Lochkovian conodonts from Podolia, Ukraine, and their stratigraphic significance

DANIEL DRYGANT and HUBERT SZANIAWSKI


In the Podolian Dniester Basin (southwestern Ukraine) the Lower Devonian marine deposits are represented by about 530 m thick continuous sequence of interlaminated carbonate and schale outcrops at several localities. Conodonts occur in most of the carbonate layers of the whole Lochkovian but are not abundant and their ramiform elements are mostly broken or lacking. Therefore, only the pectiniform, Pa elements of twenty five stratigraphically important conodont species occurring in the region are discussed and two new species, Caudicriodus schoenlaubi and Pandorinellina? parva are proposed. The hypothetical phylectic relationships within the main representatives of the icriodontid and spathognathodontid genera, Caudicriodus, Zieglerodina, and Pandorinellina? are traced. Comparison of the previously published and newly obtained data revealed discrepancies in the hitherto used interpretation of some of the conodont taxa and their stratigraphic ranges. Contrary to the earlier reports, Caudicriodus postwoschmidti does not occur in the lower Lochkovian but only in the middle part of the Chortkiv Formation, high above the Monograptus uniformis Zone. Based on new material and verification of the previous determinations, a modified scheme of the Lochkovian conodont zonation in Podolia is proposed. Conodont zones: Caudicriodus hesperius, C. transiens, C. postwoschmidti, C. serus, and ?Caudicriodus steinachensis are distinguished. The zones are correlated with conodont zonations in other regions—Barrandian, Cantabrian Mountains, Pyrenees, and Nevada. Biostratigraphy of the Siluro–Devonian transition and Lochkovian is integrated with the carbon isotope stratigraphy.

Key words: Conodonta, evolution, stratigraphy, Devonian, Lochkovian, Podolia, Ukraine.

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Introduction

One of the most complete Silurian–Lower Devonian sections in the world is exposed in the Dniester Basin of Ukraine. This essentially undeformed and continuous sedimentary sequence is situated on the southwestern margin of the East European Platform (Fig. 1). The Lower Devonian succession is interpreted to be a regressive unit composed of flysch-like shales with limestone interbeds. In the upper part of the succession, the open marine sediments pass gradually and diachronically into the terrigenous Old Red facies. The strata are well exposed in many localities, mainly along the high and steep slopes of the Dniester and its tributaries. Podolian sections are rich in fossils, which have been intensively investigated since the 19th century (see Szajnocha 1889; Kozlowski 1929; Nikiforova and Priedtiechensky 1968; Nikiforova et al. 1972). Papers devoted to the Early Devonian conodonts from Podolia were hitherto published by Mashkova (1968a, b, 1970, 1971, 1972, 1979) and Drygant (1971, 1974, 1984, 2010).

After the appointment of the Global Stratotype Section for the Silurian–Devonian boundary at Klonk in Czech Republic, most investigators became interested in detailed stratigraphy of the stratotype section and its correlation with sections of similar age in other regions: Cantabrian Mts, Carnic Alps, Sardinia, as well as Nevada, Texas, and Alaska (Carls 1969; Carls und Gandl 1969; Klapper and Murphy 1975; Schönlaub 1980a, b; Barrick et al. 2005). As a result, the Podolia region became virtually forgotten. Considering the insufficient documentation of some stratiographically significant conodont species described from Podolia, and insufficient knowledge of their distribution in sections, the whole Lochkovian sequence and the transitional Silurian/Devonian section were re-investigated in order to verify the conodont ranges and to improve the interregional correlations. Some of
sensitivity to facial fluctuations greatly complicate stratigraphic different facies. Their provincialism in distribution and sen−
on the great differentiation of the conodont assemblages in also confirm and better document some earlier observations their evolutionary development and stratigraphic ranges. We recognition of the conodont species occurring in the region, tensive field investigations of both authors of the present pa−
108; however, the latter paper was devoted not only to the Lochovian but also to the Middle and Upper Devonian, which in Western Ukraine is known from numerous borehole cores. The paper was based on the collections of conodonts gathered by its author before 2006, while the present study is based on new collection obtained later as a result of the ex−
tensive field investigations of both authors of the present pa−
Correlations. To solve the stratigraphic problems a collective project of comprehensive paleontological and geochemical investigations of the Siluro-Devonian transition beds and Lower Devonian sections has been conducted in last years. This paper is one of the series of publications presenting re−
sults of the project (see Malkowski et al. 2009; Babiński 2010, 2012; Olempska et al. 2011; Filipiak at al. 2012; Olempska 2012; Racki et al. 2012; Voichyshyn and Sza−

Institutional abbreviations.—SMNH, State Museum of Nat−
rnal History, National Academy of Sciences of Ukraine, Lviv, Ukraine; ZPAL, Institute of Paleobiology, Polish Aca−
demy of Sciences, Warszawa, Poland. The specimen and simple notations provided in Fig. 8 and 10–13 are explained as folows: Ivanye Zolote-52/515 m ZPAL C.207/28: Ivanye Zolote-52, name and number of the outcrop (see Fig. 1); /515 m, position of sample (in meters) above the S–D boundary (see Fig. 3); ZPAL C.20, number of the collection in ZPAL; 7, number of the SEM stub; 28, number of specimen on the stub; Dnistrove-105/1 SMNH D1123b: Dnistrove-105, name and number of the outcrop (see Fig. 1); /1, number of sample (see Fig. 3); SMNH D1123b, collection number in SMNH.

**Geological and stratigraphic setting**

**Stratigraphy and deposition**

The Lower Devonian succession in Podolia represents two different lithological and stratigraphic units: the open-marine, shallow water, calcareous–argillaceous Tyver Group and the red colored, terrigenous Dniester Member of the Old Red Formation (Fig. 2). The lower sequence, up to 530 m in

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Fig. 2. General stratigraphy of the Lower Devonian strata in Podolia (modified after Drygant 2010). Traditional, local division terms are used. Abbreviations: Fm., Formation; Mb., Member.
thickness, is highly fossiliferous and represents an uninterrupted continuation of the Silurian deposition cycle. The Dniester Member is about 1200 m thick but contains mainly the agnathan fish remains (see Nikiforova et al. 1972; Voi-

chysyn 2011).

Both the series form a continuous Siluro-Lower Devonian unit which forms an independent structural complex on the southwestern margin of the East European Platform (Fig. 1). It is separated from the Ordovician and Middle Devonian deposits by regional stratigraphic gaps. The lithological lower boundary of the Tyver Group, corresponding approximately to the biostratigraphic S-D boundary, is placed 3.2 m above the top of the Dzvenyhorod Formation (upper part of Skala Group, Pridolian in age) which in the upper part is composed of lumpy clayey limestone and marl beds with numerous brachiopods, ostracods, bivalves, trilobites, crinoids, and corals. Of the conodonts, the limestone contains numerous “Ozarkodina” eosteinhornensis (Walliser, 1964) and Delotaxis detorta (Walliser, 1964). Both of the species are characteristic for the upper part of the Dzvenyhorod Formation and do not occur in higher levels (Fig. 3). The Pridoli–Lochkovian boundary has been established 3.2 m above the lithological boundary of the Skala Group, in the middle part of the inter-

bedding layers of shale and limestone, where Monograptus uniformis angustidens Prībyl, 1940, Acastella heberti (Gos-

selet, 1888), Clorinda pseudolinguifera Kozłowski, 1929, Globoseptaena emarginata (Barrande, 1879), and Zieglerodina remscheidensis (Ziegler, 1960) occur (Nikiforova et al. 1972; Nikiforova 1977).

However, it should be mentioned that Monograptus uniformis angustidens is known in Podolia exclusively from this level, while Pristograptus transgrediens (Perner, 1899), which in other regions is characteristic for the uppermost graptolite zone of the Silurian, is not known in Podolia at all.

