On Classification of Pridoli (Silurian)-Lochkovian (Devonian) Spathognathodontidae (Conodonts)

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This paper was finished in 2001 and was to be part of a volume dedicated to our friend and colleague Gilbert Klapper on occasion of his retirement of University of Iowa after a distinguished scientific career characterized by his numerous and seminal contributions to the study of Silurian and Devonian conodonts. The paper it is published now separately owing to the long delay of the planned volume.
ON CLASSIFICATION OF PRIDOLI (SILURIAN)-LOCHKOVIAN (DEVONIAN)
SPATHOGNATHODONTIDAE (CONODONTS)

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ABSTRACT
The Spathognathodontidae are common conodonts in the Pridoli (Silurian) and Lochkovian (Devonian) in the areas investigated, Nevada, Spain, Germany, and the Czech Republic, and form the basis of most of the biostratigraphic zonation within the interval. This paper continues the subdivision of the genus *Ozarkodina* Branson & Mehl, 1933, which, since Silurian-Devonian conodont workers changed-over to multielement taxonomy around 1970, has included a large and diverse group of taxa; discusses the nomenclature of the type species of *Ozarkodina*, *O. typica* Branson & Mehl; describes *Wurmiella* n. gen. (type species *Ozarkodina tuma* Murphy & Matti); describes *Zieglerodina* n. gen. (type species *Spathognathodus remscheidensis* Ziegler); and the need for further subdivision of *Ozarkodina*. *Pandorinellina* Müller & Müller is maintained as a genus separate from *Ozarkodina* because its skeletal apparatus is reconstructed with an alate Sa element that has a denticulate posterior process (diplododellan) rather than the Sa of *Ozarkodina*, which normally is without a posterior process.

INTRODUCTION
The Spathognathodontidae, a large family of conodonts with sexmembrate or septemmembrate apparatuses that include carminate Pa elements, are common conodonts in Pridoli and Lochkovian strata and form the basis of most biostratigraphic zonation within the interval. The latest comprehensive classification for the group (Sweet, 1988) included most Late Silurian-Early Devonian Spathognathodontidae in a single genus, *Ozarkodina* Branson & Mehl, 1933. Since 1971, *Criteriognathus* Walliser, 1972, *Amydrotaxis* Klapper & Murphy, 1980, *Flaj sella* Valenzuela-Ríos & Murphy, 1997, and *Lanae* Murphy & Valenzuela-Ríos, 1999 have been erected based on taxa that had formerly been grouped within *Ozarkodina*. They are joined by *Pandorinellina* Müller & Müller, 1957, *Ancyrodelloides* Bischoff & Sannemann, 1958 (= *Cruci o d us* Bardashev, 1991), *Eognathodus* Philip, 1965, and *Kimognathus* Mashkova, 1978 to form the current Early Devonian Spathognathodontidae, which as Sweet (1988, p. 89) has remarked, "is superficially quite heterogeneous".

We currently identify five generic-rank spathognathodontid clades that are present in Pridoli strata and cross the boundary into the Lochkovian (Figure 1). These are:
Figure 1. - Spathognathodontid genera (exclusive of Amydrotaxis) that cross the Silurian-Devonian boundary. Spacing of the boundaries of stratigraphic units represents convenience in depicting events discussed in the text and does not represent current inferences concerning the time span of the units. Abbreviations are as follows: MD – Middle Devonian; L-M S – Lower-Middle Silurian; C – ‘Ozarkodina’ crispa; F – Flajsella; K – Kockelella; P – Pterospathodus; Ps - Polygnathoides siluricus Zone; S - ‘Ozarkodina’ snajdri; CO43 and Lag Vas 6 – approximate positions of erratic boulders from northern Germany; Ut 12 – Bed 12 in the U topolů section, Radotín Valley, near Prague, Czech Republic; U – approximate position of the Untenrüden section, Rhenish Slate Mountains, Germany
in the Pridoli and earliest Devonian in spite of many citations. (5) The clade exemplified by Amydrotaxis johnsoni, type species, Spathognathodus johnsoni Klapper, 1969, whose apparatus reconstruction is reasonably well documented (Klapper & Murphy, 1980; Murphy & Matti, 1983; Mawson, 1986), is now known as Mawson (1986, p. 40) predicted, from several levels of the Pridoli of Nevada as well as from the Lochkovian.

Ozarkodina, Wurmiella, and Amydrotaxis have been recognized as independent clades for some time, but material here attributed to Zieglerodina has been amalgamated (Ziegler, 1960; Walliser, 1964; Klapper & Murphy, 1975; Denkler & Harris, 1988) with the additional lineages of the Late Silurian and earliest Devonian and has been assigned to 'Ozarkodina'. The origins and compositions of the latter groups have not been clarified. However, at least four spathognathodontid apparatuses exclusive of Amydrotaxis are present in the Upper Silurian and Lower Devonian strata of the U topolů section southwest of Prague, Barrandian area, Czech Republic. The faunas there are made up partly of the easily recognizable Wurmiella and Ozarkodina and partly of more than two additional kinds of elements attributable to spathognathodontid apparatuses instead of only the one kind that would be expected if previous taxonomic hypotheses for handling this material were true. One hypothesis (Walliser, 1964, p. 86; Klapper & Murphy, 1975, p. 41) maintains that the morphologic variety resulted from an indivisible, highly variable series of populations. The other (Barnett, 1971; Denkler & Harris, 1988, p. B6; Jeppsson, 1989, p. 30) explained the variability as an ecophenotypic response of such populations to environmental conditions. Our classification is constructed to reflect that the additional kinds of apparatus found at U topolů are representative of independent, contemporaneously evolving and radiating clades. In our classification, the entire apparatus is taken into account, which serves to restrict explanations dependent upon infraspecific variability of the Pa element. Without this more analytical approach to the classification, the current practice would continue to classify Pridoli-Lochkovian specimens of this general morphology as either of two poorly understood taxa, the so-called “eosteinhornensis” or “remscheidensis” groups.

In this paper we propose to: 1) revise the generic-rank classification of the Spathognathodontidae and make the required nomenclatorial adjustments; 2) restrict Ozarkodina to the morphology characterized by Ozarkodina typica Branson & Mehl, 1933; 3) describe Wurmiella new genus; and 4) describe Zieglerodina new genus.

CONVENTIONS

The element notation of Sweet & Schönlaub (1975), conventional orientations, and the element terminology proposed in Murphy & Valenzuela-Ríos (1999) with minor additional elements are used. We agree with Walliser’s (1972, p. 75) modus operandi with respect to the nomenclature of conodonts.

Much of the taxonomy discussed here deals with the type specimens of Branson & Mehl (1933), who designated them as “cotypic”. They are syntypes in the present nomenclature and we refer to them as such below.

Currently the International Commission on Stratigraphy recognizes the Pridoli as a Series. We suggest that the rank of Stage is more compatible with comparable length units in other systems, but, for the present, we use the internationally agreed upon rank.

LIST OF DESCRIPTIVE TERMS USED IN THIS PAPER

α - angle between processes in lateral view.
arched - descriptive term referring to an element whose basal profile is regularly curved in lateral view as in an ellipse, spiral or circle.
angulate - descriptive term referring to an element whose processes are individually nearly straight but are at an angle to one another in lateral view.
bent - descriptive term referring to an element whose processes are straight in upper or lower view but abruptly change direction.
blade - the continuous part of the process excluding the denticles.
blade height - measured from the base of the anterior edge of the cusp to the junction of a basal platform lobe and the anterior blade in lateral view.
bowed - descriptive term referring to an element that has a regular curvature in upper or lower view.
cockscomb – a set of denticles at the anterior end of the blade of the Pa element that are set off from the remainder of the blade by their greater height.
process - one branch of an element including both the denticles and blade.
sexmembrete – referring to a skeletal apparatus with six kinds of elements.
septemmembrete – referring to a skeletal
apparatus with seven kinds of elements. Shoulder – inflation of the blade above a basal platform lobe that extends out from a ledge.

APPARATUS RECONSTRUCTION

Purnell & Donoghue (1998) have reconstructed Carboniferous apparatuses with seven mirror-image pairs of elements plus one symmetrical element. The Lochkovian apparatus described by Mashkova (1972) consists of 13 elements and one only partially preserved element, and the Sa element is lacking. These data suggest that Silurian-Early Devonian taxa had one pair each of Pa, Pb, and M elements, two pairs of Sc elements, two pairs of Sb elements, and that a symmetrical Sa element belongs at least to some individuals. Our reconstructions are guided by these data.

