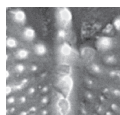


# Revision of the Frasnian Late Devonian conodont genus *Ancyrodella*

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This paper revises all the species of the Frasnian Late Devonian genus *Ancyrodella*. Seventeen species are recognized, as well as several intraspecific morphotypes not considered separate species. Illustrated specimens are all from collections from the Canning Basin, Western Australia, but publications of global Devonian tropical localities are also reviewed in the synonymies. The taxonomic approach herein is one using the controversial “vertical chronospecies” based primarily on the Pa elements’ platform outline and the pattern of secondary carinae and keels, if present. Multielement reconstructions have been few. In view of the widespread confusion and variable application of species names, zonations based on the succession of *Ancyrodella* species appear premature. • Key words: conodonts, Frasnian Stage, Late Devonian, Canning Basin, Western Australia.

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The Frasnian conodont *Ancyrodella* has not had a comprehensive taxonomic treatment at the genus level for many years, not since two papers by García-López (1986, 1987) in which she presented a phylogeny for the entire genus, as did Ziegler (1962a) at a much earlier stage of knowledge. Other papers since the 1980s have dealt only with some of the species of *Ancyrodella*, whether for taxonomic or biostratigraphic purposes. This is in contrast to three other Frasnian genera, *Palmatolepis* (e.g., Ziegler 1962a, b; Helms 1963; Ziegler & Sandberg 1990; Klapper & Foster 1993; Dzik 2002; Klapper 2007a, b), *Ancyrognathus* (e.g., Klapper 1990, Sandberg *et al.* 1992) and *Polygnathus* (e.g., Ziegler *et al.* 2000, Ovnatanova & Kononova 2001). Thus, a taxonomic revision of all *Ancyrodella* species is overdue.

The purpose of this paper is entirely taxonomic; the biostratigraphy of *Ancyrodella* has been treated in many papers. The chronostratigraphic definition and GSSP for the lower boundary of the Frasnian Stage is positioned on what was then thought to be the lowest occurrence of *A. rotundiloba* early form (Klapper *et al.* 1993; Becker *et al.* 2012, fig. 22.7 = *A. pristina* in current terminology). At the stratotype section, Col du Puech de la Suque in the Montagne Noire, however, Liao *et al.* (2019) reported a lower occurrence of *A. pristina* approximately 30 cm below the current GSSP. Of course, it would be possible to lower the GSSP this small stratigraphic interval at the stratotype section. Before this lower occurrence of *A. pristina* was known, however, another possibility of revision

for the GSSP was suggested by Racki & Wrzolek (1989, p. 233, fig. 1) and Klapper (2000, p. 154). This was to revise the position of the base of the Frasnian to coincide with the lowest occurrence *A. rotundiloba* s.s. (= late form in earlier terminology), because that is part of a lineage, whereas *A. pristina* enters known sections as a cryptogene.

## A Taxonomic controversy

Dzik (1985, pp. 72–74; 1990, fig. 4) advocated horizontally defined chronospecies (that is, use of a population approach), both for ammonoids and conodonts, as opposed to vertically defined chronospecies in his terminology. The latter he terms “typologic”, which implies basing fossil species on a highly limited sample of specimens. It can be said, however, that some practitioners of the vertical concept can and have also analyzed large samples from fossil populations. A fundamental issue is whether or not the vertical as well as the horizontal approach to species definition demonstrates the full range of intraspecific variation, a feature that has often been ignored in much recent conodont literature (Klapper & Vodrážková 2013).

Dzik (2002, e.g., fig. 49; Dzik *et al.* 2018, fig. 10) used a zonation for the Frasnian based on the succession of species of *Ancyrodella* that “seems much more reliable as the basis for time correlation than the evolution of palmatolepidids [*Palmatolepis* and *Mesotaxis*], widely used for this purpose” (*op. cit.* 2002, p. 621). He recom-

mended such a zonation despite stating the caveat that “*Ancyrodella* species are generally very variable and the status of the majority of them is questionable” (*op. cit.*, p. 618). If this is correct, then how can a zonation based on species of *Ancyrodella* be practicable? In an attempt to answer this question, the synonymies in the Systematic Paleontology section herein indicate that many of the species have been deeply conflated. Recently, Piszarszewska *et al.* (2020) used a Frasnian zonation based on *Ancyrodella* species that is subject to the same reservations as Dzik’s zonation.

Dzik (2002, p. 617) criticized a number of authors of papers involving *Ancyrodella* (from Klapper 1985 to Gouwy & Bultynck 2000, seven papers in all) for using “the vertical (typological) species concept which is highly inappropriate for such a variable and ontogenetically sensitive character as these conodonts’ platform shape”.

Nevertheless, is Dzik’s use of a horizontal species concept superior *in practice* to a vertical approach, which it is according to his theoretical viewpoint? In Dzik *et al.* (2018, fig. 3) *Ancyrodella nodosa*, the defining species of its eponymous zone, is illustrated by five specimens. Leaving aside the juvenile specimen (Dzik *et al.* 2018, fig. 3k) and a fragmentary and poorly preserved specimen from one of the two Vietnam sections of the 2018 paper (fig. 3o), the three Polish specimens represent two distinct species in the vertical taxonomic approach used herein (fig. 3l, m = *A. nodosa* and 3n = *A. lobata*). The specimens in fig. 3l–n are from the same Holy Cross Mts section and sample but Dzik has not in either paper shown intermediates between the two “vertical” species, the differences of which are outlined in the Systematic Paleontology section. Dzik (2002, fig. 26) used biometrics, involving platform element length and density of tubercles, on earlier species of *Ancyrodella*, but did not publish biometrics supporting his horizontal concept of *A. nodosa*. Platform shape of the Pa (P1) element, which Dzik (*op. cit.*, p. 617) discounted as too variable, is in contrast heavily weighted in the taxonomic approach used herein.

This paper attempts to analyze all species of *Ancyrodella* here considered valid, by means of comparisons and nearly complete synonymies. Specimens illustrated in the literature that are not well enough preserved or not provided with critical lower views, when such are needed, are not listed in the synonymies in most instances. Unfortunately, not all the valid species could be illustrated from the available Canning Basin material at this time, but all are represented in the published literature.

## Systematic paleontology

This analysis focuses on the Pa element of *Ancyrodella* (in the system of notation used by Sweet 1988 and his earlier

papers). The diagnoses are limited to the distinguishing morphologic characteristics of the species. Multielement reconstructions have been few, primarily that of Schülke (1997); two other partial reconstructions are cited in the synonymies. The photographs on Figure 1B–R and all of Figure 3A–I were taken with a Canon D50 digital camera mounted on a Leitz Aristophot with a 50 mm Milnar lens. Figure 1A and Figure 2A–K were taken with the same Aristophot and lens but with a Leica M back and Kodak Technical Pan film. All specimens on Figures 1–3 are from the Canning Basin and are deposited in the Geological Survey of Western Australia (GSWA) collections with numbers following the letter F. As a matter of presentation only, the genus is divided into four groups.

### Genus *Ancyrodella* Ulrich & Bassler, 1926

*Type Species.* – *Ancyrodella nodosa* Ulrich & Bassler, 1926.

#### *Ancyrodella rotundiloba* Group

The group includes *A. binodosa*, *A. crosbiensis*, *A. pristina*, *A. recta*, *A. rotundiloba* s.s., *A. rugosa*, and *A. triangulata*.

#### *Ancyrodella binodosa* Uyeno, 1967

- 1967 *Ancyrodella rotundiloba binodosa* n. subsp.; Uyeno, pp. 4, 5, pl. 1, figs 2, 4, 5 [fig. 2 = holotype].
- [non] 1970 *Ancyrodella prima* sp. nov.; Khalymbadzha & Chernysheva, pp. 88, 89, pl. 1, figs 1, 2 [= transitional between *A. binodosa* and *A. pristina*].
- 1973 *Ancyrodella rotundiloba binodosa* Uyeno. – Ziegler, pp. 35, 36, *Ancyro* pl. 1, fig. 4 [reillustration of holotype].
- 1974 *Ancyrodella rotundiloba binodosa* Uyeno. – Uyeno, pp. 24, 25, pl. 1, figs 4–6 [fig. 5 = reillustration of Uyeno 1967, pl. 1, fig. 4; non fig. 2 = *A. pristina*]; pl. 2, figs 2, 3, 5 [fig. 2 = reillustration of holotype; fig. 3 = Uyeno 1967, pl. 1, fig. 5].
- [non] 1981 *Ancyrodella binodosa* Uyeno. – Bultynck & Hollard, p. 38, pl. 10, fig. 4 [= transitional between *A. binodosa* and *A. pristina*].
- 1982 *Ancyrodella binodosa* Uyeno. – Bultynck, p. 56, pl. 1, figs 18, 25, 28–30 [only].
- 1982 *Ancyrodella binodosa* Uyeno. – Mouravieff, pp. 112, 113, pl. 1, figs 1–3, 9, 11, 13, 21 [only; fig. 8? = juvenile]; pl. 2, figs 2, 3.
- 1983 *Ancyrodella binodosa* Uyeno delta morphotype. – Bultynck, p. 165, figs 1.12–1.15 [non figs 1.16–1.20 = transitional between *A. binodosa* and *A. pristina*].
- 1986 *Ancyrodella binodosa* Uyeno. – García-López, p. 450, pl. 1, figs 1–3 [non figs 4, 5 = ?].

- 1987 *Ancyrodella binodosa* Uyeno. – García-López, pp. 58, 59, pl. 1, figs 1–3 [*non* figs 4, 5 = ?; same illustrations as preceding reference].
- 1989 *Ancyrodella binodosa* Uyeno. – Sandberg, Ziegler & Bultynck, pp. 209, 210, fig. 2.1, pl. 1, figs 1, 2.
- 1991 *Ancyrodella* sp. aff. *A. binodosa* Uyeno. – Irwin & Orchard, p. 206, pl. 2, fig. 2.
- 1993 *Ancyrodella binodosa* Uyeno. – Racki & Bultynck, pl. 7, figs 7, 8.
- 1999 *Ancyrodella binodosa* Uyeno. – Lazreq, pp. 57, 58, pl. 3, figs 4–7.
- 2007 *Ancyrodella binodosa* Uyeno. – Gouwy, Haydukiewicz & Bultynck, p. 388.
- 2013 *Ancyrodella binodosa* Uyeno. – Gouwy, Liao & Valenzuela-Rios, pp. 322, 323, fig. 6d–g.
- 2013 *Ancyrodella binodosa* Uyeno. – Gholamalian *et al.*, p. 143, pl. 1, figs 14–19.
- 2017 *Ancyrodella binodosa* Uyeno. – Ovnatanova *et al.*, p. 1045, 1046, pl. 8, fig. 8.

**Diagnosis.** – *Ancyrodella binodosa* is restricted to specimens with a single large node on each anterior lobe, but extends to rarer forms with 1–2 tiny posterior denticles.

**Remarks.** – *Ancyrodella binodosa* characteristically has only a single large node on each circular anterior lobe (e.g., Uyeno, 1974, pl. 2, fig. 5; Bultynck, 1982, pl. 1, figs 25, 28–30). Exceptional forms have at most 1–2 small denticles posterior of the anterior large nodes (e.g., Uyeno 1967, pl. 1, fig. 4b). The species should be restricted to these forms. The delta morphotype of *A. binodosa* sensu Bultynck & Jacobs (1981, pl. 9, figs 3, 4, 7, 8) has more posterior nodes, except the juvenile in fig. 5, and is considered herein as transitional between *A. binodosa* and *A. pristina* (see synonymy for the latter). This restricted concept of *A. binodosa* is in agreement with the discussion and species definition of Gouwy *et al.* (2007, p. 388).

Juveniles of *A. binodosa* are difficult to distinguish from those of later *Ancyrodella* species such as *A. pristina* and *A. rotundiloba* s.s., if taken out of stratigraphic context. Therefore, confident identification should be based on large, adult specimens as emphasized by Gouwy *et al.* (2007, *op. cit.*).

There are transitional specimens between *A. binodosa* and *A. pristina*, as indicated in their synonymy lists, including the *A. prima* holotype. These are not assigned to either species.

“Occurring with *Ancyrodella binodosa* in sample ‘F 27 top’ at Blauer Bruch, near Bad Wildungen, Germany, a locality notable for the abundant sequential occurrence of species of *Ancyrodella*, is a small specimen identified as *Ancyrodella* sp. (Sandberg *et al.* 1989, pl. 1, figs 7, 8 and text-fig. 4). This specimen, which displays two pointed conical denticles protruding laterally from the

blade, is now considered to represent another early species of *Ancyrodella* rather than an unidentifiable juvenile” (C.A. Sandberg, written communication, February 24, 2021).

### ***Ancyrodella crosbiensis* Kralick, 1994**

- 1981 *Polygnathus cristatus* Hinde. – Huddle, pp. b28, b29, pl. 9, figs 11–19; pl. 10, figs 1–18.
- 1994 *Ancyrodella crosbiensis* n. sp.; Kralick, p. 1387, figs 5.1–5.2, 5.5–5.6 [fig. 5.5, 5.6 = holotype].
- 2020 *Ancyrodella crosbiensis* Kralick. – Kirchgasser *in* Kirchgasser *et al.*, p. 209, fig. 5h, i.

**Diagnosis.** – *Ancyrodella crosbiensis* does not have a marked depression between the posterior end of the free blade and the beginning of the carina. There are 2–5 diagonal rows of nodes on either side of, and converging posteriorly toward the carina at the anterior end of the platform.

**Remarks.** – In contrast to *A. crosbiensis*, the Pa element of *A. rotundiloba* s.s. has a marked depression in which there is a distinct gap in denticulation or tiny nodes between the free blade and carina. Although most illustrated specimens of *A. crosbiensis* have a small pit like that of *A. rotundiloba* s.s., exceptions which have a pit resembling that of *A. pristina* are the holotype (Kralick 1994, fig. 5.5) and the specimens of Huddle (1981, pl. 10, figs 6, 14). *Ancyrodella rotundiloba* s.s. does not have diagonal rows of nodes anteriorly (= rostral ridges of Huddle, 1981, p. b28 and explanation of the specimen in pl. 10, fig. 6).

### ***Ancyrodella pristina* Khalymbadzhia & Chernysheva, 1970**

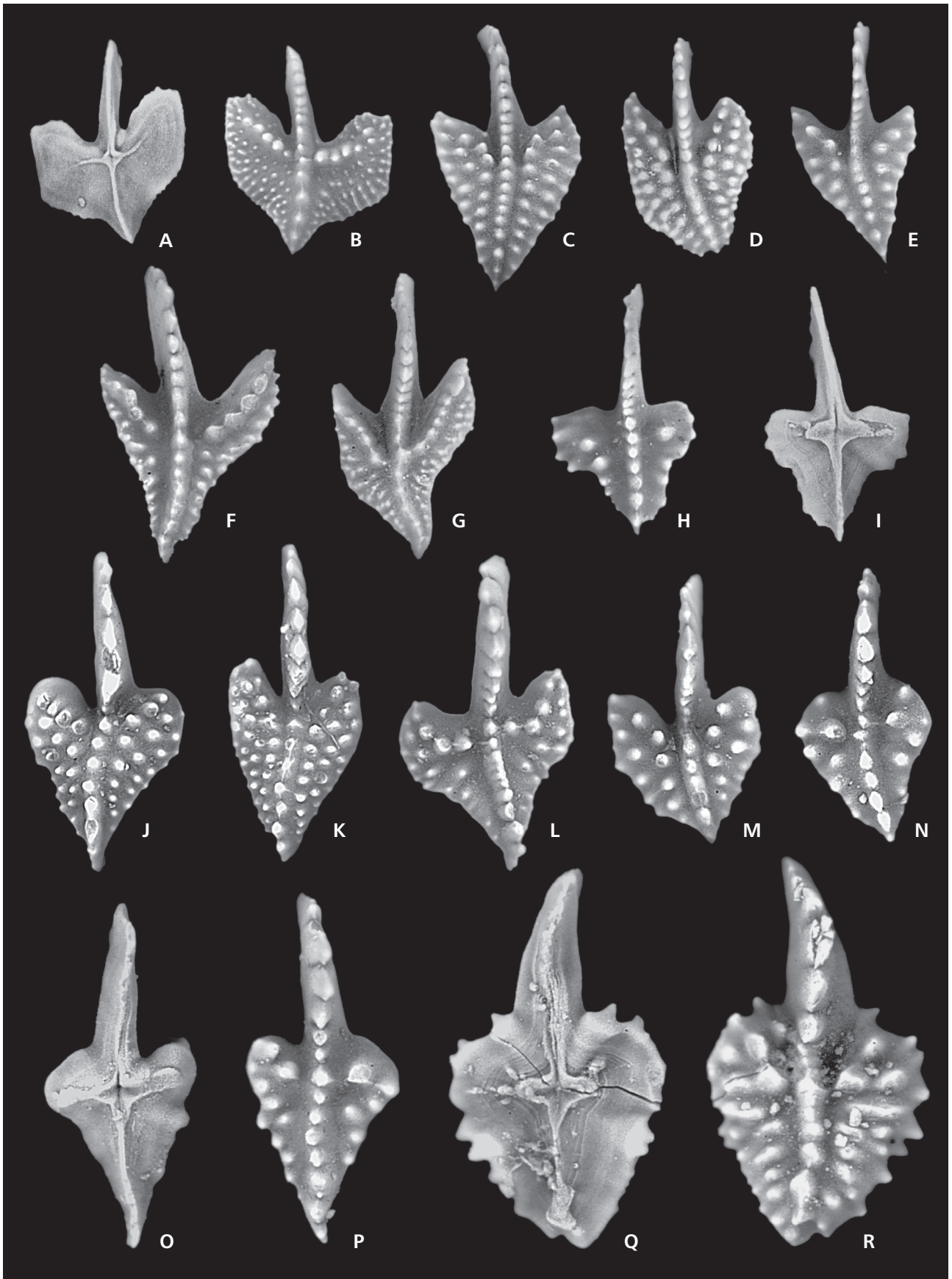
Figure 1N–P

- 1967 *Ancyrodella rotundiloba* subsp. A; Uyeno, p. 5, pl. 1, fig. 3 [only; reillustrated under same designation by Uyeno, 1974, pl. 2, fig. 6; figs 7, 9 probably belong to the same species].
- 1970 *Ancyrodella pristina* sp. nov.; Khalymbadzhia & Chernysheva, pp. 89, 90, pl. 1, figs 3–8 [figs 5–7 = holotype].
- 1970 *Ancyrodella rotundiloba* (Bryant). – Kirchgasser, pp. 343, 344, pl. 65, figs 5, 6, 9 [fig. 8 = ?].
- 1971 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Szulczewski, p. 15, pl. 1, fig. 4 [only].
- 1974 *Ancyrodella rotundiloba binodosa* Uyeno. – Uyeno, pp. 24, 25, pl. 1, fig. 2 [only].
- 1976 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Druce, pp. 62–64, pl. 9, figs 1–5, 7 [only].
- 1981 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Bultynck & Hollard, p. 38, pl. 10, fig. 7.
- 1981 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Huddle, pp. b19, b20, pl. 1, figs 11–13 [only].

