C, D and F).

SERIES 2

The most juvenile elements have a relatively slender free blade with four narrow denticles and a basal cavity that extends under the entire element (Fig. 3U, V). The development of the

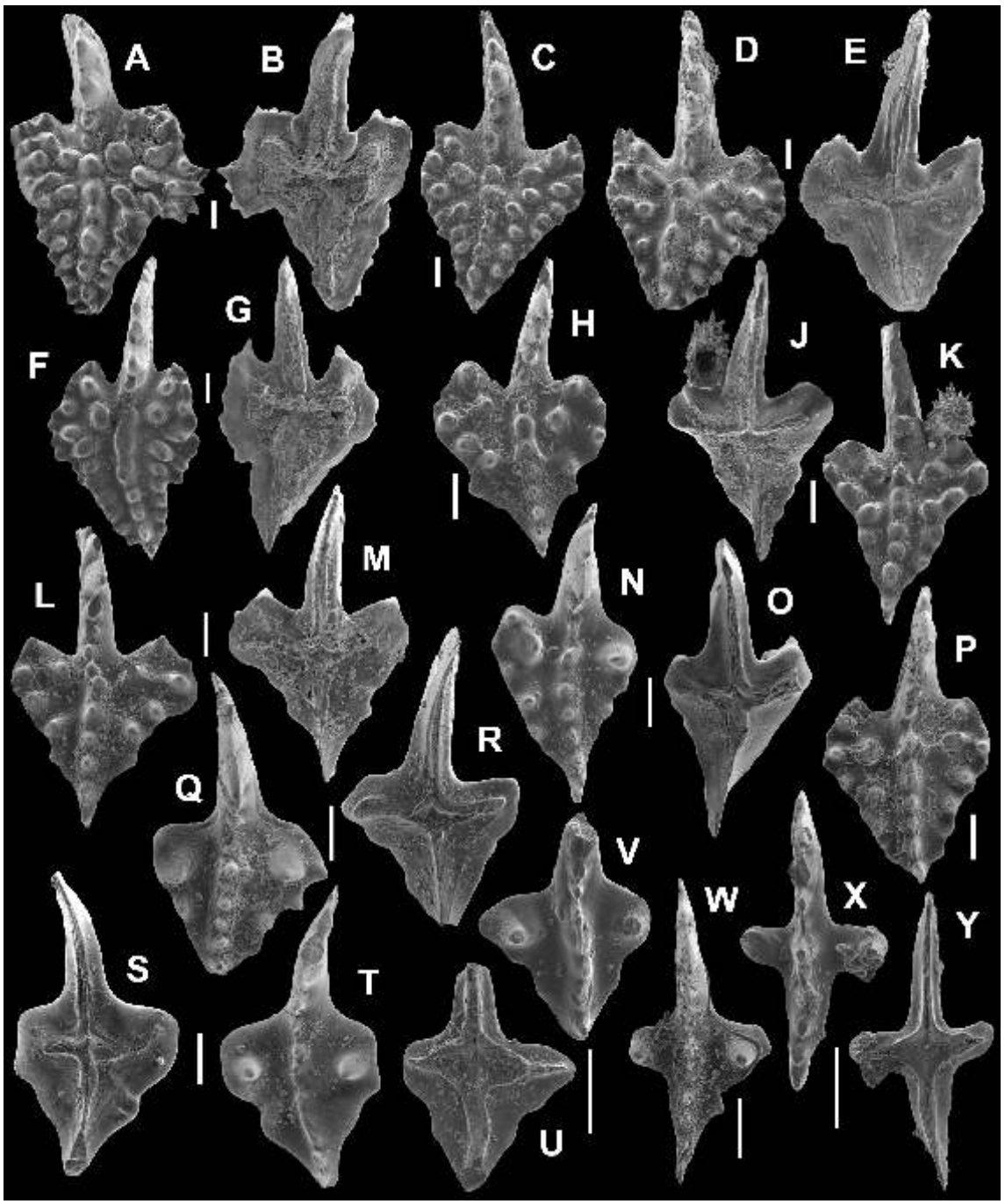

Fig. 2. Ontogenetic series 1, P_1 elements of *Ancyrodella pristina* Khalymbadzha and Chernysheva (1970)