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A persistent problem encountered in the compilation of this paper has been the lack of specific terms for structures that look alike but are not homologous. We have tried to address this problem by consultation with the following colleagues. In this respect, we thank especially Otto H. Walliser and Gilbert Klapper for their thoughtful discussions of the paper. They also permitted us free use of their extensive collections. Norman M. Savage reevaluated his reconstruction of Ozarkodina philipi (Savage et al., 1977) for us and commented on this paper. Raymond Ethington evaluated the type specimen of Ozarkodina typica Branson & Mehl, 1933 for us and permitted loan of the specimen. Philip Donoghue verified that the holotype of Prioniodella inclinata Rhodes, 1953 is missing from the Birmingham collection. Carlo Corradini and James Barrick read early versions of the manuscript and made valuable suggestions. We appreciate the detailed reviews of Walter Sweet and Anita Harris and incorporate many of their suggestions. Ivo Chlupáč shared his extensive knowledge of the Barrandian with us, secured permission to collect samples, and demonstrated the stratigraphy of the area in the field. Falk Lehnhoff assisted in the Barrandian field work. This study has been supported by Humboldt Foundation, Spanish DGICYT Research Project PB 98-1558 and MCYT-FEDER Research Project BTE 2003-01609 and National Science Foundation Grant EAR 981 4354. The paper constitutes a contribution to IGCP 499. To finish this paper J.I.VR. was supported by an Intramural Research Grant of the University of Valencia (Estades curtes en alters universitatus).

SYSTEMATIC PALEONTOLOGY

Family SPATHOGNATHODONTIDAE Hass, 1959

We follow Walliser (1972) and Sweet (1988) in classifying spathognathodontids and polygnathids in separate families because, in addition to the reasons given by them, the development of the platforms of the Pa elements in the two groups is different. In the spathognathodontid apparatus, the platform develops from the base of the blade as basal platform lobes; in the polygnathid apparatus, the platform develops from ledges in the upper part of the blade. Bardashev et al. (2002) have classified the group of taxa generally with sulcate upper blades that are intermediate between the two as Eognathoidae.

Genus OZARKODINA Branson & Mehl 1933

Type species.- Ozarkodina typica Branson & Mehl, 1933 (= Spathodus primus Branson & Mehl, 1933; Prioniomentus bicusciatus Branson & Mehl, 1933; Plectospathodus flexuosus Branson & Mehl, 1933; Trichognathus symmetrissima Branson & Mehl, 1933; Hindeodella confluens Jeppsson, 1975).

Diagnosis.- A spathognathodontid genus with a sexmembrate apparatus, in which Pa elements are characterized by a high anterior, sail-like or fan-like cockscomb separated from the rest of the denticles by a slight offset of the denticle row, a space, or an abrupt change in style of denticulation; small basal platform lobes and correspondingly small basal cavity with its anterior margin in the anterior half of the blade, and correspondingly with a stepped lower profile; Pb element with high relatively erect cusp; M and transition-series elements with small basal cavities, crowded denticles and white matter that reaches almost to the base of the blade, Sa normally alate without posterior process (trichonodellan).

Discussion.- Multielement Ozarkodina Branson & Mehl, 1933 (= Spathognathodus Branson & Mehl, 1941) is currently accepted by conodont workers as the taxon of choice to house poorly understood spathognatho-dontid taxa. 'Ozarkodina'...
included what we consider as the four main genera shown in Figure 1, as well as Amydrotaxis, and some of the taxa mentioned in the introduction. Even after several revisions and separation of several generic units, 'Ozarkodina' includes several clades and requires further restriction, some of which is proposed and justified below.

Jeppsson (1969) made the first apparatus reconstruction of Ozarkodina based on material from the siluricus Zone (Ludlow) of Gotland. In it he showed that the white matter roots in the apparatus elements almost reach the base of the blade and that this kind of distribution of the white matter is distinctive. In the classification proposed here, Ozarkodina is restricted to those taxa closely resembling Jeppsson’s reconstruction (1969, figs. 1A-C, E-F, not D; figs. 2 A-C, E-F not D). However, instead of the Sc element included by him (1969, figs. 1D, and 2D), we agree with Klapper et al. (1981: W163, 165) that his subsequently figured specimen (Jeppsson, 1975, pl. 7, fig. 1) is representative of the Sc element.

Characters generally associated in apparatuses of the kind Jeppsson described are: 1) The Pa element has a high anterior cockscomb set off from the remainder of the element, (2) the basal platform begins to widen anterior of the midpoint, and (3) the Pa element tapers conspicuously to the posterior in lateral view. (4) In all elements, the denticles are densely crowded. 5) The Pb element has a high, relatively erect cusp and a blunt anterior end. 6) The ramiform elements have small basal cavities, their blades are compressed and high, and do not have ledges (note the relatively low blade and ledge of the excluded specimen in Jeppsson, 1969, fig. 2D). 7) The Sa element is normally trichonodellan, in some cases, slightly asymmetrical and in one case, with a denticulate posterior process. (8) Processes of the Sc element are oriented so that the anterior process angles obliquely down and away from the posterior process when the latter is oriented horizontally.

The Ozarkodina apparatus is commonly present in the Upper Silurian (Ludlow, Pridoli). All the potential type species for multielement Ozarkodina were originally described by Branson & Mehl (1933) from a sample of the Bainbridge Limestone at Lithium, Missouri (Figures 2.1-2.15). The section at Lithium contains only a single bed of shale (Rexroad & Craig, 1971; Klapper, personal communication, June, 2000) and, because Branson & Mehl derived their material from shale, new collections of well-preserved material from the shale bed would be desirable. However, Branson & Mehl's collection shows that preservation in the shale bed is poor whereas preservation in the neighboring limestone beds is excellent. Rexroad & Craig's (1971) material collected from limestone beds above and below the type bed is not specifically located in the outcrop and could have come from any of the three lower units of their columnar section. Thus, we have chosen to represent the Ozarkodina apparatus by well-preserved material loaned to us by Gilbert Klapper (Figs. 2.1-2.7), which comes from a bed 29-39 cm above the shale unit. The entire apparatus is present and the Pb elements are morphologically like the lectotype of Ozarkodina typica Branson & Mehl (Figs. 2.9-2.11). However, the compelling reason for this choice is that this apparatus, in reality, is what most authors have used as the model for the species and it is what we use below.

Branson & Mehl (1933, p. 51) designated "Ozarkodina typica Branson & Mehl, n. sp." as the "genotype" of Ozarkodina. Therefore, Ozarkodina typica Branson & Mehl, 1933 is the type species of Ozarkodina, regardless of any subsequent action (ICZN). Jeppsson (1969, p. 13), in the course of apparatus reconstruction, treated Ozarkodina as a subjective junior synonym of Hindeodella Bassler, 1925. Jeppsson's (1969, 1975) concept of including all taxa with hindeodellan elements in Hindeodella has been reviewed by Klapper & Philip (1971, p. 441) who subjectively decided to use Ozarkodina as the generic name for species with the apparatus under consideration. We concur with their action, which requires the use of Ozarkodina typica as the name of the type species of the genus (Klapper & Philip, 1971). Walliser (1972) also came to this conclusion. Jeppsson (1969, p. 17), however, as first reviser, had chosen the name confluens to represent the taxon from among Branson and Mehl's six names pertaining to the taxon. Thus, Ozarkodina typica became a subjective junior synonym of “Hindeodella confluens” (Jeppsson, 1969, 1975). Jeppsson used Swedish material for his apparatus reconstruction of “H. confluens” rather than material from the type locality and he did not choose a lectotype for confluens. The Sc element that he chose in his first reconstruction (1969, fig. 2d) probably does not belong to the rest of the apparatus that he depicted as the “Hindeodella” apparatus because it has a strong ledge at the base of the denticles.

Rexroad & Craig (1971) restudied Branson & Mehl’s (1933) material and made additional collections through the section at Lithium. They also refigured what they interpreted to be Branson &
Mehl’s syntypes and claimed they belonged to at least two different taxa (1971, p. 690). They chose figure 23 of Branson & Mehl (1933) as lectotype because one of the remaining specimens "represents a Ligonodina" (presumably pl. 70, fig. 21) and the other was "broken into several pieces" after photography. The lectotype (University of Missouri, Columbia C-157-3) has alternating denticle sizes and a strong ledge, both characters that do not occur in the taxon identified as ‘Ozarkodina confluens’ in the recent literature (compare Fig. 2.3). It also differs from Branson & Mehl’s drawings in the relative sizes of the denticles although it certainly is the same specimen. Finally, it differs from the Sc elements shown by Jeppsson (1969, 1975). Thus, the name, 'Ozarkodina confluens' (= Hindeodella confluens) is attributable only to the "lectotype" because the type specimen belongs to an unknown apparatus and, in addition, is too incomplete to be identified with confidence.

Jeppsson (1975, pl. 7, fig. 1), in a second reconstruction, depicted an Sc element that fits the characteristics of the other apparatus elements. It is the one that we assign to the Ozarkodina typica apparatus.