The Tyver Group (Superhorizon) for a long time has been subdivided into lithological and stratigraphical units: the Borschchiv, Chortkiv, and Ivanye horizons and Khudykivtsi, Mytkiv, Chortkiv, and Ivanye formations (Fig. 2) (see Nik-

tiforova et al. 1972).

**Borschchiv Horizon.**—In the lithological subdivision the unit is divided into two parts: Khudykivtsi and Mytkiv formations.

The Khudykivtsi Formation is exposed in the Dniester escarpments from the village Dnistrov in the east to the Nich-

lava estuary in the west (Fig. 1). It is developed in the form of the flysch-like interbedding of shallow-water, detrital, partly clayey limestone and dark grey shale. Their total thickness is about 57 m. Most of the layers are rich in fossils. The most important for stratigraphy are graptolites (Monograptus uniformis angustidens Prībyl, 1940), trilobites (Warburgella rugulosa Alth, 1874, Acasterella heberti elsaana R. and E. Richter, 1954, A. tiro R. and E. Richter, 1954), brachiopods (Resserella elegan
tuloides Kozłowski, 1929, Clorinda pseudolinguifera Kozłowski, 1929, Globoseptaena emarginata [Havlíček, 1967], Cyrtina praeecedens Kozłowski, 1929), and conodonts (Zieglerodina remscheidensis [Ziegler, 1960], Caudicriodus woschmidtii [Ziegler, 1960], C. hes

perius [Klapper and Murphy, 1975], Delotaxis cristagalli [Ziegler, 1960]). In the north–eastern part of Podolia, near Terebovlya and on the banks of the river Tayna, the Khu-

dykivtsi strata are gradually replaced by the Tseliyiv lumpy limestone (Drygant 1984, 2000).

The Mytkiv Formation, about 136 m in thickness, crop out on the Dniester escarpments between the villages Khudykivtsi and Zozulyntsi and along the river Nichlava. The strata are composed mainly of dark grey shale with thin interbeds and lenses of gray clayey limestone, partially detrital. Frequent ag-

glomerations of the brachiopod shells form thin coquina layers and lenses. Most of the limestone beds are fossiliferous and contain numerous assemblages of brachiopods (Lanceomyo-
nia borealiformis [Siemiradzki, 1906], Plectodonta maria Kozłowski, 1929, Cyrtrina praecedens Kozłowski, 1929), trilobites (Warburgella rugulosa Alth, 1874, Homalonotus roemeri Comte, 1959), ostracods (Opi
toplaspyx gyratus Abu-
shik, 1968, Ochescapha podolica [Abushik, 1968]), cono-
donts (Zieglerodina remscheidensis [Ziegler, 1960], Caudi-
criodus transiens [Cars and Gandl, 1969], Caudicriodus had-
nagyi [Chatterton and Perry, 1977]), brinoids, bryozoans, and others (see Nikiforova et al. 1972; Drygant 1984).

**Chortkiv Horizon and Formation.**—Lower boundary of the unit has been established after the diachronic appearance of the organogenous-detrital limestone layer in the midst of the mudstone rocks. In the outcrops located along the Dnie-

ster and its tributary Seret, in the vicinity of the villages Kolodribka, Syn’kiv, Vynohradiv, Horodok, and Chortkiv the formation is composed of dark grey claystone inter-

bedded with thin (1–10, rarely 20 cm) layers of the fine grained, detrital limestone. Abundance of the limestone layers increase toward the top. Total thickness of the Formation is about 205 m. Assemblages of fossils in the limestone layers are taxonomically diverse but not much different from those in the underlying beds. However, except for most com-

monly occurring brachiopods (Mutationella podolica Kozłowski, 1929, Howeella zaleszczyniensis Kozłowski, 1929), ostracods (Cornikloedenia inornata [Alth, 1874], C. binata Abushik, 1971, Evlanella rubeli Krandijevsky, 1963), cono-
donts (Caudicriodus postwoschmidtii [Maskhova, 1968], Zieglerodina mashkovae [Drygant, 1984]), also remnants of the agnathan fishes (Theolodus oervigi Talima, 1966 and Podolaspis lerichei [Zych, 1927]) are abundant (see Nik-

iforova et al. 1972; Drygant 1984).

**Ivanye Horizon and Formation.**—Deposits of the unit crop out along the escarpments of the Dniester (in the vicinity of Dobrivlyany, Zalishchyky, Ivanye Zolote, and Ustechko). They represent the latest Lower Devonian, open marine sedi-
ments in Podolia. Total thickness of the Formation is about 130 m. Its lower boundary is established at the first appear-
ance of the cherry-red claystone packet. The lower part, about 60 m thick, comprises claystone and marlstone beds, rhythmically interbedded with thin layers and lenses of the

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detrital or bioclastic (mainly ostracod) limestone. In the upper part, named Zalishchyk Beds, about 70 m in thickness, the quantity of argillaceous material gradually increases, and in its uppermost part quite thick layers of the mudstone occur. Fossils in the Ivanye strata are still abundant but their diversity gradually decreases. In its uppermost part only a few of the endemic species of brachiopods and ostracods occur, mainly *Mutationella podolica* Kozlowski, 1929 and *Leper-

Fig. 3. Stratigraphic range of conodonts in the Lochkovian sequence of Podolia. A. Lower part. B. Upper part (see next page). D., Devonian; S., Silurian.
ditia tyraica Schmidt, 1873. Tentaculites are still relatively abundant. Rarely occur also gigantostracans of the genus Pterygotus (Nikiforova et al. 1972), agnathans (Zascinaspis heinitzi [Brotzen, 1933], Irregulareaspis stensioi Zych, 1927) and acanthodians (Voichyshyn 2001, 2011; Voichyshyn and Szaniawski 2012). Conodonts are rare and abundant in some layers only. They are represented mainly by Zieglerodina serrula (Drygant, 1984) and Pandorinellina? parva sp. nov.

The area of outcrop of the Ivanye Formation is much smaller than that of the Chortkiv because of the gradual shrinking of the marine basin. Also the area is shifted westwards, to the Teisseyre–Tornquist Zone (or Trans-European Suture Zone) (Fig. 1). The upper boundary of the Ivanye Formation is diachronic and corresponds to the bottom of the Podolian old facies (= Terebovlya Formation) which begins from the sandstone and mudstone that are typical for the Ustechko Beds of the Dniester Member (Fig. 2).

The age of the uppermost part of the Ivanye Formation is not determined as yet. Nikiforova and Priedtiechiensky (1968: 35), based on the fish remains, proposed to correlate those deposits with the upper Gedinian (= upper Lochkovian–Pragian). Later Nikiforova et al. (1972: 125), based on the results of the conodont studies of Mashkova (1968b, 1970) correlated the Ivanye strata with Luesma Beds in the Iberian Mts, Spain and assigned it to the upper part of the lower Gedinian
However, the conodonts described by Mashkova (1968b) were obtained not from the Ivanye but from the Chortkiv strata. As a result of the present investigations the conodont species characteristic for the Pragian, Caudicriodus? steinachensis (Al Rawi, 1977), has been found in the Ivanye Formation, what suggests that marine sedimen-

Fig. 4. Carbon isotope ($\delta^{13}$C) trends in the Lochkovian sections of Barrandian (Požáry Quarry), Cantabrian Mountains and Podolia. Subdivision of the Lochkovian after Slavík et al. (in press). Isotope curves, from Barrandian and Cantabrian Mountain after Buggisch and Mann (2004), from Podolia after Malkowski et al. (2009). On the right—electric resistance of isochronic rocks in the nearest deep borings in Podolia (for location see Fig. 1), after Drygant (2000).

Abbreviations: C., Caudicriodus; I., Icriodus; O., Ozarkodina; D, Devonian; S, Silurian; Fm., Formation; Mb., Member. For legend see Fig. 3.
tation in Podolia continued until the late Lochkovian and possibly even until the earliest Pragian.

The stratigraphy of the Dniester Member is not well understood because of its monotonous deposits and scarcity of stratigraphically important fossils.

