

The new genus *Walliserognathus* and the origin of *Polygnathoides siluricus* (Conodonts, Silurian)

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Abstract. The new genus *Walliserognathus* is described to host the species *posthamatus* (Walliser). The genus is monospecific. The shape of P1 and P2 elements of *Walliserognathus posthamatus*, characterized by a small platform along the whole elements, and its stratigraphic distribution limited to the *Ancoradella ploeckensis* Zone suggest that the species may have been the bridge in the phylogenesis from *Wurmiella* to *Polygnathoides*.

Key words: conodonts, taxonomy, phylogeny, Silurian, *Walliserognathus* n. gen., *Polygnathoides siluricus*.

INTRODUCTION

Walliser (1964) described the morphospecies *Spathognathodus inclinatus posthamatus* from the Ludlow of Cellon (Carnic Alps) to include carminate elements with a narrow platform along the entire length of both sides of the elements. In terms of multielement taxonomy, the taxon was later named *Ozarkodina excavata posthamata*, as were the other form subspecies of *Spathognathodus inclinatus*. It should be noted that at that time the apparatus was still not known, and only a possible P2 element had been tentatively suggested by Jeppsson (1974). After the revision of late Silurian ozarkodinids by Murphy et al. (2004), all representatives of the ‘*excavata* Group’ were placed in the genus *Wurmiella*, and therefore in all recent papers the taxon under discussion is called *Wurmiella posthamata* (Walliser, 1964). However, the P2 element of the species does not fit with the characteristics of *Wurmiella*, mainly because its basal cavity is restricted to the lower part of the element and is not visible in lateral view as in the P2 elements of *Wurmiella*. Therefore we introduced here the new genus *Walliserognathus* to host the species *posthamatus*.

Polygnathoides siluricus Branson & Mehl, 1933 is one of the more widespread and better known conodont taxa of the Silurian. Its P1 element with a wide platform of rhomboidal shape is diagnostic and very easy to recognize, and its global distribution in a limited interval of the Ludfordian makes it a perfect index species. As a

result, the *P. siluricus* Zone has been included in all the Silurian zonation schemes as a range zone, since Walliser (1964) introduced it in the first biozonation scheme of the Silurian. In all the succeeding schemes the *P. siluricus* Zone always possesses the same definition with the lower and upper boundaries defined by the First Appearance Datum (FAD) and by the Last Appearance Datum of the species, respectively (e.g. Aldridge & Schönlaub 1989; Corradini & Serpagli 1999; Jeppsson et al. 2006; Cramer et al. 2011; Corradini & Corriga 2012; Corradini et al. 2015). For a summary on Silurian conodont biostratigraphy see Corradini et al. (2015). However, despite the numerous elements collected from all over the world, the ancestor of *P. siluricus* is still not known and is generally referred to an unidentified ozarkodinid (e.g. Sweet 1988, pp. 93–94).

In this paper we propose that *P. siluricus* evolved from *Walliserognathus posthamatus* (Walliser, 1964). The latter is a characteristic but relatively rare taxon documented only from the *Ancoradella ploeckensis* Zone that became extinct just before the FAD of *P. siluricus* and has some morphologic features intermediate between *Wurmiella excavata* and *P. siluricus*.

MATERIAL

This study is based on collections from several sections and localities in the Carnic Alps, Sardinia and Morocco and on a thorough bibliographical investigation. The

figured specimens come from various sections in those areas: Cellon (Walliser 1964; Corradini et al. 2015), Rauchkofel Boden (Schönlaub 1980; Schönlaub et al. 2017), Hoher Trieb and Cuestalta (authors' unpublished data) in the Carnic Alps, Genna Ciuerciu (Barca et al. 1995; Corradini et al. 1998, 2009b) and Su Forreddu (authors' unpublished data) in Sardinia and Atrous 7 (Corriga et al. 2014a, 2014b) in Morocco.

The material is stored in the Museo Friulano di Storia Naturale (MFSNgp), Museo di Paleontologia 'Domenico Lovisato' of Cagliari University (MDLCA), Museo di Paleontologia of Modena and Reggio Emilia University (IPUM) and at the Geoscience Centre of Georg-August University Göttingen (GZG). Precise information and repository numbers of illustrated specimens are reported in the caption of Fig. 1.

SYSTEMATIC PALAEOLOGY

The taxa are presented in stratigraphic and phylogenetic order.

Class CONODONTA Pander, 1856
 Order OZARKODINIDA Dzik, 1976
 Family SPATHOGNATHODONTIDAE Hass, 1959
 Genus *Walliserognathus* n. gen.

Type species. *Spathognathodus inclinatus posthamatus* Walliser, 1964.

Derivatio nominis. To honour Prof. Otto H. Walliser, who described the species *posthamatus*, for his studies on Silurian conodonts.

Diagnosis. An ozarkodinid characterized by a small platform developed on both sides of the blade in P1 (carminate to carminiplanate) and P2 (angulate to anguliplanate) elements and with the ovoidal/polygonal partly inverted basal cavity.

Remarks. The genus *Walliserognathus* differs from all the Silurian genera previously attributed to *Ozarkodina* ('*Ozarkodina*', *Ozarkodina*, *Wurmiella* and *Zieglerodina*) in the presence of the small but well-developed platform in P1 and P2 elements. The P1 element also differs from those of *Ozarkodina* and *Zieglerodina* in its denticulation pattern, which is made of denticles of more or less equal size along the entire length of the element, and in the partially inverted basal cavity. The symmetrical and partially inverted basal cavity of the P2 element does not fit with those of the P2 elements of *Wurmiella*, which have an asymmetrical basal cavity more developed in the inner side, visible in lateral view.

The development of the platform in *Walliserognathus* may be somewhat similar to the unrelated Devonian

genus *Tortodus* (Weddige, 1977). The latter has a small well-developed platform in the posterior part of the element and bears a free blade anteriorly.

Species attributed. The only species attributed to *Walliserognathus* n. gen. is *Walliserognathus posthamatus* (Walliser, 1964).

Wurmiella? hamata (Walliser, 1964) has a very small partial platform in the holotype (Walliser, 1964, pl. 18, fig. 26), but it is not well developed in all the specimens. Therefore this species is not included in *Walliserognathus*, although it may be reconsidered when the P2 element is described.