A, B — PM X 3205; **C** — PM X 3206; **D, E** — PM X 3207; **F, G** — PM X 3208; **H** — PM X 3209; **J, K** — PM X 3210; **L, M** — PM X 3211; **N, O** — PM X 3212; **P** — PM X 3213; **Q, R** — PM X 3214; **S, T** — PM X 3215; **U, V** — PM X 3216; **W** — PM X 3217; **X, Y** — PM X 3218; specimens all from sample 6 and all vertical scale bars 150 μm

platform is relatively symmetrical but prominent nodes do not appear early in ontogeny (Fig. 3S, U; compare with elements of same size Fig. 2X) until the platform has already taken on a pronounced v-shaped outline (Fig. 3O). The outline of the platform to the posterior is relatively regular in early stages of development (Fig. 3U, S and O), with sharp indentations to the margin occurring only on one side of the platform (Fig. 3M, O). In more juvenile specimens, the first added nodes are larger than incipient nodes (Fig. 3M) but through ontogeny nodes take on a more regular size (Fig. 3F, H and K) although in sample 7, there are relatively few transitional examples between Figure 2K, M. The anterior platform margins on juvenile specimens are slightly angled to the posterior only in the most juvenile specimens (Fig. 3U) but quickly become straight to slightly curved to the posterior (Fig. 3F, H, K, M and O). In juvenile specimens, the large basal pit extends under the whole element (Fig. 3T, V) but more mature specimens basally resemble those from series 1 with poorly developed, occasionally curved to the anterior, sec-