- 1981 *Ancyrodella binodosa* Uyeno. – Bultynck & Jacobs, pp. 16, 17, pl. 8, figs 1–14; pl. 9, figs 1, 2, 6 [non figs 3–5, 7, 8 = transitional between *A. binodosa* and *A. pristina*].
- 1982 *Ancyrodella binodosa* Uyeno. – Bultynck, p. 56, pl. 1, figs 19–24 [only].
- 1982 *Ancyrodella binodosa* Uyeno. – Mouravieff, p. 112, pl. 1, figs 4, 5, 10, 12, 14–20 [only].
- 1983 *Ancyrodella binodosa* Uyeno. – Bultynck, p. 165, figs 1.21–1.27, 1.32–1.34.
- 1985 *Ancyrodella rotundiloba* (Bryant) early form. – Klapper, pp. 24, 26, 27, pl. 1, figs 1–20; pl. 2, figs 5–12; pl. 3, figs 5–9 [misprinted as late form; corrected in distributed reprints], 10, 11.
- 1989 *Ancyrodella pristina* Khalymbadzha & Chernysheva. – Sandberg, Ziegler & Bultynck, pp. 210, 211, figs 2.2–2.4, pl. 1, figs 3, 4, 9, 10, 13, 14.
- 1989 *Ancyrodella soluta* n. sp.; Sandberg, Ziegler & Bultynck, pp. 211, 212, figs 2.5–2.7, pl. 1, figs 5, 6, 11, 12 [only].
- 1989 *A. sp. n.* – Racki & Wrzolek, pp. 234, 236, fig. 1 [drawing of specimen in Klapper 1985, pl. 1, figs 11, 12 = *A. pristina*].
- 1992 *Ancyrodella rotundiloba* (Bryant) early form sensu Klapper (1985)? – Uyeno, p. 128, pl. 15, figs 5, 6, 15, 16.
- 1992 *Ancyrodella rotundiloba* (Bryant) early form sensu Klapper (1985). – Uyeno, p. 128, pl. 15, figs 7, 8.
- 1993 *Ancyrodella pristina* Khalymbadzha & Chernysheva. – Racki & Bultynck, pl. 6, fig. 1; pl. 7, fig. 5 [upper view of same specimen], fig. 6 [= ?].
- 1993 *Ancyrodella soluta* Sandberg, Ziegler, & Bultynck. – Racki & Bultynck, pl. 6, figs 2, 3, 7 [fig. 7, because of the pit size, not the outline]; pl. 7, figs 1, 2, 9, 10 [figs 3, 11 = ?, because the outline is that of *A. rotundiloba* s.s., but the pit is not shown].
- 1993 *Ancyrodella pristina* Khalymbadzha & Chernysheva. – Ji & Ziegler, pp. 53, 54, pl. 1, figs 7–9.
- 1994 *Ancyrodella rotundiloba* (Bryant) early morphotype. – Kirchgasser, pp. 123, 125, pl. 1, figs a–i, pl. 2, figs a–k, n–p.
- 1994 *Ancyrodella rotundiloba* (Bryant). – Kralick, p. 1387, figs 4.7, 4.8; 5.3, 5.4, 5.7, 5.8 [only; the pit in fig. 5.7 is transitional between *A. pristina* and *A. rotundiloba*].
- 1998a *Ancyrodella pristina* Khalymbadzha & Chernysheva. – Spalletta & Perri, p. 197, pl. 2.1.1, fig. 6.
- 1999 *Ancyrodella pristina* Khalymbadzha & Chernysheva. – Lazreq, p. 60, pl. 3, figs 8, 9, 13.
- 1999 *Ancyrodella soluta* Sandberg, Ziegler & Bultynck. – Lazreq, p. 60, pl. 3, fig. 10.
- 2000 *Ancyrodella rotundiloba* (Bryant, 1921) early form. – Klapper, pl. 1, figs 1, 5 [reillustration of Klapper, 1985, pl. 3, figs 5, 6].
- 2005 *Ancyrodella rotundiloba* (Bryant, 1921) early form of Klapper (1985). – Uyeno & Wendte, p. 163, pl. 1, figs 1, 2.
- 2005 *Ancyrodella rotundiloba* (Bryant, 1921) late form of Klapper (1985). – Uyeno & Wendte, p. 163, pl. 1, figs 4, 5.
- 2007 *Ancyrodella rotundiloba pristina* Khalymbadzha & Chernysheva. – Aboussalam & Becker, pp. 364, 365, fig. 9k, l, o–r [interpreted herein as an ontogenetic series, rather than different morphotypes].
- 2007 *Ad. rotundiloba binodosa*. – Aboussalam & Becker, p. 359, fig. 9m, n [i, j may represent an early ontogenetic stage].
- 2007 *Ancyrodella pristina* Khalymbadzha & Chernysheva. – Miller, p. 446, fig. 2l–y [in 2e and 2j the pit appears to be too small for this species; in 2b and 2g the pit is covered by basal plate; in fig. 3h, j the pit also seems too small for *A. pristina*].
- 2007 *Ancyrodella rotundiloba*. – Over, p. 1202, figs 11.18, 11.21.
- 2008 *Ancyrodella pristina* Khalymbadzha & Chernysheva. – Liao & Valenzuela-Ríos, pp. 2, 3, 7, fig. 6j [6i = ?].
- 2008 *Ancyrodella soluta* Sandberg, Ziegler, & Bultynck. – Liao & Valenzuela-Ríos, p. 7, fig. 6k–p.
- 2008 *Ancyrodella binodosa* Uyeno. – Ovnatanova & Kononova, p. 1080, 1155, pl. 26, fig. 3 [only; figs 1, 2 = possibly juveniles of *A. pristina*].
- 2012 *Ancyrodella rotundiloba* (early morphotype = *rot. pristina*). – Becker *et al.*, p. 569, fig. 22.7d, e.
- 2013 *Ancyrodella pristina* Khalymbadzha & Chernysheva. – Gouwy, Liao & Valenzuela-Ríos, p. 323, fig. 6l, m.
- 2013 *Ancyrodella pristina* “transitional form with *Ad. rotundiloba* (Bryant, 1921)”. – Gouwy, Liao & Valenzuela-Ríos, p. 332, fig. 6n, o.
- 2013 Transitional form between *Ancyrodella binodosa* Uyeno, 1967 and *Ancyrodella pristina* Khalymbadzha & Chernysheva, 1970. – Gouwy, Liao & Valenzuela-Ríos, p. 332, fig. 6i, j.

**Figure 1.** All photograph magnifications are ×40. Abbreviations: see Appendix: Localities of illustrated specimens; FZ = Frasnian Zone. • A, B – *Ancyrodella alata* Glenister et Klapper 1966, lower and upper views of F54956, TH 370-A, FZ 4. • C–F – *Ancyrodella nodosa* Ulrich et Bassler 1926; C–E – upper views of F54957–54959, WMcP 365-4, 9, 11, FZ 5; F – upper view of F54960, HS 364-18, FZ 11. • G – *Ancyrodella hamata* Ulrich et Bassler 1926, upper view of F54961, HS 364-71, FZ 13b. • H, I, L – *Ancyrodella africana* García-López 1981; H, I – upper and lower views of F54962, TH 370-D, FZ 4; L – upper view of F54963, TH 370-B, FZ 4. • J, K – *Ancyrodella rugosa* Branson et Mehl 1934, upper views of F54964–54965, Capped-Oncolite locality, sample 3, FZ 4. • M – *Ancyrodella devonica* García-López 1986, upper view of F54966, TH 370-I, FZ 4. • N–P – *Ancyrodella pristina* Khalymbadzha & Chernysheva 1970; N – upper view of F54967, Outcamp Hill, FZ 2; O, P – lower and upper views of F54968, Outcamp Hill, FZ 2. • Q, R – *Ancyrodella rotundiloba* (Bryant, 1921), lower and upper views of F54969, Outcamp Hill, FZ 2.





- 2013 *Ancyrodella pristina* Khalymbadzhia & Chernysheva. – Liao & Valenzuela-Rios, pp. 346, 347, fig. 6a, b.
- 2013 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Liao & Valenzuela-Rios, pp. 347, 348, fig. 6f [only].
- 2013 *Ancyrodella rotundiloba* (Bryant, 1921) early form. – Gholamalian *et al.*, p. 143, pl. 1, figs 1–13.
- 2014 *Ancyrodella pristina* Khalymbadzhia & Chernysheva. – Bahrami *et al.*, p. 184, pl. 1, fig. 17.
- 2016 *Ancyrodella rotundiloba pristina* Khalymbadzhia & Chernysheva. – Klapper & Kirchgasser, p. 537, figs 7.5, 7.10.
- 2017 *Ancyrodella pristina* Khalymbadzhia & Chernysheva. – Ovnatanova *et al.*, pp. 1049, 1050, pl. 11, fig. 7.
- 2017 *Ancyrodella soluta* Sandberg, Ziegler & Bultynck. – Ovnatanova *et al.*, pp. 1055, 1056, pl. 29, fig. 6 [only].
- 2019 *Ancyrodella rotundiloba soluta* Sandberg, Ziegler & Bultynck. – Telnova, Soboleva & Sobolev, p. 259, fig. 4.1.
- 2019 *Ancyrodella rotundiloba pristina* Khalymbadzhia & Chernysheva. – Özkan *et al.*, p. 216, figs 6.13, 6.14.
- 2020a *Ancyrodella* [as *Ad.*] *rotundiloba pristina*. – Becker *et al.*, p. 75, figs 62.17, 62.18.
- 2020 *Ancyrodella* [as *Ad.*] *rotundiloba pristina*. – Aboussalam *et al.*, p. 148, fig. 20.6.

**Diagnosis.** – *Ancyrodella pristina* is distinguished from *A. rotundiloba* s.s. by having a basal pit that is more extensive laterally. Neither species has well developed secondary keels.

**Remarks.** – *Ancyrodella pristina* Khalymbadzhia and Chernysheva was proposed as a new species in 1970 (pp. 89, 90, pl. 1, figs 3–8; holotype = figs 5–7). The species was mostly long overlooked until the paper of Sandberg, Ziegler and Bultynck (1989, pp. 210, 211; the exception was Ziegler 1973, p. 35). Sandberg *et al.* treated the taxon as a separate species of *Ancyrodella* although some later authors (Aboussalam & Becker 2007; Klapper & Kirchgasser 2016 considered *pristina* as a subspecies of *A. rotundiloba*). Sandberg *et al.* (*op. cit.* fig. 2, a diagram of their evolutionary hypothesis) proposed a further new species termed *A. soluta*, which they regarded as transitional between *A. pristina* and *A. rotundiloba*. The analysis of the current revision, however, indicates that *pristina* and some of the specimens identified as *soluta* are intraspecific variants of the one taxon. Compare specimens in Sandberg *et al.* 1989, p. 199, figs 2.5, 2.7 identified as *soluta* with fig. 2.4 determined as *pristina*, as well as pl. 1, figs 3, 4, 9, 10 = *pristina*, with pl. 1, figs 5, 6, 11, 12 identified as *soluta*. Gouwy *et al.* (2007, p. 389) regarded the *soluta* holotype “as an extreme form in the range of variation of *An. pristina*, close to *An. rotundiloba*”. The holotype of *A. soluta*, however (Sandberg *et al.* 1989, pl. 2, figs 1, 2), fits well within the range of variation of

*A. rotundiloba* s.s. as considered herein. [A specimen that was termed a “transitional specie (sic) between *Ancyrodella rotundiloba pristina* and *Ancyrodella rotundiloba soluta*” by Zhang *et al.* (2019, p. 9, fig. 6.1) is indeterminate. Without a lower view this specimen cannot be identified with confidence as to whether it is *A. pristina* or *A. rotundiloba*]. Similarly, without lower views showing the pit size, specimens identified as *A. soluta* (Ji & Ziegler, 1993, pl. 1, figs 5, 6) cannot be determined whether they are *A. pristina* or *A. rotundiloba*. This is exemplified by specimens that have closely similar platform outlines and upper surfaces, but distinctly different pit sizes (Gouwy *et al.* 2013, fig. 6n, o *versus* fig. 6p, q)

A second difference from the Sandberg *et al.* 1989 evolutionary hypothesis is the identification of two specimens shown in their figs 2.8 and 2.10 (also as photographs in pl. 3, figs 1, 2, 8, 9), which were represented as characteristic of *Ancyrodella rotundiloba*. Instead, these specimens are characteristic of *A. recta* as has been noted previously by Kralick 1994 (p. 1387) and Klapper 2000 (pp. 154, 156). The two species are conspicuously different as shown in Klapper (2000, pl. 1, figs 2–4, 8 = *A. recta*; figs 6, 7, 9–14 = *A. rotundiloba*, lectotype = figs 13, 14) [see under *A. rotundiloba* for discussion].

The pit is more extensive laterally in *A. pristina* than in *A. rotundiloba* s.s. and is commonly larger, e.g., Klapper, 1985, pl. 1, figs 1, 4, 6, 8, 10, 14, 15, 18, 20 = *pristina* (= “early form” of *rotundiloba* in the terminology of that paper); pl. 2, figs 6, 7, 9, 11; pl. 3, figs 5, 8, 10 = *pristina* (5 and 8 were misprinted as the “late form” but corrected to “early form” in distributed reprints as noted in Klapper & Kirchgasser 2016, p. 537). In contrast, the pit is smaller in *rotundiloba* s.s. (so-called “late form” of Klapper 1985, e.g., pl. 2, figs 1, 4, pl. 3, figs 1, 3; Klapper 2000, pl. 1, fig. 1 = *pristina*, figs 6, 11, 12, 14 = *rotundiloba*; Gouwy *et al.* 2013, fig. 6o = *pristina*, fig. 6q = *rotundiloba* s.s.). The platform outline is generally more nearly triangular in *A. pristina* versus more heart-shaped in *A. rotundiloba* s.s. although there is some overlap in shape. Consequently, the species level distinction is more reliably based on the pit. Bultynck & Jacobs (1981, pl. 8, figs 1–12, their alpha morphotype of *A. binodosa*) illustrated an excellent ontogenetic series of *A. pristina*.

#### ***Ancyrodella recta* Kralick, 1994**

- 1957 *Ancyrodella rotundiloba* (Bryant). – Bischoff & Ziegler, p. 42, pl. 16, figs 5, 10, 12, 17 [only].
- 1958 *Ancyrodella rotundiloba* (Bryant). – Ziegler, pp. 44, 45, pl. 11, fig. 12 [only].
- 1959 *Ancyrodella rotundiloba* (Bryant). – Krebs, p. 384, pl. 1, fig. 15.
- 1966 *Ancyrodella rotundiloba alata* n. subsp.; Glenister & Klapper, pp. 799, 800, pl. 86, figs 1, 2 [only].