Walliserognathus posthamatus (Walliser, 1964)
 Figure 1A–J

- 1962 *Spathognathodus* n. sp. g Walliser, fig. 2.29.
 1964 *Spathognathodus inclinatus posthamatus* n. subsp.; Walliser, p. 78, pl. 7, fig. 12; pl. 19, figs 1–5.
 1964 *Ozarkodina media* Walliser; Walliser, pl. 26, figs 26, 30? (only).
 1965 *Polygnathoides?* sp.; Van den Boogard, figs 6, 7.
 1967 *Spathognathodus inclinatus posthamatus* Walliser; Flajs, pl. 4, fig. 10.
 1971 *Ozarkodina excavata posthamata* (Walliser); Klapper in Ziegler, p. 233, *Ozarkodina*, pl. 1, fig. 8.
 1975 *Ozarkodina excavata excavata* (Walliser); Klapper & Murphy, pl. 6, fig. 13 (only).
 1975 *Spathognathodus inclinatus posthamatus* Walliser; Schönlaub & Zezula, pl. 2, figs 6, 7.
 1976 *Spathognathodus inclinatus posthamatus* Walliser; Ebner, pl. 3, figs 8, 9.
 1976 '*Spathognathodus*' *inclinatus posthamatus* Walliser; Schönlaub et al., p. 131, pl. 3, fig. 6.
 1984 *Ozarkodina excavata posthamata* (Walliser); Kozur, pl. 2, fig. 7.
 1998 *Ozarkodina excavata posthamata* (Walliser); Sarmiento et al., pl. 1, fig. 15.
 2005 *Ozarkodina inclinata posthamata* (Walliser); Jin et al., pl. 2, fig. 22.
 2010 *Wurmiella posthamata* (Walliser); Barrick et al., fig. 4G, H.
 2013 *Wurmiella inclinata posthamata* (Walliser); Wang, p. 143, pl. 53, figs 7–9, 29.
 2016 *Wurmiella inclinata posthamata* (Walliser); Wang, p. 164, pl. S-5, fig. 10.
 2017 *Wurmiella? posthamata* (Walliser); Schönlaub et al., pl. 2, fig. 13.
 2017 *Wurmiella? posthamata* (Walliser); Corradini et al., fig. 7.7.

Original diagnosis. (Walliser 1964, p. 78, German; P1 element). *Spathognathodus inclinatus* (Rhodes) with a narrow platform on both sides of the low blade and without lateral processes.

Emended diagnosis. An ozarkodinid with P1 (carminate to carminiplanate) and P2 (angulate to anguliplanate) elements characterized by a small platform developed along the whole element on both sides of the blade.

Description. Only P1 and P2 elements are known with certainty.

The P1 element of *Walliserognathus posthamatus* is a spathognathodiform element with the upper and lower margins of the blade more or less parallel. Most specimens are laterally curved close to the posterior end, whereas others are almost straight. The denticles are robust, closely spaced and laterally expanded, more or less of equal size along the whole element and may be slightly smaller close to the posterior end; the cusp is sometimes only slightly larger than the adjacent denticles. The blade is characteristically expanded at the level of insertion of the denticles, forming an evident narrow platform extending along the whole element that gradually tapers to the extremities. The partially inverted basal cavity is larger under the cusp and continues as a deep groove under the whole element.

The P2 element is ozarkodiniform (angulate to anguliplanate), with an angle of about 130° between the two robust and straight processes. The cusp is high, laterally compressed and posteriorly reclined. The strong denticles are closely spaced, laterally compressed and posteriorly reclined. An evident ledge is present along the whole element at the level of the insertion of the denticles. The small, partially inverted, symmetrical basal cavity is located below the cusp where it has a more or less rhomboidal outline. It is not connected with the ledge margins and continues as deep grooves under the processes.

Remarks. The narrow platform of the P1 elements is very diagnostic and distinguishes *Wa. posthamatus* from all the other Silurian ozarkodinids. Most specimens have the posterior part laterally deflected, whilst others are almost straight. Ebner (1976, pl. 3, figs 10, 11) illustrated a specimen with transitional features between *Wu. excavata* and *Wa. posthamatus*, bearing an incipient small ledge that does not reach the distal parts of the element. *Wurmiella? hamata* may have a small ledge, but differs from *Wa. posthamatus* in the strongly curved posterior end and the presence of a lateral process.

Jeppsson (1974) suggested that the P2 element figured by Walliser (1964) in pl. 26, fig. 26 may belong to the apparatus of '*S.*' *posthamatus*, due to the evident ledge along the whole element. Also the specimen

figured by Walliser (1964) in pl. 26, fig. 30 shows the same features and may belong to *Wa. posthamatus*. Both these specimens came from sample C19, together with the holotype (P1) of the species. The only P2 element, so far attributed to the species with certainty, was illustrated by Barrick et al. (2010, fig. 4H).

The shape of the P2 element excludes a possible attribution of the species to *Wurmiella*. In fact, P2 elements of *Wurmiella* have 'an asymmetrical basal platform that is higher on the inner side so that the basal cavity is seen in inner lateral view' (Murphy et al. 2004, p. 10). The basal cavity of *Walliserognathus posthamatus* is limited below the element and does not reach the inner part of the element; therefore it is not visible in lateral view.

A small enlargement of the central part of the platform may occur in a few P2 elements (Fig. 1H), which somewhat resembles that of the P2 element of *P. siluricus*, but is definitely much less developed and without the characteristic triangular outline of the latter. Walliser (1964) reported the occurrence of some elements of '*Polygnathoides emarginatus*' (now the P2 element of *P. siluricus*) from the *A. ploeckensis* Zone (samples 18A, 18B). However, the restudy of the original collection (Corradini et al. 2015) has demonstrated that those P2 elements have a small platform without the characteristic triangular flange of P2 of *P. siluricus* and actually are P2 elements of *Wa. posthamatus*, whose P1 occur in these samples.