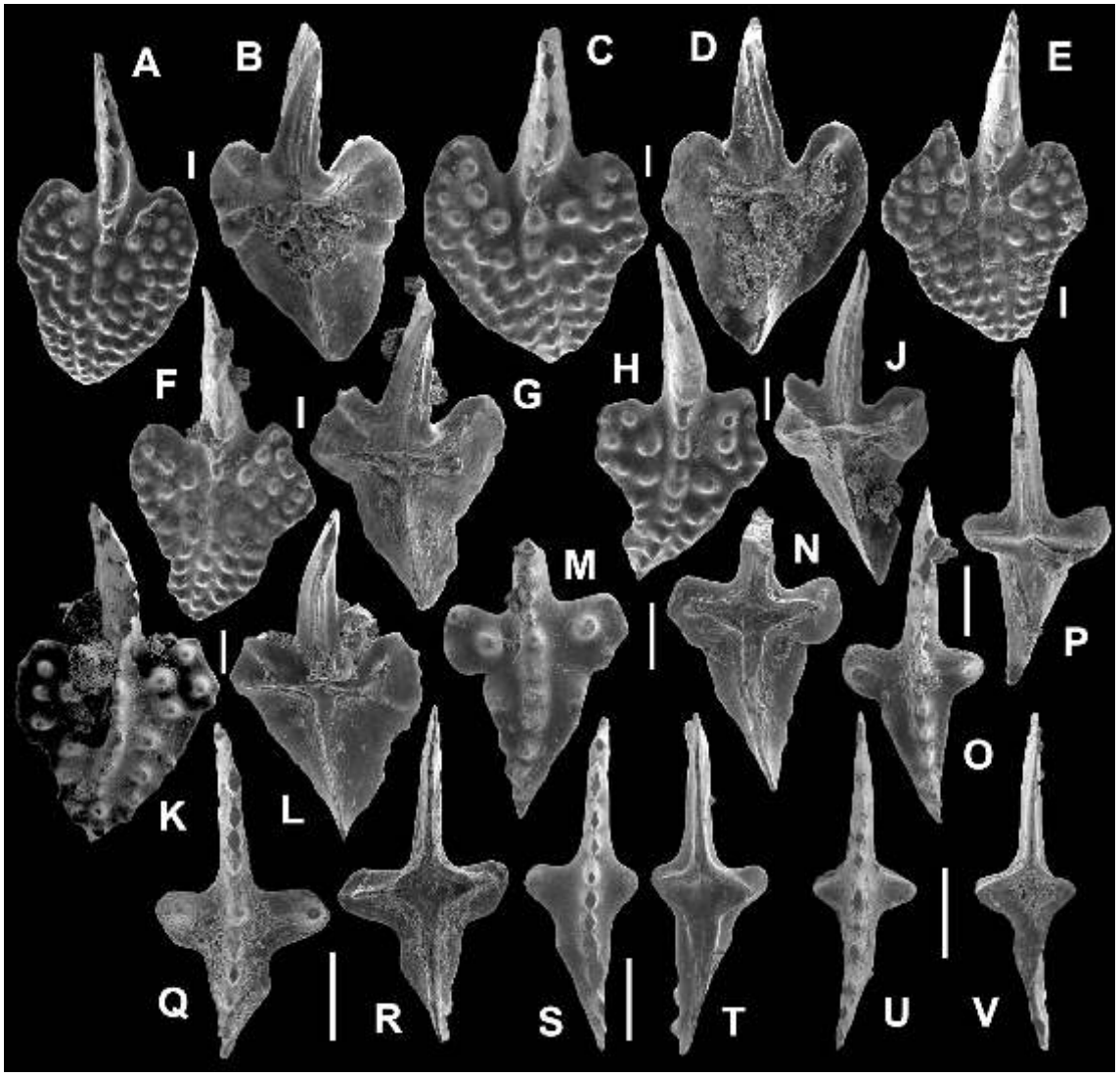

Fig. 3. P_1 elements from sample 7, ontogenetic series 2 and *Ancyrodella rotundiloba* (Bryant, 1931) unless stated

A, B — PM X 3219; **C, D** — PM X 3220; **E** — PM X 3221; **F, G** — PM X 3222; **H, J** — *Ancyrodella pristina* Khalymbadzha and Chernysheva, 1970, series 1, PM X 3223; **K, L** — PM X 3224; **M, N** — PM X 3225; **O, P** — PM X 3226; **Q, R**— *Ancyrodella pristina* Khalymbadzha and Chernysheva, 1970, series 1, PM X 3227; **S, T** — PM X 3228; **U, V** — PM X 3229; all vertical scale bars 150 μm

ondary keels and a less extensive basal pit (Fig. 3G, J and L). The platform nodes on the most adult specimens are arranged in a single antero-posterior row either side of the carina but on the lobes are more randomly arranged (Fig. 3F, H and K). The margins of adult specimens are irregular, but are often extended laterally on the outer lobe (Fig. 3F, H).

SERIES 3

The youngest specimens are adenticulate with an elongate and slender free blade with 4–5 narrow denticles (Figs. 4X and 5Y). Nodes are developed at tips of early platforms with distinctly asymmetrical arrangement either side of central line; one side angled slightly to the anterior (Fig. 4V). When first nodes are developed, the platform is distinctly cross-shaped and there is no development of platform to posterior (Figs. 4V and 5Y). As platform develops all anterior margins are curved inwards towards the junction between the free blade and carina with maximum anterior extent of platform always on inner margin. When platform develops laterally from single nodes either side of the carina, margins in these specimens often depressed leaving an arrow head-like platform projection at the posterior (Figs. 4T and 5U, W). Faint lateral ridge either side of carina first visible at this point and present in all older specimens as ridge (Figs. 4H, L, P and 5H, N, P), and later as row of well-developed nodes form a cruciform at the platform mid-point (Figs. 4A, B, D, F and 5A, D, F, H). The large basal pit of the youngest specimens extends under the entire central area and later secondary keels extend almost to the platform margin (Figs. 4U, W, X and 5X). Through ontogeny the basal pit covers less and less of the lower surface and the secondary keels become less well developed (Figs. 4E, J, K and 5G, J, L) with one secondary keel curving to the anterior throughout ontogeny when devel-