For some years results of the geochemical investigations have been very helpful in establishing stratigraphic correlations. Especially useful are studies of the carbon and oxygen stable isotopes ($\delta^{13}C$ and $\delta^{18}O$) content changes in rocks and calcium carbonate shells. Such investigations made in the Lower Devonian sections of different regions strongly indicate the global geological coeval events and perturbations which correspond to the stratigraphic divisions (Buggisch and Mann 2004). Results of such investigations of the Lower Devonian sections in Podolia (Malkowski et al. 2009) help greatly in their detailed correlation with corresponding sections in the Barrandian and Cantabrian Mountains (Fig. 4). Moreover, the isotopic composite curves of the Podolian sections are very similar to the curves showing changes of the electric resistance (self-potential logging) of rocks of the same age in borings situated also in Podolia but further to the north (for example boring Darakhiv-1) and on the south-west margin of the East European Platform (for example boring Zahaypil'-1) (Figs. 1, 4).

Discussion on the conodont distribution and zonations

Insufficient knowledge of the relationship between the Lochkovian conodont taxa, and their irregular distribution in coeval sediments of different regions has caused different interpretations of stratigraphic ranges of the species and, as a result, incorrect interregional correlations. Based on new material, we propose an emended conodont zonation for Podolia and its correlation with other regions.

The *Caudicriodus woschmidti* (or *C. hesperius*) Conodont Zone has been recognized as the lowermost unit of the Devonian, and its base as the Pridoli/Lochkovian boundary. On the same level (or close to the lower boundary of Devonian) in different sections the conodonts “*Ozarkodina* eosteinhornensis” (Walliser, 1964), *Ozarkodina typica* Branson and Mehl, 1933, and *Delotaxis detorta* (Walliser, 1964) disappear (Walliser 1964; Drygant 1971; Barrick et al. 2005; Slavík et al. in press). In the stratotype section at Klonk the electric resistance (self-potential logging) of rocks of the same age in borings situated also in Podolia but further to the north (for example boring Darakhiv-1) and on the south-west margin of the East European Platform (for example boring Zahaypil'-1) (Figs. 1, 4).

Except previous information about occurrence of *Icriodus woschmidti* Ziegler, 1960 and *Spathognathodus remscheidensis* Ziegler, 1960 in Khudykivtsi Formation (Drygant 1967, 1968a, b; Mashkova 1968a), Mashkova (1968b) described two new icriodontid species from the Lower Devonian of Podolia (*Icriodus eolatericrescens* and *I. woschmidti postwoschmidti*). She established also a new *Icriodus eolatericrescens* Conodont Zone, above the zone she named “*Icriodus woschmidti* s. s.” To the former she assigned the Khudykivtsi and Mytkiv formations, and the lowermost part (about 20 m) of the Chortkiv Formation (together 205 m). To the latter zone she assigned the middle part of the Chortkiv strata (about 120 m). After additional investigations (Mashkova 1970) the boundary between the zones was moved down and correlated with the first appearance of *I. woschmidti postwoschmidti* Mashkova, 1968, *I. eolatericrescens* Mashkova, 1968, and *I. angustoides bidentatus* Carls and Gandl, 1969 in the upper part of the Mytkiv strata (130 m above the base of the Lower Devonian). As a result, the *Icriodus eolatericrescens* Zone became thicker, and coincides with the disappearance of *I. woschmidti* and the appearance of *I. w. postwoschmidti*. In about the same time Carls (1969), based on the distribution of *I. transiens* Carls and Gandl, 1969 in Chortkiv Formation of Podolia and in the Luesma Beds of Iberian Mountains (Spain), correlated the *I. eolatericrescens* Zone with the uppermost part of Lower Gedinnian. Later on, Mashkova (1979) changed her own interpretations. She came to the conclusion that the *I. woschmidti* Zone represents only the lower part (20 m) of Khudykivtsi (former Tayna) Formation while *I. w. postwoschmidti* Zone (upper Khudykivtsi and Mytkiv strata, about 110 m). Both of the zones were correlated by her with the stratigraphic interval of *Monograptus uniformis uniformis* Graftolite Zone. However, in the zone the *Caudicriodus hesperius* and *C. transiens* are present but not the *C. postwoschmidti* (see Fig. 3). In such a zonation the upper Mytkiv strata (about 60 m) and whole Chortkiv and Ivanye formations (together 400 m) were assigned to the *I. eolatericrescens* Zone. As a result, the previous *I. postwoschmidti* Zone became substituted by a new “*I. postwoschmidti* Zone” established in distinctly different biostratigraphical interval of the Lochkovian deposits.

More extensive investigations of the Devonian conodonts in the Podolian section have shown that the species identified as *Icriodus eolatericrescens* Mashkova, 1968 and *I. angustoides bidentatus* Carls and Gandl, 1969 (Mashkova 1968b, 1970) represent in fact juvenile specimens of *I. woschmidti transiens* Carls and Gandl, 1969, *I. w. postwoschmidti* Mashkova, 1968 and *I. serus* Drygant, 1984 and do not have significant value for detailed correlations (Drygant 1984, 1994). It has been also shown that *I. woschmidti* sensu stricto occurs rarely in most of the Lower Devonian sections (see Carls 1969; Barrick et al. 2005; Carls et al. 2007; Corradini and Corriga 2012; Slavík et al. in press). As a consequence, identification of the *I. woschmidti* Zone without other characteristic conodonts is hardly possible. Besides, the fact that the holotype of *I. w. postwoschmidti* (Mashkova, 1968) is incompletely preserved (its spur is broken off) caused different inter-
pretations of its intraspecific variability and stratigraphic distribution. Klapper and Murphy (1975) based on the material from the lower Lochkovian of Nevada stated that some representatives of Icriodus, related to I. woschmidti Ziegler, 1960 significantly differ from it in morphology and described them as new subspecies I. w. hesperius Klapper and Murphy, 1975. Because of the lack of icriodontids in the higher part of the section the next conodont zone (corresponding to the upper part of the graptolite Monograptus uniformis Zone) in Nevada has been established according to the range of Ozarkodina eurekaensis Klapper and Murphy, 1975. The Ozarkodina eurekaensis Zone has been considered later as equivalent of Icriodus postwoschmidti Zone (Klapper and Ziegler 1979; Barrick and Klapper 1992) which, however, has in Podolia much higher stratigraphic position, above Icriodus eolatericrescens Zone sensu Mashkova 1970 (but not sensu Mashkova 1979). Because some of the publications of Mashkova (1968b, 1970, 1971) did not contain information that I. w. postwoschmidti has been found only in the upper part of the Icriodus eolatericrescens Zone its range has been correlated, in other regions, with the upper part of the lower Lochkovian only (Barrick et al. 2005). Bultynck (1976) has been con-

Fig. 5. A. Probable phyletic relationships within Caudicriodus, based on the evidence of the Podolian collection. B. Similar forms in other regions. D., Devonian; S., Silurian; Fm., Formation. For legend see Fig. 3.
vinced that *Icriodus eolaticrescens* Mashkova, 1968, *I. angustoides bidentatus* Carls and Gandl, 1969, and *I. w. transiens* Carls and Gandl, 1969 are junior synonyms of *I. w. postwoschmidti* Mashkova, 1968. As a result, stratigraphic range of *Caudicriodus hesperius*, *C. woschmidti*, and *C. postwoschmidti* is not established and the interregional correlation of the Lochkovian stratigraphic units based on icriodontid conodonts lacks firm foundations. It was not possible also to correlate correctly the range of Podolian zones with conodont zonation in other regions.

According to the present stratigraphic investigations the lower Lochkovian section of the Podolian sequence is about 105 m thick (Figs. 4, 5). Its top is situated in lower part of the Mytkiv Formation, approximately 50 m above the bottom. Its range nearly correspond to that of the *Monograptus uniformis* Zone. The middle Lochkovian section is about 240 m thick, and the upper about 70 m thick. As mentioned above the age of the upper part of the Ivanye Formation (about 115 meters) is not quite certain. Fossils occurring in the sediments are not diversified and not sufficient for precise age determination. Judging from the presence of *Caudicriodus? steinhornensis* (Al-Ravi, 1977) (unfortunately one specimen only; Figs. 3, 5) some meters beneath the top of the formation it seems possible that its uppermost part belong to the Pragian.