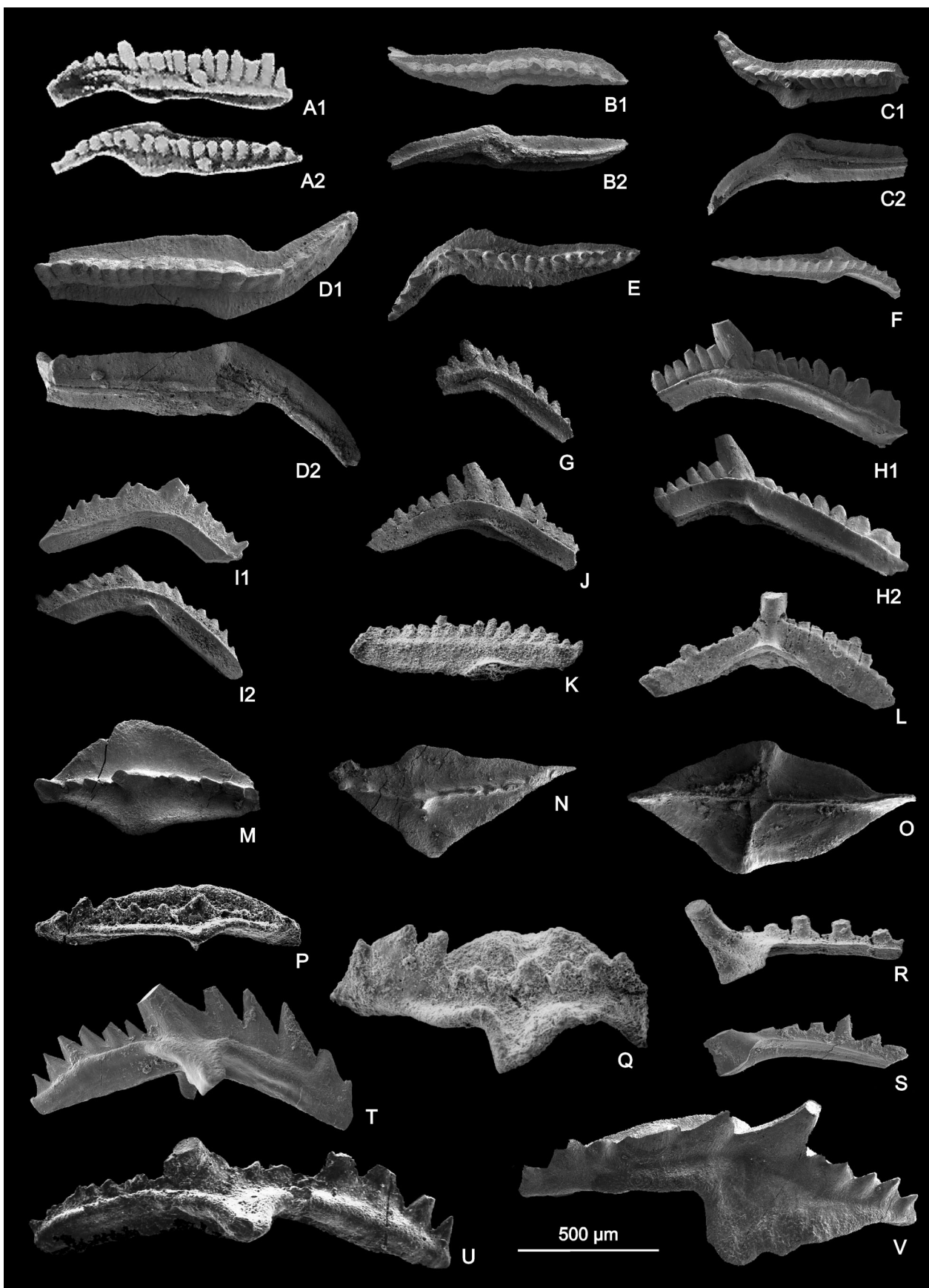
The other elements of the apparatus are still unknown, even if in our material samples with *Wa. posthamatus* contain a few broken and poorly preserved M elements similar to those of *P. siluricus*. Similar elements are present in the Walliser (1964) collection of the Cellon section from the upper part of the *A. ploeckensis* Zone and likely may be associated with *Wa. posthamatus*.

Stratigraphic range. The species occurs only within the *A. ploeckensis* Zone (Ludlow), having its FAD in the lower part of the zone and ranging up to its top.

Geographic distribution. The species has been reported from the Carnic Alps (e.g. Walliser 1964; Corradini & Corrigan 2012; Corradini et al. 2015; Schönlaub et al. 2017), Sardinia (Corradini & Serpagli 1999; Corrigan et al. 2009), the Graz Palaeozoic (Ebner 1976), Spain (Sarmiento et al. 1998), Hungary (Kozur 1984), Gotland (Jeppsson 1974), North America (Klapper & Murphy 1975; Barrick et al. 2010) and China (Wang 2013, 2016).

Genus *Polygnathoides* Branson & Mehl, 1933

Type species. *Polygnathoides siluricus* Branson & Mehl, 1933.



Original description. More or less lanceolate, deeply concave plates, bearing a median longitudinal crest consisting of a row of laterally compressed, sharp-edged, more or less discrete, pointed denticles; one near mid-length conspicuously larger than the others in most specimens (Branson & Mehl 1933 p. 50).

Species attributed. The only species attributed to the genus *Polygnathoides* Branson & Mehl is *Polygnathoides siluricus* Branson & Mehl, 1933.