As no holotype had been chosen for the form taxon, Ozarkodina typica Branson & Mehl, 1933, Walliser (1964, p. 61) designated the syntype figured by Branson & Mehl (1933, pl. 3, fig. 44) as the lectotype. Rexroad & Craig (1971, p. 694, pl. 80, fig. 35) refigured the same specimen, which has an incomplete posterior process and cannot be attributed with confidence to any species-rank taxon. Thus, the taxon with the name typica would normally also be regarded as indeterminate. G. Klapper (2001, oral communication), however, regards it as the only possible Pb element available from the type material for reconstruction of the Ozarkodina apparatus. R. Ethington (2001, oral communication) kindly examined this specimen for us and reported the following observations: the distribution of the white matter reaches nearly to the base of the blade; the white matter in the roots of the denticles shows overgrowth and elimination of denticles; the basal cavity is small. These are all features that are characteristic of the topotypic Pb elements of conventional Ozarkodina typica, but not of the other Pb elements from the type locality at Lithium (Figs. 2.1-2.7). Ethington subsequently loaned us the lectotype and other Pb elements from the original collection, which are refigured here (Figs. 2.9-2.11). As a consequence of the above interpretations, as well as ICZN article 68b, the name of the type specimen for the taxon in question is Ozarkodina typica Branson & Mehl, 1933. The use of this name also stabilizes nomenclature of the genus. Walliser and Wang (1989) have already used this nomenclature, but without elaboration.

Although previous analyses of Late Silurian Ozarkodina (as limited here) have resulted mostly in classification at the informal morph (Klapper & Murphy, 1975) or subspecies level (Männik & Viira, 1990; Jeppsson et al. 1994), Fordham (1991) also considered a separation on a generic level of some spathognathodontid taxa, particularly Ozarkodina typica and the stock attributed here to Wurmiella n. gen. However, because the cladistic evidence used by Fordham may be interpreted as implying morphological convergence, we do not follow his nomenclatorial suggestions.

Classification of Ozarkodina species.- Several species of Ozarkodina with overlapping ranges are present in the Ludlow and Pridoli and suggest a minor radiation of the clade in the interval. This is confirmed by the presence in glacial erratic boulders of northern Germany of two different Ozarkodina Sa elements. One kind has only lateral processes (= trichonodellan), and the other (represented by a single specimen) has a denticulate posterior process (= diplododellan). Other Late Silurian Ozarkodina are described from the Baltic region by Viira (1983, 1994, 2000). With the addition of an Ozarkodina n. sp. from the Barrandian, four species are now known from the Pridoli. In addition to the Barrandian O. n. sp., they include Ozarkodina typica Branson and Mehl, O. ambiguus (Viira, 1983), and O. nasuta (Viira,1983). A fifth species may be present at the Silurian-Devonian stratotype section at Klonk as suggested by Pa element fragments from bed 18. The apparatuses of ‘O.’ inordinata (Viira, 2000) and ‘O.’ denticulata (Viira, 2000), also from the Baltic region, have not been reconstructed and their Pa elements are not typical of Ozarkodina. For these reasons, we query their assignment to Ozarkodina.

Stratigraphic distribution.- Confirmed species of Ozarkodina are known from the Early Llandovery to the base of the Devonian. The Early Llandovery presence of Ozarkodina in Australia is clearly established by Bischoff (1987) with Ozarkodina masurensis Bischoff and followed in the later Llandovery by O. cadiaensis Bischoff, O. bathurstensis Bischoff, and O. waugoolaensis Bischoff. The origin of Ozarkodina is, thus, at least as old as earliest Llandovery, but we have not
evaluated the Late Ordovician records of Ozarkodina mentioned by Sweet & Bergstrom (1972, p. 38).

Although some authors (Nicoll & Rexroad, 1969; Rexroad & Nicoll, 1971; Fordham, 1991, p. 132) have suggested that ‘Ozarkodina’ hadra (late Llandovery, celloni Zone) may be the ancestor of the later Ozarkodina, its apparatus has not been reconstructed and it is equally likely at this point that one of Bischoff’s taxa represents the main line of descent.

The Ludlow and Pridoli were times of high numbers of species within the genus, but the numbers diminished markedly in the Late Pridoli and the clade disappeared just above the base of the Devonian. Its last occurrence is slightly above the base of the Devonian in bed 12 of the U topolů section, near Prague, Czech Republic (Fig. 1). So far as we know, there exists no Ozarkodina younger than that occurrence, although some Devonian taxa may be related.

Comments on Early Devonian ‘Ozarkodina’ and Pandorinellina. - The history of Ozarkodina is complicated by a lack of record in the lower Lochkovian (uniformis Zone), which has yielded only the Ozarkodina from bed 12 at U topolů, one bed above the first occurrence of Monograptus uniformis angustidens. The next earliest recorded Devonian taxon, perhaps arising out of Ozarkodina because of similarities in their Pa elements, is the Middle Lochkovian Pandorinellina optima (Moskalenko, 1966). The reason for classifying P. optima and other Early Devonian species as Pandorinellina originally was that the apparatus reconstruction for the Middle-Late Devonian Pandorinellina insita (Stauffer), type species of Pandorinellina, has an alate Sa element with a denticulate posterior process (= diplododellan; Klapper & Philip, 1971, fig.1) whereas the element assigned to the Sa position in Ozarkodina typica is alate, but normally lacks a posterior process (= trichonodellan). Pandorinellina insita differs also in having alternating large and small denticles in the M and transition-series elements that are not present in the O. typica apparatus. Klapper (personal communication, January 31, 1997) regards the P. insita reconstruction as highly probable, but that it may, in addition, have an Sd element that has a right-angle bend, whereas only a slight lateral bend is present in the anterior process of the Sc element. Most reconstructed Early Devonian taxa assigned to Pandorinellina also have denticles of alternating sizes in the transition-series elements. This differs from the reconstructions of Silurian Ozarkodina by Jeppsson (1969; 1975) and Klapper & Murphy, (1975), which show that the denticles change size progressively along the processes. Because of these differences, we use Pandorinellina for P. insita and Early Devonian taxa with Ozarkodina-style Pa elements that are reconstructed with a diplododellan Sa. We use Ozarkodina for those taxa with a trichonodellan Sa, and the other characteristics of O. typica, but would distribute the other described taxa currently classified as ‘Ozarkodina’ in other genera.

This use does not affect Criteriognathus Walliser, 1972, with Spathognathodus steinhornensis Ziegler, 1956 as its type species. Criteriognathus steinhornensis was reconstructed from a bedding plane assemblage and discrete conodonts from the Turkparida Formation, Fana Mountains, Tadjikistan with a diplododellan Sa element (Mashkova, 1972, pl. 2, figs. 1-6, not pl. 1). Klapper & Murphy (1975, p. 40) remarked that “the P element is close, but not identical with steinhornensis”. On the basis of stratigraphic position and similarity of the Pa element, they inferred that steinhornensis was a Pandorinellina because it probably had a diplododellan Sa element. However, steinhornensis cannot be referred to Pandorinellina because its Pa element is nearly equidentate, has a large, heart-shaped basal cavity, commonly has an ornamented basal platform lobe, and the position of the basal platform lobes posterior of the midpoint of the element are characters not found in Pandorinellina. If the character of the Sa element were a decisive unifying criterion, Criteriognathus would become a junior synonym of Pandorinellina. However, the possession of diplododellan Sa elements by several otherwise unrelated Silurian and Devonian taxa suggests that diplododellan Sa elements are a common parallel development in a number of lineages. Silurian species with denticulate posterior processes are known from: 1) a Late Ludlow specimen figured as 'Hindeodella cf. wimani' by Jeppsson (1975, pl. 12, fig. 1a-d; probably not Ozarkodina); 2) a specimen from a north German erratic boulder (PC-A940) with the typical Ozarkodina distribution of white matter and associated with other elements of O. typica; 3) a Late Ludlow diplododellan element from another erratic boulder (PC-Chon 1) from the Baltic region and associated with "O. 'snajdri' transitional to 'O. crispa"; and 4) several different diplododellan elements from bed 12 of the U topolů section, Radotin Valley, Czech Republic. Late Early Devonian diplododellan Sa elements are known especially from contemporaneous Emsian clades, such as Polygnathus and Pandorinellina.
Polygnathus almost certainly has its origin in Eoggnathodus, which does not have a diplododellan Sa in current reconstructions (Klapper & Philip, 1971; Murphy et al., 1981) and is not considered close to Criteriognathus. Evidently, denticulate posterior processes of Sa elements appear independently and heterochronously in several clades and do not always signify identity. However, once they are developed, all descendents probably retain this morphologic feature and we consider it a characteristic of Criteriognathus and Pandorinellina that separates them from Zieglerodina and Ozarkodina, respectively.

Pandorinellina optima is thought to have given rise to P. philipi in the late Pragian or early Emsian. P. exigua and P. expansa continue this lineage. P. paleothorpei (Telford, 1975) may constitute a peculiar side branch and has been assigned to Bipennatus by Mawson (1993).