The oldest Lochkovian deposits of the *Monograptus uniformis* Graptolite Zone or *Caudicriodus hesperius* Conodont Zone are represented by the Khudykivtsi Formation and lower part (about 45 m) of the Mytkiv Formation (Fig. 4). In the deposits quite common are: *Caudicriodus hesperius* (Klapper and Murphy, 1975), *C. woschmidti* (Ziegler, 1960), *Zieglerodina remscheidensis* (Ziegler, 1960), and *Delotaxis cristagalli* (Ziegler, 1960). The Late Silurian species "*Ozarkodina* eostehornensis* (Walliser, 1964), *Ozarkodina typica* Branson and Mehl, 1933, and *Delotaxis detorta* (Walliser, 1964) are still present at the lowermost Khudykivtsi strata but about 3.2 m above the bottom disappear. In the higher layers of the Mytkiv deposits *C. hesperius* and *C. woschmidti* are replaced by *Caudicriodus transiens* (Carls and Gandl, 1969), *C. hadnagyi* (Chatterton and Perry, 1977), and *C. ruthmawsonae* Drygant, 2010 (Fig. 5). Other species found in the formation include *Zieglerodina remscheidensis* (Ziegler, 1960), *Caudicriodus alcoleae* (Carls, 1969), *Lanea omoalpha* (Murphy and Valenzuela-Rios, 1999), *Pseudooneotodus beckmannii* (Bischoff and Sannemann, 1958), and *Panderodus unicostratus* (Branson and Mehl, 1933). However, the specimens of *Zieglerodina remscheidensis* from the Mytkiv strata are clearly different from their lowermost Lochkovian ancestors. It is worthy to mention that most of these earliest representatives of the species are very similar to each other but there are also some specimens with clearly visible characteristic features of the new varieties which later on evolve into different morphotypes of *Zieglerodina remscheidensis* or another species, *Z. mashkovaei* (Drygant, 1984), *Z. flabellicauda* (Sorrentino, 1989), *Z. planilingua* (Murphy and Valenzuela-Rios, 1999), *Z. prosoplatys* (Mawson, Talent, Molloy, and Simpson, 2003) (Fig. 6).

Results of the conodont investigations from the Podolian sections show that range of the *Caudicriodus hesperius* Conodont Zone corresponds to the *Monograptus uniformis* Graptolite Zone. The *Caudicriodus postwoschmidti* Zone belongs to the middle Lochkovian and is separated from the earlier one by a large stratigraphic interval (Mytkiv Formation and lower part of the Chortkiv Formation) which belongs to the here established *Caudicriodus transiens* Zone (Fig. 7). Results of the new investigations convinced us that the opinions about occurrence of *Z. remscheidensis* in the middle and upper Lochkovian strata and the co-occurrence
of Caudicriodus postwoschmidti and C. hesperius in the lower part of the M. uniformis Zone (Schönlau 1985; Chlupáč and Hladil 2000) have been caused by incorrect identification of the species. Also, the stratigraphic schemes in which Caudicriodus postwoschmidti Zone was placed directly above the Caudicriodus woschmidti Zone (Maskhova 1979; Weddige 1996; Bultynck 2003) have been based on insufficient knowledge of their distribution.

In the lower part of the Chortkiv Formation, besides of the Caudicriodus transiens (Carls and Gandl, 1969), we found numerous Zieglerodina mashkovae (Drygant, 1984) and rare specimens of Pseudooneotodus beckmanni (Bischoff and Sannemann, 1958). In the middle part of the formation Zieglerodina mashkovae and Caudicriodus postwoschmidti are comparatively common while in upper beds infrequent Caudicriodus schoenlaubi sp. nov. and Pandorinellina? sp. are present. The first of them do not differ significantly from the middle Lochkovian specimens known from the northwestern Spain and, as we suppose, wrongly identified as Icriodus vincentum Carls, 1975 (Garcia-Lopez et al. 2002: pl. 2: 5). It is worthy to note that conodonts from the middle part of the Chortkiv deposits are very well preserved, represented by different elements of apparatuses and different stages of ontogenetic development.

In the Ivanye Formation conodonts are rather rare, represented mainly by Zieglerodina and Pandorinellina? Aside from their Pa elements Pb, Sa, Sb, Sc also occur as well as M elements of unidentified species of Zieglerodina or Pandorinellina? (Fig. 8), which until now were not described from the Lochkovian deposits. Also in the lower part infrequent Caudicriodus serus (Drygant, 1984) are present, while in the upper part Pandorinellina? parva sp. nov., Pandorinellina steinhornensis (Ziegler, 1956), Peleksygnathus csakyi (Chaterton and Perry, 1977) and Pedavis cf. breviramus Murphy and Matti, 1982 are found. In the middle beds of the formation conodonts have not been found.

Just below the top of the Ivanye Formation one specimen of the species characteristic for Pragian, Caudicriodus? steinachensis (Al-Ravi, 1977) was found (Fig. 3). The almost complete disappearance of the icriodontids in the beds and simultaneous dominance of the ozarkodinids is probably a result of the environmental changes, which can be observed in the gradual increase of the terrigenous material in sediments preceding ingress of the Old Red facies.

Conclusions

Based on the stratigraphic distribution of conodont species (Fig. 3) and phyletic relationships within Caudicriodus (Fig. 5) five regional conodont zones in the Lochkovian of Podolia are distinguished: Caudicriodus hesperus, Caudicriodus transiens, Caudicriodus postwoschmidti, Caudicriodus serus, and Caudicriodus? steinachensis (Fig. 7).

The Caudicriodus hesperus Zone corresponds in its stratigraphic range to the Monograptus uniformis Graptolite Zone. Its lower boundary is defined by the disappearance of “Ozar-kodina” eosteinhornensis (Walliser, 1964) s. s. and Delotaxis detorta (Walliser, 1964). Conodonts occurring in this zone are: Zieglerodina remsemdehnsis (Ziegler, 1960), Z. podolica Drygant, 2010, Z. planilingua (Murphy and Valenzuela-Rios, 1999), Z. prosoplatys (Mawson, Talent, Molloy, and Simpson, 2003), Pandorinellina camelfordensis (Farrell, 2003), Delotaxis cristagalli (Ziegler, 1960), and the newly discovered within the zone Pandorinellina? formosa Drygant, 2010. Characteristics for lower part of the zone are the morphologi-
cal modifications of *Caudicriodus woschmidti*, which moving upwards gradually become more similar to *C. transiens* (Carls and Gandl, 1969) and other co-occurring species of icriodontids. Therefore single specimens of such transitional forms are not informative for interregional correlations.

Very characteristic modification of the conodonts from the transitional Silurian/Devonian beds is also the great increase of size of the *Wurniella excavata excavata* (Branson and Mehl, 1933), which gave rise to *Wurniella excavata maxima* (Drygant, 1984) in *Caudicriodus hesperius* Zone. Contrary to that, representatives of *Zieglerodina* and *Pandorinellina* gradually decrease in size during the Lochkovian.

Characteristic conodonts for the *Caudicriodus transiens* Zone, except for the guide species, are *Caudicriodus ruthmawsonae* Drygant, 2010, *C. hadnagyi* (Chatterton and Perry, 1977) and *C. alcoleae* (Carls, 1969). Species disappearing in the zone include *Zieglerodina remscheidensis* (Ziegler, 1960) and *Pandorinellina? formosa* Drygant, 2010.

The *Caudicriodus postwoschmidti* Zone is characterized by the comparatively common occurrence of the name giving species and *Zieglerodina mashkovae* (Drygant, 1984), the rare occurrence of *Pandorinellina? sp.* and first appearance of *Caudicriodus schoenlaubi* sp. nov. and transitional forms from *Caudicriodus postwoschmidti* to *Caudicriodus serus*. Occurring within the *Caudicriodus serus* Zone are the guide species (not abundant), *Zieglerodina serrula* (Drygant, 1984), and *Pandorinellina? parva* sp. nov.