Polygnathoides siluricus Branson & Mehl, 1933

Figure 1M–V

- 1933 *Polygnathoides siluricus* Branson & Mehl, p. 50, pl. 3, figs 39–42.
- 1933 *Polygnathellus emarginatus* Branson & Mehl, p. 49, pl. 3, fig. 38.
- 1957 *Polygnathoides emarginatus* (Branson & Mehl); Walliser, p. 45, pl. 1, figs 35, 36.
- 1957 *Polygnathoides siluricus* Branson & Mehl; Walliser, p. 45, pl. 1, fig. 34.
- 1964 *Neoprioniodus latidentatus* Walliser, p. 50, pl. 29, figs 34, 35.
- 1964 *Polygnathoides emarginatus* (Branson & Mehl); Walliser, p. 66, pl. 18, figs 1, 2, 4, 5 (only).
- 1964 *Polygnathoides siluricus* Branson & Mehl; Walliser, p. 66, pl. 8, fig. 19; pl. 17, figs 1–11.
- 1972 *Polygnathoides emarginatus* (Branson & Mehl); Link & Druce, pp. 83, 84, pl. 8, figs 15–20.
- 1972 *Polygnathoides siluricus* Branson & Mehl; Link & Druce, pp. 84, 85, pl. 8, figs 13, 14.
- 1974 *Polygnathoides siluricus* Branson & Mehl; Feist & Schönlaub, figs 7.10, 7.13.
- 1975 *Polygnathoides siluricus* Branson & Mehl; Klapper & Murphy, p. 56, pl. 8, figs 16–21.
- 1976 *Polygnathoides siluricus* Branson & Mehl; Ebner, p. 290, pl. 2, figs 4–7.
- 1976 *Polygnathoides emarginatus* Branson & Mehl; Ebner, p. 290, pl. 2, figs 9, 10 (only).
- 1976 *Polygnathoides siluricus* Branson & Mehl; Uyeno, pl. 41.1, figs 19, 20.
- 1980 *Polygnathoides siluricus* Branson & Mehl; Chlupac et al., pl. 17, fig. 4.
- 1980 *Polygnathoides emarginatus* (Branson & Mehl); Chlupac et al., pl. 17, fig. 5.
- 1981 *Polygnathoides emarginatus* (Branson & Mehl); Uyeno, p. 46, pl. 9, figs 24, 25.
- 1981 *Polygnathoides siluricus* Branson & Mehl; Uyeno, p. 47, pl. 9, figs 22, 23, 26–29.
- 1983 *Polygnathoides siluricus* Branson & Mehl; Jeppsson, fig. 1A, B (only).
- 1984 *Polygnathoides siluricus* Branson & Mehl; Kozur, pl. 3, fig. 6.
- 1988 *Polygnathoides siluricus* Branson & Mehl; Dégardin, pl. 3, figs 1, 2.
- 1992 *Polygnathoides siluricus* Branson & Mehl; Barca et al., pl. 11, figs 10–12.
- 1995 *Polygnathoides siluricus* Branson & Mehl; Barca et al., pl. 4, fig. 1.
- 1998 *Polygnathoides siluricus* Branson & Mehl; Sarmiento et al., pl. 1, fig. 10.
- 1998 *Polygnathoides siluricus* Branson & Mehl; Männik & Malkowski, pl. 1, figs 1, 4.
- 1998 *Polygnathoides siluricus* Branson & Mehl; Serpagli et al., pl. 1.2.2, figs 13, 14, 16 (only).

Fig. 1. A–J, *Walliserognathus posthamatus* (Walliser, 1964); A, lateral (A1) and upper (A2) views of P1 element Wa 519/3, holotype, Cellon section, sample C19 (refigured after Walliser 1964, pl. 19, fig. 2); B, upper (B1) and lower (B2) views of P1 element MDLCA 30414, Su Forreddu section, sample SFR A; C, upper (C1) and lower (C2) views of P1 element MFSNgp 49431, Rauchkofel Boden section, sample RKB 325; D, upper (D1) and lower (D2) views of P1 element MDLCA 30395, Rauchkofel Boden section, sample RKB X; E, upper view of P1 element MFSNgp 49432, Rauchkofel Boden section, sample RKB X; F, upper view of P1 element MFSNgp 49433, Hoher Trieb section, sample HT 2; G, lateral view of P2 element MDLCA 30415, Su Forreddu section, sample SFR A; H, lateral (H1) and lower-lateral (H2) views of P2 element MFSNgp 49434, Rauchkofel Boden section, sample RKB 325; I, lateral (I1) and lower-lateral (I2) views of P2 element MFSNgp 49435, Hoher Trieb section, sample HT 2; J, lateral view of P2 element MFSNgp 49436, Rauchkofel Boden section, sample RKB X. **K, L,** *Wurmiella excavata* (Branson & Mehl, 1933); K, lateral view of P1 element IPUM 29025, Genna Ciurciu section, sample GCIU 0; L, lateral view of P2 element IPUM 29026, Genna Ciurciu section, sample GCIU 20. **M–V,** *Polygnathoides siluricus* Branson & Mehl, 1933; M, upper view of P1 element MFSNgp 49437, Cuestalta section, sample CUE 1; N, upper view of P1 element MDLCA 30389, Rauchkofel Boden section, sample RKB 2; O, lower view of P1 element MFSNgp 49438, Cuestalta section, sample CUE 1; P, upper-lateral view of P1 element IPUM 25898, Genna Ciurciu section, sample GCIU 4; Q, upper-lateral view of P1 element IPUM 29027, Genna Ciurciu section, sample GCIU 1; R, lateral view of M element IPUM 29028, Genna Ciurciu section, sample GCIU 2; S, lateral view of M element MFSNgp 49439, Hoher Trieb section, sample HT 4; T, lateral view of P2 element GZG 1612-540C-3725-2, El Atrous 7 section, sample AT 7 12; U, lateral view of P2 element IPUM 29029, Genna Ciurciu section, sample GCIU 2; V, upper-lateral view of P2 element MFSNgp 43440, Cuestalta section, sample CUE 1.