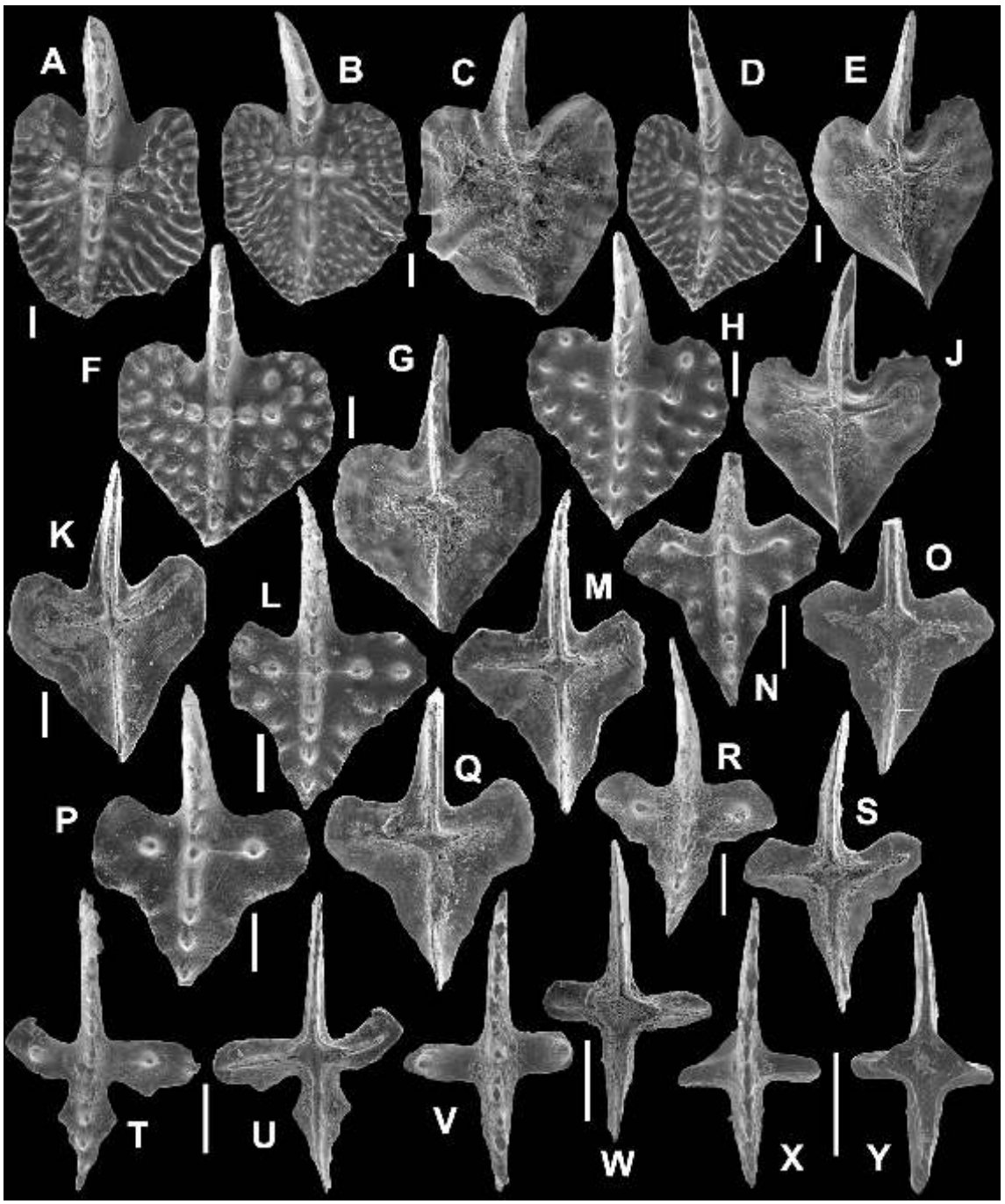

Fig. 4. Ontogenetic series 3, P_1 elements of *Ancyrodella recta* Kralick (1994)

A — PM X 3230; **B, C** — PM X 3231; **D, E** — PM X 3232; **F, G** — PM X 3233; **H, J** — PM X 3234; **K** —— PM X 3235; **L, M** — PM X 3236; **N, O** — PM X 3237; **P , Q —** PM X 3238; **R, S** — PM X 3239; **T, U** — PM X 3240; **V, W** — PM X 3241; **X, Y** — PM X 3242; specimens all from sample 7 and all vertical scale bars 150 μm

oped (compare Figs. 4E, T and 5L, X). When secondary keels have almost disappeared in older specimens, the lower surface becomes crenulated to the posterior (Figs. 4C and 5G) and the basal margin develops a collar-like thickening at the anterior margin where the free blade meets the platform (Figs. 4C, E, H and 5E, G, J). The outline of the margin of the platform in these gerontic specimens becomes more ovoidal (Figs. 4A, B and 5A, D, F) compared to the arrowhead-like outlines of the younger specimens. The nodes become more and more crowded on these adult specimens, coalescing into ridges that fan to the posterior with mid-element cruciform arrangement still prominent (Figs. 4A, B and 5A, D, F).