Based on the studied material it is possible to distinguish in the Podolian section a continuously developing lineage of the Lochkovian icriodontids: *Caudicriodus hesperius–C. transiens–C. postwoschmidti–C. serus*. Their earliest representatives, occurring near the Silurian/Devonian boundary, are elongated and represent typical forms of the *C. hesperius* and *C. woschmidti* species, as well as intermediate forms between them (Fig. 5). In the lower part of the middle Lochkovian, directly above the *Monograptus uniformis* Graptolite Zone, one can observe considerable widening of the element platform, concentration of the denticles, decrease of the angle between the axis of the spindle and postero-lateral process and the shortening of the process. *Caudicriodus hesperius* has comparatively short and wide platform with the inner and outer sides slightly convex. Some of its morphological features, for example the outline of basal cavity are close to those in *Caudicriodus? steinachensis* Al−Rawi, 1977 (Fig. 5).

Great importance for biostratigraphy is also possessed within representatives of the genera *Zieglerodina* and *Pandorinellina*? Based on the stratigraphical ranges of the species, gradual changes of their morphology and occurrence of transitional forms two developmental lineages can be observed: (i) *Zieglerodina remscheidensis–Z. mashkovae–Z. serrula*, (ii) *Z. remscheidensis–Pandorinellina? formosa–P.? parva* (Fig. 6).

Generally the Lower Devonian conodont assemblages from Podolia, especially those of the middle and upper Lochkovian, are rather poor in terms of number of specimens and taxonomical diversification, except for the upper part of lower Lochkovian where the number of species is slightly greater. However, results of the investigations show that Podolia can be one of the best regions in which almost the whole history of the icriodontid development during Lochkovian is recorded.

**Material**

The field investigations have been conducted in the years 2006–2010 in the natural outcrops situated on the escarp-
ments of the Dniester river and its tributaries (Fig. 1, Table 1). Twenty one outcrops, 10–60 m in thickness, representing the whole marine sedimentary sequence of the Lochkovian, were sampled. The samples for conodonts were collected from the calcareous layers only. Unfortunately, they are in minority in most of the sections. To maximize the diversity, some of the sections have been sampled two or even three times. The collections of conodonts from the localities described earlier by the first author (Drygant 1974, 1984, 2010) were re-examined.

All together about 3000 complete conodont elements were collected but in many samples only their fragments were found. Studied conodonts are represented mainly by species belonging to the families Spathognathodontidae and Icriodontidae but only the pectiniform elements were taken into account for stratigraphic correlations. Other elements of their apparatuses, in most of our samples, are not present at all or are rare and mostly broken. Probably because of that they were not reported from the region at all. Only in some layers we have found ramiform and coniform elements comparatively well preserved. However, because they are not numerous and usually co-occur with pectiniform elements of more than one species their specific determination would be uncertain and not useful for stratigraphy.

Color alteration index of the Lochkovian conodonts from Podolia is about 2 and thus the distribution of white matter cannot be well studied.

### Systematic palaeontology

The symbols informing about position of the conodont elements in the apparatus are after Sweet and Schönlaub (1975). Terminology used in the description of *Caudicriodus* is after Murphy and Cebecioglu (1984).

**Phylum Chordata** Bateson, 1886

**Class conodonta** Eichenberg, 1930

**Family Icriodontidae** Müller and Müller, 1957

**Genus Caudicriodus** Bultynck, 1976

*Type species:* *Icriodus woschmidti* Ziegler, 1960; Rhenish Slate Mountains, Hüinghaus Beds, lower Lochkovian.

**Remarks.**—Apparatuses of the *Caudicriodus* species are composed of the typical icriodontid Pa elements and five pairs of different coniform elements (see Serpagli 1982). All the coniform elements of *Caudicriodus* from Podolia were earlier assigned to the form species: *Rotundacodina quadratibasis* Drygant, 1974, *R. elegans* Carls and Gandl, 1969, *R. noguerensis* Carls and Gandl, 1969, *R. dubia* (Rhodes, 1953), *Drepanodus? curvatus* (Rhodes, 1953), *Acodina plicata* Carls and Gandl, 1969, *A. curvata* Stauffer, 1940, *A. retracta* Carls and Gandl, 1969 (Drygant 1974) and to *Rotundacodina rotunda* Drygant, 1984 (Drygant 1984). However, the rare preservation of the M and transition series elements and their occur-

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rence with Pa elements of different species restricts the reconstruction of the apparatuses to a few exceptional cases. Because of that only the Pa elements are determined and illustrated in the paper.

Ontogenetic development of *Caudicriodus transiens* (Carls and Gandl, 1969), *C. postwoschmidti* (Mashkova, 1968), and *C. serus* (Drygant, 1984) shows that their juvenile forms (Figs. 9, 10N, Q–S, U) strongly differ from the mature. In some cases (Mashkova 1968b, 1970) the juveniles were described as separate species and subspecies, e.g. *Caudicriodus eolatericrescens* (Mashkova, 1968), *C. angustoides angustoides* (Carls and Gandl, 1969), *C. angustoides bidentatus* (Carls and Gandl, 1969). Besides we noticed that among the left and right mature forms of Pa elements of some species (*Cau−dicriodus transiens, C. postwoschmidti, C. schoenlaubi, and C. serus*) considerable morphological difference occurs (Figs. 5, 9). The general shape of the elements is similar but their outline is different. Similar asymmetry of the conodont elements within one apparatus has been described in detail by Lane (1968).

*Caudicriodus hesperius* (Klapper and Murphy, 1975)

Figs. 9A, 10A, B.

For synonymy see Drygant (2010) and include:

- 2010 *Caudicriodus hesperius* (Klapper and Murphy); Drygant 2010: 56, pl. 2: 1, 2, 14−16.

**Material.**—Eleven Pa elements and thirty seven coniform elements (not separated from the elements of *C. woschmidti*) from the lower part of the Khudykivtsi Formation, Tseliyiv Formation and lower part of Mytkiv Formation. Numbers of sections and samples: 14/−1,3, 16 and 25 m, 14V/5, 104/1, 37/1, 12/1a (Fig. 3).

**Remarks.**—Pa elements of the species characterize comparatively elongated spindle (0.9−1.0 mm) and occurrence of 4−5 transverse ridges which are formed by connected denticles of the lateral and median rows. In the juvenile specimens the longitudinal rows are not developed and the transverse ridges are flattened. Postero-lateral process long, straight, laterally compressed, bears a single ridge of denticles. Inner and outer lobes undenticulated. Basal cavity lobe-like, expanded behind the second transverse ridge. Primary and secondary cusps high and approximately equal in height.

The platform gets suddenly wider immediately behind the second or third transverse ridge. The angle between the median longitudinal row (axis of the spindle) and the postero-lateral process is up to 135° and does not differ much from the angle in the holotype and paratype (115−145°).

Representatives of the species differ from *Caudicriodus woschmidti* (Ziegler, 1960) by the lobe-like, expanded platform and possession of narrow, long, and straight postero-lateral process.

Elements assigned to the *Icriodus woschmidti hesperius* by Schönlaub (1980b: pl. 6: 5 and 1980a: pl. 19: 1, 12) are close in outline of the basal cavity to the transitional forms between *Caudicriodus woschmidti* (Ziegler, 1960) and *C. ruthmawsonae* Drygant, 2010. Specimens identified by Simpson (1998) as *Icriodus woschmidti hesperius* are closest in morphology and denticulation to the transitional forms between the genera *Pedavis* and *Caudicriodus*.

**Stratigraphic and geographic range.**—Uppermost part of Pridoli(?) and lower Lochkovian—the *Caudicriodus hesperius* Zone. Podolia, Sardinia, Morocco, Nevada, Texas, Western North America, Canadian Arctic Archipelago, and Australia (Queensland and New South Wales).
Caudicriodus woschmidti (Ziegler, 1960)

Figs. 9B, 10C, D.