- 1998 *Polygnathoides siluricus* Branson & Mehl; Corradini et al., pl. 1.3.1, fig. 15.
- 1998 *Polygnathoides siluricus* Branson & Mehl; Ferretti et al., pl. 2.2.2, figs 1, 2.
- 2001 *Polygnathoides siluricus* Branson & Mehl; Corradini et al., pl. 1, fig. 22.
- 2002 *Polygnathoides siluricus* Branson & Mehl; Talent et al., pl. 3, fig. 1.
- 2005 *Polygnathoides emarginatus* Branson & Mehl; Jin et al., pl. 1, figs 17–19.
- 2005 *Polygnathoides siluricus* Branson & Mehl; Jin et al., pl. 2, figs 3–5.
- 2009 *Polygnathoides siluricus* Branson & Mehl; Corrigan et al., pl. 2, fig. 6.
- 2009a *Polygnathoides siluricus* Branson & Mehl; Corradini et al., pl. 1, fig. 8.
- 2009b *Polygnathoides siluricus* Branson & Mehl; Corradini et al., pl. 1, fig. 15.
- 2009 *Polygnathoides siluricus* Branson & Mehl; Ferretti et al., pl. 1, fig. 3.
- 2010 *Polygnathoides siluricus* Branson & Mehl; Slavík et al., p. 402, fig. 3A–U.
- 2013 *Polygnathoides siluricus* Branson & Mehl; Rytina et al., pl. 1, figs 14, 15.
- 2013 *Polygnathoides emarginatus* Branson & Mehl; Wang, pp. 136, 137, pl. 56, figs 13–15, 18, 19 (only).
- 2013 *Polygnathoides siluricus* Branson & Mehl; Wang, p. 137, pl. 56, figs 7–12.
- 2014b *Polygnathoides siluricus* Branson & Mehl; Corrigan et al., fig. 5E–I.
- 2016 *Polygnathoides siluricus* Branson & Mehl; Wang, p. 150, pl. S-5, fig. 11.
- 2017 *Polygnathoides siluricus* Branson & Mehl; Spiridonov et al., fig. 4C, R, U.

Diagnosis. P1 element carminiplanate with a more or less rhomboidal platform and transversely extended pit; P2 element anguliplanate with well-developed subtriangular platform on inner side; M element dolabrate with well-spaced round teeth and a large basal cavity.

Remarks. The complete apparatus is still not known. It is now widely accepted that the P2 element is represented by the form species *Polygnathoides emarginatus* (Branson & Mehl, 1933) (e.g. Klapper & Murphy 1975; Slavík et al. 2010; Corrigan et al. 2014b). Jeppsson (1983, fig. 1A–E) gave a tentative incomplete reconstruction of the apparatus based on an association from Gotland where the S0 element was missing. Sweet (1988, fig. 5.40) presented this reconstruction without elaboration in the text. However, as Slavík et al. (2010) already pointed out, Jeppsson’s reconstruction cannot be confirmed in associations from other localities and is disregarded. Uyeno (1981) suggested that the M element could have

been represented by elements assignable to the form species *Neoprioniodus latidentatus* Walliser, 1964, and Corrigan et al. (2014b, fig. 5I) recorded a similar M element from Morocco. Slavík et al. (2010, fig. 3D, G, T) illustrated possible S1 elements from Bohemia.

The M elements in our collections from Sardinia and the Carnic Alps, corresponding to the form species *Neoprioniodus latidentatus*, are always associated with P1 and P2 elements of *P. siluricus*. Also a few elements similar to the S1 figured by Slavík et al. (2010) are present. Therefore we may support his suggestion, even if more investigation of the S elements of the apparatus is necessary.

The P1 element of *P. siluricus* shows a wide variability in the shape of the platform. In upper view it has a more or less rhomboidal shape, with the minor axis variable in length. A few specimens are narrow, whereas others have a very wide platform in their central part. The upper surface can be more or less flat, or may be strongly undulated in the central part, where a distinct crease may occur, often more pronounced on one side. In lower view, the basal pit is transversely extended, and short secondary keels are present in larger elements.

Stratigraphic range. The species is exclusive to the eponymous *P. siluricus* Zone (Ludfordian).

Geographic distribution. *Polygnathoides siluricus* has a global distribution. It has been reported from the Carnic Alps (e.g. Walliser 1964; Corradini & Corrigan 2012; Corradini et al. 2015; Schönlaub et al. 2017), Sardinia (e.g. Corradini & Serpagli 1999; Corrigan et al. 2009), Czech Republic (e.g. Slavík et al. 2010), the Graz Palaeozoic (Ebner 1976), Spain (Sarmiento et al. 1998), French Pyrenees (Dégardin 1988), Montagne Noir (Feist & Schönlaub 1974), Morocco (Rytina et al. 2013; Corrigan et al. 2014b), Hungary (Kozur 1984), Gotland (Jeppsson 1974), Lithuania (Spiridonov et al. 2017), Poland (Männik & Malkowski 1988), North America (Branson & Mehl 1933; Klapper & Murphy 1975; Barrick et al. 2010; Uyeno 1976, 1981), China (Wang 2013, 2016 and references herein), Australia (Link & Druce 1972; Talent et al. 2002) and Argentina (Gómez 2015; Garcías 2016).

PHYLOGENY

Elements of *Wu. excavata* with a small enlargement of the blade at the base of the denticles are well known from several stratigraphic levels within the Ludlow. In *Wa. posthamatus* this ledge is very wide and a true platform is developed at both sides of the blade along the whole element. It likely evolved from the elements

of *Wu. excavata* characterized by an enlarged blade near the base of the *A. ploeckensis* Zone (Fig. 2). The development of the platform resulted in that the basal cavity became partially inverted with a somewhat polygonal outline. In the P2 element of *Wa. posthamatus* the development of the small platform constrained the small, partially inverted basal cavity to the lower part of the element and made it not visible in lateral view, differing from that of *Wurmiella*.

Polygnathoides siluricus has a wide rhomboidal platform that may have derived from *Wa. posthamatus* by the lateral enlargement of the platform in the central part of the element (Fig. 2). The denticulation became stronger and the basal cavity changed from partially inverted in *Wa. posthamatus* to fully inverted in *P. siluricus*. The transition is evidenced by the occurrence of early forms of *P. siluricus* from the base of the *P. siluricus* Zone, characterized by a narrow and/or almost not undulated platform (e.g. Walliser 1964, pl. 17, fig. 6). In these elements the basal cavity is similar to that of *Wa. posthamatus*, and its lateral extensions are not always present: they are more developed in specimens with a large, undulated platform.

A similar evolution is observable also in the P2 element, where the small platform of *Wa. posthamatus* enlarged laterally to the cusp into the more developed

subtriangular one of *P. siluricus*. It should be noted that a few P2 elements of *Wa. posthamatus* already have a slightly enlarged platform in the inner part of the element. As in the P1 element, the denticulation became stronger and the lower part of the element suffered a similar evolution, with the basal cavity not modified, but the grooves changed to keels.