The Pa elements within the Pandorinellina philipi-P. exigua-P. expansa lineage seem to represent anagenetic evolution within the Emsian, but their Pb and Sa elements, as presently reconstructed, do not. The sequence of Pa elements shows a progressive expansion of the basal cavity posteriorly with P. exigua in the intermediate position (Klapper, 1969; Uyeno & Mason, 1975). However, the Pb elements do not follow a simple progression. Initially, in P. philipi, the Pb element has a long, low posterior process in which the denticles near the cusp are small and lower than the more distal ones (Savage et al., 1977). The tendency to diminish the size of denticles just behind the cusp is more advanced in P. expansa whose Pb element has a space without denticles immediately behind the cusp. In contrast to the other two, P. exigua, the supposedly intermediate form based on the Pa elements, is reconstructed with normal Pb elements (Mawson, 1987, pl. 40, figs. 9-11) with no hint of denticle diminution. Possibly, this discrepancy can be resolved by using the Pb element illustrated by Lane & Ormiston (1979, pl. 6, figs. 25, 26) in the exigua reconstruction. It is similar to the one figured by Savage et al. (1977, pl. 1, figs. 13-17) for P. philipi. Morphologically, this Pb with its shorter denticles just behind the cusp also recalls the gape behind the cockscomb of the Pa element of P. exigua and fits better in the proposed anagenetic sequence from P. philipi to P. expansa.

The Pandorinellina philipi Sa element has a very long, denticulate posterior process (Savage et al., 1977, pl. 1, figs. 30-33). In P. exigua, the posterior process is very short and non-denticulate (Mawson, 1987, pl. 40, figs. 12, 13). P. expansa again has the long, denticulate process (Uyeno & Mason, 1975, pl. 1, fig. 16). We hope that new studies of these Emsian taxa will resolve this enigma.

The apparatus of taxa in the group exemplified by ‘Ozarkodina’ buchanensis (Philip, 1966) has been reconstructed with a trichodollellan Sa. Thus, it would make an ideal descendent of Ozarkodina based on that fact and similarities in their Pa elements. However, the other elements of the apparatus do not appear to be compatible with descent from the already highly specialized elements of Ozarkodina. In addition, ‘O.’ buchanensis is separated from Ozarkodina by a stratigraphic interval ranging from just above the S-D boundary to the middle Pragian. This is also the case with some other Australian forms, such as, ‘O.’ prolata Mawson, 1987 and ‘O.’ paridens (Wilson, 1989) and the European ‘O.’ carinthiaca (Schultze, 1968). Until such time as the connection to Ozarkodina can be shown, we assign them to Ozarkodina.

‘Ozarkodina’ frankenwaldensis Bischoff & Sannemann, 1958, from the middle Lochkovian of Germany has a Pa element like Pandorinellina. However, too little is known about the variation of the Pa element and nothing is known of its apparatus to do more than suggest a relationship with either Ozarkodina or Pandorinellina.

Genus WURMIELLA n. gen.

Type species.- Ozarkodina excavata subspecies tuma Murphy & Matti, 1983, pl. 1, figs. 3-9.

Diagnosis.- A spathognathodontid genus whose species have a sexmembrate apparatus characterized primitively by processes without strong size variation of adjacent denticles and Pa elements with relatively small, narrow basal platform lobes that lack ornamentation; Pb elements with a cusp much larger than the other denticles and slight asymmetry of the basal platform so that the lobe on the inner side is elevated.

Derivation of Name.- To honor Professor Adolf Wurm, Würzburg, who stimulated research on the Devonian of the Frankenwald.

Discussion.- The genus characterized by species with the widespread and abundant apparatus usually identified as ‘Ozarkodina excavata’ or ‘O. wurmi’ is given the name Wurmiella n. gen.
choose *Ozarkodina tuma* Murphy & Matti, 1983 (here Figs. 2.16-2.28) as type species of *Wurmiella* because several uncertainties surround the type specimens of the two most frequently cited taxa in the clade, *Neoprioniodus excavatus* (Branson & Mehl, 1933), the type of the multielement species *Ozarkodina* excavata, and *Spathognathodus wurmi* Bischoff & Sannemann 1958, the type of *Ozarkodina* wurmi.

In the case of *excavatus* (based on M elements = the form species *Prioniodus excavatus* Branson & Mehl, 1933), the two syntypes (Branson & Mehl, 1933, pl. 3, figs. 7, 8) from the Bainbridge Limestone, Lithium, Missouri were figured as drawings. The drawings are clear as to the shape of the basal cavity, the lack of an anterior process, and the denticles being in contact at their bases, but their incomplete posterior processes and the poor preservation of the denticles preclude definite classification. Walliser's (1957, p. 46) designation of a lectotype (the additional designation of a "Holotypus", in the explanation of pl. 2, fig. 17, is probably a residue from an earlier manuscript) did not change the quality of the syntypes. However, his expanded concept of the taxon allowed much greater variability of the spacing and position of the denticles because it emphasized the curvature of the lower profile of the element rather than the characteristics of the denticles. We agree that curvature of the element may be an important characteristic, but not in this case in which the characteristics of the denticulation are more critical.

The lectotype and the other syntype of *Prioniodus excavatus* have been lost. As a result, Rexroad & Craig (1971, p. 692, pl. 80, not pl. 81, fig. 7) introduced a neotype that comes from an unspecified level in units A or B of the Bainbridge Limestone at Lithium. Denticles on the blade of the neotype are discrete with interspaces of nearly equal width. This choice of a neotype is within the enlarged concept of the taxon given by Walliser (1964), but differs from the figure of the lectotype, which has denticles that are in contact at their bases (Branson & Mehl, 1933, pl. 3, fig. 8), i.e., not separated basally by a U-shaped interspace. The occurrence of three Pa morphotypes in Rexroad & Craig's figures (pl. 80, figs. 19-24, 25-31) suggests that the small differences in the M elements may reflect their affiliation with different apparatuses and therefore are important differences. In any case, Rexroad & Craig (1971) have altered the concept of the single-element species based on the M element. We regard *Prioniodus excavatus* Branson and Mehl, 1933 as a *nomen dubium* because the neotype does not have the same morphology as the lectotype and may not represent the same taxon as the lectotype. In addition, it is not clear to which apparatus either of them belongs.

The first reconstruction of an apparatus of *Wurmiella* was given by Walliser (1964, p. 14, 18-19) who combined six form taxa in his "Conodonten Apparat H", but left it in open nomenclature.

Next, Jeppsson (1969, fig. 3) suggested an apparatus reconstruction for *Wurmiella* whose elements came from unspecified beds of the Öved-Ramsåsa Group (Ludlow-Pridoli) in southern Sweden. He identified his elements with form taxa established by Branson & Mehl (1933), Rhodes (1953), and Walliser (1957), and he chose the M element, *Prioniodus excavatus* Branson & Mehl 1933 as the type of the multielement species. We reject Jeppsson's identification of his M element (1969, fig. 3C) with the lectotype of *Prioniodus excavatus* because Jeppsson's specimen has a denticulate anterior process and the denticles of the posterior process are widely separated. In addition, Jeppsson's (1969) specimen differs from the neotype of *N. excavatus*.

As for the other elements in Jeppsson's reconstruction, the Sa element identified as *Trichonodella excavata* Branson & Mehl, 1933 differs from the lectotype of *T. excavata*, which has been refigured by Rexroad & Craig (1971, pl. 79, fig. 43) (see also Figs. 2.29-2.36 for depiction of apparatus from the Bainbridge Limestone at Lithium, Missouri). In the Swedish Sa specimen, "the part of the basal cavity that rises up on the posterior side of the cusp is narrow, has parallel or nearly parallel margins, and tapers to a point" (Jeppsson, 1969, p. 20), whereas, in the lectotype it is wider and the apex is bluntly rounded. The Swedish Pb element has a ledge at the base of the denticles and an almost straight lower profile as opposed to no ledge and an angulate or arched lower profile in the Bainbridge toptype material loaned to us by Gilbert Klapper from his sample at 29-39 cm above the type bed. The Swedish Pb element has discrete, closely spaced denticles (five on the anterior and eight on the posterior process). The synonymized syntypes of *Ozarkodina simplex* Branson and Mehl 1933 were stated to have eight or nine anterior appressed denticles. Additional toptype material figured by Rexroad & Craig (1971, pl. 80, figs. 26-29) has shorter posterior processes. The Swedish Sb element has a wider angle between the processes than the
various morphotypes figured from the Bainbridge. The Swedish Sc element has a nearly straight lower profile, discrete, equally spaced denticles, and its anterior process almost in line with the posterior process, as opposed to the arched lower profile, needle-shaped denticles, and right angle bend between the processes in Klapper’s Bainbridge specimens. According to all the differences mentioned, the apparatus figured by Jeppsson (1969, fig. 3) is not demonstrated in the Bainbridge specimens and cannot bear the name of a Bainbridge species. Thus, this taxon is not suitable as a type species for the new genus, *Wurmiella*.

Jeppsson (1969, p. 18) also placed *Prionodella inclinata* Rhodes, 1953 in synonymy with *Hindeodella excavata*. This synonymy needs verification because the holotype for *inclinata* designated by Rhodes (1953, p. 374) has never been figured. Rexroad & Craig (1971, pl. 80, fig. 25) refigured one of the paratypes from the Rhodes collection at Birmingham (CIIC2b) as the "lectotype". However, a lectotype can be chosen only if no holotype was designated originally. The holotype previously has not been declared lost, but P. Donoghue (personal communication, 9/2000) has searched the Birmingham collection and has certified that the holotype is indeed lost. We, therefore, designate the paratype refigured by Rexroad & Craig as the neotype and resurrect the taxon *inclinatus* Rhodes, because the denticlement of the neotype differs in significant ways from the Pa elements found in the Bainbridge fauna.