- 1967 *Ancyrodella rotundiloba* (Bryant). – Müller & Clark, p. 908, pl. 115, fig. 8; text-figs 5d, 6i [there are two figures labeled i, the upper one appears to be *A. recta*], 6k–m, p, r, x [only].
- 1967 *Ancyrodella rotundiloba* (Bryant). – Clark & Ethington, pp. 29, 30, pl. 2, figs 9, 13 [only].
- 1969 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Pölsler, p. 404, pl. 4, figs 5, 6 [only].
- 1970 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Khalymbadza & Chernysheva, pp. 92–94, pl. 2, figs 1, 2 [only].
- 1970b *Ancyrodella rotundiloba alata* Glenister & Klapper. – Seddon, p. 94, pl. 7, fig. 4 [only].
- 1971 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Szulczewski, p. 15, pl. 2, fig. 6 [only].
- 1973 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Ziegler, pp. 29–31, Ancyro pl. 1, fig. 2 [only; reillustration of Ziegler, 1958, pl. 11, fig. 12b].
- 1974 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Uyeno, p. 24, pl. 1, fig. 3 [only].
- 1976 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Druce, pp. 64, 65, pl. 11, fig. 4 [only].
- 1980 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Klapper, p. 112, pl. 3, fig. 33.
- 1981 *Ancyrodella rotundiloba* aff. *alata* Glenister & Klapper. – Bultynck & Hollard, p. 38, pl. 9, figs 15, 16 [only].
- 1981 *Ancyrodella rotundiloba alata* Glenister & Klapper, 1966. – Huddle, pp. b20, b21, pl. 2, figs 20–24 [only; pl. 1, figs 25–27 are too small for confident identification].
- 1981 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Bultynck & Jacobs, pp. 17, 18, pl. 10, fig. 9 [only].
- 1982 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Bultynck, p. 57, pl. 2, fig. 3 [only].
- 1983 *Ancyrodella rotundiloba rotundiloba*. – Bultynck, p. 165, fig. 1.37 [only; = reillustration of Bultynck 1982, pl. 2, fig. 3].
- 1985 *Ancyrodella alata* Glenister & Klapper, early form. – Klapper, pp. 27, 28, pl. 4, figs 5, 6 [only], pl. 5, figs 7–10, 13–16 [only]; pl. 6, figs 9–12.
- 1985 *Ancyrodella alata* Glenister & Klapper, late form. – Klapper, pp. 27, 28, pl. 6, figs 5–8 [only].
- 1987 *Ancyrodella rotundiloba* (Bryant). – Fuchs, pl. 3, fig. 2.
- 1989 *Ancyrodella rotundiloba* (Bryant). – Sandberg, Ziegler & Bultynck, pp. 212, 213, pl. 2, figs 9, 10 [only]; pl. 3, figs 1, 2 [reillustration of Ziegler 1958, pl. 11, fig. 12; drawing of same specimen on text-fig. 2.8]; figs 8, 9 [reillustration of Bischoff & Ziegler 1957, pl. 16, fig. 10; drawing of same specimen on text-fig. 2.10].
- 1989 *Ancyrodella rotundiloba* (Bryant). – Vandelaer *et al.*, p. 331, pl. 1, fig. 1.
- 1992 *Ancyrodella alata* Glenister & Klapper. – Yatskov & Kuz'min, p. 89, pl. 2, fig. 4 [only].
- 1993 *Ancyrodella alata* Glenister & Klapper. – Racki & Bultynck, pl. 9, fig. 3 [only].
- 1993 *Ancyrodella africana* García-López. – Racki & Bultynck, pl. 9, fig. 6 [only].
- 1994 *Ancyrodella rotundiloba* (Bryant). – Weary & Harris, p. 224, pl. 2, figs 15–18 [only].
- 1994 *Ancyrodella rotundiloba* (Bryant). – Sandberg, Hasenmueller & Rexroad, p. 250, pl. 1, fig. 7.
- 1994 *Ancyrodella recta* n. sp.; Kralick, p. 1387, 1390, figs 3.5, 3.6, 3.11, 3.12, 4.11, 4.12, 6.1, 6.2, 6.5, 6.6, 6.9, 6.10 [figs 6.1, 6.2 = holotype].
- 2000 *Ancyrodella recta* Kralick. – Klapper, pp. 154, 156, 158, pl. 1, figs 2, 3 [reillustration of holotype]; figs 4, 8 [reillustration of Klapper 1985, pl. 6, figs 7, 8].
- 2000 *Ancyrodella rotundiloba* (Bryant). – Gouwy & Bultynck, p. 40, pl. 1, figs 1, 2.
- 2001 *Ancyrodella alata* Glenister & Klapper. – Savage & Yudina, pp. 287, 288, pl. 1, figs 10–12 [only].
- 2001 *Ancyrodella* cf. *A. alata* Glenister & Klapper. – Savage & Yudina, p. 288, pl. 1, figs 1–3 [only].
- 2004 *Ancyrodella recta* Kralick. – Klapper, Uyeno *et al.*, p. 377, figs 5.1, 5.2, 5.7–5.9.
- 2005 *Ancyrodella recta* Kralick. – Uyeno & Wendte, p. 163, pl. 1, figs 12, 13.
- 2007 *Ancyrodella recta* Kralick. – Miller, pp. 448, 449, figs 4a–y, 5a, 5d–y.
- 2008 *Ancyrodella rotundiloba* - *Ancyrodella recta*. – Liao & Valenzuela-Rios, pp. 7, 13, fig. 6q, r.
- 2013 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Liao & Valenzuela-Rios, p. 347, figs 6c, d.
- 2016 *Ancyrodella recta* Kralick. – Klapper & Kirchgasser, p. 552, figs 7.15, 7.16.
- 2017 *Ancyrodella recta* Kralick. – Ovnatanova *et al.*, pp. 1050, 1053, pl. 14, figs 3, 5 [only]; pl. 16, fig. 5 [only]; pl. 23, figs 2, 3, 8 [fig. 7 = ?]; pl. 31, fig. 4.
- 2017 *Ancyrodella rugosa* Branson & Mehl. – Ovnatanova *et al.*, p. 1055, pl. 9, fig. 3.
- 2020 *Ancyrodella recta* Kralick. – Kirchgasser *in* Kirchgasser *et al.*, p. 210, figs 6k, 9c–e.
- 2020 *Ancyrodella alata* Glenister & Klapper. – Kirchgasser *in* Kirchgasser *et al.*, p. 210, fig. 6c [only].

**Diagnosis.** – *Ancyrodella recta* has straight margins of the anterior inner platform and commonly curved outer margins, a small basal pit, and thin short secondary keels, the inner one directed anteriorly, the outer directed laterally.

**Remarks.** – A significant number of identifications of *Ancyrodella rotundiloba* prior to the establishment of *A. recta* by Kralick (1994) resulted in a heterogeneous taxonomic concept of the former species. This has since been clarified by the recognition of *A. recta* (see respective synonymies). For the main comparison with *A. rotundiloba* s.s., see under the latter. In *A. recta*, the anterior



outer platform is usually curved, but it can be straight (e.g., Kralick 1994, figs 3.11, 6.9). It is always curved in *A. rotundiloba* s.s.

Miller's 2007 paper represents a major contribution to the ontogenetic variation in the early species of *Ancyrodella* (that is, *A. pristina*, *A. rotundiloba*, and *A. recta*). All the specimens in his figure 5 (except b, c) represent *A. recta* and are from sample 8, which also has *A. rotundiloba* (fig. 1; 5b, c) but not *A. pristina*. The distinctive juveniles of *A. recta* in figure 5 are matched by those in figure 4 and were so identified by Miller, but differ from the juveniles in ontogenetic series 2 from sample 7 (fig. 3).

# *Ancyrodella rotundiloba* (Bryant, 1921) s.s.

Figure 1Q, R

- 1921 *Polygnathus rotundilobus* Spec. Nov.; Bryant, pp. 26, 27, pl. 12, figs 1–6, text-fig. 7 [fig. 1 = lectotype selected by Ziegler 1958, p. 44].
- 1933 *Polygnathus tuberculata* Hinde, 1879. – Branson & Mehl, pp. 148, 165, pl. 11, fig. 9 [non fig. 2 = lectotype of *Polygnathus tuberculatus* Hinde, selected by Bryant 1921, p. 25; see Klapper 2017, p. 219].
- 1934 *Polygnathus rotundiloba* Bryant. – Huddle, pp. 102, 103, pl. 8, figs 36, 37.
- 1957 *Ancyrodella rotundiloba* (Bryant). – Bischoff & Ziegler, p. 42, pl. 16, fig. 7 [only].
- 1966 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Glenister & Klapper, p. 799, pl. 85, figs 9–13.
- 1967 *Ancyrodella rotundiloba* (Bryant). – Müller & Clark, p. 908, pl. 116, fig. 1 [non figs 2–5 = ? *A. sp.*; text-fig. 5a–c, e, non 5d = *A. recta* Kralick, 1994].
- 1967 *Ancyrodella rotundiloba* subsp. A. – Uyeno, p. 5, pl. 1, fig. 6 [only]; [reillustrated by Uyeno 1974, pl. 2, fig. 8].
- ? 1967 *Ancyrodella rotundiloba* subsp. A. – Uyeno, p. 5, pl. 1, fig. 1 [specimen has pit not unlike that of *A. pristina*, but platform outline is that of *A. rotundiloba*; reillustrated by Uyeno 1974, pl. 2, fig. 1]
- 1970 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Khalymbadzha & Chernysheva, pp. 91, 92, pl. 1, figs 9–12.
- 1972 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Klapper & Philip, p. 99, pl. 2, figs 1–5 [multielement reconstruction].
- 1973 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Ziegler, pp. 29–31, Ancyro pl. 1, fig. 1 [only; reillustration of lectotype].
- 1976 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Druce, pp. 62–64, pl. 9, fig. 6 [only]; pl. 10, figs 1–3; pl. 12, fig. 1.
- 1976 *Ancyrodella rotundiloba alata* Glenister & Klapper, 1966. – Druce, pp. 64, 65, pl. 11, figs 1–3 [only].
- 1980 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Klapper, p. 112, pl. 3, figs 34, 35.
- 1981 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Huddle, pp. b19, b20, pl. 1, figs 1–3, 6–8, 16, 17 [only; figs 1, 2 = reillustration of lectotype; non figs 4, 5, 14, 15 = ? *A. triangulata* Kralick; non figs 11–13 = *A. pristina*]; pl. 3, figs 20, 21.
- 1981 *Ancyrodella rugosa* Branson & Mehl. – Huddle, pp. b21, b22, pl. 3, figs 16, 17 [only].
- 1981 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Bultynck & Jacobs, pp. 17, 18, pl. 10, figs 1–8 [only].
- 1982 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Bultynck, pp. 56, 57, pl. 1, figs 26, 27; pl. 2, figs 1, 2 [only].
- 1982 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Mouravieff, p. 113, pl. 2, fig. 4.
- 1983 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Bultynck, p. 165, figs 1.35, 1.36 [only; 1.35 = reillustration of Bultynck 1982, pl. 1, fig. 26].
- 1985 *Ancyrodella rotundiloba* (Bryant) late form. – Klapper, pp. 24, 26, 27, pl. 2, figs 1–4; pl. 3, figs 1–4, 12; pl. 4, figs 9–12; pl. 8, figs 9, 10; pl. 11, figs 3, 4; text-fig. 3e–j, m, n.
- 1989 *Ancyrodella rotundiloba* (Bryant). – Sandberg, Ziegler & Bultynck, pp. 212, 213, text-fig. 2.9 [reillustration of Bischoff & Ziegler 1957, pl. 16, fig. 7; non text-figs 2.8, 2.10 = *A. recta*]; pl. 3, figs 5, 6 [reillustration of same specimen as in text-fig. 2.9]; fig. 7 = [reillustration of lectotype].
- 1989 *Ancyrodella soluta* n. sp. – Sandberg, Ziegler & Bultynck, pp. 211, 212, pl. 2, figs 1–4 [only; figs 1, 2 = holotype].
- 1989 *Ancyrodella rotundiloba* (Bryant). – Racki & Wrzolek, pp. 234, 236, text-fig. 1, specimen from bed 46 [drawing of specimen in Klapper 1985, pl. 4, figs 11, 12].
- 1994 *Ancyrodella rotundiloba* (Bryant) late morphotypes. – Kirchgasser, p. 125, pl. 2, figs l, m, q, r.
- 1994 *Ancyrodella rotundiloba* (Bryant). – Weary & Harris, p. 224, pl. 2, figs 9, 10, 19–21 [only].
- 1994 *Ancyrodella rotundiloba* (Bryant). – Kralick, p. 1387, figs 3.15–3.24 [3.21, 3.22 = reillustration of lectotype]; figs 5.9–5.11 [only].
- 2000 *Ancyrodella rotundiloba* (Bryant) late form. – Klapper, p. 158, pl. 1, figs 6, 7, 9–14 [10, 11 = reillustration of Klapper 1985, pl. 4, figs 11, 12; 13, 14 = reillustration of lectotype].
- 2004 *Ancyrodella rotundiloba* (Bryant) late form. – Klapper et al., p. 377, fig. 5.6.
- 2007 *Ancyrodella rotundiloba* (Bryant, 1931 [sic]). – Miller, pp. 447, 449, figs 3a–g, k, l; 5b, c.
- 2013 *Ancyrodella rotundiloba* (Bryant) late form of Klapper (1985). – Gouwy, Liao & Valenzuela-Ríos, pp. 323, 324, fig. 6p, q.
- 2013 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Liao & Valenzuela-Ríos, pp. 347, 348, fig. 6e [only].
- 2016 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Klapper & Kirchgasser, pp. 534, 537, figs 7.8, 7.9.



- 2017 *Ancyrodella rotundiloba* (Bryant). – Ovnatanova *et al.*, p. 1053, 1055, pl. 14, fig. 1 [only].
- 2017 *Ancyrodella soluta* Sandberg, Ziegler & Bultynck. – Ovnatanova *et al.*, pp. 1055, 1056, pl. 5, fig. 8; pl. 23, fig. 1 [only; figs 4–6 = *A. sp.*, 3 juveniles without lower views].
- 2019 *Ancyrodella rotundiloba rotundiloba* Bryant [sic]. – Telnova, Soboleva & Sobolev, p. 259, fig. 4.3.
- 2020 *Ancyrodella rotundiloba rotundiloba* Branson & Mehl [sic]. – Kirchgasser in Kirchgasser *et al.*, p. 210, fig. 6i.

**Diagnosis.** – *Ancyrodella rotundiloba* s.s. has a medium-sized pit and lacks well developed secondary carinae and secondary keels. Only exceptionally are there a few small nodes or the faint suggestion of incompletely developed keels in that position.

**Remarks.** – In contrast to *Ancyrodella rotundiloba* s.s., *A. recta* has a straight anterior inner platform margin, a distinctly smaller pit, and thin secondary keels. The latter are lacking in *A. rotundiloba*, although exceptionally there are either a few small nodes or incipient, extremely weakly developed secondary keels under the anterior lobes. The anterior inner platform margin of the latter is always curved. Furthermore in *A. rotundiloba*, there is a marked depression between the posterior end of the free blade and the carina that is occupied by either a small gap in denticulation or one to two tiny nodes. In *A. recta*, however, this denticulation gap is shorter, equivalent to the space of one tiny node that is characteristically absent. The denticulation gap in *A. rotundiloba* was first noted and shown by Müller & Clark (1967, p. 905, text-fig. 2).

The specimen illustrated by Soboleva & Sobolev (2019, fig. 6n, o) appears to be transitional between *Ancyrodella rotundiloba* and *A. rugosa*. The faint secondary keels are much better developed than in the former and are in the pattern but not nearly as strong as in the latter species.

#### ***Ancyrodella rugosa* Branson & Mehl, 1934**

Figure 1J, K

- 1934 *Ancyrodella rugosa* n. sp.; Branson & Mehl, p. 239, pl. 19, figs 15, 17 [= holotype].
- 1957 *Ancyrodella rugosa* Branson & Mehl. – Bischoff & Ziegler, p. 42, pl. 16, fig. 13.
- 1958 *Ancyrodella rugosa* Branson & Mehl. – Ziegler, p. 45.
- 1959 *Ancyrodella rugosa* Branson & Mehl. – Krebs, p. 384, pl. 1, fig. 14.
- 1968 *Ancyrodella rugosa* Branson & Mehl. – Pollock, p. 428, pl. 61, fig. 1.
- 1970b *Ancyrodella rugosa* Branson & Mehl. – Seddon, p. 94, pl. 7, figs 2, 3.
- 1971 *Ancyrodella sinecarina* sp.n.; Szulczewski, pp. 16, 17, pl. 1, figs 5, 6.
- 1971 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Szulczewski, p. 15, pl. 1, fig. 3 [only].
- 1974 *Ancyrodella gigas* Youngquist. – Uyeno, pp. 23, 24, pl. 1, figs 1, 8, 9.
- 1976 *Ancyrodella rugosa* Branson & Mehl. – Druce, p. 66, pl. 3, fig. 4.
- 1979 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Baliński, p. 75, pl. 20, figs 6, 7.
- 1981a *Ancyrodella rugosa* Branson & Mehl. – Perri & Spalletta, p. 294, pl. 1, fig. 7.
- 1981 *Ancyrodella rugosa* Branson & Mehl. – Huddle, pp. b21, b22, pl. 3, figs 1–15, 18, 19 [only].
- 1982 *Ancyrodella rugosa* Branson & Mehl. – Bultynck, pp. 38, 57, pl. 2, figs 11, 13–16.
- 1983 *Ancyrodella rugosa* Branson & Mehl. – Bultynck, p. 165, figs 1.30, 1.31 [= reillustration of Bultynck 1982, figs 13b, 14, respectively].
- 1985 *Ancyrodella rugosa* Branson & Mehl. – Klapper, p. 30, pl. 11, figs 1, 2, 5–14, text-fig. 3u, v.
- 1989 *Ancyrodella rugosa* Branson & Mehl. – Vandelaer *et al.*, p. 331, pl. 1, figs 3, 4.
- 1991 *Ancyrodella rugosa* Branson & Mehl. – Uyeno, p. 158, pl. 4, figs 10, 11.
- 1992 *Ancyrodella rugosa* Branson & Mehl. – Yatskov & Kuz'min, p. 89, pl. 2, fig. 2 [only; fig. 5 = indet. juvenile].
- 1993 *Ancyrodella rugosa* Branson & Mehl. – Racki & Bultynck, pl. 8, figs 9–12.
- 1994 *Ancyrodella rugosa* Branson & Mehl. – Weary & Harris, p. 217, pl. 1, figs 14, 15.
- 1994 *Ancyrodella* aff. *An. rugosa* Branson & Mehl. – Weary & Harris, p. 217, pl. 2, fig. 22.
- 1994 *Ancyrodella rugosa* Branson & Mehl. – Kralick, p. 1393, figs 3.7, 3.8, 3.13, 3.14, 4.9, 4.10.
- 2000 *Ancyrodella rugosa* Branson & Mehl. – Gouwy & Bultynck, pp. 40, 42, pl. 1, figs 3–6.
- 2001 *Ancyrodella rotundiloba* (Bryant). – Savage & Yudina, p. 288, pl. 2, figs 1–4.
- 2003 *Ancyrodella rugosa* Branson & Mehl. – Over *et al.*, p. 222, pl. 1, figs 18, 19.
- 2005 *Ancyrodella rugosa* Branson & Mehl. – Uyeno & Wendte, p. 163, pl. 1, figs 10, 11.
- 2006 *Ancyrodella rugosa* Branson & Mehl. – Piszczowska *et al.*, p. 625, fig. 13a.
- 2007 *Ancyrodella rugosa* Branson & Mehl. – Gouwy *et al.*, p. 389, fig. 15h.
- ? 2007 *Ancyrodella rugosa*. – Over, p. 1202, figs 11.11, 11.19 [11.11 = ? *A. lobata*].
- 2016 *Ancyrodella rugosa* Branson & Mehl. – Klapper & Kirchgasser, p. 534, figs 7.13, 7.14, 7.17, 7.18.