ONTOGENETIC TRENDS

Morphological trends within P_1 elements of *Ancyrodella* have been given different weighting taxonomically and have contributed to disagreements on the early phylogeny and

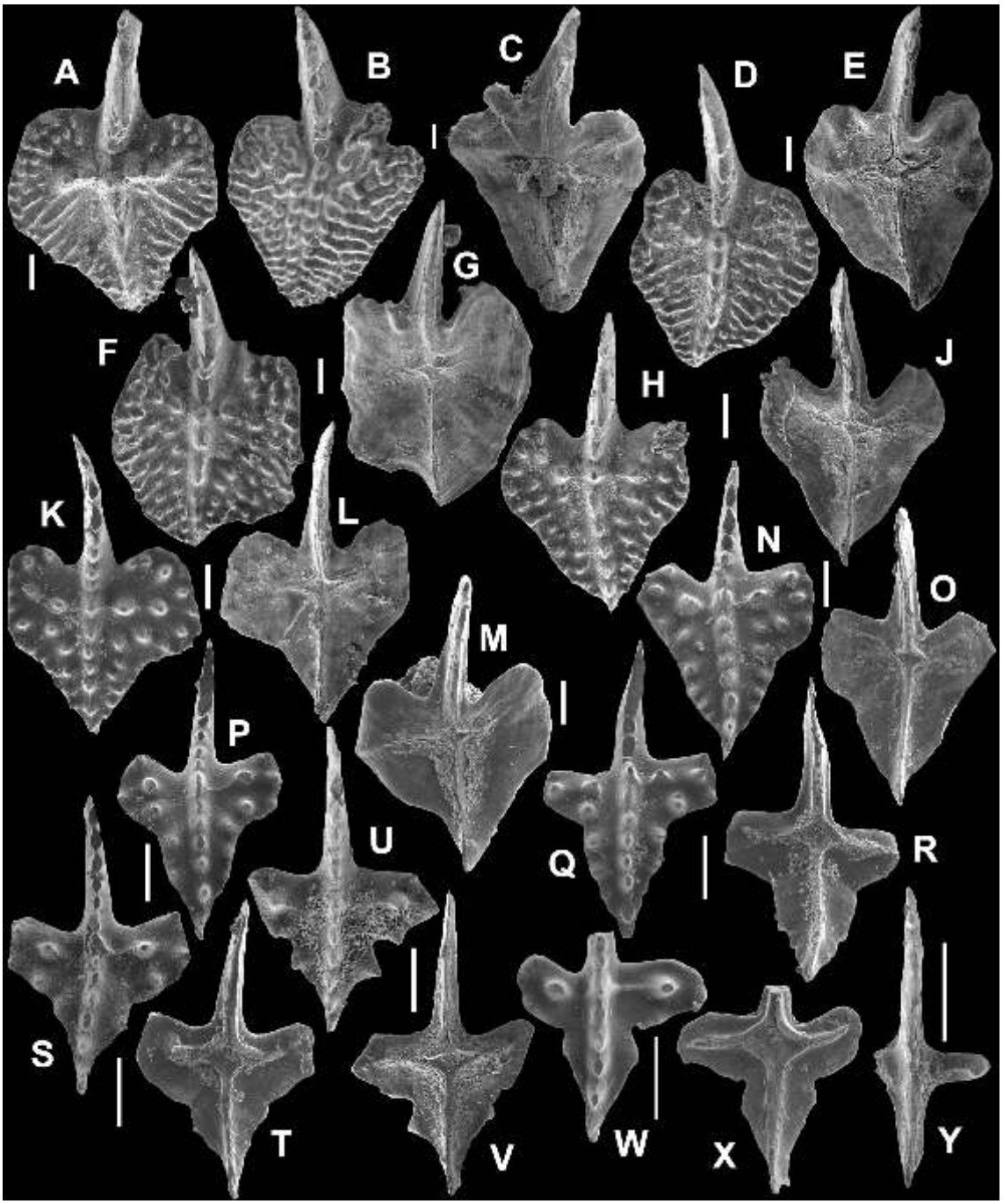

Fig. 5. Ontogenetic series 3, P_1 elements of *Ancyrodella recta* Kralick (1994) unless stated