CONCLUSIONS

The main results of this paper on middle Ludlow conodonts may be summarized as follows:

- the new genus *Walliserognathus* is introduced to host the species *Wa. posthamatus* (Walliser, 1964);
- only the P1 and P2 elements of *Wa. posthamatus* are known with certainty;
- an M element of the apparatus of *P. siluricus* is suggested, and the proposal of the S1 element by Slavik et al. (2010) is supported;
- morphological features of P1 and P2 elements suggest that *Wa. posthamatus* evolved from *Wu. excavata* near the base of the *A. ploeckensis* Zone; later, at the base of the *P. siluricus* Zone, *Wa. posthamatus* gave rise to *P. siluricus*.

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REFERENCES

- Aldridge, R. J. & Schönlaub, H. P. 1989. Conodonts. In *A Global Standard for the Silurian System* (Holland, C. H. & Bassett, M. G., eds), *National Museum of Wales, Geological Series*, **9**, 274–279.
- Barca, S., Ferretti, A., Massa, P. & Serpagli, E. 1992. The Hercynian Arburese Tectonic Unit of SW Sardinia. New stratigraphic and structural data. *Rivista Italiana di Paleontologia e Stratigrafia*, **98**, 119–136.
- Barca, S., Corradini, C., Ferretti, A., Olivieri, R. & Serpagli, E. 1995. Conodont biostratigraphy of the “Ockerkalk” (Silurian) from Southeastern Sardinia. *Rivista Italiana di Paleontologia e Stratigrafia*, **100**(1994), 459–476.
- Barrick, J. E., Klapper, G., Kleffner, M. A. & Karlsson, H. R. 2010. Conodont biostratigraphy and stable isotope chemostratigraphy of the lower Henryhouse Formation (Gorstian–early Ludfordian, Ludlow, Silurian), southern Oklahoma, USA. *Memoirs of the Association of Australasian Palaeontologists*, **39**, 51–70.
- Branson, E. B. & Mehl, M. G. 1933. Conodonts from the Bainbridge Formation (Silurian) of Missouri. *University of Missouri Studies*, **8**, 39–52.

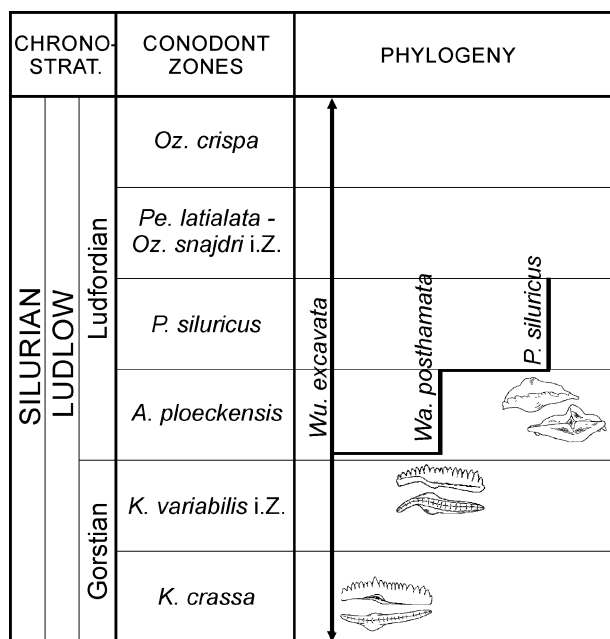


Fig. 2. Phylogeny and stratigraphic distribution of *Walliserognathus posthamatus* and *Polygnathoides siluricus*, aligned to the Ludlow biozonation scheme by Corradini et al. (2015). Sketch drawings of P1 elements after Walliser (1964). Abbreviations: *A.*, *Ancoradella*; *K.*, *Kockeella*; *Oz.*, *Ozarkodina*; *Pe.*, *Pedavis*; *P.*, *Polygnathoides*; *Wa.*, *Walliserognathus*; *Wu.*, *Wurmiella*.