**Diagnosis.** – *Ancyrodella rugosa* has two anteriorly directed secondary carinae and secondary keels, many nodes of uniform size, and a heart-shaped platform outline.

**Remarks.** – The Pa element of *Ancyrodella rugosa* has a similar platform outline to that of *A. rotundiloba* s.s. The crucial difference, however, is the distinct development of the two anteriorly directed secondary carinae and secondary keels in *A. rugosa*, as opposed to only a few small nodes or incipient, weakly developed keels in *A. rotundiloba*. *Ancyrodella rugosa* also differs in having many more nodes of uniform size on the platform. The gap between the free blade and the carina is generally more prominent in *A. rugosa*, but it also contains one to two small nodes as in *Ancyrodella rotundiloba* s.s.

The many more nodes of uniform size in *A. rugosa* contrasts with that in *A. nodosa*, in which there is a row of nodes parallel to, and on either side of the posterior carina. The specimen identified as *A. rugosa* by Dzik (2002, fig. 25c; Dzik *et al.* 2018, fig. 3p) has both the quasi-trapezoidal platform outline of *A. lobata* (see remarks there) and a row of separated nodes bisecting the outer platform margin just posterior of midlength, in contrast with its absence in *A. rugosa*.

The specimen identified as *A. sp. cf. A. rugosa* by Uyeno (1991, pl. 4, figs 8, 9) has a platform outline like that of *A. recta*, but the prominent gap between the free blade and the carina is a characteristic of *A. rugosa*. The specimen is considered as intermediate between the two species. Importantly, this prominent gap is absent in *A. nodosa*.

#### ***Ancyrodella triangulata* Kralick, 1994**

- 1981 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Huddle, pp. b20, b21, pl. 1, figs 9, 10, 23, 24 [only].
- ? 1981 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Huddle, pp. b19, b20, pl. 1, figs 4, 5, 14, 15 [only].
- 1981 *Ancyrodella rugosa* Branson & Mehl. – Huddle, pp. b21, b22, pl. 1, figs 18, 19 [only].
- 1985 *Ancyrodella alata* Glenister & Klapper. – Klapper, pp. 27, 28, pl. 5, figs 9, 10 [only].
- 1992 *Ancyrodella rotundiloba* (Bryant). – Yatskov & Kuz'min, p. 89, pl. 2, fig. 3.
- 1994 *Ancyrodella triangulata* n. sp.; Kralick, pp. 1390, 1393, figs 3.3, 3.4, 3.9, 3.10, 4.1–4.4, 6.3, 6.4, 6.7, 6.8, 6.11, 6.12 [figs 11, 12 = holotype, same as 3.3, 3.4].
- 2005 *Ancyrodella triangulata* Kralick. – Uyeno & Wendte, p. 163, pl. 1, figs 6, 7.
- 2017 *Ancyrodella recta* Kralick. – Ovnatanova *et al.*, pp. 1050, 1053, pl. 14, figs 2, 4, 6 [only]; pl. 16, fig. 1 [only].
- 2019 *Ancyrodella triangulata*. – Zhang *et al.*, p. 9, fig. 6.2.

**Diagnosis.** – In *Ancyrodella triangulata* both the secondary carinae and secondary keels are directed anteriorly and both the outer and inner platform margins are straight.

**Remarks.** – *Ancyrodella triangulata* differs from *A. recta* in the secondary carinae and secondary keel patterns. Both structures are directed anteriorly in *A. triangulata*, whereas only the inner ones are so directly in *A. recta* and the outer ones are directly laterally.

#### ***Ancyrodella alata* Group**

The group includes *Ancyrodella africana* s.s., *A. devonica*, *A. alata*, and *A. pramosica*.

#### ***Ancyrodella africana* García-López, 1981 s.s.**

Figures 1H, I, L

- 1966 *Ancyrodella rotundiloba* (Bryant) n. subsp.; Krebs & Ziegler, p. 736, pl. 1, figs 8, 9 [only].
- 1976 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Druce, p. 62–64, pl. 9, fig. 4 [only].
- 1978 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Orchard, p. 928, pl. 114, figs 29, 30 [only].
- 1981 *Ancyrodella africana* n. sp.; García-López, pp. 264, 265, pl. 1, figs 1–14 [figs 1–3 = holotype].
- 1982 *Ancyrodella rugosa* Branson & Mehl. – Mouravieff, p. 114, pl. 3, fig. 2.
- 1982 *Ancyrodella gigas* Youngquist. – Mouravieff, p. 114, pl. 3, fig. 4, 5, 7.
- 1985 *Ancyrodella africana* García-López. – Klapper, pp. 28, 29, pl. 8, figs 15–18 [only], pl. 9, figs 1–8 [only].
- 1985 Specimens transitional between *A. africana* García-López and *A. gigas* Youngquist. – Klapper, p. 34, pl. 10, figs 7, 8, 11, 12, text-figs 3cc–dd [same as 7, 8].
- 1986 *Ancyrodella africana* García-López. – García-López, p. 453, pl. 2, figs 10–23 [same illustrations as in her 1981 paper, figs 10–12 = holotype], text-fig. 3.
- 1986 *Ancyrodella mouravieffi* n. sp.; García-López, p. 449, pl. 1, figs 17–24 [figs 17–20 = holotype], pl. 2, figs 1–6, text-fig. 3.
- 1986 *Ancyrodella rugosa* Branson & Mehl. – Bultynck, p. 276, pl. 1, figs 7, 8.
- 1987 *Ancyrodella africana* García-López. – García-López, pp. 57, 58, pl. 2, figs 8–19 [8, 9 = holotype and = 10, 11 of her 1986 paper; 10, 11 = 13, 14 of her 1986 paper; 12, 13 = 16, 17; 14, 15 = 18, 19; 16, 17 = 20, 21; 18, 19 = 22, 23], text-fig. 11 [see synonymy].
- 1987 *Ancyrodella mouravieffi* García-López. – García-López, pp. 63, 64, pl. 1, figs 13–21 [13–17 = holotype], pl. 2, figs 1–4, text-fig. 11.
- 1989 *Ancyrodella africana* García-López. – Vandelaer *et al.*, p. 329, pl. 1, figs 6, 7.
- 1989 *Ancyrodella gigas* Youngquist beta morphotype. – Vandelaer *et al.*, pp. 329, 330, pl. 2, fig. 7 [only].
- 1993 *Ancyrodella africana* García-López. – Racki & Bultynck, pl. 9, fig. 8 [only].

- 1993 *Ancyrodella pramosica* Perri & Spaletta [sic]. – Racki & Bultynck, pl. 9, fig. 5.
- 1993 *Ancyrodella gigas* Youngquist. – Ji & Ziegler, p. 52, pl. 1, fig. 12 [non fig. 11 = indet. fragment].
- 1999 *Ancyrodella rotundiloba* (Bryant). – Lazreq, p. 60, pl. 3, figs 14, 15 [only].
- 2000 *Ancyrodella africana* García-López. – Gouwy & Bultynck, p. 40, pl. 1, figs 7, 8.
- 2002a *Ancyrodella africana* [transitional with] *Ancyrodella gigas*. – García-López & Sanz-López, p. 160, pl. 2, figs 12, 13.
- 2002a *Ancyrodella africana* García-López. – García-López & Sanz-López, p. 160, pl. 2, fig. 14.
- 2002b *Ancyrodella africana* García-López. – García-López & Sanz-López, pp. 198, 200, pl. 2, figs 25, 26 [reillustration of García-López 1981, pl. 1, figs 4, 5], pl. 3, figs 1, 2 [reillustration of García-López 1981, pl. 1, figs 11, 12].
- 2002b *Ancyrodella mouravieffi* García-López. – García-López & Sanz-López, p. 198, pl. 2, figs 23, 24 [= reillustration of holotype, García-López 1986, pl. 1, figs 17, 18].
- 2003 *Ancyrodella africana* García-López. – Over *et al.*, p. 222, pl. 1, fig. 4.
- 2007 *Ancyrodella africana* García-López. – Gouwy *et al.*, p. 388, fig. 151.
- 2007 *Ancyrodella alata* Glenister & Klapper late form of Klapper, 1989. – Gouwy *et al.*, p. 388, fig. 151 [only].
- 2007 *Ancyrodella africana*. – Over, p. 1202, fig. 11.20.
- 2009 *Ancyrodella pristina* Khalymbadza & Chernysheva. – Li *et al.*, p. 530, pl. 1, figs 6, 7.
- 2012 *Ancyrodella africana* García-López. – Liao & Valenzuela-Ríos, pp. 821–823, fig. 4a–l.
- 2012 *Ancyrodella mouravieffi* García-López. – Liao & Valenzuela-Ríos, pp. 824, 826, fig. 5i–l.
- 2012 *Ancyrodella devonica* García-López. – Liao & Valenzuela-Ríos, pp. 823, 824, fig. 4m–p.
- 2013 *Ancyrodella africana* García-López. – Gholamalian *et al.*, p. 143, pl. 1, figs 20, 21.
- 2014 *Ancyrodella africana* García-López. – Rodríguez-Cañero & Martín-Algarra, p. 48, fig. 9.19.
- 2014 *Ancyrodella mouravieffi* García-López. – Rodríguez-Cañero & Martín-Algarra, p. 48, fig. 9.16.
- 2015 *Ancyrodella africana* García-López. – Becker & Aboussalam, p. 118, pl. aii-2, figs 6, 7.
- 2017 *Ancyrodella africana* García-López. – Ovnatanova *et al.*, pp. 1041, 1045, pl. 11, figs 8, 10 [only].
- 2020a *Ancyrodella* [as *Ad.*] *africana*. – Becker *et al.*, p. 75, fig. 62.19 [62.20 = ?].
- 2020 *Ancyrodella* [as *Ad.*] *africana*. – Aboussalam *et al.*, p. 149, fig. 20.12.

**Diagnosis.** – In *Ancyrodella africana* the platform outline is distinctly asymmetrical in that the inner lobe extends farther to the anterior than the outer lobe and they are of

different shape. The outer lobe has an extra secondary keel only in some specimens. The inner secondary keel is directed anteriorly, the outer one(s) directed laterally.

**Remarks.** – The platform outline of the two species, *Ancyrodella africana* and *A. mouravieffi*, of García-López (1986, 1987) is essentially the same. The specimens of *A. mouravieffi* in the cited papers are larger than those of *A. africana* (they are illustrated at different magnifications) suggesting that those of the former represent later ontogenetic stages. There is a short accessory keel on the outer lobe in some specimens of *A. africana* but it is lacking in others, as well as in *A. mouravieffi* (see text-fig. 11 of the 1987 paper). The inner lobe extends farther to the anterior than the outer lobe making the outline highly asymmetrical in both species. Furthermore, the two lobes are of different shape. The platform outline is viewed here as the most highly weighted character for species separation, suggesting their synonymy.

The specimen of Gouwy & Bultynck (2000, pl. 1, figs 7, 8) is highly representative of *A. africana* s.s. The specimens illustrated by Klapper (1985, pl. 10, figs 7, 8, 11, 12) because of their platform outline are interpreted here as large growth stages of *A. africana* s.s. The specimens of Mouravieff (1982, pl. 3, figs 2, 7) and Bultynck (1986, pl. 1, figs 7, 8) are closely comparable and interpreted to represent this late ontogenetic stage.

### ***Ancyrodella devonica* García-López, 1986**

Figure 1M

- ? 1967 *Ancyrodella rotundiloba* (Bryant). – Clark & Ethington, pp. 29, 30, pl. 2, fig. 10 [only].
- 1969 *Ancyrodella rotundiloba rotundiloba* (Bryant). – Pölsler, p. 404, pl. 4, figs 7, 8 [only].
- 1981 *Ancyrodella rotundiloba* aff. *alata* Glenister & Klapper. – Bultynck & Hollard, p. 38, pl. 10, fig. 8 [only].
- 1985 *Ancyrodella gigas* Youngquist. – Klapper, p. 29, pl. 10, figs 3–6 [only].
- 1985 *Ancyrodella africana* García-López. – Klapper, pp. 28, 29, pl. 8, figs 11–14, 19–22 [only], pl. 9, figs 9–16 [only], text-figs 3s, t, aa–bb [s, t same as pl. 8, figs 20, 19; aa–bb same as pl. 9, figs 12, 11, respectively].
- 1985 *Ancyrodella alata* Glenister & Klapper, early form. – Klapper, pp. 27, 28, pl. 5, figs 1–6 [only].
- 1986 *Ancyrodella devonica* n. sp.; García-López, p. 448, pl. 3, figs 1–10 [figs 1–3 = holotype], text-fig. 3.
- 1987 *Ancyrodella devonica* García-López. – García-López, pp. 60, 61, pl. 3, figs 1–6 [1–3 = holotype], text-fig. 11 [see synonymy].
- 1993 *Ancyrodella africana* García-López. – Racki & Bultynck, pl. 9, fig. 7 [only].
- 2002b *Ancyrodella devonica* García-López. – García-López



- & Sanz-López, p. 200, pl. 3, figs 3, 4 [= reillustration of holotype, García-López 1986, pl. 3, figs 1, 2].
- 2005 *Ancyrodella africana* García-López. – Uyeno & Wendte, p. 163, pl. 1, figs 14, 15.
- 2006 *Ancyrodella africana* García-López. – Pisarzowska *et al.*, p. 625, fig. 13c.
- 2016 *Ancyrodella africana* García-López. – Klapper & Kirchgasser, pp. 534, 552, figs 7.3, 7.4.
- 2017 *Ancyrodella africana* García-López. – Ovnatanova *et al.*, pp. 1041, 1045, pl. 15, figs 1, 6 [only].

**Diagnosis.** – *Ancyrodella devonica* is closely similar to *A. africana* s.s. but the anterior lobes are more nearly symmetrical in the former. Both secondary keels, if well developed, may be directed slightly to the anterior.

**Remarks.** – García-López (1987, p. 60) synonymized the small specimens of Klapper (1985, pl. 10, figs 3–6) in *A. devonica*. Although those specimens were placed in *A. nodosa* by Klapper & Kirchgasser (2016, p. 537) they show the definitive outline of *A. devonica*.

Additionally, Klapper (1985, pl. 8, figs 11–14, 19–22, pl. 9, figs 9–16), by inclusion of the specimens cited, expanded the concept of *Ancyrodella africana*, as correctly questioned by García-López (1987, pp. 57, 58). I agree that these specimens do not belong in *A. africana* s.s. and by their inclusion herein in *A. devonica* to some extent expands the concept of that species. However, the Montagne Noire specimens (Klapper 1985, pl. 8, figs 11, 12, 20, 21 and pl. 9, figs 11, 12) in the very slight asymmetry of the platform outline provide a relationship with the types of *A. devonica*.

# ***Ancyrodella alata* Glenister & Klapper 1966**

Figure 1A, B

- 1966 *Ancyrodella rotundiloba alata* n. subsp.; Glenister & Klapper, pp. 799, 800, pl. 85, figs 1–8 [only; figs 7, 8 = holotype].
- 1969 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Pölsler, p. 404, pl. 4, figs 1–4.
- 1970 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Khalymbadzhia & Chernysheva, pp. 92–94, pl. 2, figs 3–9 [only].
- 1970b *Ancyrodella rotundiloba alata* Glenister & Klapper. – Seddon, p. 98, pl. 9, figs 5, 6 [only].
- 1972 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Klapper & Philip, p. 99, pl. 2, figs 6–13 [multielement reconstruction].
- 1973 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Ziegler, pp. 33, 34, Ancyro pl. 1, fig. 3 [reillustration of holotype].
- 1974 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Uyeno, p. 24, pl. 1, fig. 7 [only].