1960 Icriodus woschmidti n. sp.; Ziegler 1960: 185, pl. 15: 16, 17, 18, 20, 21, 22.

1976 Caudicriodus woschmidti (Ziegler 1960); Bultynck 1976: 21 [partim], text-fig. 1, 3: 1–2; 4: 1–4 [‘non fig. 3; 3, 4, 5 = ?Caudicriodus hesperius’ (Klapper and Murphy, 1975)].


2010 Caudicriodus woschmidti (Ziegler 1960); Drygant 2010: 57, pl. 2: 3, 6–13.

For more extensive synonymy see Drygant (2010).

Material.—20 specimens from lower part of the Khudykivtsi Formation. Sections and samples: 14/4a, 7, 8, 14V/4, 6, 104/1, 105/1.

Remarks.—Morphology of the Podolian Pa elements, especially the outline of basal cavity and denticulation of the spine, as well as the outline of spur and postero-lateral process (Fig. 5) agree in all details with the holotype (Ziegler 1960: pl. 15: 16a–c). The platform is slightly sigmoidal in upper view, comparatively narrow, gradually widening from the anterior end to the first transverse ridge. Spindle elongated (0.9–1.2 mm), with maximum five transverse ridges and anterior immaturate denticle. Its denticulation identical to that in Caudicriodus hesperius but the distance between transverse ridges is slightly larger.

Postero-lateral process short or a little elongated, usually weakly curved, with pointed end, bears a single ridge of denticles. Inner and outer lobes undenticulated. Basal cavity expanded behind the second or third transverse ridge. The primary cusp higher than the secondary one. The angle between the median longitudinal row and postero-lateral process bigger than 130°. In very small juvenile specimens (with 1–3 transverse ridges) the postero-lateral process and spur are lacking (Fig. 9B). Variations in morphology of adult specimens from Podolia has been illustrated in Drygant (2010: pl. 2: 6–13).

The specimens assigned to Icriodus woschmidti, known from Celtiberia (Carls 1975: pl. 2: 19, 21) and Tennessee (Broadhead and McComb 1983: fig. 3H–J) differ from the Podolian specimens by the less expanded basal cavity (Fig. 5).

Stratigraphic and geographic range.—Lower part of Caudicriodus hesperius Zone in Podolia (Fig. 3), Rhenish Slate Mountains (Germany), Iberian Chains, central Pyrenees and Guadarrama Mountains (Spain), Sardinia, Marocco, New South Wales and Victoria (Australia), Northwestern Canada, Appalachians.

Caudicriodus ruthmawsonae Drygant, 2010

Fig. 10F, H.

1968 Icriodus woschmidti Ziegler 1960; Drygant 1968b: 46 [partim], fig. 1 [‘non fig. 2–4 = Caudicriodus postwoschmidti’ (Mashkova, 1968)].


1984 Icriodus woschmidti transiens Carls and Gandl; Drygant 1984: 134 [partim], pl. 16: 7, 9–11 [‘non 5, 6, 8, 12–16’].

1990 Icriodus woschmidti postwoschmidti Mashkova; Olivieri and Serpagli 1990: 63, pl. 1: 15 [only].

1995 Icriodus postwoschmidti Mashkova; Colquhoun 1995: pl. 1: 4 [only].


2005 Icriodus eolatericrescens Mashkova; Barrick et al. 2005: pl. 3: 11.

2010 Caudicriodus ruthmawsonae nov. sp.; Drygant 2010: 59, pl. 3: 1, 2, 6.

Material.—Twelve Pa elements from the Mytkiv Formation and lower part of the Chortkiv Formation. Sections and samples: 16/4, 12/1a, 2, 17/4b, 18/5, 5d, 45/170 and 180 m, 13/260 m.

Remarks.—Pa elements of the species possess straight margins of the platform and lateral processes. Spindle long (0.89–0.96 mm) and narrow, with maximal 6 transverse ridges in which the denticles of the middle-row are smaller than those of the lateral rows. Lateral denticles of the transverse ridges are connected with the denticles of middle row by thin transverse ridges. Postero-lateral process triangular, elongated, denticulated or smooth. Spur well developed, fused with the postero-lateral lobe form together a process of the rhomboidal wing shape. Inner margin of the spur and outer margin of the postero-lateral process parallel. Primary cusp higher than the secondary and the denticles of the transverse ridges.

The species differs from the related Caudicriodus woschmidti (Ziegler, 1960) and C. hesperius (Klapper and Murphy, 1975) by the outline of platform which has straight margins, triangular form of the processes and wider inner side. From the C. transiens (Carls and Gandl, 1969) it differs by narrower platform and straight margins of lobes. The specimen illustrated by Olivieri and Serpagli (1990: 63, pl. 1: 15) as Icriodus woschmidti postwoschmidti Mashkova, 1968 differs from that species by the outline of platform and wider space between the transverse ridges but does not differ much from C. ruthmawsonae.

Stratigraphic and geographic range.—Upper part of Caudicriodus.


http://dx.doi.org/10.4202/app.2011.0124
Caudicriodus hadnagyi (Chatterton and Perry, 1977)  
Fig. 10J, L.
2010 *Caudicriodus* hadnagyi (Chatterton and Perry, 1977); Drygant 2010: 59, pl. 3: 4, 5.

**Material.**—Five complete Pa elements from the Mytkiv Formation and lower part of the Chortkiv Formation. Sections and samples: 12/2, 18/5, 18/5d, 45/185 m, 13/260 m.

**Remarks.**—Podolian specimens differ from the holotype by a bigger size, regular denticulation of the spindle and well developed spur. Platform enlarged in the posterior half, spindle elongated (0.9–1.1 mm) with 4–5 transverse ridges which are similar in morphology to those in *Caudicriodus woschmidti*. Postero-lateral process triangular, short and undenticulated. Spur well developed, on line with the postero-lateral process. Inner lobe weakly developed, posteriorly directed. Primary cusp prominent, directed posteriorly. The secondary cusp of the same height or somewhat smaller.

The Podolian Pa elements of the species differ from the closest species *Caudicriodus ruthmawsonae* by occurrence of prominent cusp, weakly developed inner lobe and expanded basal cavity in its mid part.

**Stratigraphic and geographic range.**—Upper part of *Caudicriodus hesperius* Zone and lower part of *Caudicriodus transiens* Zone; Podolia and Delorme Formation of Northwest−Canada.

**Caudicriodus transiens** (Carls and Gandl, 1969)
Figs. 9C, 10E, I.

**Pa element**
1968 *Icriodus eolatericrescens* sp. n.; Mashkova 1968b: 942 [partim].
1970 *Icriodus angustoides bidentatus* Carls and Gandl, 1969; Mashkova 1970: fig. 1: 1–6 [form juv.].
1975 *Icriodus postwoeschmidtii* Mashkova; Klapper in Ziegler 1975: 155 (partim). *Icriodus* plate 5: 5 (non 3, 4 = *Caudicriodus postwoeschmidtii* [Mashkova, 1968] and 6 = *Caudicriodus hesperius* [Klapper and Murphy, 1975]).
1984 *Icriodus woschmidti transiens* Carls and Gandl, 1969; Drygant 1984: 134 [partim], pl. 16: 5, 6, 8, 12–16 [non 7, 9–11 = *Caudicriodus ruthmawsonae* Drygant, 2010].
2010 *Caudicriodus transiens* (Carls and Gandl, 1969); Drygant 2010: 60, pls. 2: 19, 3: 7–15.