A — PM X 3243; **B, C** — *Ancyrodella rotundiloba* (Bryant, 1931) late form, PM X 3244; **D, E** — PM X 3245; **F, G** — PM X 3246; **H, J** — PM X 3247; **K, L** — PM X 3248; **M** — PM X 3249; **N, O** — PM X 3250; **P** — PM X 3251; **Q, R** — PM X 3252; **S, T** — PM X 3253; **U, V** — PM X 3254; **W, X** — PM X 3255; **Y** — PM X 3256; specimens all from sample 8 and all vertical scale bars 150 μm

biostratigraphy of *Ancyrodella*. These include changes in platform size and outline, changes in size and shape of the basal pit, secondary keels and changes in the size and distribution of nodes on the platform surface (Kralick, 1994). The three ontogenetic series outlined above show variations in all of these factors. However, comparing them shows a few common trends that could be of use when elucidating the taxonomy of early *Ancyrodella* species:

1. There are clear size differences between the most juvenile specimens of each ontogenetic series at the start of development of nodes and lateral extensions to the platform.

2. There are distinct initial lateral developments of the platform for each series.

3. Although basal body obscures some of the cavities in the studied material, there is a general trend from juvenile specimens with cavities that cover most of the basal surface to adult specimens with cavities that are not so extensive across the

platform. Measurements of platform width to cavity size ratios may not therefore be a good way to compare between species.

4. The shape of secondary keels on the lower surface does not change through ontogeny, but, instead they extend less and less to the platform margins. García-López (1986) suggested that the variation of the outline of the platform is closely related to the development of the keel on the lower side and established a new phylogeny on this basis.

5. Folds and collars on the lower surface only become evident late in ontogeny.

6. The outline of the margin in upper view is variable. In juvenile specimens it is often controlled by the incipient addition of a node on the platform surface (see particularly series 1). In gerontic specimens, extensions to the margins can cause significant differences in platform outlines (see Figs. 2A, 4A and 5A). Platform shape analysis may not therefore be such as useful tool for *Ancyrodella* as has been shown for *Palmatolepis* (e.g., Klapper and Foster, 1993).

TAXONOMICAL DISCUSSION

SERIES 1

The prominent nodes on younger specimens of this series are very similar to *A. binodosa* alpha morphotype as identified by Bultynck (1983, fig. 1.24, 26). However the specimens figured here differ from the alpha morphotype specimens of *A. binodosa* of Bultynck and Jacobs (1981, pl. 8, figs. 1–12), as they have lateral keels developed in both the juvenile (Fig. 2U) and more adult specimens (Fig. 2J). Only juvenile specimens in the ontogenetic series described here, resemble *A. binodosa* as figured in upper view by Uyeno (1967, pl. 1, figs. 2 and 5) originally as *Ancyrodella rotundiloba binodosa* sp. nov. However, comparison of the size of the specimen figured by Uyeno (1967, pl. 1, fig. 4) with the specimens in series 1 shows that the series 1 specimens have many more nodes by the time they reach this size. Sandberg *et al.* (1989) considered the holotype (Uyeno, 1967, pl. 1, fig. 2) of *A. binodosa* Uyeno (1967) to be a small specimen and to resemble small specimens of younger species of *Ancyrodella*. A possibility that cannot be discounted here is that series 1 represents a mixture of *A. binodosa* and a younger species of *Ancyrodella*. This may well be the case as figure 5 of Uyeno (1967) is very close to some of the most juvenile specimens in series 1. There has been much discussion on the criteria for distinction of *A. binodosa* from early forms of *A. rotundiloba*. Klapper (1985) argued that *A. binodosa* cannot be distinguished from early *A. rotundiloba* on the basis of juvenile specimens that he considered virtually identical and remarked that it is unfortunate that the holotype for *A. binodosa* should be a relatively small specimen. Bultynck and Jacobs (1981) preferred to use pit size as the main criteria for distinction. However, that can't be tested on the material illustrated here as most of the specimens have basal body filling the cavity.