- 1979 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Baliński, p. 75, pl. 2, fig. 5 [only].
- 1981a *Ancyrodella rotundiloba alata* Glenister & Klapper. – Perri & Spalletta, pp. 293, 294, pl. 2, figs 1–3.
- 1981 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Huddle, pp. b20, b21, pl. 2, figs 1–19 [only].
- 1982 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Bultynck, p. 57, pl. 2, figs 4–8 [fig. 10 = ? *A. sp.*].
- 1983 *Ancyrodella rotundiloba alata*, typical form. – Bultynck, p. 165, figs 1.39, 1.40 [reillustration of figs 5 and 8 of 1982 paper, 1.38 = fig. 10 of 1982 paper].
- 1985 *Ancyrodella alata* Glenister & Klapper, early form. – Klapper, pp. 27, 28, pl. 4, figs 1–4, 7, 8 [only], pl. 5, figs 11, 12 [only].
- 1985 *Ancyrodella alata* Glenister & Klapper, late form. – Klapper, pp. 27, 28, pl. 6, figs 1–4 [only], pl. 7, figs 1–11.
- 1986 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Ji *et al.*, p. 97, pl. 1, figs 1, 2.
- 1987 *Ancyrodella alata* Glenister & Klapper. – Fuchs, pl. 3, fig. 3 [only].
- 1989 *Ancyrodella alata* Glenister & Klapper. – Sandberg, Ziegler & Bultynck, p. 226, pl. 4, figs 10, 11.
- 1989b *Ancyrodella rotundiloba rotundiloba* Glenister & Klapper [sic, probably a typographical error as *A. r. alata* was meant, see Ji & Ziegler 1993, p. 51 and Ji 1989b, p. 306, sample YT-16]. – Ji, p. 316, pl. 3, figs 10–13.
- 1991 *Ancyrodella alata* Glenister & Klapper late form *sensu* Klapper (1985). – Uyeno, p. 158, pl. 4, figs 4–6.
- 1992 *Ancyrodella alata* Glenister & Klapper. – Yatskov & Kuz'min, p. 89, pl. 2, fig. 6 [only].
- 1993 *Ancyrodella alata* Glenister & Klapper. – Racki & Bultynck, pl. 9, figs 1, 2 [only].
- 1993 *Ancyrodella alata* Glenister & Klapper. – Ji & Ziegler, p. 51, pl. 1, figs 1–3.
- 2001 *Ancyrodella alata* Glenister & Klapper. – Savage & Yudina, pp. 287, 288, pl. 2, figs 5–7 [only].
- 2001 *Ancyrodella cf. A. alata* Glenister & Klapper. – Savage & Yudina, p. 288, pl. 2, figs 8–10 [only].
- 2003 *Ancyrodella alata* Glenister & Klapper. – Over *et al.*, pl. 1, figs 16, 17.
- 2007 *Ancyrodella alata* Glenister & Klapper late form of Klapper 1989. – Gouwy *et al.*, p. 388, fig. 15j [only].
- 2007 *Ancyrodella alata*. – Over, p. 1202, figs 11.14–11.17.
- 2008 *Ancyrodella alata* Glenister & Klapper. – Ovnatanova & Kononova, pp. 1079, 1080, pl. 26, figs 4, 5.
- 2009 *Ancyrodella alata* Glenister & Klapper. – Li *et al.*, p. 533, pl. 1, figs 1, 2.
- 2009 *Ancyrodella rotundiloba* (Bryant). – Li *et al.*, p. 530, pl. 1, figs 8, 9.
- 2016 *Ancyrodella alata* Glenister & Klapper. – Gatovsky *et al.*, p. 66, pl. 1, fig. 10.
- 2016 *Ancyrodella alata* Glenister & Klapper. – Klapper & Kirchgasser, p. 552, figs 7.1, 7.2, 7.6, 7.7, 7.11, 7.12.

- 2017 *Ancyrodella alata* Glenister & Klapper. – Ovnatanova *et al.*, p. 1045, pl. 10, fig. 7; pl. 11, fig. 9; pl. 15, figs 2–5; pl. 16, fig. 3; pl. 17, figs 1–5; pl. 22, figs 6, 7; pl. 29, fig. 7; pl. 31, fig. 2 [only]; pl. 8, fig. 11[?]; pl. 23, fig. 9[?]; pl. 31, fig. 3 [= ? *A. africana*].
- 2020 *Ancyrodella alata* Glenister & Klapper. – Kirchgasser *in Kirchgasser et al.*, p. 210, fig. 6f, g [only].

**Diagnosis.** – *Ancyrodella alata* has the inner lobe directed anteriorly and the outer lobe laterally or slightly to the posterior. Well-developed secondary keels are under both lobes; the outer lobe may have an accessory keel directed anteriorly in some morphotypes.

**Remarks.** – *Ancyrodella alata* is closely related to *A. pramosica* but they differ in the platform outline of the Pa elements. The inner lobe of *A. pramosica* is generally both slenderer and more strongly directed to the anterior. The secondary keels of *A. alata* are in most instances not as extensive as in *A. pramosica*, in which they extend at least to the crimp. But some specimens of *A. alata* have equally extensive secondary keels.

Huddle (1981, pl. 2, figs 1–19) showed the range of variation in his New York Frasnian material of *A. alata*, including a morphotype with an accessory keel directed anteriorly on the outer lobe. Klapper (1985, pl. 7, figs 1, 2) illustrated one such specimen. Ji & Ziegler (1993, p. 52) proposed a new species, *A. huddlei*, for this morphotype, based on Huddle's (1981, pl. 2, figs 7–10, 12–21) specimens, with the holotype in figs 12–14. But Ji & Ziegler's (1993, pl. 1, fig. 10) one photographed specimen is shown only in upper view and has a quite different outline from Huddle's specimens assigned to their new species. Ji & Ziegler's cited specimen has the characteristic outline of *A. alata*, except for the strong inner curvature of the posterior carina. The stratigraphic source of the two specimens in the drawings of Ji & Ziegler (1993, text-figs 8.13, 8.14) is not given. *Ancyrodella huddlei* is regarded herein as an intraspecific variant of *A. alata*.

The multielement reconstruction of *Ancyrodella alata* (Klapper & Philip 1972, pl. 2, figs 6–13) illustrates 6 elements, lacking only the Sd element, presumably due to lack of preservation.

#### ***Ancyrodella pramosica* Perri & Spalletta, 1981**

- 1966 *Ancyrodella rotundiloba alata* n. subsp.; Glenister & Klapper, pp. 799, 800, pl. 86, figs 3, 4 [only].
- 1966 *Ancyrodella rotundiloba* (Bryant) n. subsp.; Krebs & Ziegler, p. 736, pl. 1, figs 6, 7 [only].
- 1968 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Pollock, p. 424, pl. 61, figs 2, 3.

- 1971 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Szulczewski, pp. 15, 16, pl. 1, figs 1, 2.
- 1976 *Ancyrodella* sp. nov. A. – Druce, p. 67, pl. 1, fig. 1.
- 1981a *Ancyrodella* sp. nov. A in Druce. – Perri & Spalletta, pp. 294, 296, pl. 2, figs 4, 5.
- 1981b *Ancyrodella pramosica* n. sp.; Perri & Spalletta, pp. 96, 98, pl. 1, figs 1–5 [fig. 3 = holotype, reillustration of fig. 4 of preceding paper], pl. 2, figs 1–5.
- 1981 *Ancyrodella rotundiloba alata* Glenister & Klapper. – Bultynck & Jacobs, p. 18, pl. 10, figs 10, 11 [fig. 12 = ?].
- 1985 *Ancyrodella pramosica* Perri & Spalletta. – Klapper, p. 28, pl. 7, figs 12–21, pl. 8, figs 1–7, text-figs 3w–z [w, x same as pl. 7, figs 16, 17; y, z same as pl. 7, figs 12, 13].
- 1985 *Ancyrodella alata* Glenister & Klapper, late form. – Klapper, pp. 27, 28, pl. 8, fig. 8 [only].
- 1986 *Ancyrodella alata* Glenister & Klapper. – Bultynck, p. 276, pl. 1, figs 10, 11.
- 1987 *Ancyrodella alata* Glenister & Klapper. – Fuchs, pl. 3, fig. 1 [only].
- 1989 *Ancyrodella pramosica* Perri & Spalletta. – Vandelaer *et al.*, pp. 330, 331, pl. 1, fig. 5.
- 1993 *Ancyrodella pramosica* Perri & Spalletta [sic]. – Racki & Bultynck, pl. 9, fig. 5.
- 2006 *Ancyrodella pramosica* Perri & Spalletta [sic]. – Pisarzowska *et al.*, p. 625, fig. 13b.
- 2007 *Ancyrodella pramosica* Perri & Spalletta. – Gouwy *et al.*, p. 389, fig. 15k.
- 2017 *Ancyrodella pramosica* Perri & Spalletta. – Ovnatanova *et al.*, p. 1049, pl. 10, fig. 6, pl. 29, fig. 5.
- [non] 2020a *Ancyrodella* [as *Ad.*] *pramosica*. – Becker *et al.*, p. 75, figs 62.24, 62.25.
- ? 2020 *Ancyrodella* [as *Ad.*] *pramosica*. – Aboussalam *et al.*, p. 149, fig. 20.22.

**Diagnosis.** – *Ancyrodella pramosica* has the inner lobe generally slenderer and more strongly directed to the anterior than in *A. alata* and has generally, though not always, more extensive secondary keels.

**Remarks.** – García-López (1987, pp. 57, 58) compared *Ancyrodella pramosica* with *A. africana*, noting the similarity of their secondary keel pattern, especially in specimens of the latter that lack an accessory keel on the outer anterior lobe. She also noted differences in the platform outline and ornament. Both species have an asymmetrical platform outline with the inner lobe projecting in an anterior direction. The anterior inner lobe in *A. pramosica* is more alate and is longer than in most specimens of *A. africana*.

The specimen of Aboussalam *et al.* (2020, fig. 20.22) is not nearly as asymmetrical as that of Pa elements of *A. pramosica* because the anterior inner lobe is directed

much more laterally than anteriorly. In this respect, it more nearly resembles *A. africana*. Also, the inner lobe of the specimens of Becker *et al.* (2020a, figs 62.24, 62.25) projects straight laterally and thus does not match the platform outline typical of *A. pramosica* (compare with Perri & Spalletta, 1981b, pls 1, 2).

### *Ancyrodella nodosa* Group

This group includes *A. gigas* s.s., *A. gigas* sensu Ziegler (1958), *A. gigas* form 2 (Klapper 1989), *A. hamata*, *A. ioides* s.s., *A. ioides* form 1, and *A. nodosa*.

### *Ancyrodella gigas* Youngquist, 1947 s.s.

- 1947 *Ancyrodella gigas* n. sp.; Youngquist, pp. 96, 97, pl. 25, fig. 23 [= holotype].
- 1947 *Polygnathus rotundiloba* Bryant. – Youngquist, p. 110, pl. 26, fig. 6.
- 1985 *Ancyrodella gigas* Youngquist. – Klapper & Lane, p. 923, fig. 14.15 [only; reillustration of holotype].
- 1989 *Ancyrodella gigas* Youngquist form 3. – Klapper, p. 457, pl. 3, fig. 13.
- 1994 *Ancyrodella gigas* Youngquist. – Sandberg *et al.*, p. 250, pl. 1, fig. 9.
- 2006 *Ancyrodella* aff. *nodosa* Ulrich & Bassler. – Savage *et al.*, pp. 178, 180, fig. 5r, s.
- 2007 *Ancyrodella gigas* Youngquist form 3 of Klapper, 1989. – Gouwy *et al.*, pp. 389, 391, fig. 15m [only].
- 2018 *Ancyrodella nodosa* Ulrich & Bassler. – Huang *et al.*, p. 65, fig. 4.11.
- 2020b *Ancyrodella* [as *Ad.*] *gigas*. – Becker *et al.*, p. 108, fig. 19.1.

**Diagnosis.** – *Ancyrodella gigas* s.s. has nearly straight secondary carinae arranged in a narrow v-shaped pattern and well developed secondary keels projecting anteriorly.

**Remarks.** – The holotype of *Ancyrodella gigas* and the very few closely similar specimens (e.g., Sandberg *et al.* 1994, pl. 1, fig. 9; Huang *et al.* 2018, fig. 4.11) have the nearly straight secondary carinae forming a distinctive V-shaped pattern at a narrow angle and raised above the posterior platform nodes. The angle is narrower and the carinae are straighter than in Pa elements of *A. nodosa*, a species that has been widely misidentified as *A. gigas* (see synonymy of *A. nodosa*). This was partly due to papers I wrote (Klapper 1985, pl. 10, figs 3–6, 9, 10, 13–16 and Klapper 1989, p. 457) in which the specimens cited in the 1985 paper were taken as exemplars of *A. gigas* form 1. But the so-called form 1 clearly belongs in *A. nodosa* as stated under that species. The confusion of *A. gigas* and *A. nodosa* also occurred before 1985.

### *Ancyrodella gigas* Youngquist sensu Ziegler, 1958

- 1957 *Ancyrodella gigas* Youngquist. – Müller & Müller, p. 1091, pl. 142, fig. 1 [only].
- 1958 *Ancyrodella gigas* Youngquist. – Ziegler, pp. 41, 42, pl. 11, fig. 8 [only].
- 1970b *Ancyrodella gigas* Youngquist. – Seddon, p. 94, pl. 7, fig. 6 [only].
- 1978 *Ancyrodella gigas* Youngquist. – Orchard, p. 926, pl. 114, fig. 4.
- 1981a *Ancyrodella gigas* Youngquist. – Perri & Spalletta, pp. 292, 293, pl. 1, fig. 4.
- 1989b *Ancyrodella gigas* Youngquist. – Ji, p. 316, pl. 3, figs 1, 2, 4, 5.
- 1998a *Ancyrodella gigas* Youngquist. – Spalletta & Perri, p. 197, pl. 2.1.1, fig. 5.
- 1999 *Ancyrodella gigas* sensu Ziegler. – Lazreq, p. 58, pl. 4, fig. 1.
- 2001 *Ancyrodella gigas* Youngquist. – Savage & Yudina, p. 288, pl. 8, figs 7–12.
- 2007 *Ancyrodella gigas*. – Over, p. 1202, fig. 11.9 [only].
- 2020a *Ancyrodella* [as *Ad.*] *nodosa* (= *gigas* M1). – Becker *et al.*, p. 81, fig. 71.15.

**Diagnosis.** – In this morphotype of *Ancyrodella gigas* the inner and outer posterior platform margins are convex lacking distinct sinuses. The secondary keels are as in *A. gigas* s.s.

**Remarks.** – The seminal paper of Ziegler (1958) led to a different concept of *Ancyrodella gigas*, labeled “*sensu* Ziegler” by Lazreq (1999). Compared with *A. gigas* s.s. it lacks well developed sinuses on both the inner and outer convex margins at slightly posterior of platform midlength.

### *Ancyrodella gigas* Youngquist form 2 sensu Klapper (1989)

Figure 3A

- 1985 *Ancyrodella gigas* Youngquist. – Klapper, p. 29, pl. 10, figs 1, 2 [only].
- cf. 1985 *Ancyrodella gigas* Youngquist. – Klapper & Lane, p. 923, fig. 14.14 [only].
- 1989 *Ancyrodella gigas* Youngquist form 2. – Klapper, p. 457, pl. 3, fig. 17.
- cf. 2006 *Ancyrodella gigas* Youngquist (form 3 *sensu* Klapper, 1988 (*sic*)). – Pisarzowska *et al.*, p. 625, fig. 13g.
- cf. 2009 *Ancyrodella gigas* Youngquist cf. form 2 of Klapper, 1989. – Klapper, p. 412, fig. 1.3, fig. 11.
- cf. 2015 *Ancyrodella gigas* Youngquist form 2. – Mahboubi *et al.*, pp. 849, 851, fig. 5a.
- cf. 2020 *Ancyrodella* [as *Ad.*] *gigas* s. str. – Aboussalam *et al.*, p. 149, fig. 20.20.



**Diagnosis.** – *Ancyrodella gigas* form 2 has a strongly convex outer posterior platform margin uninterrupted by a sinus. Secondary keels are as in *A. gigas* s.s.

**Remarks.** – The form 2 morphotype of *Ancyrodella gigas* has the outer posterior platform margin formed by a convex curve without development of a sinus and an incurved posterior carina. In contrast, the holotype of *A. gigas* (reillustrated by Klapper & Lane 1985, fig. 14.15) has well developed sinuses at slightly posterior of platform midlength and the posterior carina is sinuous rather than incurved. The morphotype here termed “cf. form 2” illustrated in Fig. 3B and those so noted in the synonymy list, have a similar platform outline to that of form 2 but the platform is covered with strong nodes instead of partly broken ridges and few nodes. The outer posterior platform outline anterior of the posterior tip is slightly concave in the specimen of Aboussalam *et al.* (2020, fig. 20.20) thus differing from others here termed “cf. form 2”, except that of Mahboubi *et al.* (2015). However, the inner platform outline is essentially the same so the “cf.” designation is appropriate.