Other (coniform) elements
1974 *Rotundacodina dubia* (Rhodes); Drygant 1974; pl. 2: 26–29.
1974 *Acodina triquetra* (Jentzsch); Drygant 1974; pl. 2: 13 [?12].
1984 *Rotundacodina dubia* Carls and Gandl; Drygant 1984: 76, pl. 1: 48–52 [non pl. 1: 47].
1984 *Acodina triquetra* (Jentzsch); Drygant 1984: 75, pl. 1: 30 [?29].
1984 *Rotundacodina noguerensis* Carls and Gandl; Drygant 1984: 77, pl. 1: 36, 37.
1984 *Rotundacodina elegans* Carls and Gandl; Drygant 1984: 76, pl. 1: 40–42.
1984 *Rotundacodina rotunda* sp. n.; Drygant 1984: 77, pl. 1: 46. For more extensive synonymy see Drygant (2010).

**Material.**—More than 120 Pa and about 300 (not separated from the elements of other *Caudicriodus* species) coniform elements from the Mytkiv Formation. Sections and samples: 12/1a, 2, 17/4v, 18/1, 5, 5d, 5e, 6, 18A/5, 45/180, and 170–180 m.

**Remarks.**—Juvenile Pa elements of the species possess narrow, wedge-shaped platform which in the later ontogeny become wider, mainly because of the better development of the spur. Number of the transverse ridges in adult specimens is up to six. Length of the spur 0.9–1.1 mm. Postero-lateral process triangular, more or less elongated, straight, laterally compressed, bears a single ridge of denticles. Inner and outer lobes undenticulated. Basal cavity lobe-like, expanded behind the second or third transverse ridge. Primary and secondary cusps high, approximately equal. The angle between anterior and postero-lateral processes not bigger than 120–140° in “right” elements and 105–125° in “left”. In stratigraphically older specimens “right” elements differ from the “left” by lack of the spur and longer postero-lateral process.

Representatives of the species differ from the related *Caudicriodus woschmidti* (Ziegler, 1960) by the laterally expanded platform and possession of straight and narrow postero-lateral process. From *C. hesperius* (Klapper and Murphy, 1975) they differ by triangular and shorter postero-lateral process, shorter inner posterior lobe and anteriorly expanded basal cavity.

All elements constructing apparatus of *C. transiens* from the Chortkiv deposits of Podolia (samples 18/5, 18/5d and 18/5e) were described and illustrated by Drygant (1974, 1984).

**Stratigraphic and geographic range.**—*Caudicriodus transiens* Zone in Podolia, Luesma Beds of Iberian Chains (Spain).

**Caudicriodus alcoleae** (Carls, 1969)
Fig. 10K.
1976 *Caudicriodus angustoides alcoleae* (Carls, 1969); Bulynck 1976: 34, pl. 4: 14, 18–28; text−fig. 2.
1980 *Icriodus woschmidti hesperius* Klapper and Murphy; Schönlaub 1980a: pl. 19: 1, 2.
1994 *Icriodus angustoides alcoleae* Carls; Valenzuela-Ríos 1994: 93, pl. 8: 9–10, 12–13, 18, 27, 34.
2003 *Caudicriodus angustoides alcoleae* (Carls); Bultynck 2003: pl. 4: 12, 13.
?non 2012 *Icriodus angustoides alcoleae* Carls; Slavík et al. in press: fig. 6: 16 [= ?C. schoenlaubi sp. nov.].

**Material.**—One Pa element from Mytkiv Formation, sample 45/175 m.

**Remarks.**—Specimen is characterized by tear-shaped, short and strongly convex platform with short spindle and lack of spur. Denticles of the transverse ridges in the lateral rows have circular base, are big and cone-shaped. Denticles of the median row are lower, joined by thin margins with themselves and with lateral denticles. Postero-lateral process short, undenticulated. The angle between median longitudinal row and postero-lateral process is about 130°. The primary cusp much bigger than the secondary.

This specimen is similar to the specimens illustrated by Bultynck (2003: pl. 1: 12, 13) from *Pedavis pesavis* Zone in Guadarrama and to the specimens illustrated by García-López et al. (2002: pl. 1: 11, 12) from *Caudicriodus alcoleae* Zone in Northwest Spain but differs from them by typical icriodontan denticulation on the spindle.

**Stratigraphic and geographic range.**—*Caudicriodus transiens* Zone in Podolia, lower Lochkovian in Barrandian, *Ancyrodelloides delta* and *Pedavis pesavis* Zones in Pyrenees, Carazo and Lebanon Formations (lower and middle Lochkovian) of Northwest Spain, middle Lochkovian of Guadarrama Mountains (Spain).

**Caudicriodus postwoschmidti** (Mashkova, 1968)

Figs. 9D, 10O, P, 11A, B.

For synonymy see Drygant (2010) and include:
1968 *Icriodus eolatericrescens* sp. n.; Mashkova 1968b: 942 [partim], fig. 1: 4–5 [juvenile form].
1985 *Icriodus* sp. n. A; Schönlaub 1985: pl. 2: 23 [only].
2004 *Latericriodus steinachensis* (Al-Rawi) eta morph Klapper and Johnson; Slavík and Hladil 2004: 144, pl. 1: 4 [only].
2010 *Caudicriodus postwoschmidti* (Mashkova); Drygant 2010: 61, pls. 3: 16–18, 4: 1–3, 6, 7.

**Material.**—More than 50 complete Pa and 16 conform elements from the Chortkiv Formation. Sections and samples: 18/5d, 13/1, 13A/2, 13/280 m, 81/370 m, 11B/1.

**Remarks.**—Among the Pa elements of this species “right” and “left” forms can be distinguished (Fig. 9D). Platform of the first one is triangular, elongated, widen behind the second (in juvenile specimens) or fourth (in adult specimens) transverse ridge. Platform of the second form shorter but wider than the first and has almost straight borders of the processes. Spindle comparatively elongated (0.7–0.9 mm), with 5–7 transverse ridges. The angle between the median row and postero-lateral processes do not exceeds 115–125°. Denticles of the lateral rows bigger than those of the median row and connected in transverse ridges and in median row. Spur well developed, can be denticulated in gerontic specimens. Postero-lateral process triangular and bears a single ridge of denticles. Primary cusp is a little bigger than secondary one.

Specimens of the related species *Caudicriodus woschmidti* (Ziegler, 1960) are characterized by elongated, less expanded platform and shorter postero-lateral process. Second related species *C. hesperius* (Klapper and Murphy, 1975) differs by short, lobe-like extension of the platform, narrower postero-lateral process and by possession of the inner posterior lobe.

The specimens illustrated by Schönlaub (1980a: pl. 19: 2, 3) and also described by Mawson (1986: 44, pl. 9: 1, 2) as *Icriodus postwoschmidti* are close in outline of platform and short triangular postero-lateral process to the transitional forms between *Caudicriodus woschmidti* (Ziegler, 1960) and *C. hesperius* (Klapper and Murphy, 1975). The specimens assigned to the species by Colquhoun (1995: pl. 1: 2, 3) and by Barrick et al. (2005: pl. 3: 9, 10, 12) have short, lobe-like extended platform with separated and well-developed outer and inner lobes. This feature is characteristic for *C. hesperius*, but not for the discussed species. The Pa elements described as *Icriodus postwoschmidti* by Barrick and Klapper (1992: 45, pl. 3: 7–12) and by Farrell (2003: 124, pl. 2: 1, 2) are closest in morphology to the *Caudicriodus hesperius*. They distinctly differ from *C. postwoschmidti* by the lobe-like platform.

Pa element from Barrandian identified by Slavík (2004: pl. 1: 4) as “*Latericriodus steinachensis* (Al-Rawi) eta morphotype Klapper and Johnson” represents the “right” form of the element in *Caudicriodus postwoschmidti*. Second specimen from Barrandian identified by Slavík (2004: pl. 1: 5) and described by Slavík and Hladil (2004: 144, pl. 1: 4) as “*L. steinachensis* (Al-Rawi, 1977) eta morph Klapper and Johnson” represents the “left” form of the element in *Caudicriodus postwoschmidti*. The elements have similar shape of platform and denticulation. Specimen of the “eta morphotype” is Lochkovian in age, probably from *Pedavis pesavis* Zone (see Slavík [2004: fig. 3 and table 2] and Slavík and Hladil [2004: figs. 2, 3, 4]). Age of the “beta morphotype” is uncertain.