The problem with using *Spathognathodus wurmi* Bischoff & Sannemann, 1958 as the type of our new genus is that the type stratum in the Frankenwald, Germany, is a condensed deposit in which conodonts of a longer interval are concentrated. Thus, the exact age and faunal association are unknown. Therefore, a taxon based on a holotype from that material is not appropriate as the type species of a genus.

According to current reconstructions, *Wurmiella* has a sexmembrane apparatus in which denticulation of most of the non-platform elements is of discrete, more or less elongate needle-shaped denticles that are lens shaped or elliptical in cross section (Jeppsson, 1972; Klapper & Murphy, 1975; Murphy & Cebecioglu, 1986). Primitively, this denticulation is more or less equidentate (as opposed to alternating sizes), but this does not totally exclude intercalation of single, small denticles, and it allows for the presence of smaller denticles near the cusps of Sc and Sb elements. All elements of *Wurmiella* show a tendency to develop morphs that have a ledge at the base of the denticles (Bischoff & Sannemann, 1958; Walliser, 1964; Murphy & Cebecioglu, 1986), although Pa morphotypes without a ledge are present through much of its stratigraphic range, mostly as small specimens, but also as large specimens in collections dominated by the ledge-bearing morphs. The basal cavity of the Pa element is mostly small and narrow and confined to the mid-section of the element, but it repeatedly develops shapes in which the basal opening bulges laterally and/or tapers gradually to the posterior end of the element. The posterior basal grooves tend to invert (Walliser, 1964; Klapper & Murphy, 1975; Murphy & Cebecioglu, 1986).

The most characteristic elements of *Wurmiella* and the ones with the most stable morphologies throughout the history of the genus are the Pb and M elements. The Pb element has a high, slightly inclined cusp, long, low processes with denticles that are much shorter than the cusp, and an asymmetrical basal platform that is higher on the inner side so that the basal cavity is seen in inner lateral view. Such elements are distinctive and they differ from other spathognathodontid Pb elements. They vary mostly in the size of the angle between the two processes, and the relative lengths of the processes, and in the number of denticles present. Morphology of the M element is also distinctive. The lower profile of the posterior process blends with that of the expansion of the basal cavity and the anterior process (if present), rather than having a sharp bend at the base of the cusp at the beginning of the posterior process. Denticle spacing and the shape of the cross section are the main variables. Transition-series elements vary mostly in the shape of the basal cavity and in its size. All elements tend to increase in size at higher stratigraphic levels. However, normal infraspecific variation, ontogenetic changes, and generally similar morphology of the Pa element within most samples have kept taxa within the clade from being well characterized.

Table 1 is a representative list of the described Silurian and Devonian taxa that we assign to *Wurmiella*. This list contains a diverse group of taxa many of which are already specialized in the Llandovery. Some of them are parts of lineages that are rare, but persist through much of the Silurian and Early Devonian relatively unchanged, such as, the arcuate forms figured from the Llandovery by Pollock et al. (1970, pl. 113, figs. 13-15) and the Lochkovian forms of Murphy & Cebecioglu (1986,
Forms with biconvex lower profile figured by Liebe & Rexroad (1977, pl. 1, fig. 26) from the Llandovery and *Wurmiella wurmi* (Bischoff & Sannemann, 1958, pl. 14 fig. 5) from the Lochkovian could also be parts of a lineage with intermittently common representatives. The distinctive Pb element is found with all of the above-cited Pa elements. Thus, we suggest that we are seeing components of several lineages, all with the basic apparatus pattern of apparatus H of Walliser (1964) and we have represented the three lineages as separate bars in Figure 1.

### Table 1.- Partial list of representative species of *Wurmiella*

<table>
<thead>
<tr>
<th>Species</th>
<th>Age</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Wurmiella wurmi</em></td>
<td>middle and upper Lochkovian</td>
<td>Bischoff &amp; Sannemann, 1958</td>
</tr>
<tr>
<td><em>Wurmiella tuma</em></td>
<td>middle Lochkovian</td>
<td>Murphy &amp; Matti, 1983</td>
</tr>
<tr>
<td><em>Wurmiella 'excavata'</em></td>
<td>Ludlow</td>
<td>Branson &amp; Mehl, 1933</td>
</tr>
<tr>
<td><em>Wurmiella inclinata?</em></td>
<td>Ludlow</td>
<td>Rhodes, 1953</td>
</tr>
<tr>
<td><em>Wurmiella inflata</em></td>
<td>Ludlow</td>
<td>Walliser, 1964</td>
</tr>
<tr>
<td><em>Wurmiella hassi</em></td>
<td>Llandovery</td>
<td>Pollock, Rexroad and Nicoll, 1970</td>
</tr>
<tr>
<td><em>Wurmiella polinclinata</em></td>
<td>Llandovery</td>
<td>Nicoll and Rexroad, 1969</td>
</tr>
<tr>
<td><em>Wurmiella eosilurica</em></td>
<td>Llandovery</td>
<td>Bischoff, 1987</td>
</tr>
<tr>
<td><em>Wurmiella australensis</em></td>
<td>Llandovery</td>
<td>Bischoff, 1987</td>
</tr>
</tbody>
</table>

**Holotype.**- Murphy & Matti, 1983, p. 7, pl. 1, figs. 3, 4; University of California, Riverside Museum 8536/2, bed 6, 55.7 feet, type section of the Bastille Limestone (Kay & Crawford, 1964, p. 439), Mill Canyon, Toquima Range, Nevada.

**Diagnosis.** A species of *Wurmiella* in which the Pa element is carminate to slightly angulate (has a straight or stepped lower profile), slightly asymmetrical basal platform with both lobes inflated, basal grooves open, deep, tapering at low angle to extremities, 11-19 anterior and 8-12 posterior denticles (depending on size), ledges and inner shoulder strongly developed.

**Description.**- Pa element (Figs. 2.16-2.19), straight or bent at position of basal cavity in basal view, laterally with arched or stepped lower profile, moderate to strong pinch zone in lower half of blade, moderately deep basal cavity, ledge and inner shoulder strongly developed, outer shoulder commonly present; Pb element (Fig. 2.20) with cusp two to three times wider than other denticles, with about 6-10 anterior and about 20 posterior denticles, $\alpha = 115-135^\circ$, basal grooves open, tapering to extremities, basal cavity asymmetrical with inner side larger; M element (Figs. 2.21, 2.22) with very small or without anterior process, posterior process evenly curved with about 16-20 discrete, very closely spaced, palisade-type denticles, basal grooves and basal cavity open, shallow; Sa element (Figs. 2.27, 2.28) trichonodellan, bowed in basal view, $\alpha$ about 150°, basal grooves open, tapering to extremities, basal cavity narrow, high, triangular almost parallel sided; Sb element (Figs. 2.23, 2.24) basal grooves open proximally, appressed distally, basal cavity narrow, high, triangular, anterior process with extremely long needle-shaped denticles; Sc element (Figs. 2.25, 2.26) with anterior process at about right angles to posterior, posterior process arched in lateral and bowed in basal views, denticles discrete, needle-shaped, size augmenting to the distal end, basal grooves open merging gradually with only slightly expanded basal cavity.

**Comparison.**- *Wurmiella tuma* Pa differs from *W. wurmi* in having a straight or angular lower profile rather than a biconvex one and has a higher number of denticles per mm (Murphy & Cebecioglu, 1986, fig. 2). It differs from the *Wurmiella* apparatus from the Bainbridge Limestone, *W. excavata*, in being larger, in having a much greater number of denticles of the palisade type, strongly developed ledge, inflated basal platform lobes or shoulders, and poorly or undeveloped cusp.
Distribution. — *Wurmiella tuma* was a short-lived species of local distribution in central Nevada where it occurs abundantly in the middle Lochkovian upper *eleanorae-trigonicus* and lower *trigonicus-pandora* β Zones of Valenzuela-Ríos & Murphy (1997). Occurrences in the COP IV, Mill Canyon, and SP VII sections of central Nevada are given in Murphy & Matti (1983, Tables 1-3).

*Wurmiella wurmi* (Bischoff & Sannemann, 1958)

*1958 Spathognathodus wurmi* Bischoff & Sannemann, pl. 14, figs. 4-10.

*1958 Plectospathodus robustus* Bischoff & Sannemann, pl. 14, figs. 11-14.

*1958 Plectospathodus extensus* Rhodes, Bischoff & Sannemann, pl. 15, figs. 11, 14, 15.

*1958 Trichonodella excavata* Branson & Mehl, Bischoff & Sannemann, pl. 15, figs. 16, 18.

*1958 Prioniodina excavata* Branson & Mehl, Bischoff & Sannemann, pl. 15, fig. 7 only.