- Chlupac, I., Kriz, J. & Schönlaub, H. P. 1980. Silurian and Devonian conodont localities in the Barrandian. In *Second European Conodont Symposium (ECOS II), Guidebook, Abstracts* (Schönlaub, H. P., ed.), *Abhandlungen des Geologischen Bundesanstalt*, **35**, 147–180.
- Corradini, C. & Corrigan, M. G. 2012. A Pridoli–Lochkovian conodont zonation in Sardinia and the Carnic Alps: implications for a global zonation scheme. *Bulletin of Geosciences*, **87**, 635–650.
- Corradini, C. & Serpagli, E. 1999. A Silurian conodont biozonation from late Llandovery to end Pridoli in Sardinia (Italy). *Bollettino della Società Paleontologica Italiana*, **37**, 255–273.
- Corradini, C., Ferretti, A., Serpagli, E. & Barca, S. 1998. The Ludlow–Pridoli Section “Genna Ciuerciu” west of Silius. *Giornale di Geologia*, **60**, Spec. Issue, 112–118.
- Corradini, C., Leone, F., Loi, A. & Serpagli, E. 2001. Conodont stratigraphy of a highly tectonised Silurian–Devonian section in the San Basilio area (SE Sardinia, Italy). *Bollettino della Società Paleontologica Italiana*, **40**, 315–323.
- Corradini, C., Ferretti, A., Corrigan, M. G. & Serpagli, E. 2009a. The reference section of the Sardinian Ockerkalk: the Silius Section. *Rendiconti della Società Paleontologica Italiana*, **3**, 209–216.
- Corradini, C., Ferretti, A., Corrigan, M. G. & Serpagli, E. 2009b. Loboliths (crinoids) and conodont biostratigraphy of the Genna Ciuerciu Section (SE Sardinia). *Rendiconti della Società Paleontologica Italiana*, **3**, 217–224.
- Corradini, C., Corrigan, M. G., Männik, P. & Schönlaub, H. P. 2015. Revised conodont stratigraphy of the Cellon section (Silurian, Carnic Alps). *Lethaia*, **48**, 56–71.
- Corradini, C., Corrigan, M. G., Ferretti, A. & Schönlaub, H. P. 2017. The Cellon section. *Berichte des Institutes für Erdwissenschaften, Karl-Franzens-Universität Graz*, **23**, 262–270.
- Corrigan, M. G., Corradini, C. & Ferretti, A. 2009. Silurian conodonts from Sardinia: an overview. *Rendiconti della Società Paleontologica Italiana*, **3**, 95–107.
- Corrigan, M. G., Corradini, C., Haude, R. & Walliser, O. H. 2014a. Conodont and crinoid stratigraphy of the upper Silurian and Lower Devonian scyphocrinoid beds of Tafilalt, southeastern Morocco. *GFF*, **136**, 65–69.
- Corrigan, M. G., Corradini, C. & Walliser, O. H. 2014b. Upper Silurian and Lower Devonian conodonts from Tafilalt, southeastern Morocco. *Bulletin of Geosciences*, **89**, 183–200.
- Cramer, B. D., Brett, C. E., Melchin, M. J., Männik, P., Kleffner, M. A., McLaughlin, P. I., Loydell, D. K., Munnecke, A., Jeppsson, L., Corradini, C., Brunton, F. R. & Saltzman, M. R. 2011. Revised correlation of Silurian Provincial series of North America with global and regional chronostratigraphic units and $\delta^{13}\text{C}_{\text{carb}}$ chemostratigraphy. *Lethaia*, **44**, 185–202.
- Dégardin, J.-M. 1988. Le Silurien des Pyrénées – Biostratigraphie, Paléogéographie. *Société Géologique du Nord, Publication*, **15**, 1–525.
- Dzik, J. 1976. Remarks on the evolution of Ordovician conodonts. *Acta Palaeontologica Polonica*, **21**, 395–455.
- Ebner, F. 1976. Das Silur/Devon Vorkommen von Eggenfeld – ein Beitrag zur Biostratigraphie des Grazer Paläozoikums. *Mitteilungen der Abteilung für Geologie, Paläontologie und Bergbau am Landesmuseum Joanneum Graz*, **37**, 275–305.
- Flajs, G. 1967. Conodontenstratigraphische Untersuchungen im Baum von Eisenerz, Nördliche Grauwackenzone. *Mitteilungen der Geologischen Gesellschaft in Wien*, **59**, 157–212.
- Feist, R. & Schönlaub, H. P. 1974. Zur Silur/Devon-Grenze in der östlichen Montagne Noire Süd-Frankreichs. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **1974**(4), 200–219.
- Ferretti, A., Corradini, C. & Serpagli, E. 1998. Wenlock–Ludlow conodonts from Perd’e Fogu (Fluminimaggiore). *Giornale di Geologia*, **60**, Spec. Issue, 156–167.
- Ferretti, A., Corradini, C., Kriz, J., Piras, S. & Serpagli, E. 2009. The Perd’e Fogu outcrop: a classical exposure of “*Orthoceras* limestone” in the Fluminimaggiore area (SW Sardinia). *Rendiconti della Società Paleontologica Italiana*, **3**, 253–264.
- Garcías, Y. V. 2016. *Estratigrafía y Bioestratigrafía de Conodontes de la Formación Los Espejos (Silúrico) en Quebrada Poblete, Talacasto, Precordillera Central*. Unpubl. Master Thesis, Universidad Nacional de San Juan, 66 pp.
- Gómez, M. J. 2015. *Estratigrafía y Bioestratigrafía de Conodontes de la Formación Los Espejos (Silúrico) en Quebrada Ancha, Talacasto, Precordillera Central*. Unpubl. Master Thesis, Universidad Nacional de San Juan, 86 pp.
- Hass, W. H. 1959. Conodonts from the Chappel Limestone of Texas. *U.S. Geological Survey Professional Paper*, **294**, 365–399.
- Jeppsson, L. 1974. Aspects of Late Silurian conodonts. *Fossils and Strata*, **6**, 1–54.
- Jeppsson, L. 1983. Silurian conodont faunas from Gotland. *Fossils and Strata*, **15**, 121–144.
- Jeppsson, L., Eriksson, M. E. & Calner, M. 2006. A latest Llandovery to latest Ludlow high-resolution biostratigraphy based on the Silurian of Gotland – a summary. *GFF*, **128**, 109–114.
- Jin, C.-T., Qian, Y.-Z. & Wang, J. L. 2005. Silurian conodont succession and chronostratigraphy of the Baizitian region in Yanbian, Panzhihua, Sichuan. *Journal of Stratigraphy*, **29**(3), 281–294 [in Chinese].
- Klapper, G. & Murphy, M. A. 1975. Silurian–Lower Devonian conodont sequence in the Roberts Mountains Formation of central Nevada. *University of California Publications in Geological Sciences*, **111**, 1–62.
- Kozur, H. 1984. Preliminary report about the Silurian to Middle Devonian sequences near Nekezensy (Southernmost Uppony Mts., Northern Hungary). *Geologisch-Paläontologische Mitteilungen Innsbruck*, **13**, 149–176.
- Link, A. G. & Druce, E. C. 1972. Ludlovian and Gedinnian conodont stratigraphy of the Yass Basin, New South Wales. *Department of National Development, Bureau of Mineral Resources, Geology and Geophysics Bulletin*, **134**, 1–136.
- Männik, P. & Malkowski, K. 1998. Silurian conodonts from the Goldap core, Poland. In *Proceedings of the Sixth European Conodont Symposium (ECOS VI)* (Szaniawski, H., ed.), *Palaeontologica Polonica*, **58**, 139–149.
- Murphy, M. A., Valenzuela-Ríos, J. I. & Carls, P. 2004. On classification of Pridoli (Silurian)–Lochkovian (Devonian)