***Ancyrodella hamata* Ulrich & Bassler, 1926**

Figures 2H; 3C, D

- 1926 *Ancyrodella hamata* new species; Ulrich & Bassler, p. 48, pl. 7, fig. 7 [= holotype, reillustrated in Huddle 1968, pl. 13, fig. 1], text-fig. 5.10.
- 1926 *Ancyrodella symmetrica* new species; Ulrich & Bassler, p. 49, pl. 8, fig. 1 [reillustrated in Huddle 1968, pl. 13, figs 2, 3].
- 1938 *Ancyrodella buckeyensis* n. sp.; Stauffer, p. 418, pl. 52, figs 17, 18, 23, 24 [figs 23, 24 = lectotype selected by Müller & Müller 1957, p. 1091].
- 1938 *Ancyrodella plena* n. sp.; Stauffer, p. 418, pl. 52, figs 21, 22.
- 1938 *Ancyrodella robusta* n. sp.; Stauffer, p. 418, pl. 52, figs 28, 29.
- 1947 *Ancyrodella lobata* Branson & Mehl. – Miller & Youngquist, pp. 502, 503, pl. 74, figs 10–12 [specimen in fig. 12 reillustrated by Klapper & Kirchgasser 2016, fig. 9.13].
- 1947 *Ancyrodella magister* n. sp.; Miller & Youngquist, p. 503, pl. 74, fig. 14 [= holotype, reillustrated by Klapper & Kirchgasser 2016, fig. 9.16].
- 1947 *Ancyrodella subrotunda* n. sp.; Miller & Youngquist, p. 503, pl. 74, fig. 17.
- 1956 *Ancyrodella* sp. – Müller, p. 1340, pl. 145, fig. 13 [only].
- 1957 *Ancyrodella buckeyensis* Stauffer. – Müller & Müller, p. 1091, pl. 136, fig. 5 [same specimen as preceding reference; *non* fig. 2 = *A.* sp. indet.].
- 1957 *Ancyrodella subrotunda* Müller & Youngquist. – Müller & Müller, p. 1092, pl. 136, fig. 6.
- 1958 *Ancyrodella buckeyensis* Stauffer. – Ziegler, p. 40, pl. 11, fig. 7.
- 1971 *Ancyrodella buckeyensis* Stauffer. – Szulczewski, p. 11, pl. 2, fig. 1.
- 1976 *Ancyrodella buckeyensis* Stauffer. – Druce, pp. 53–55, pl. 1, figs 2, 4; pl. 2, figs 2, 4, 5 [only].
- 1976 *Ancyrodella nodosa* Ulrich & Bassler. – Druce, pp. 61, 62, pl. 8, fig. 1 [only].
- 1978 *Ancyrodella nodosa* Ulrich & Bassler. – Orchard, p. 928, pl. 114, fig. 3.
- 1981a *Ancyrodella buckeyensis* Stauffer. – Perri & Spalletta, p. 292, pl. 1, fig. 1.
- 1985 *Ancyrodella nodosa* Ulrich & Bassler. – Olivieri, p. 282, pl. 3, figs 3, 4.
- 1987 *Ancyrodella nodosa* Ulrich & Bassler. – Fuchs, pl. 3, figs 5, 7, ?10.
- 1989a *Ancyrodella nodosa* Ulrich & Bassler. – Ji, p. 294, pl. 1, figs 27, 28.
- 1989b *Ancyrodella nodosa* Ulrich & Bassler. – Ji, p. 316, pl. 3, fig. 6.
- 1992 *Ancyrodella nodosa* Ulrich & Bassler. – Uyeno, p. 72, pl. 16, figs 1–5 [only].
- 1992 *Ancyrodella nodosa* Ulrich & Bassler. – Savage, p. 280, figs 4.13, 4.14.
- 1992 *Ancyrodella nodosa* Ulrich & Bassler. – Helsen & Bultynck, p. 152, pl. 1, fig. 5.
- 1997 *Ancyrodella buckeyensis* Stauffer. – Over, pp. 172, 174, figs 11.1–11.9 [fig. 11.7 = reillustration of lectotype, synonymy].
- 1999 *Ancyrodella nodosa* Ulrich & Bassler. – Lazreq, pp. 58, 60, pl. 4, figs 7, 8.
- 2000 *Ancyrodella buckeyensis* Stauffer. – Over & Rhodes, p. 109, fig. 6.1.
- 2004 *Ancyrodella buckeyensis* Stauffer. – Klapper *et al.*, p. 383, fig. 5.5 [synonymy].
- 2006 *Ancyrodella nodosa* Ulrich & Bassler. – Savage *et al.*, p. 178, fig. 5v–x [only].
- 2007a *Ancyrodella* [as *An.*] *buckeyensis* Stauffer. – Klapper, tables 1–3.
- 2007 *Ancyrodella buckeyensis* Stauffer. – Over, pp. 1201, 1202, figs 11.1–11.3.
- 2009 *Ancyrodella buckeyensis* Stauffer. – Navas-Parejo *et al.*, p. 115, figs 3.1, 3.2.
- 2013 *Ancyrodella buckeyensis* Stauffer. – Savage, p. 7, figs 5.1, 5.2, 5.26–5.28, 6.26–6.29.
- 2016 *Ancyrodella hamata* Ulrich & Bassler. – Klapper & Kirchgasser, pp. 537, 539, figs 9.13–9.18.
- 2019 *Ancyrodella hamata* Ulrich & Bassler. – Savage, p. 484, figs 7.20, 7.21 [same specimen as Savage 2013, figs 6.26, 6.27], 8.22–8.24 [same specimen as *op. cit.*, figs 5.1, 5.2], 9.27–9.32, 11.18–11.21, 12.21–12.23 [same specimen as *op. cit.*, figs 5.26–5.28].
- [*non*] 2020a *Ancyrodella* [as *Ad.*] *hamata* (= *gigas* M2). – Becker *et al.*, p. 75, fig. 62.23 [= ? *A.* sp. indet.].

**Diagnosis.** – *Ancyrodella hamata*, with extremely rare exception, lacks posterior rows of nodes parallel to the carina. Secondary keels project anteriorly.

**Remarks.** – *Ancyrodella hamata* was an unused name after its initial proposal in 1926, with the exception of the paper by Müller & Müller 1957, who used it for the closely related species *A. nodosa*, until its revival by Klapper & Kirchgasser (2016, pp. 537, 539). Huddle (1968, p. 6) and Klapper & Lane (1985, p. 925) had treated *A. hamata* as a junior synonym of *A. nodosa*, which were published in the same paper. But the two can be distinguished although there is some intergradation, especially in the platform outline (see Klapper & Kirchgasser 2016, fig. 9). Commonly the outlines are distinct, however. The specimen in fig. 9.14 of that paper has the posterior rows of nodes parallel to the carina, the distinguishing characteristic of *A. nodosa* that is almost always absent in *A. hamata*. But this specimen has the characteristic outline of *A. hamata* so it is identified as such. It should not be necessary to emphasize that because there are some transitional specimens need not mean that the two taxa are the same species.

The Pa element identified as *A. hamata* by Becker *et al.* (2020a, fig. 62.23) has an extremely different outline from that characteristic of *A. hamata*. Furthermore, the platform outline of their Morocco specimen is not at all similar to *A. gigas* form 2 of Klapper (1989), nor is that morphotype similar to *A. hamata*.

# ***Ancyrodella ioides* Ziegler, 1958 s.s.**

Figure 2B–D

- 1958 *Ancyrodella ioides* n. sp.; Ziegler, pp. 42, 43, pl. 11, figs 2, 3 [only; fig. 2 = holotype].
- 1970 *Ancyrodella ioides* Ziegler. – Khalymbadza & Chernysheva, pp. 97, 102, pl. 2, figs 18, 19.
- 1973 *Ancyrodella ioides* Ziegler. – Ziegler, pp. 23, 24, Ancyro pl. 1, fig. 6 [only; reillustration of holotype].
- 1982 *Ancyrodella ioides* Ziegler. – Mouravieff, p. 113, pl. 2, fig. 9.
- 1987 *Ancyrodella ioides* Ziegler. – Fuchs, pl. 3, fig. 6.
- 1989a *Ancyrodella ioides* Ziegler. – Ji, p. 294, pl. 1, figs 23, 24 [only].
- 1992 *Ancyrodella ioides* Ziegler. – Helsen & Bultynck, p. 152, pl. 1, fig. 3.
- 1999 *Ancyrodella ioides* Ziegler. – Lazreq, p. 58, pl. 4, fig. 2.
- 2013 *Ancyrodella ioides* Ziegler. – Savage, p. 9, figs 7.15, 7.16 [only].
- 2016 *Ancyrodella ioides* Ziegler. – Gatovsky *et al.*, p. 66, pl. 1, fig. 8.
- 2019 *Ancyrodella ioides* Ziegler. – Savage, p. 484, figs 5.23, 5.24 [only; same specimen as Savage 2013, figs 7.15, 7.16].

- 2020b *Ancyrodella* [as *Ad.*] *ioides*. – Becker *et al.*, p. 106, fig. 18.13.

**Diagnosis.** – *Ancyrodella ioides* s.s. completely lacks a platform posterior of the secondary carinae.

**Remarks.** – The Pa element of *Ancyrodella ioides* s.s. is characterized by a posterior carina and secondary carinae but otherwise lacks platform development. The blade and carina are gently incurved and the outer secondary carina in distinctly and strongly reclined posteriorly.

# ***Ancyrodella ioides* form 1 new morphotype**

Figure 2E–G

- 1958 *Ancyrodella ioides* n. sp.; Ziegler, pp. 42, 43, pl. 11, fig. 4 [only].
- 1966 *Ancyrodella nodosa* Ulrich & Bassler. – Glenister & Klapper, pp. 798, 799, pl. 86, figs 11, 12 [only].
- 1970 *Ancyrodella nodosa* Ulrich & Bassler. – Khalymbadza & Chernysheva, pp. 96, 97, pl. 2, figs 12, 13 [only].
- 1970a *Ancyrodella ioides* Ziegler. – Seddon, p. 753, pl. 16, fig. 6.
- 1970a *Ancyrodella nodosa* Ulrich & Bassler. – Seddon, p. 753, pl. 16, fig. 5.
- 1971 *Ancyrodella ioides* Ziegler. – Szulczewski, pp. 12, 13, pl. 5, fig. 1.
- 1973 *Ancyrodella ioides* Ziegler. – Ziegler, pp. 23, 24, Ancyro pl. 1, fig. 5 [only].
- 1976 *Ancyrodella ioides* Ziegler. – Druce, pp. 58, 59, pl. 4, figs 3, 4 [only; figs 1, 2 are too small for confident identification].
- 1981a *Ancyrodella ioides* Ziegler. – Perri & Spalletta, p. 293, pl. 1, fig. 2.
- 1982 *Ancyrodella nodosa* Ulrich & Bassler. – Mouravieff, pp. 113, 114, pl. 2, fig. 8; pl. 3, fig. 8 [only].
- 1983 *Ancyrodella nodosa* Ulrich & Bassler. – Boogaard, p. 3, pl. 1, fig. 5 [only].
- 1989 *Ancyrodella nodosa* Ulrich & Bassler. – Orchard, p. 42, pl. 1, fig. 5.
- 1989a *Ancyrodella ioides* Ziegler. – Ji, p. 294, pl. 1, figs 25, 26 [only].
- 1989b *Ancyrodella ioides* Ziegler. – Ji, p. 316, pl. 3, fig. 7.
- 1993 *Ancyrodella ioides* Ziegler. – Ji & Ziegler, pp. 52, 53, pl. 2, figs 1–3.
- 1998 *Ancyrodella nodosa* Ulrich & Bassler. – Bultynck *et al.*, p. 66, pl. 6, fig. 4.
- 2007a *Ancyrodella* [as *An.*] *buckeyensis* transitional with [as tr. w.] *An. ioides*. – Klapper, tabs 2a, 2b, 3.
- 2008 *Ancyrodella nodosa* Ulrich & Bassler. – Ovnatanova & Kononova, pp. 1080, 1081, 1155, pl. 26, figs 11–13 [only].
- 2013 *Ancyrodella ioides* Ziegler. – Savage, p. 9, figs 5.23–5.25 [only].



**Figure 2.** All photographs are upper views, magnifications  $\times 40$ . • A – homeomorph of *Ancyrodella ioides* Ziegler 1958 s.s., F54970, HS 364-70, FZ 13a. • B–D – *Ancyrodella ioides* Ziegler 1958 s.s., F51422 [previously illustrated in Klapper 2009, fig. 1.3.3], F54971–54972, all from HS 364-34, FZ 12. • E–G – *Ancyrodella ioides* form 1 new morphotype, F54973–54975, HS 364-43, 45, 43, FZ 12. • H – *Ancyrodella hamata* Ulrich & Bassler 1926, F54976, HS 364-71, FZ 13b. • I, J, K – *Ancyrodella nodosa* Ulrich & Bassler 1926; I, J – F54977–54978, HS 364-12, FZ 11; K – F54979, HS 364-18, FZ 11 [This specimen is identified with some question].



- 2013 *Ancyrodella ioides* Ziegler. – Tagarieva, p. 308, fig. 7s.  
 2013 *Ancyrodella ioides* Ziegler. – Bahrami *et al.*, p. 380, figs 7p, q [fig. 7r = ?].  
 2019 *Ancyrodella ioides* Ziegler. – Savage, p. 484, figs 6.19–6.21, 12.18–12.20 [same specimen as Savage 2013, figs 5.23–5.25] [only].

**Diagnosis.** – The form 1 morphotype of *Ancyrodella ioides* s.s. has an extremely narrow platform posterior of the secondary carinae.

**Remarks.** – The new morphotype designated here as *Ancyrodella ioides* form 1 has heretofore always been included within *A. ioides* without qualification, as seen in the above synonymy. However, it differs consistently by the development of an extremely narrow platform posterior of the secondary carinae. The transitional nature of the two morphotypes is evidenced by the specimen illustrated by Savage (2019, fig. 12.18), which has an incipiently developed outer platform posterior of the secondary carina that is distinctly reclined as in *A. ioides* s.s. The Canning Basin specimens of form 1 such as those in Fig. 2E and 2G also have an incipiently developed outer platform although the secondary carina is only slightly reclined. The difference between *A. ioides* s.s. and form 1 is small indicating they should be considered as morphotypes within the one species. The single unique specimen from Horse Spring in FZ13a (Fig. 2A), termed as a homeomorph of *A. ioides* s.s., has a triangular platform posterior of the secondary carinae with small rows of nodes adjacent to and parallel to the posterior carina.

# ***Ancyrodella nodosa* Ulrich & Bassler, 1926**

Figures 1C–F, 2I–K

- 1926 *Ancyrodella nodosa* new species; Ulrich & Bassler, p. 48, pl. 1, figs 10–13 [fig. 10 = lectotype selected by Ziegler 1958, p. 44], text-figs 5.8, 5.9.  
 1956 *Ancyrodella* sp. – Müller, p. 1340, pl. 145, figs 12, 14 [only].  
 1957 *Ancyrodella hamata* Ulrich & Bassler. – Müller & Müller, pp. 1091, 1092, pl. 136, fig. 4.  
 1958 *Ancyrodella nodosa* Ulrich & Bassler. – Ziegler, p. 44, pl. 11, fig. 1.  
 1958 *Ancyrodella gigas* Youngquist. – Ziegler, pp. 41, 42, pl. 11, fig. 10 [only; fig. 17 = ?, shown in an oblique lateral view].  
 1959 *Ancyrodella buckeyensis* Stauffer, 1938. – Krebs, p. 384, pl. 1, fig. 6.  
 1966 *Ancyrodella gigas* Youngquist. – Anderson, p. 403, pl. 48, figs 10, 14.  
 1966 *Ancyrodella nodosa* Ulrich & Bassler. – Glenister & Klapper, pp. 798, 799, pl. 86, figs 5, 6, 9, 10 [only; figs 7, 8 = transitional morphotype between *A. nodosa* and *A. hamata*].  
 1968 *Ancyrodella nodosa* Ulrich & Bassler. – Huddle, pp. 6, 7, pl. 13, figs 7–10 [only; reillustrations of Ulrich & Bassler, pl. 1, figs 10, 11, 12, 13, respectively].  
 1970 *Ancyrodella nodosa* Ulrich & Bassler. – Khalymbadzha & Chernysheva, pp. 96, 97, pl. 2, figs 10, 11 [only].  
 1970b *Ancyrodella nodosa* Ulrich & Bassler. – Seddon, p. 94, pl. 7, fig. 18.  
 1970b *Ancyrodella gigas* Youngquist. – Seddon, p. 94, pl. 7, fig. 7 [only].  
 1971 *Ancyrodella gigas* Youngquist. – Szulczewski, p. 12, pl. 4, fig. 1 [only].  
 1971 *Ancyrodella nodosa* Ulrich & Bassler. – Szulczewski, pp. 14, 15, pl. 2, fig. 4; pl. 5, figs 2–4 [only].  
 1971 *Ancyrodella rugosa* Branson & Mehl. – Szulczewski, p. 16, pl. 2, fig. 5.  
 1971 *Ancyrodella* sp. A; Szulczewski, p. 17, pl. 5, fig. 6.  
 1976 *Ancyrodella nodosa* Ulrich & Bassler. – Druce, pp. 61, 62, pl. 7, figs 1–3; pl. 8, figs 2, 3 [only].  
 1976 *Ancyrodella gigas* Youngquist. – Druce, pp. 57, 58, pl. 3, figs 1, 2 [only].  
 1981a *Ancyrodella lobata* Branson & Mehl. – Perri & Spalletta, p. 293, pl. 1, fig. 5 [only].  
 1981 *Ancyrodella gigas* Youngquist. – Bultynck & Jacobs, p. 24, pl. 9, figs 9–11.  
 1983 *Ancyrodella nodosa* Ulrich & Bassler. – Boogaard, p. 3, pl. 1, fig. 3 [only].  
 1985 *Ancyrodella gigas* Youngquist. – Klapper, p. 29, figs 3ee–ff [non fig. gg = *A. gigas* holotype]; pl. 10, figs 9, 10, 13–16 [only; figs 9, 10 = same specimen as figs 3ee–ff; non figs 3–6 = *A. devonica*].  
 1985 *Ancyrodella nodosa* Ulrich & Bassler. – Klapper & Lane, pp. 925, 927, figs 14.6, 14.7, 14.10, 14.11.  
 1989 *Ancyrodella gigas* Youngquist form 1. – Klapper, p. 457.  
 1989 *Ancyrodella gigas* Youngquist alpha morphotype. – Vandelaer *et al.*, pp. 329, 330, pl. 2, fig. 5.  
 1989 *Ancyrodella gigas* Youngquist beta morphotype. – Vandelaer *et al.*, pp. 329, 330, pl. 2, fig. 6 [only].  
 1992 *Ancyrodella nodosa* Ulrich & Bassler. – Savage, p. 280, figs 4.13, 4.14.  
 1992 *Ancyrodella nodosa* Ulrich & Bassler. – Helsen & Bultynck, p. 152, pl. 1, fig. 5.  
 1993 *Ancyrodella nodosa* Ulrich & Bassler. – Ji & Ziegler, p. 53, pl. 2, fig. 11 [fig. 12 = ?].  
 2000 *Ancyrodella gigas* Youngquist. – Gouwy & Bultynck, p. 40, pl. 1, figs 9, 10 [only; the specimen in figs 11, 12 is not well enough preserved for confident identification].  
 2002 *Ancyrodella nodosa* Ulrich & Bassler. – Dzik, p. 590, fig. 25f, 25h [only].