Original diagnosis. — A species of the genus *Spathognathodus* with the following characteristics: long anterior half with convex aboral margin, posterior half as long as or one third shorter with concave aboral margin. Oral margin of the blade enlarged, ledge-like, with strong, nearly equal-sized denticles. Oval basal cavity mostly expanded more strongly on one side. [Translated from German]

Revised diagnosis. — A species of *Wurmiella* with a combination of the following characteristics in the Pa element: biconcave or convexo-concave lower margin in lateral view; moderate shoulder on inner side of the blade above the basal platform lobe; ledges at the base of the denticles; 17 to 27 denticles (depending on size of the element).

Description. — Pa element gently twisted, slightly more strongly near extremities; basal cavity small, asymmetrical, inner side more expanded; basal grooves appressed at distal ends; upper margin in lateral view biconvex; ledge normally developed on inner side at base of denticles; flanks of blade inflated below ledge and with narrow pinch zone close to lower margin; height of both parts (anterior and posterior) of blade about equal; thicker (wider) and higher denticles concentrated near centers of anterior and posterior parts of blade; cusp not strongly developed; at position of basal cavity ledge bulges laterally to form shoulder on inner side of all specimens and in some specimens on both inner and outer sides; dente number varies from 17–27, counting all germ denticles and depending on size of element; denticles straight, stout, with elliptical cross sections, and blunt to moderately sharp tips.

Comparison. — See *W. tuma* above.

Occurrence. — The species avoids very shallow-water facies and occurs in the middle Lochkovian of Barrandian of the Czech Republic (U topolů section, beds 15, 16, 17A); of the central Pyrenees and of the Guadarrama, Spain (beds 22-25 in the Gerri 1.1 section, beds 10-14 at the Gerri 1.2 section, and beds 13-36b at the Segre section in the central Spanish Pyrenees; beds 12-15, of the Frankenwald section in Germany (Transgressions Horizont); of central Nevada (beds 9E through 13J, SP VII section, Windmill Limestone, at Coal Canyon). A similar form, shown as cf. in Figure 1, occurs in beds 20-27 in the Guadarrama section of central Spain (Carls, 1969).

Genus ZIEGLERODINA new genus

Type species. — *Spathognathodus remscheidensis* Ziegler, 1960: 194. pl. 13, figs. 4a-b

Derivation of the name. — To honor the late Professor Willi Ziegler, former Director of the Senckenberg Museum und Forschungsinstitut, Frankfurt am Main, leading conodont researcher and magnanimous facilitator of conodont research.

Diagnosis. — A genus of the Family Spathognathodontidae with an apparatus that has the following combination of characters: Pa element carminate, straight or slightly bowed in basal view; lobes of small, subcircular basal platform without ornament; denticles lenticular, of unequal sizes; with enlarged cusp. Pb element angulate pectiniform of the kind figured by Ziegler (1960, pl. 15, fig. 15). M element dolabrate with long, steeply descending posterior process. Processes of transition-series elements with lanceolate cross section and no pronounced outer ledges, with alternating large and sets of small denticles, small basal cavities; posterior blades of Sb and Sc elements tend towards inversion of the basal grooves and undulation of the blades in maturity. Sa element alate with short but high lateral processes, no posterior process; α 65 to almost 90º, with short posterior extension of basal cavity, and with a narrow anterior median sulcus with flat bottom that may continue on the cusp.
Discussion. - The Pa elements from bed f at Untenrüden, have four characteristics in common: irregular denticulation, open, parallel-sided basal grooves, position of the basal cavity, and lack of ornamentation on the basal platform lobes. The shape of the lateral profiles and the arrangement, number, and size of the individual denticles is variable. However, the cusp is almost always much larger than the surrounding denticles and the cockscomb normally has one or two very large denticles whose position is variable. Irregularity of the denticles is extreme.

Ziegler figured non-platform elements from several taxa at Untenrüden. We reconstruct the apparatus of Zieglerodina, therefore, from a combination of localities where Pa elements of other species of Zieglerodina are present with non-platform elements that are similar to those found at Untenrüden. These localities include bed 40 in the Cellon section of the Carnic Alps (Walliser, 1964; Figures 3.25, 3.29-3.32), erratic glacial boulders from the North German plain of Silurian age, and material from bed 12 of the U topolů section in the Radotín Valley near Prague, Czech Republic. The Pb elements recovered by Carls from Untenrüden are shown in Figure 3.9 – 3.12. The cusp in some of these specimens is noticeably more inclined than in the specimens figured by Ziegler (1960, pl.15, figs. 13-15) and perhaps they belong to a separate taxon, but it is not possible to determine whether the observed variation results from tectonics or genetics. If genetics controls the variation, the most likely relationship is the one between those Pb elements with the more erect cusp and the *remscheidensis* Pa because of the tendency for the denticles in the *remscheidensis* Pa elements to be erect. Note that this kind of Pb is also present in the assemblages from Cellon 40 (Figure 3.29), C 2/7 (Figure 2.42), Co 43 (Figure 3.37), and Lag Vas 6 (Figure 3.43).

Comparison. - The apparatus of Zieglerodina differs from that of *Critieriognathus* Walliser 1972 in the position and shape of the basal platform lobes of the Pa element, in the possession of the undulatory blades in the transition-series elements, and in the Sa element that lacks a posterior process. It differs from *Ozarkodina* Branson & Mehl, 1933 in the more posterior position and shape and, generally, the larger size of the basal platform lobes, the alternation of denticle sizes, undulation of the processes of the transition-series elements, and less deep distribution of white matter in all elements. It differs from Wurmiella in the *denckmanni* vs. *media* style Pb element, the more acute angle between the cusp and posterior process in the M element, and the undulation of the processes, alternation of denticle sizes, and the smaller basal cavities of the Sb and Sc elements.

Zieglerodina remscheidensis (Ziegler, 1960)


*1960 Spathognathodus remscheidensis* n. sp.
Ziegler, p. 194, pl. 13, figs. 1, 2, 4, 5, 7.
.1960 Spathognathodus cf. frankenwaldensis
Bischoff & Sannemann, Ziegler, pl. 13, fig.13.
not 1964 Spathognathodus steinhornensis
Ziegler, Walliser, p. 87, pl. 20, fig. 26 (= cf. paucidentata Murphy & Matti, 1983); pl. 21, figs. 1, 2 (= paucidentata Murphy & Matti, β morph).
not 1975 Ozarkodina remscheidensis (Ziegler),
Carls, p. 411, pl. 2, figs. 16-18.

Holotype.- Specimen figured by Ziegler, 1960, pl. 13, fig. 4a, b, from the Ockrige Kalke, bed e at Untenrüden, Rhenish Slate Mountains, Germany.

Diagnosis. - A Zieglerodina in which mature Pa elements have the following combination of properties: variable denticle size, anterior part of cockscomb with zero to three small to moderate-sized denticles and a second part mainly formed by one very high and wide denticle; four to seven, normally unequal smaller denticles follow; cusp high and wide; posterior blade with about six to seven denticles that vary in size. Lower profile is straight, arched or sigmoidal. Basal platform lobes occupy up to one quarter of the length, begin slightly anterior of midpoint, have no ornament; outline of mature basal platform broadly heart-shaped, tapering rapidly to basal groove posteriorly; basal grooves parallel sided. Blade length 5 to 6 times height.

Description. - Pa element (Figs. 3.1-3-8) with simply vaulted basal platform lobes without terraces or ornament, located mainly in posterior half of element, not constricted where they join blade; outline of basal platform nearly circular in small specimens, wider than long and heart shaped in larger specimens; with narrowly tapering to parallel-sided, open posterior basal groove; lateral profile with prominent anterior cockscomb with denticle arrangement variable but commonly with anterior 0-3 denticles small, followed by a very large and high denticle or pair of denticles; high and wide cusp, with strong size variation in remaining denticles. Pb elements (Figs. 3.9, 3.11) angulate pectiniform with
equally wide anterior denticles increasing in height progressively posteriorly almost to height of wide and high cusp, posterior denticles shorter and more even in height. Transition-series elements (Figs. 3.20-3.24) with denticles alternating in size, but irregularly spaced and staggered, without outer ledge, and with subtle undulation of blade that causes lower profiles to have shape of series of small waves; larger denticles may cause swellings that reach almost to base of inner side of blade and contribute to undulation; denticles of Sb and Sc elements strongly reclined posteriorly, especially cusp and thicker denticles of Sb, curve inwardly; cusp of Sc may have round cross section and attenuated apex, basal view shows processes evenly curved without angle at basal cavity; basal cavity very small, commonly basal grooves appressed or parallel sided; Sa element alate without posterior process, small, with short, high blades and \( \alpha = 65 \) to 80°.

**Discussion.** Of the M elements figured by Ziegler (1960, pl. 15, figs. 8, 9, and 23), those with high blade and no ledge (pl. 15, figs. 9, 23) most closely resemble the other members of the apparatus. This is the common form in Carls’ collection from Untenrüden (Figure 3.14-3.16, 3.19) and is also present at Cellon and in the glacial erratic boulders (Figures 3.38, 3.42).

Sa elements are not common at Untenrüden. However, one of them is distinctive because the cusp is recessed and lies in a channel between the lateral processes (Ziegler, 1960, pl. 15, fig. 1b), but it lacks alternation of denticle sizes of the Sb and Sc elements. The other specimen (Ziegler, 1960, pl. 15, fig. 2) has alternation of denticle sizes, although not well shown in the figure, like the earlier taxa from Cellon 40 (Figures 3.30, 3.31) and those from the erratic boulders (Figures 3.41, 3.45).