Some specimens illustrated in series 1 (Fig. 2) appear to be closer to specimens illustrated as *A. pristina* and *A. soluta* by Sandberg *et al.* (1989) with morphotypes 1 and 2 of *A. soluta* (Fig. 2C, P) 2 and 3 of *A. pristina* (Fig. 2N) represented. Klapper (2000) considered *A. soluta* to coincide with the early form of *A. rotundiloba* with the holotype representing an intermediate between early and late forms of the species. It should also be noted that the basal pit of the holotype of *A. soluta* is clearly smaller than in all other figured specimens assigned to *A. soluta*. Kralick (1994) considered *A. pristina* and *A. soluta* to be too similar to be identified apart. According to Sandberg *et al*. (1989, p. 211), "In our evolutionary scheme, once the size of the cavity has decreased somewhat and additional nodes have been inserted between the marginal nodes and the carina, a specimen is considered to be more advanced and to have evolved to *A. soluta* n. sp." However, the ontogenetic series 1 illustrated here shows that marginal nodes are inserted during ontogeny with cavity size relative to the total size of the platform also a function of ontogeny. If the sample was considered to have contained a mixture of *A. soluta* and *A. pristina* specimens as is suggested above, then nodes would not have been added and cavity size would not have decreased as evenly as it does in ontogenetic series 1. This confirms that Kralick (1994) was probably right to consider *A. soluta* and *A. pristina* synonymous. In this case, the identification of *A. pristina* is preferred as it has priority over *A. soluta*. It has also been suggested (Bultynck, pers. comm.) that there is no difference between the holotypes of *A. pristina* and *Ancyrodella prima* and that *A. prima* has page priority. However, the types have not been examined as part of the current study so *A. pristina* is retained herein. The more juvenile material described here fits the diagnosis for *A. pristina* of Sandberg *et al*. (1989, p. 211) as emended from Khalymbadzha and Chernysheva (1970), which states that it "is characterised by a lanceolate to triangular platform with rounded or straight anterior margins and a moderately large cruciform to T-shaped basal cavity. The upper surface ornamentation consists of two large nodes, one on either side of the carina and several small marginal nodes, mainly posterior to the large nodes."

The question remains as to whether the material from series 1 should be called early *A. rotundiloba* (*sensu* Klapper, 1985) or be identified as *A. pristina* (*sensu* Sandberg *et al.*, 1989). When distinguishing early and late forms of *A. rotundiloba*, Klapper (1995, p. 23) used the following criteria "a decrease in the size of the pit from relatively large to one of moderate size permits recognition of stratigraphically early and late forms of the species even though the two forms intergrade." All of the ontogenetic series show that the width of the basal pit changes through ontogeny but depth cannot be accurately determined because basal body fills most specimens in the material studied herein. Pit size/depth would not seem to be a good criterion to decide between early and late forms in the material described here. As a result, the identification of *A. pristina* has been retained.

SERIES 2

The juveniles of this series are distinct from those of series 1 as prominent nodes do not appear as early in ontogeny (Fig. 3S, U) as they do in similar sized elements in series 1 (Fig. 2X). However, Figure 3 also contains some elements that are common to series 1 (compare Fig. 2W with 3Q and Fig. 2F, G with 3H, J). Figure 3U is also comparable to a specimen figured as *Ancyrodella* sp. but present in the same sample as both *A. pristina* and *A. soluta* (Sandberg *et al.*,1989; pl. 1, figs. 7–8).

Series 2 may well represent a mixture of taxa as Figure 3A–E include specimens that some workers would consider to be *A. rotundiloba* (Sandberg *et al*., 1989, pl. 3, figs. 2, 4; Kralick, 1994, figs 3.21–24; Iudina, 1995, fig. 2). Kralick (1994, p. 1387) and Klapper (2000, p. 154), both identify the specimen in Sandberg *et al*. (1989, pl. 3, figs. 1, 2) as *A. recta*. Furthermore, Klapper (2000, p. 156) states: "*Ancyrodella rotundiloba* in the sense of Sandberg *et al*. (1989) primarily refers to specimens of *A. recta* . . .". However, the ontogenetic series shown here is distinct from that of *A. recta* (see discussion in next section). Only a few specimens show characteristics of series 1 so it is suggested that Figure 3 could mainly represent an ontogenetic series of *A. rotundiloba* but with minor numbers of *A. pristina* in the same sample.