- 2003 *Ancyrodella gigas* Youngquist form 1 of Klapper (1989). – Over *et al.*, p. 222, pl. 1, fig. 5.
- 2006 *Ancyrodella nodosa* Ulrich & Bassler. – Savage *et al.*, p. 178, fig. 6g, h [only].
- 2006 *Ancyrodella gigas* Youngquist (form 1 *sensu* Klapper, 1988 (*sic*)). – Piszarszewska *et al.*, p. 625, fig. 13d, e.
- 2007 *Ancyrodella gigas* Youngquist form 1 of Klapper, 1989. – Gouwy *et al.*, pp. 389, 391, fig. 15n [only].
- 2007 *Ancyrodella nodosa* Ulrich & Bassler. – Over, pp. 1202, 1206, fig. 11.8.
- 2007 *Ancyrodella gigas*. – Over, p. 1202, figs 11.10, 11.12, 11.13 [only].
- 2008 *Ancyrodella gigas* Youngquist. – Ovnatanova & Kononova, pp. 1080, 1155, pl. 26, figs 6, 8.
- 2008 *Ancyrodella nodosa* Ulrich & Bassler. – Ovnatanova & Kononova, pp. 1080, 1081, 1155, pl. 26, fig. 15 [only; figs 14, 16 = juveniles that are too small for confident identification].
- 2008 *Ancyrodella rugosa* Branson & Mehl. – Ovnatanova & Kononova, pp. 1081, 1082, pl. 26, fig. 7.
- 2013 *Ancyrodella gigas* Youngquist. – Tagarieva, p. 308, fig. 7o.
- 2013 *Ancyrodella nodosa* s.s. – Over *et al.*, p. 13, fig. 7a.3.
- 2015 *Ancyrodella gigas* Youngquist Morphotype 1: Klapper (1985) [*sic*]. – Becker & Aboussalam, p. 118, pl. aii-2, figs 2, 3.
- 2016 *Ancyrodella nodosa* Ulrich & Bassler. – Gatovsky *et al.*, p. 66, pl. 1, fig. 4.
- 2016 *Ancyrodella nodosa* Ulrich & Bassler. – Klapper & Kirchgasser, pp. 537, 538, figs 9.1–9.12 [fig. 9.4 = reillustration of lectotype; additional synonymy].
- 2017 *Ancyrodella nodosa* Ulrich & Bassler. – Ovnatanova *et al.*, pp. 1046, 1049, pl. 41, figs 3, 5 [only].
- 2017 *Ancyrodella rotundiloba* (Bryant). – Königshof *et al.*, p. 525, fig. 4.2.
- 2018 *Ancyrodella nodosa* Ulrich & Bassler. – Dzik *et al.*, p. 331, fig. 3l (photo reversed), 3m [only; reillustrations of Dzik 2002, fig. 25f, 25h].
- 2019 *Ancyrodella rugosa* Branson & Mehl. – Nazarova *et al.*, p. 91, pl. 3, fig. 15.
- 2020b *Ancyrodella* [as *Ad.*] *nodosa*. – Becker *et al.*, p. 106, fig. 18.1.
- 2020 *Ancyrodella* [as *Ad.*] *nodosa* (= *gigas* M1). – Aboussalam *et al.*, p. 149, fig. 20.8.

**Diagnosis.** – *Ancyrodella nodosa* has posterior rows of nodes closely parallel to, and on both sides of the carina. Secondary keels project anteriorly.

**Remarks.** – As stated in the diagnosis of *A. nodosa* (Klapper & Kirchgasser 2016, p. 537): “Each secondary carina meets or comes close to a slightly curved row of nodes that parallels the posterior carina and is separated from it by an adcarinal trough.” In their figures 9.1, 9.3

(paralectotype), 9.4 (lectotype), 9.7, 9.9, 9.10 the specimens have the meeting of the secondary carinae and the posterior node-rows, but there is a conspicuous one-denticle gap on the inner (fig. 9.11) or outer side (fig. 9.12). This variable gap or non-gap is a characteristic feature of *A. nodosa* Pa elements and the posterior node-rows may be weakly developed in some specimens that are nevertheless included here within the intraspecific variation of the species (*e.g.*, Müller 1956, pl. 145, fig. 14; Müller & Müller 1957, pl. 136, fig. 4, outer but not inner side; Ziegler 1958, pl. 11, fig. 10a; Glenister & Klapper 1966, pl. 86, fig. 6, inner side node-row is weak; Savage *et al.* 2006, fig. 6g, outer posterior node-row well developed but lacks node-row on inner side). The specimens in Fig. 21 and J also have only weakly developed posterior node rows, but do have the characteristic platform outline of *A. nodosa*.

Based on the evidence of the types of Ulrich & Bassler’s species (as reillustrated by Huddle 1968, Klapper & Kirchgasser 2016), as well as the many other specimens now placed in *A. nodosa*, *A. gigas* Youngquist form 1 proposed by Klapper (1989, p. 457) is identical with *A. nodosa*. This is because *most* of the specimens originally given in that paper as examples of form 1 are the same as *A. nodosa* (according to the synonymy above; note that the specimens cited in Klapper 1985, pl. 10, figs 3–6 are not included herein in *A. nodosa*, but rather in *A. devonica*).

### *Ancyrodella curvata* Group

This group includes *A. curvata* s.s., *A. curvata* early form, and *A. lobata*.

### *Ancyrodella curvata* (Branson & Mehl, 1934) s.s.

- 1934 *Ancyrognathus curvata* new species; Branson & Mehl, p. 241, pl. 19, figs 6, 11 [= lectotype selected by Ziegler 1958, p. 41].
- 1957 *Ancyropenta asteroideus* (Stauffer). – Müller & Müller, p. 1093, pl. 136, figs 7, 8.
- 1962 *Ancyrodella curvata* (Branson & Mehl). – Ethington & Furnish, pp. 1261, 1262, pl. 172, figs 12–20.
- 1966 *Ancyrodella curvata* (Branson & Mehl). – Anderson, p. 403, pl. 48, figs 6, 9, 11, 13 [only].
- 1966 *Ancyrodella curvata* (Branson & Mehl). – Glenister & Klapper, p. 798, pl. 86, figs 13–15.
- 1970b *Ancyrodella curvata* (Branson & Mehl). – Seddon, p. 94, pl. 7, figs 12, 13.
- 1971 *Ancyrodella curvata* (Branson & Mehl). – Szulczewski, pp. 11, 12, pl. 3, fig. 5, pl. 4, figs 4, 5.
- 1976 *Ancyrodella curvata* (Branson & Mehl). – Druce, pp. 55–57, pl. 1, fig. 3.
- 1978 *Ancyrodella curvata* (Branson & Mehl). – Orchard,

- p. 926, pl. 114, figs 2, 10 [figs 8, 9, 20 = indet. juveniles].
- 1981 *Ancyrodella curvata* (Branson & Mehl). – Bultynck & Hollard, p. 38, pl. 10, fig. 12.
- 1981 *Ancyrodella lobata* Branson & Mehl. – Bultynck & Jacobs, p. 24, pl. 9, fig. 12 [only].
- 1982 *Ancyrodella curvata* (Branson & Mehl). – Mouravieff, p. 114, pl. 3, figs 10, 11 [only].
- 1984 *Ancyrodella curvata* (Branson & Mehl). – Matthews & Riddolls, p. 34, pl. 6, figs 1, 2, 7.
- 1985 *Ancyrodella curvata* (Branson & Mehl). – Olivieri, p. 280, pl. 3, fig. 6.
- 1986 *Ancyrodella curvata* (Branson & Mehl). – García-López, p. 454, pl. 3, figs 17–19.
- 1987 *Ancyrodella curvata* (Branson & Mehl). – García-López, pp. 59, 60, pl. 3, figs 11–13, text-fig. 11.
- 1987 *Ancyrodella curvata* (Branson & Mehl). – Fuchs, pl. 3, fig. 9 [only]; pl. 16, fig. 13.
- 1989 *Ancyrodella curvata* (Branson & Mehl) late form. – Klapper, p. 457, pl. 3, fig. 20.
- 1992 *Ancyrodella curvata* (Branson & Mehl). – Sandberg *et al.*, p. 74, pl. 4, fig. 2 [only; termed as late morphotype].
- 1992 *Ancyrodella curvata* (Branson & Mehl). – Helsen & Bultynck, p. 152, pl. 1, fig. 1.
- 1993 *Ancyrodella curvata* (Branson & Mehl). – Ji & Ziegler, pp. 51, 52, pl. 2, fig. 4 [only].
- 1995 *Ancyrodella curvata* (Branson & Mehl). – Schülke, p. 65, pl. 14, figs 12, 13.
- 1997 *Ancyrodella curvata* (Branson & Mehl). – Schülke, pp. 42–44, pl. 1, fig. 10; pl. 2, figs 1–8, 10–20 [multielement reconstruction].
- 1997 *Ancyrodella curvata* (Branson & Mehl) (late form). – Over, p. 174, figs 11.10–11.14.
- 1998 *Ancyrodella curvata* (Branson & Mehl) late form. – Bultynck *et al.*, pp. 55, 66, pl. 6, figs 1, 2.
- 1998 *Ancyrodella curvata* (Branson & Mehl) latest form. – Bultynck *et al.*, pp. 55, 65, 66, pl. 5, figs 8–10; pl. 6, fig. 3.
- 1998b *Ancyrodella curvata* (Branson & Mehl). – Spalletta & Perri, p. 205, pl. 2.2.1, fig. 1.
- 1999 *Ancyrodella curvata* (Branson & Mehl). – Lazreq, p. 58, pl. 4, figs 3, 4.
- 1999 *Ancyrodella curvata* (Branson & Mehl). – Schülke, p. 64, pl. 11, figs 20–23 (partial multielement reconstruction).
- 2000 *Ancyrodella curvata* (Branson & Mehl) late form. – Gouwy & Bultynck, pp. 40, 49, pl. 2, figs 1–3.
- 2000 *Ancyrodella curvata* (Branson & Mehl) latest form. – Gouwy & Bultynck, p. 40, 49, pl. 2, fig. 4.
- 2002 *Ancyrodella lobata* Branson & Mehl. – Dzik, p. 590, fig. 27d [only].
- 2002 *Ancyrodella curvata* Branson & Mehl [sic]. – Dzik, p. 590, fig. 27g, h [only].
- 2006 *Ancyrodella curvata* Branson & Mehl [sic]. – Savage *et al.*, p. 178, fig. 5n–q.
- 2007 *Ancyrodella curvata* (Branson & Mehl) late form of Klapper, 1989. – Gouwy *et al.*, p. 389, fig. 15t.
- 2007 *Ancyrodella curvata* (Branson & Mehl) late form. – Over, p. 1202, figs 11.4, 11.7.
- 2013 *Ancyrodella curvata* (Branson & Mehl). – Tagarieva, p. 308, fig. 7m, n.
- 2013 *Ancyrodella curvata* (Branson & Mehl). – Bahrami *et al.*, pp. 382, 384, fig. 7n, t.
- 2018 *Ancyrodella curvata* Branson & Mehl [sic]. – Dzik *et al.*, p. 331, fig. 3c, d [only; c = reillustration of Dzik 2002, fig. 27g; d (photo reversed) = reillustration of Dzik 2002, fig. 27h].
- 2020a *Ancyrodella* [as *Ad.*] *curvata* late morph. – Becker *et al.*, p. 81, fig. 71.20.
- 2020b *Ancyrodella* [as *Ad.*] *curvata* late form. – Becker *et al.*, pp. 106, 108, figs 18.20, 19.12.

**Diagnosis.** – *Ancyrodella curvata* s.s. has a well defined outer posterior lobe formed by distinct sinuses on both the anterior and posterior sides. This lobe has a strong accessory carina.

**Remarks.** – *Ancyrodella curvata* s.s. (= *A. curvata* late form of Klapper 1989, both late and latest forms of Bultynck *et al.* 1998 and Gouwy & Bultynck 2000) differs from the early form of Klapper (1989) by the presence of a distinct outer posterior lobe that is demarcated by sinuses on either side of the lobe. Compare for example, the early form (Klapper 1989, pl. 3, figs 18, 19) with the late form (*op. cit.*, fig. 20). Both morphs have a distinct accessory carina on the outer side posterior of midlength. There is a transition, however, between the two morphs as is well illustrated by the three specimens in Sandberg *et al.* (1992, pl. 4, fig. 1 = *A. curvata* early morphotype, fig. 2 = *A. curvata* s.s. or late morphotype, and fig. 3 = intermediate morphotype in their designations). The intermediate morphotype has only a slight incipient sinus developed between the tips of the outer accessory carina and the posterior carina. The intermediate morphotype seems to be relatively infrequent (and is included herein within the *A. curvata* early form). The existence of the transition justifies treating the two as morphotypes of the same species.

Ethington & Furnish (1962), Over (1997), and Schülke (1997) have illustrated ontogenetic series for the *A. curvata* s.s. Pa (P1) element. Furthermore, Schülke (1997, pl. 2, figs 1–8, 10–20) proposed a multielement reconstruction for this species lacking only the Sd element.

Branson & Mehl (1934) originally included their new species *curvata* within *Ancyrognathus* so the authors' names must be in parentheses as it subsequently became a changed genus combination.



***Ancyrodella curvata* (Branson & Mehl, 1934) early form**

- 1958 *Ancyrodella curvata* (Branson & Mehl). – Ziegler, pp. 40, 41, pl. 11, fig. 5.
- 1966 *Ancyrodella curvata* (Branson & Mehl). – Anderson, p. 403, pl. 48, figs 2, 4 [only].
- 1970a *Ancyrodella curvata* (Branson & Mehl). – Seddon, p. 753, pl. 16, figs 3, 4.
- 1970b *Ancyrodella lobata* Branson & Mehl. – Seddon, p. 94, pl. 7, figs 15, 17 [only].
- 1971 *Ancyrodella lobata* Branson & Mehl. – Szulczewski, pp. 13, 14, pl. 3, fig. 3 [only].
- 1976 *Ancyrodella lobata* Branson & Mehl. – Druce, pp. 59–61, pl. 5, fig. 1 [only].
- 1981a *Ancyrodella curvata* (Branson & Mehl). – Perri & Spalletta, p. 292, pl. 1, fig. 3.
- 1982 *Ancyrodella curvata* (Branson & Mehl). – Mouravieff, p. 113, pl. 2, figs 10–13 [only].
- 1987 *Ancyrodella curvata* (Branson & Mehl). – Fuchs, pl. 3, fig. 8 [only].
- 1989 *Ancyrodella curvata* (Branson & Mehl) early form. – Klapper, p. 457, pl. 3, figs 18, 19.
- 1989 *Ancyrodella curvata* (Branson & Mehl). – Vandelaer *et al.*, p. 329, pl. 3, fig. 1.
- 1992 *Ancyrodella curvata* (Branson & Mehl). – Sandberg *et al.*, p. 74, pl. 4, figs 1, 3 [only; 1 termed as early morphotype, 3 as intermediate morphotype].
- 1993 *Ancyrodella curvata* (Branson & Mehl). – Ji & Ziegler, pp. 51, 52, pl. 2, fig. 5 [only].
- 2000 *Ancyrodella curvata* (Branson & Mehl) early form. – Gouwy & Bultynck, pp. 40, 49, pl. 2, figs 5, 6.
- 2000 *Ancyrodella curvata* (Branson & Mehl). – Çapkinoglu & Gedik, p. 84, pl. 3, fig. 16.
- 2007 *Ancyrodella curvata* (Branson & Mehl) early form of Klapper, 1989. – Gouwy *et al.*, p. 389, fig. 15p–s.
- 2020a *Ancyrodella* [as *Ad.*] *curvata* early morph. – Becker *et al.*, p. 81, fig. 71.19.
- 2020b *Ancyrodella* [as *Ad.*] *curvata* early form. – Becker *et al.*, p. 106, fig. 18.12.