The Sb elements figured by Ziegler (1960, pl. 15, figs. 6, 7, 11) represent two forms both of which have alternation of denticles sizes. Two such forms are in Carls’ collection (Figures 3.21-3.23). The Zieglerodina at Cellon (Figure 3.25) also has a similar Sb element.

Ziegler (1960, pl. 15, figs. 3, 4) figured only a single kind of Sc element from Untenrüden and Carls also subsequently recovered only this kind of element (Figure 3.24). As in the other elements assigned to the taxon, it has the high walled processes with alternation of denticle sizes and lacks a ledge. This kind of Sc is also present at Cellon in bed 40, and in the erratic boulders Co 43 (Figure 3.40) and Lag Vas 6 (Figure 3.47).

Bultynck (1971, p. 12, figs. 4-10) distinguished seven Pa element morphotypes obtained also from Untenrüden, bed f, immediately above the type stratum. Mainly his morphotypes gamma, delta, and epsilon correspond to the holotype and paratypes. Bultynck's short and stout morphotype, \( \epsilon' \) (1971, fig. 9), also occurs in the unit d1ey of the Luesma Formation in Celtiberia (Carls and Gandl, 1969, pl. 19, fig. 2) together with and just above *Ancyrodelloides carlisi*. As this Celtiberian material is comparatively young and is not accompanied by the morphotypes close to the holotype, the morphotype \( \epsilon' \) might be considered as a separate taxon that survived the stock around the holotype of *Z. remscheidensis*.

Beginning with the description of 'Spathognathodus steinhornensis eosteinhornensis' Walliser, 1964 (Figs. 2.45-2.47; Figs. 3.33-3.35), the taxon *remscheidensis* has generally been thought to have a Pa element with comparatively wide variation of denticle sizes, whereas a rather even denticulation was thought to characterize the supposedly congeneric or even conspecific taxon *eosteinhornensis*. Therefore, the mere presence of uneven denticulation has usually induced the identification of 'remscheidensis'. Most of these taxa are considered by us to be outside the limits of *Z. remscheidensis*. Our revision restricts the identifications of *Z. remscheidensis* to mainly European occurrences of early Lochkovian age morphologically close to the Untenrüden material.

Many early writers classified Zieglerodina *remscheidensis* as a subspecies of *Criteriognathus steinhornensis* (Ziegler, 1956). The type locality of *steinhornensis* yields Sa elements with denticulate posterior processes (= diplododellan) as constituents of the corresponding apparatus. Thus, *Criteriognathus* would become a junior synonym of *Pandorinellina* if the character of the Sa element were a decisive unifying criterion. However, as discussed above on p. 7, the possession of diplododellan Sa elements by several otherwise unrelated Silurian and Devonian taxa suggests that diplododellan Sa elements are a common parallel development in a number of lineages.
ADDITIONAL SPATHOGNATHODONTID GENERA

Other genera with different kinds of Pa elements are clearly present in the latter half of the Silurian. Examples are: all of the different morphs of ‘Ozarkodina’ eosteinhornensis (Walliser), ‘Ozarkodina’ snajdri (Walliser), ‘Ozarkodina’ crispa (Walliser), and ‘Ozarkodina’ douroensis Uyeno. Only the first of these is of interest here (New Genus W, below) because it represents a plexus of forms constituting what we interpret as one of the main clades crossing the Silurian-Devonian boundary. We use open nomenclature to incorporate these forms because we wish to direct attention to them, but currently we do not have the documentation needed for a generic characterization.

New Genus W

Characteristic species. - Spathognathodus eosteinhornensis Walliser 1964.

Alternating denticle sizes appear in the pelagic facies of the Cellon section at bed 39A, one sample below the appearance of New Genus W eosteinhornensis (Walliser, 1964). However, the alternation of denticle sizes begins much earlier in the shallow-water facies of the Baltic region. On Gotland, it is reported first from member b of the Hamra Formation (Jeppsson et al., 1994, fig. 4 h). In samples from erratic boulders of Carls’ collection at Braunschweig, it occurs in almost all samples that contain Delotaxis elegans elegans. In North America, at least one specimen of Branson & Mehl’s material from the siluricus Zone at Lithium (Rexroad & Craig, 1971, pl.79, fig. 22) has alternation of denticle sizes. Thus, apparatuses that show alternation of denticle sizes in the transition-series elements are present from well down in the Ludlow onward. This suggests that we should look for the origin of Zieglerodina and New Genus W in the Ludlow. The two spathognathodontid genera that have been described from the Ludlow and that could serve as ancestors are Ozarkodina and Wurmiella.

An origin in Ozarkodina has the difficulty that the Ozarkodina apparatus is already specialized as early as Llandovery. The other potential ancestor, Wurmiella, also has documented occurrences in the Llandovery (Bischoff, 1987). Still, there are no obvious linkages among these taxa at present.

Hypothesized apparatus for new genus W. - In order to determine the elements of the New Genus W apparatus we started with bed 40 of the Cellon section in the Carnic Alps, Austria, type bed for eosteinhornensis. We first eliminated the elements of Wurmiella. After that, along with their Pa elements, we subtracted the Sb and Sc elements that most resemble those associated with the holotype of Zieglerodina remschiedensis, that is, those without ledges, with irregular and staggered denticulation, and undulating blades. There remained slender and elongate Sb and Sc elements with an alternation of denticles sizes that have low blades with nearly straight lower profiles (vs. wave like), with a ledge at the base of the denticle row on the inner sides, and a small but distinct basal cavity. These appear to characterize New Genus W because, among the relevant Sb and Sc elements in the Cellon material, they differ most from the Untenrüden material of Z. remschiedensis and may be attributed to the accompanying Pa element of eosteinhornensis. The presence of ledges and regular alternation of denticle size, and absence of undulation in the Sc and Sb elements are the main criteria derived from the transition series elements for the separation of the two genera.

It is not clear from the material available if the transition series elements have more than one pair of Sb and Sc elements. No diplododellan Sa element has been found in the type stratum of W eosteinhornensis, thus, one of the trichonodellan Sa elements present there probably belongs to its apparatus.

Comparison. - New genus W differs from Criteriognathus in the shape of the basal platform lobes of the Pa element and the Sa element lacks a posterior process; from Ozarkodina Branson & Mehl, 1933 it differs in the more posterior position, subquadrate shape, and generally larger size of the basal platform lobes, the shallower distribution of white matter, and the alternation of denticles in the Sb and Sc elements; from Wurmiella it differs in the alternation of denticles in the Sb and Sc elements, the larger more quadrate shape and more posterior position of the Pa basal platform lobes, the angulate relation of the posterior process to the cusp of the M element, and the much higher cusp in the Pb element of Wurmiella; from Zieglerodina n. gen. in having a large, subquadrate, posterior, commonly ornamented basal platform and transition-series elements with a ledge at the base of the denticles but no undulation of the posterior blades.

‘Ozarkodina’ planilingua Murphy & Valenzuela-Rios was interpreted as an early member
of the clade and the branch that later led to *Lanea* and *Ancyrodelloides* (Murphy & Valenzuela-Ríos, 1999), but the only documentation of the relationship is the stratigraphic position of *O.‘ planilingua* in the Upper Silurian and Lower Devonian.

**Genus W eosteinhornensis** (Walliser)
Figures 2.45-2.47; 3.26-3.28; 3.33-3.35

*1964. Spathognathodus steinhornensis
eosteinhornensis n. ssp. Walliser, p. 85, pl. 20, figs. 19, 20, 21 (upper specimen = holotype), 22, only; not 21 (lower specimen).

.1980. Ozarkodina steinhornensis
eosteinhornensis Walliser, Schönlaub, pl. 3, figs. 10, 12, 13 15. only.

*Holotype.* Specimen figured in Walliser, 1964, pl. 20, fig. 21 (upper specimen), Cellon section, bed 40, near Plöcken Pass, Carnic Alps, Austria.

*Original diagnosis.* (Translated from German) “A subspecies that is almost homeomorphic with the typical *S. steinhornensis* Ziegler, whose basal cavity mostly is less distinctly heart-shaped than in the typical subspecies.”

*Original description.* (Translated from German) “The holotype shows an almost even development of the denticles. The expanded basal cavity lies behind the midpoint and is asymmetric. In its anterior part, its edge joins the blade at a high angle while it joins it in a gentler curve posteriorly, so that the basal cavity when seen from above seems broadly heart-shaped with its tip pointing posteriorly. From the middle of one side of the basal platform, a ridge runs up to the blade; the ridge is slightly notched above so that a sort of denticle is formed. Within the range of variation are forms that have almost completely equal denticles up to such that resemble *S. steinhornensis* remscheidensis in this respect. The basal cavity can be relatively small to extremely expanded, with or without the presence of a denticle, is typically heart-shaped to nearly right angled and its maximum width lies somewhere between the midpoint and the posterior one third of the blade of the conodont. All these characteristics may be combined interchangeably. A dependence of one from the others is not established.”