SERIES 3

Juvenile specimens in series 3 have a very distinctive early growth of the posterior part of the platform in an arrowhead-like shape (Figs. 4T and 5U, W). The characteristic cruciform appearance on the platform surface of specimens in ontogenetic series 3 has also been shown for the late form of *A. rotundiloba* from the Montagne Noire, which also have large nodes on either side of the carina (Klapper, 1985, pls. 1–3). However, in these specimens the cross is made by only one or two prominent nodes rather than up to 4 in the series 3 material (Figs. 4B, F and 5A, F). The ontogenetic series is consistent with the diagnosis of Kralick (1994) for *A. recta*, which is characterised by a straight margin on the inner lobe, a moderately sized pit, secondary keels moderately to well developed and the inner keel curved anteriorly. Kralick (1994) distinguished *A. recta* from late forms of *A. rotundiloba* on platform outline (shape and orientation of anterior lobes) and secondary keel development saying that these in *A. rotundiloba* are at most incipiently developed. Klapper *et al.* (2004) are also in agreement with this. However, the more juvenile specimens in samples 7 and 8 in lower view have well developed keels (Figs. 4K, M, O, S, U, W and 5R, T, V, X). As with sample 7, minor numbers of adult *A. rotundiloba* specimens are present (Figs. 3A–E and 5B). It would seem that ontogenetic series 3 probably represents mainly *A. recta* mixed with some late forms of *A. rotundiloba*.

BIOSTRATIGRAPHICAL SIGNIFICANCE

Regardless of whether the identifications of the taxa present in the ontogenetic series obtain general agreement, series 1 shows evidence of growth of a typical late Givetian "early *rotundiloba*-type" *Ancyrodella* while series 3 shows a typical early Frasnian "late *rotundiloba*" *Ancyrodella*, as *A. recta* is seen (Kralick, 1994) as a transition form between late *A. rotundiloba* and *A. alata*. Distinct size and early growth shape differences in the juvenile specimens can also be recognised and can potentially be used to distinguish forms from the late Givetian from those of the early Frasnian. This has proved difficult in the past (see Taxonomic Discussion section). Previously, the use of the first occurrence of *Ancyrodella* species to mark the Middle–Upper Devonian boundary was brought into question as lack of knowledge of taxa ancestral to *A. rotundiloba* gave rise to the argument by Sandberg *et al*. (1989) that the first occurrence could be a biofacies first occurrence (Racki and Wrzolek, 1989). Documentation of the ontogenetic series of *A. pristina* will be useful for the knowledge of early *Ancyrodella* taxa, particularly in the late Givetian. The problems with using P_1 element taxonomy alone have been highlighted by the debates surrounding the use of *A. rotundiloba* for defining the Middle–Upper Devonian boundary. Future studies could be focussed towards morphometric studies, particularly in size variations between taxa at juvenile stages of growth. Although this contribution has suggested some taxonomic criteria are more important than others, it is possible that considering conodonts in a multielemental context may well be the way forward in studies of biostratigraphy and phylogeny. This concept has already been tried for *Ancyrodella* by Klapper and Philip (1971, 1972), Schülke (1997) and Dzik (2002). With regards to the Kozhym River section, it would be interesting to carry out bed by bed studies to test the ontogenetic series described here and to more accurately place the Middle–Upper Devonian boundary that, on the occurrence *A. recta* and of late forms of *A. rotundiloba* in sample 7, should be placed somewhere between samples 6 and 7.

CONCLUSIONS

Ontogenetic series showing predominantly *Ancyrodella pristina* and *Ancyrodella recta* have been illustrated. There is a general trend from juvenile specimens with laterally more extensive basal pits to adult specimens with smaller pits compared to the width of the platform.

Juvenile specimens of both series can be distinguished by their size at the onset of platform and node growth and can be used in biostratigraphy to recognise typical late Givetian and early Frasnian forms.

The shape of secondary keels on lower surfaces does not change through ontogeny, but instead they extend less and less to the platform margins.

Folds and collars on the lower surface only become evident in the most adult specimens.

Platform outline is variable and is controlled in juveniles by the addition of nodes to the platform margin; gerontic specimens sometimes have additional projections to the lateral margins. Detailed morphometric studies of P_1 element platform outlines may therefore have limited value.

Future studies on ontogenetic series, particularly the morphometrics of juveniles of early species of *Ancyrodella*, are important for ensuring that conodonts continue to be useful to correlate the Middle–Upper Devonian boundary.

Detailed bed by bed sampling of the Kozhym River section would be a good step in that direction and is needed to accurately place the Middle–Upper Devonian boundary in that section.

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