- Spathognathodontidae (Conodonts). *University of California, Riverside Campus Museum Contribution*, **6**, 1–25.
- Pander, C. H. 1856. *Monographie der Fossilen Fische des Silurischen System der Russisch-Baltischen Gouvernements*. Petersburg, 83 pp.
- Rytina, M.-K., Becker, R. T., Aboussalam, Z. S., Hartenfelds, S., Helling, S., Stichling, S. & Ward, D. 2013. The allochthonous Silurian–Devonian in olistostromes at “the Southern Variscan front” (Tinerhir region, SE Morocco) – Preliminary data. In *International Field Symposium “The Devonian and Carboniferous of Northern Gondwana” – Morocco 2013* (Becker, R. T., El Hassani, A. & Tahiri, A., eds), *Documents de l’Institut Scientifique, Rabat*, **27**, 11–21.
- Sarmiento, G. N., Sanz-Lopez, J. & Garcia-Lopez, S. 1998. Silurian conodonts from the Iberia Peninsula – an update. In *Proceedings of the 6th International Graptolite Conference (GWG-IPA) & 1998 Field Meeting, IUGS Subcommission on Silurian Stratigraphy* (Gutierrez-Marco, J. C. & Rabano, I., eds), *Temas Geológico-Mineros ITGE*, **23**, 119–124.
- Schönlaub, H. P. 1980. Carnic Alps. In *Second European Conodont Symposium (ECOS II), Guidebook, Abstracts* (Schönlaub, H. P., ed.), *Abhandlungen der Geologischen Bundesanstalt*, **35**, 5–57.
- Schönlaub, H. P. & Zezula, G. 1975. Silur-Conodonten aus einer Phyllonitzone im Muralpen-Kristallin (Lungau/Salzburg). *Verhandlungen der Geologisches Bundesanstalt*, **1974**, 253–269.
- Schönlaub, H. P., Exner, C. & Nowotny, A. 1976. Das Altpaläozoikum des Katschberges und seiner Umgebung (Österreich). *Verhandlungen der Geologisches Bundesanstalt*, **1976**, 115–145.
- Schönlaub, H. P., Corradini, C., Corrigan, M. G. & Ferretti, A. 2017. Litho-, chrono- and conodont bio-stratigraphy of the Rachkofel Boden Section (Upper Ordovician–Lower Devonian), Carnic Alps, Austria. *Newsletters on Stratigraphy*, **50**, 445–469.
- Serpagli, E., Corradini, C. & Ferretti, A. 1998. Conodonts from a Ludlow–Pridoli section near Silius Village. *Giornale di Geologia*, **60**, Special Issue, 112–118.
- Slavík, L., Kříž, J. & Carls, P. 2010. Reflection of the mid-Ludfordian Lau Event in conodont faunas of Bohemia. *Bulletin of Geosciences*, **85**, 395–414.
- Spiridonov, A., Stankevič, A., Gečas, T., Šilinskas, T., Brazauskas, A., Meidla, T., Ainsaar, L., Musteikis, P. & Radzevičius, S. 2017. Integrated record of Ludlow (Upper Silurian) oceanic geobioevents – Coordination of changes in conodont, and brachiopod faunas, and stable isotopes. *Gondwana Research*, **51**, 272–288.
- Sweet, W. C. 1988. *The Conodonta: Morphology, Taxonomy, Paleoecology, and Evolutionary History of a Long-Extinct Animal Phylum*. Oxford University Press, New York, 212 pp.
- Talent, J. A., Mawson, R., Simpson, A. & Brock, G. A. 2002. Ordovician–Carboniferous of the Townsville Hinterland: Broken River and Camel Creek regions, Burdekin and Clark River basins. *Macquarie University Centre for Ecostratigraphy and Palaeobiology Special Publication*, **1**, 1–82.
- Uyeno, T. T. 1976. Summary of conodont biostratigraphy of the Read Bay Formation and its type sections and adjacent areas, eastern Cornwallis island, District of Franklin. *Geological Survey of Canada Paper*, **77-1B**, 211–216.
- Uyeno, T. T. 1981. Stratigraphy and conodonts of the upper Silurian and Lower Devonian rocks in the environs of the Boothia uplift, Canadian Arctic Archipelago. Part II – Systematic study of conodonts. *Geological Survey of Canada Bulletin*, **292**, 39–75.
- Van den Boogard, M. 1965. Two conodont faunas from the Paleozoic of the Betic of Malaga near Veloz Rubio, S.E. Spain. *Koninklijke Nederlandse Akademie van Wetenschappen Proceedings, Series B*, **68**, 33–37.
- Walliser, O. H. 1957. Conodonten aus dem oberen Gotlandium Deutschlands und der Karnischen Alpen. *Notizblatt des Hessischen Landesamtes für Bodenforschung*, **85**, 28–52.
- Walliser, O. H. 1962. Conodontenchronologie des Silurs (= Gotlandiums) und des tieferen Devons mit besonderer Berücksichtigung der Formations-grenze. In *Internationalen Arbeitstagung über die Silur/Devon-Grenze und die Stratigraphie von Silur und Devon, Bonn–Bruxelles 1960, Band 2* (Erben, H. K., ed.), pp. 281–287. E. Schweizerbart’sche Verlagsbuchhandlung, Stuttgart.
- Walliser, O. H. 1964. Conodonten des Silurs. *Abhandlungen des Hessischen Landesamtes für Bodenforschung zu Wiesbaden*, **41**, 1–106.
- Wang, C.-Y. 2013. *Silurian Conodonts in China*. Chinese University of Science and Technology Press, Hefei, 230 pp. [in Chinese].
- Wang, C.-Y. 2016. *Conodont Biostratigraphy in China*. Zhejiang University Press, Hangzhou, 380 pp. [in Chinese].
- Weddige, K. 1977. Die conodonten der Eifel-Stufe im Typusgebiet und in benachbarten Faziesgebieten. *Senckenbergiana Lethaea*, **58**, 271–419.
- Ziegler, W. (ed.). 1971. *Catalogue of Conodonts, Vol. 1*. E. Schweizerbart’sche Verlagsbuchhandlung, Stuttgart, 504 pp.

Uus perekond *Walliserognathus* ja *Polygnathoides siluricus*’e päritolu (Conodonta, Silur)

Carlo Corradini ja Maria G. Corrigan

On kirjeldatud uus konodondiperekond *Walliserognathus*, milles on seni teada ainult üks liik: *W. posthamatus* (Walliser). Nimetatud liigi P1 ja P2 elementide morfoloogia ning liigi stratigraafiline levik lubab oletada, et tegemist on perekondade *Wurmiella* ja *Polygnathoides*’e fülogeneetilise vahelülga.