*Revised diagnosis.* A species whose Pa element has a large basal platform that lies in the posterior half of the element, a wedge-shaped posterior groove that is open to the posterior tip of the element and generally one or both platform lobes ornamented by a ridge or denticle. Fusion and blunting of the denticles in the region of the cusp are common.

**Discussion.* The taxon *eosteinhornensis* is restricted here mostly to forms of the kind found in bed 40 at Cellon, type locality for the taxon. Pa elements from the type bed in both the Göttingen and Braunschweig collections of Walliser and Carls, respectively, all have wedge-shaped posterior grooves, a deep, parallel-sided anterior basal groove and at least one of the basal platform lobes with a sub-rectangular outline that is constricted where it joins the blade. They vary in the character of the denticles in the cusp region and the number and presence or absence of a cusp and platform denticles or ridges, and with the presence or absence of a small anterior cockscomb. The denticles around the position of the cusp in larger specimens are commonly fused or blunted so that their tips are chisel-shaped. This phenomenon can involve one or many of the denticles, can extend over most of the length of the element, and can occur in specimens with or without platform denticles (Figures 2.45-2.47, 3.33, 3.34).

We put the forms with platform sculpture or denticle fusion in *eosteinhornensis* s. s. (Figure 1). These are further subdivided into three morphs as follows:

\[ \tau \] (for type) – without fusion of the denticles and with 1 or two platform denticles or ridges (Walliser, 1964, pl. 20, figs. 20, 21 upper; Figure 3.35);

\[ \alpha \] – with denticle fusion and platform ridge or denticles (Walliser, 1964, pl. 20. figs. 19, 22; Figures 2.45-2.47, 3.33-3.34).

\[ \beta \] – with denticle fusion, without ornamentation of the basal platform lobe (not shown).

The *eosteinhornensis* apparatus was first discussed by Walliser (1964, p. 14) in open nomenclature as Apparatus J. Klapper (1973, p. 243) subsequently substituted *Plectospathodus alternatus* (Walliser, 1964) for *P. flexuosus* in the Sb position. We agree that the specimens figured by Walliser (1964, pl. 30, figs. 15, 16) are not part of the *eosteinhornensis* apparatus (probably belong to *Ozarkodina typica*), but suggest that Walliser’s
(1964) pl. 30, figures 18, 20, and 22 are the appropriate interpretation of the identity of the Sb element.

Stratigraphic position.- Walliser (1964, T. 2) gave an extended range for the taxon, essentially encompassing the entire Pridoli of the present classification. At Cellon, bed 33 (Walliser's non figured collection) yielded a specimen with a large basal platform lobe and a small platform ridge connecting to an enlarged cusp. We include it in *eosteinhornensis* s.s., but not in one of the morphs because the posterior end is broken. We have also found it in bed 13 at U topolů, which is Early Devonian in age.

CONCLUSIONS

Our study of Barrandian, German, Iberian, Baltic erratic boulder, and Nevadan faunas has led us to conclude that the Pridoli-Lower Lochkovian sequences of the world have rich, undescribed faunas of mainly regional distribution, but that contain a few taxa of more cosmopolitan distribution that will enable correlation. These faunas also contain many unusual, even bizarre, Pa elements for which the apparatuses are not clear or for which we know of no potential apparatus elements. Most of them remain unclassified. This paper initiates the required analysis by segregating two of the obvious groups of taxa in the new genera *Wurmiella* and *Zieglerodina* and by restricting *Ozarkodina* to the forms closely allied with *O. typica*.

‘*Ozarkodina’ eosteinhornensis* (Walliser, 1964) should also be segregated from *Ozarkodina* in a separate genus, but the documentation of the apparatus is currently too weak to distinguish it from the large number of other undescribed taxa that we have recovered from our study areas.

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FIGURE 2 (All elements X 32)

1-7. **Ozarkodina typica** Branson & Mehl
   Bainbridge Limestone, Lithium, Missouri, Gilbert Klapper Locality 29-39 cm above shale bed from which Branson & Mehl obtained syntypes of the taxon, not coated so as to show the distribution of white matter.
   1, 2. Pa element, lateral views. SUI 98529, 98530.
   3. Sc element lateral view, note direction of the anterior process down and oblique to posterior process. SUI 98531.
   4. M element showing sharp bend of the basal profile between cusp and posterior process. SUI 98532.
   5. Sa element. SUI 98533.

8-15. **Ozarkodina typica** Branson & Mehl
   Bainbridge Limestone, Lithium, Missouri, syntypes of **Ozarkodina typica** Branson & Mehl, 1933. All are Pb elements, University of Missouri Type Collection unnumbered specimens.
   8. Syntype shows anterior process.
   9, 10, 11. Lectotype, broken across the cusp and between cusp and anterior process so that α appears larger than in unbroken specimens.
   12, 13. Syntype, lateral and oblique basal views, showing true size of α, distribution of white matter and shape of the basal cavity.
   14. Syntype, showing distribution of white matter and strongly inclined cusp.
   15. Syntype, showing more erect cusp, true size of α, and distribution of white matter.

16-28. **Wurmiella tuma** (Murphy & Matti)
   Windmill Limestone, Coal Canyon (SP VII section), northern Simpson Park Range, and Bastille Limestone, Mill Canyon (MC section), Toquima Range, Nevada.
   16-19. Pa element. top view UCR 8776/6 (SP VII 13J), basal, and lateral views UCR 8536/8 (MC 6), lateral view. UCR 8536/1 (MC 6).
   20. Pb element lateral view. UCR 8776/viii-49 (SP VII 13J)
   21, 22. M element, lateral and oblique basal views. UCR 8776 (SP VII 13J)
   23, 24. Sb element, lateral and oblique basal views. UCR 8776/vii-27 (SP VII 13J)
   25, 26. Sc element inner lateral and outer lateral views. UCR 8776/vii-37 (SP VII 13J)
   27, 28. Sa element posterior and basal views. UCR 8776/vii-38 (SP VII 13J)

29-36. **Wurmiella excavata** (Branson & Mehl)
   Bainbridge Limestone, Lithium, Missouri. Gilbert Klapper locality 29-39 cm above the shale bed from which Branson & Mehl obtained the syntypes.
   32-36. Not coated to show the distribution of the white matter.
   29. Sb element. SUI 98536.
   30, 31, and 33. Pa elements, lateral views. SUI 98537, 98538, 98539.
   32. Pb element. SUI 98540.
   34. Sc element. SUI 98541.
   35, 36. Sa element, anterior and posterior views. SUI 98542.

37-44. **Zieglerodina** sp. (= **Hindeodella steinhornensis** n. ssp. 2 Jeppsson, 1975)
   Silurian glacial erratic from north German plain, C2/7, Forschungsinstitut Senckenberg, Frankfurt am Main.
   37-40. All elements uncoated to show distribution of white matter.
   37, 38. Pa elements, lateral and top views, SMF 69952. Note macrodevelopment of the second denticle in the fan and high distribution of the white matter.
   39, 40. Pa elements, SMF 69953, 69954.
   41. M element, SMF 69955. Note white matter hardly penetrates the blade.
   42. Pb element, 69956, lateral view, with irregular sizes of posterior denticles.
   43, 44. Sb elements, 69957, 69958, with irregular denticulation and larger denticles causing minor undulation of the blade.

45-47. New Genus **W** oesteinhornensis (Walliser)
   U topolů section, Radotín Valley, SW Prague, Czech Republic, bed 13. Pa element, lateral, basal, and top views for comparison with **Ozarkodina** and **Zieglerodina** Pa elements. Depository Czech Republic National Museum.
1–24. Rhenish Slate Mountains, Germany, Section at Untenrüden, bed f. Senckenberg Forschungsinstitut (SMF 69905-69929).
   1. *Zieglerodina remscheidensis* (Ziegler) Pa element, lateral view.
   2. *Zieglerodina remscheidensis* (Ziegler) Pa element, lateral and slightly oblique basal views.
   9, 11. *Zieglerodina remscheidensis* (Ziegler) Pb elements, lateral views.
   10, 12. Undetermined Pb elements.
   17. *Wurmiella* ?
   18. Undetermined Sa element.
   20. *Zieglerodina remscheidensis* (Ziegler) Sa element, posterior and anterior views.

25–35. Section at Cellon, bed 40 Carnic Alps, Austria. Forschungsinstitut Senckenberg, Frankfurt am Main (SMF 69930-69939).
   25. *Zieglerodina* sp. Sb element, outer lateral and basal views.
   29. *Zieglerodina* sp. Pb element.
   30. *Zieglerodina* sp. Sa element, anterior and posterior views.
   31. *Zieglerodina* sp. Sa element.
   32. *Zieglerodina* sp. Sc element.

36–47. Specimens from glacial erratic boulders from northern Germany.
   42–47. *Zieglerodina* sp. Apparatus from Lag Vas 6, glacial erratic boulder. Forschungsinstitut Senckenberg, Frankfurt am Main (SMF 69946-69951).