**Diagnosis.** – *Ancyrodella curvata* early form lacks the well demarcated outer posterior lobe that is developed in *A. curvata* s.s., but shares a strong accessory carina in the same outer posterior position. The platform outline is close to trapezoidal.

**Remarks.** – The early form of *Ancyrodella curvata* has a well developed accessory carina on the outer side posterior of midlength (*e.g.*, Klapper 1989, pl. 3, figs 18, 19; Gouwy & Bultynck 2000, pl. 2, fig. 11). In contrast, in that same position in *A. lobata*, a carina is either absent or at most represented by a row of several separated nodes (*e.g.*, Druce 1976, pl. 5, fig. 2a, pl. 6, figs 1a, 2b, 3a; Dzik 2002, fig. 27c). Both have a characteristic almost trapezoidal platform outline.

***Ancyrodella lobata* Branson & Mehl, 1934**

Figure 3E–I

- 1934 *Ancyrodella lobata* n. sp.; Branson & Mehl, pp. 239, 240, pl. 19, fig. 14; pl. 21, figs 22, 23 [fig. 22 = lectotype selected by Ziegler 1958, p. 43; fig. 22 is the upper view of the specimen on pl. 19, fig. 14].
- 1957 *Ancyropenta longidenticulata* n. sp.; Müller & Müller, p. 1093, pl. 136, fig. 3; pl. 137, figs 1, 2 [fig. 1 = holotype].
- 1958 *Ancyrodella lobata* Branson & Mehl. – Ziegler, p. 43, pl. 11, figs 6, 9.
- 1966 *Ancyrodella lobata* Branson & Mehl. – Anderson, p. 403, pl. 48, figs 15, 16.
- 1968 *Ancyrodella lobata* Branson & Mehl. – Mound, pp. 470, 471, pl. 65, figs 7–12.
- 1970a *Ancyrodella lobata* Branson & Mehl. – Seddon, p. 753, pl. 16, fig. 2.
- 1970b *Ancyrodella lobata* Branson & Mehl. – Seddon, p. 94, pl. 7, figs 8–11, 14 [only; fig. 16 = ?].
- 1971 *Ancyrodella lobata* Branson & Mehl. – Szulczewski, pp. 13, 14, pl. 3, figs 1, 2, 4 [only]; pl. 4, figs 2, 3.
- 1971 *Ancyrodella gigas* Youngquist. – Szulczewski, p. 12, pl. 2, fig. 3 [only].
- 1976 *Ancyrodella lobata* Branson & Mehl. – Druce, pp. 59–61, pl. 5, fig. 2 [only]; pl. 6, figs 1–3.
- 1976 *Ancyrodella buckeyensis* Stauffer. – Druce, pp. 53–55, pl. 2, fig. 3 [only].
- 1976 *Ancyrodella gigas* Youngquist. – Druce, pp. 57, 58, pl. 3, fig. 3 [only].
- 1981 *Ancyrodella lobata* Branson & Mehl. – Bultynck & Hollard, p. 38, pl. 10, figs 9–11.
- 1981a *Ancyrodella lobata* Branson & Mehl. – Perri & Spalletta, p. 293, pl. 1, fig. 6 [only].
- 1981 *Ancyrodella lobata* Branson & Mehl. – Bultynck & Jacobs, p. 24, pl. 9, fig. 13 [only].
- 1982 *Ancyrodella lobata* Branson & Mehl. – Mouravieff, p. 114, pl. 3, fig. 6.
- 1985 *Ancyrodella lobata* Branson & Mehl. – Olivieri, pp. 280, 282, pl. 3, fig. 5.
- 1985 *Ancyrodella lobata* Branson & Mehl. – Klapper & Lane, pp. 923, 925, figs 14.12, 14.13, 14.16, 14.17.
- 1986 *Ancyrodella lobata* Branson & Mehl. – García-López, p. 454, pl. 3, figs 11–16.
- 1987 *Ancyrodella lobata* Branson & Mehl. – García-López, pp. 62, 63, pl. 3, figs 7–10.
- 1989 *Ancyrodella lobata* Branson & Mehl. – Klapper, 1989, p. 457.
- 1989 *Ancyrodella lobata* Branson & Mehl. – Vandelaer *et al.*, p. 330, pl. 2, figs 1, 2.
- 1989 *Ancyrodella* aff. *lobata* Branson & Mehl. – Vandelaer *et al.*, p. 330, pl. 2, figs 3, 4.
- 1992 *Ancyrodella lobata* Branson & Mehl. – Helsen & Bultynck, p. 152, pl. 1, fig. 4.

- 1992 *Ancyrodella* sp. A. – Helsen & Bultynck, p. 152, pl. 1, fig. 6.
- 1992 *Ancyrodella nodosa* Ulrich & Bassler. – Uyeno, p. 72, pl. 16, fig. 6 [only].
- 1993 *Ancyrodella lobata* Branson & Mehl Morphotype 1. – Ji & Ziegler, p. 53, pl. 2, figs 8–10.
- 1993 *Ancyrodella lobata* Branson & Mehl Morphotype 2. – Ji & Ziegler, p. 53, pl. 2, figs 6, 7.
- 1999 *Ancyrodella lobata* Branson & Mehl. – Lazreq, p. 58, pl. 4, figs 5, 6.
- 1999 *Ancyrodella rotundiloba* (Bryant). – Lazreq, p. 60, pl. 4, figs 9, 10 [only].
- 2000 *Ancyrodella lobata* Branson & Mehl. – Çapkinoğlu & Gedik, p. 84, pl. 3, fig. 15.
- 2002 *Ancyrodella rugosa* Branson & Mehl. – Dzik, p. 590, fig. 25c.
- 2002 *Ancyrodella nodosa* Ulrich & Bassler. – Dzik, p. 590, fig. 25e [only].
- 2002 *Ancyrodella lobata* Branson & Mehl. – Dzik, p. 590, fig. 27a–c [only].
- ? 2006 *Ancyrodella nodosa* Ulrich & Bassler. – Savage *et al.*, p. 178, figs 6q, w–y [only].
- ? 2006 *Ancyrodella gigas* Youngquist. – Savage *et al.*, p. 180, fig. 5y, z.
- 2006 *Ancyrodella curvata* (Branson & Mehl) early form. – Piszarska *et al.*, p. 625, fig. 13f.
- 2007 *Ancyrodella lobata* Branson & Mehl. – Gouwy *et al.*, p. 389, fig. 15o.
- 2007 *Ancyrodella curvata* early form. – Over, p. 1202, figs 11.5, 11.6.
- 2012 *Ancyrodella lobata* Branson & Mehl. – Liao & Valenzuela-Rios, p. 824, figs 5a, b [only; fig. 5c–h too fragmentary for confident identification].
- 2012 *Ancyrodella lobata* Branson & Mehl. – Mossoni *et al.*, p. 19, fig. 5.2.
- 2012 *Ancyrodella curvata* Branson & Mehl [sic]. – Mossoni *et al.*, p. 19, fig. 5.3.
- 2012 *Ancyrodella nodosa* Ulrich & Bassler. – Mossoni *et al.*, pp. 19, 21, fig. 5.1.
- 2013 *Ancyrodella lobata* Branson & Mehl. – Bahrami *et al.*, p. 380, fig. 7m, o.
- 2018 *Ancyrodella curvata* Branson & Mehl [sic]. – Huang *et al.*, p. 65, fig. 4.10.
- 2018 *Ancyrodella rugosa* Branson & Mehl. – Dzik *et al.*, p. 331, fig. 3p (photo reversed) [reillustration of Dzik 2002, fig. 25c].
- 2018 *Ancyrodella nodosa* Ulrich & Bassler. – Dzik *et al.*, p. 331, fig. 3n [only; reillustration of Dzik 2002, fig. 25e].
- 2018 *Ancyrodella lobata* Branson & Mehl. – Dzik *et al.*, p. 331, fig. 3h–j [only; reillustrations of Dzik 2002, fig. 27a–c].
- 2020 *Ancyrodella* [as *Ad.*] *lobata*. – Aboussalam *et al.*, p. 149, fig. 20.21.

**Diagnosis.** – *Ancyrodella lobata* has a similar platform outline to that of *A. curvata* early form but lacks the strong accessory carina on the outer side posterior of midlength.

**Remarks.** – *Ancyrodella lobata* differs from the early form of *A. curvata*, which have closely similar platform outlines, by the absence of a well developed accessory carina on the outer side just posterior of midlength. That position in *A. lobata* has at most a row of several separated nodes or no such nodes. This is the essential contrast with the *A. curvata* early form. The characteristic almost trapezoidal outline distinguishes both taxa from other species of the genus, including especially *A. nodosa*.

The range of intraspecific variation in *Ancyrodella lobata* is well exemplified by specimens illustrated in Dzik *et al.* 2018 (fig. 3h–j, n, p) all identified herein as *A. lobata*, whereas those authors identified fig. 3n as *A. nodosa*, fig. 3p as *A. rugosa*, and the other three as *A. lobata*. The row of several separated nodes bisecting the outer side just posterior of midlength is absent (fig. 3h) to weak but distinct in the other four specimens that are united by the almost trapezoidal platform outline and the straight secondary carinae set at a narrow angle in all but the specimen in fig. 3p, in which the carinae are only slightly curved. But the curvature of the secondary carinae of *A. nodosa* is much stronger (*e.g.*, Dzik *et al.* 2018, fig. 3l, m) and they form a much wider angle.

The specimens of Savage *et al.* (2006, figs 5y, z; 6q, w–y) have a platform outline somewhat resembling that of *A. lobata* but apparently lack the characteristic outer posterior accessory keel.

## Summary

In his monograph on conodonts and ammonoids of the Frasnian of the Holy Cross Mountains, Poland, Dzik (2002, p. 618) stated that “*Ancyrodella* species are generally very variable and the status of the majority of them is questionable”. The analysis and synonymies prepared for the present revision of all the *Ancyrodella* species, demonstrates how inconsistently these species

**Figure 3.** All photographs are upper views, magnifications ×40. • A – *Ancyrodella gigas* Youngquist form 2 Klapper 1989, F54980, WMcP 365-15, FZ 6. • B – *Ancyrodella gigas* Youngquist cf. form 2 Klapper 1989, F51424 [previously illustrated in Klapper 2009, fig. 1.3.11], HS 364-4a, FZ 7. • C, D – *Ancyrodella hamata* Ulrich & Bassler 1926, F54981–54982, HS 364-9, 25, FZ 10, 11. • E, F, G–I – *Ancyrodella lobata* Branson & Mehl 1934; E, F – F54983–54984, HS 364-16, FZ 11; G–I – F54985–54987, HS 364-5, FZ 8.



have been identified and in fact conflated. Thus, any zonation based on *Ancyrodella* species will remain questionable until the taxonomy is stabilized. A step in that direction is the purpose of the taxonomic revisions proposed herein. All seventeen species of *Ancyrodella* considered as valid are the subject of this paper, as well as several morphotypes that are intraspecific variants and not separate species.

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The late Philip E. Playford, former director of the Geological Survey of Western Australia, was the principal investigator of the Canning Basin Devonian reef complexes from the 1950s' field seasons for almost every year thereafter until the publication of the monograph by Playford, Hocking & Cockbain (2009). Phil provided the Survey's logistical support, including field vehicles, and assistance in my collecting especially in 1992 and 1995, but also gave critical advice on localities and stratigraphy in the other years (1988, 1990, and 1993). Furthermore, he provided a number of additional collections for conodont processing, including that of GSWA 135107. Robert S. Nicoll then of the Australian Geological Survey Organisation, Canberra, together with Richard W. Brown set up the initial field work in 1988, and greatly assisted in the measuring and collecting of the sections, especially the most important one at Horse Spring (Klapper 2007a). The late Michael R. House of Hull and Southampton Universities gave inestimable advice in the field in 1990, 1993, and 1995, as well as collecting several critical conodont samples in 1989 in addition to his main ammonoid collecting. Ralph Thomas Becker of Münster University also participated in the conodont and ammonoid sample collecting in those four field seasons. Raimund Feist of Montpellier University collected trilobites in the highest Frasnian beds at Horse Spring in the 1995 field season. My longtime colleague, the late William (Bill) T. Kirchgasser of the SUNY College at Potsdam and I collected many sections together in 1990 and had originally planned on writing a joint paper on Canning Basin Frasnian conodonts, including the genera *Ancyrodella*, *Ancyrognathus*, and *Mesotaxis*. The writing of that paper unfortunately did not begin, however, primarily because we instead worked off and on from 1989 until 2014 in the research and writing of the New York Frasnian paper that was not published until 2016 (Klapper & Kirchgasser 2016).

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## Appendix

Localities of illustrated specimens, all from the Canning Basin, Western Australia. Frasnian Zone (FZ) given in the figure caption for each specimen.

Capped-Oncolite locality, Sadler Limestone, section on west flank of McWhae Ridge, section of Nicoll (1984, section WCB 811, p. 131, fig. 5 loc.1, fig. 6; Klapper 2009, p. 410), AMG Zone 52,  $_{92088E}$   $_{7926291N}$ , capped oncolite bed is directly overlain by the straight nautiloid bed, sample 3 is from the top of the nautiloid bed, 20–32 cm above base of bed. Collected by GK and W.T. Kirchgasser, 1990.

Horse Spring (HS, section 364), Virgin Hills Formation, northern Horse Spring Range, base of section about 200 m SSE of Horse Spring, base of section is at GPS AMG Zone 52,  $_{86077E}$   $_{7985602N}$ ; the F/F boundary in this section is at GPS AMG Zone 52,  $_{86034E}$   $_{7985650N}$ . Description also in Klapper (2007a, p. 536; 2009, p. 410). Location shown in Becker & House (1997, fig. 2 and F/F boundary in fig. 6). Bed numbers and stratigraphic position are given in meters above base of section from which specimens illustrated in figs 1–3 were derived (see also Klapper 2007a, tables 1–3). Bed numbers are all preceded by section number 364: 4a = 0.64–0.79, 5 = 0.93–1.05, 9 = 1.8–2.0, 12 = 2.5–2.6, 16 = 3.75–3.9, 18 = 4.1–4.3, 25 = 5.7–6.0, 34 = 8.15–8.35, 43 = 10.7–10.8, 45 = 11.0–11.25, 70 = 31.1–31.25, 71 = 31.9–32.0. Measured and collected by GK, R.S. Nicoll, and R.W. Brown in 1988 (additional re-collections in 1990 and 1995, Klapper 2007a, p. 536).

Outcamp Hill, Sadler Limestone, SW end of Pillara Range, about 1.3 km NE of the hill, Limestone Billy Hills area, AMG Zone 51,  $_{92200E}$   $_{7961950N}$ , spot sample collected by Philip E. Playford in 1999, PEP field book 19, p. 33 bottom, point 45, sample GSWA 135107.

Timanites Hill (TH, section 370), Gogo Formation, central Bugle Gap area (= WAPET D locality of Glenister & Klapper (1966, p. 836, fig. 1, tab. 9), location also shown in Becker & House (1997, fig. 2, 370 indicated in Bugle Gap). AMG Zone 52,  $_{88200E}$   $_{7932400N}$ . Fuller description given in Klapper & Kirchgasser (2016, p. 552). Bed designations and stratigraphic position are given in

meters above base of exposed section, from which specimens illustrated in fig. 1 were derived. Bed designations are all preceded by section number 370: 1 = 5.3 (with goniatite *Timanites*), A = approximately 5.7, B = 5.9, stylioline limestone with abundant *Timanites*, D = 8.8, top of brachiopod bed; top of hill = 10.2. Collected by R.S. Nicoll and GK, 1988; W.T. Kirchgasser and GK, 1990.

West McPhee Knoll (WMcP, section 365), about 1.2 km WSW of the knoll, Old Bohemia Valley, description in Klapper (2007a, p. 537; 2009, p. 410), location shown in Becker & House (1997, fig. 2, 365 indicated NW of Teichert Hills). Base of section is at AMG Zone 52,  $193800E$   $7936500N$ . Bed numbers and stratigraphic position are given in meters above base of section from which specimens illustrated in figs 1, 3 were derived. Bed designations are all preceded by section number 365: Gogo Formation: 4 = 23.9–23.95. Virgin Hills Formation: 9 = 41.70–41.75, 11 = 55.1–55.2, 15 = 65.25–65.3. Measured and collected by R.S. Nicoll, GK, and R.W. Brown, 1988.