**Stratigraphic and geographic range.**—*Caudicriodus postwoschmidti* Zone (middle Lochkovian) in Podolia, upper Lochkovian in Cantabrian Mountains, Carnic Alps, and Barrandian.

**Caudicriodus schoenlaubi** sp. nov.

Fig. 11C–I.

1985 *Icriodus* sp. n. A; Schönlaub 1985a: pl. 2: 17, 20 [only].

http://dx.doi.org/10.4202/app.2011.0124
2007 Icriodus steinachensis Al-Rawi eta morphotype Klapper and Johnson; Slavík et al. 2007: fig. 3: 4 [only].
2012 Icriodus angularoides alcoleae Carls; Slavík et al. (in press): fig. 6: 16.

Etymology: In honor of the Austrian geologist Hans Schönlaub, who first illustrated specimens of this species.

Type material: Holotype: well-preserved “left” Pa element ZPAL C.20/8.5 (Fig. 11D). Paratypes: “right” Pa element ZPAL C.20/8.6 (Fig. 11E).

Type locality: Outcrop 81, left side of the Dniester, above the village Vynohradiv (Fig. 1, Table 1), sample 81/380 m.

Type horizon: Upper part of Chortkiv Formation, middle–upper Lochkovian.

Material.—Eight (including holotype) complete Pa elements from the Chortkiv Formation. Sections and samples: 5/320 340, 81/360 m, 380 m, 11/375 m.

Diagnosis.—Platform of Pa element wide and comparatively short with the drop-like outline of basal cavity. Spindle with maximum six straight or slightly curved transverse ridges. Postero-lateral process short. Spur developed only in adult forms.

Description.—Platform of Pa elements very wide and comparatively short, expanded in posterior part of the spindle. “Right” forms differ from the “left” by gradual widening of basal cavity and its drop-like outline. Platform of the “left” forms suddenly gets wider approximately behind the fourth transverse ridge. Spindle about 0.71–1.22 mm long, straight or slightly curved, with maximum six transverse ridges. Spur developed only in the mature forms. Postero-lateral process short, with rounded tip. Denticles of the transverse ridges and the median row joined. Those of the lateral rows are bigger and have circular base. Primary and secondary cusps equal in size and not higher than the denticles of the transverse ridges. Angle between the median row and postero-lateral process about 110–120°.

Remarks.—New species differs from the closest Caudicriodus serus (Drygant, 1984) by expanded, drop-like platform, less developed spur in the “left” forms and convex outer border of the platform opposite to the second transverse ridge.

Some specimens of the new species (Figs. 5, 11I) are similar to the specimen from the middle Lochkovian of Northwestern Spain, but close to the new species. Icriodus vinearum Carls, 1969 (García-López et al. 2002: pl. 2: 5), which differs from the typical forms by narrower and longer platform (compare with Carls 1975: pls. 2: 22–28, 3: 31–33).

The specimen from the uppermost Lochkovian, illustrated by Slavík et al. (2007: figs. 3, 4) as “Icriodus steinachensis Al-Rawi eta morphotype Klapper and Johnson, 1980” and characterized by straight spindle, wide platform in front of the postero-lateral process and spur merged with the inner posterior lobe is probably not an “eta morphotype” of Caudicriodus? steinachensis but close to the new species.

Material.—16 complete Pa elements from upper part of the Chortkiv Formation. Numbers of sections and samples: 4/8v, 11/4, 11A/6, 7, 9, 11B/1, 11/375 m.

Remarks.—Pa elements of this species characterize short and wide platform, short postero-lateral process, diversification of the elements into “right” and “left” elements differing in morphology of platform and spindle. The platform gets wider behind the fourth transverse ridge and is the widest approximately opposite the second transverse ridge. Outer bord of platform in all elements slightly curved. Spur of the “right” elements not developed, inner border of the platform bowed. Spur of the “left” elements short, triangular and less edged. Spindle straight or slightly curved, elongated (0.8–1.0 mm), with 4–6 transverse ridges. The transverse ridges in some forms slightly flattened, the denticles of the lateral rows have circular base and are less thicker than denticles of median row. Denticles of median row joined by thin margins with themselves and with lateral denticles. Postero-lateral process short, triangular, with rare and small denticles. Angle between the median row and postero-lateral processes about 95–110°. Primary cusp bigger and higher than the secondary.

Caudicriodus serus differs from related Caudicriodus postwoschmidtii (Mashkova, 1968) by the outline of platform, curved spindle and lesser angle between the median row and postero-lateral process (Fig. 9D, E).

Outline of the platform in our specimens is closest to the specimen from the Lower Pragian of Spain, illustrated by Carls (1969: pl. 3: 10) as representative of his new subspecies Icriodus angularoides castilianus Carls, 1969. It differs from the typical specimens of the subspecies, as well as from the Caudicriodus serus by a bigger number and density of the transverse ridges and by a gradual reduction of the spindle width, anteriorly and posteriorly from its middle.

The specimen described by Slavík and Hladil (2004: 144, pl. 1: 2) as the “Latericriodus steinachensis (Al-Rawi, 1977)” eta morph Klapper and Johnson” differs from the species by straight spindle and triangular postero-lateral process with undentlicated edge. In our opinion its morphology is closest to Caudicriodus serus.

Material.—Caudicriodus serus Zone (middle–upper Lochkovian) in Podolia and probably the uppermost Lochkovian in Barrandian.

Caudicriodus? steinachensis (Al-Rawi, 1977), eta morphotype of Klapper and Johnson, 1980 Fig. 11M.
1965 *Icriodus bilatericrescens* Ziegler; Philip 1965: 103, pl. 9: 30–32.
1979 *Icriodus steinachensis* Al-Rawi, 1979; Lane and Ormiston 1979: pl. 4: 28, 29.
1982 *Icriodus steinachensis* Al-Rawi eta morph; Murphy and Matti 1982: 58, pl. 5: 31, 36.
1994 *Icriodus steinachensis* (Al-Rawi) eta morph Klapper and Johnson; Mawson and Talent 1994: 47, fig. 9K–N.
2004 *Latericriodus steinachensis* (Al-Rawi) eta morph Klapper and Johnson; Slavik 2004: pl. 1: 5 [= Caudicriodus. postwoschmidtii (Mashkova, 1968)].
2004 *Latericriodus steinachensis* (Al-Rawi) eta morph Klapper and Johnson; Slavik and Hlädl 2004: 144, pl. 1: 3 [non pl. 1: 2 = ?Caudicriodus. serus (Drygant, 1984) and pl. 1: 4 = C. postwoschmidtii (Mashkova, 1968)].
2007 *Latericriodus steinachensis* (Al-Rawi) eta morph Klapper and Johnson; Suttner 2007: 24, pls. 8, 2, 8–10, 9: 1, 5, 6, 8.
2007 *Icriodus steinachensis* (Al-Rawi) eta morph Klapper and Johnson; Slavik et al. 2007: fig. 3: 2, 3 [non fig. 2: 4 = Caudicriodus schoenlaupi sp. nov.].

**Material.**—One Pa element from the upper part of Ivanye Formation. Section and sample 2A/10.

**Remarks.**—Our specimen possesses three transverse ridges and represents an intermediate ontogenetic stage. The platform is slightly curved, narrow in anterior part and expanded behind the second transverse ridge. Spindle is a little curved, transverse ridges flattened, spur short but well-developed. Postero-lateral process short, undenticated. The angle between that and spindle about 90°. Outer lobe well-developed. Primary cusp higher than the secondary. Podolian specimen differs from the typical mature “*Icriodus steinachensis* eta morphotype” by narrower platform, undenticated postero-lateral process and bigger space between the transverse ridges.

The taxon “*I. steinachensis* eta morphotype” is referred to *Caudicriodus* questionably because its Pa element (Murphy and Cebecioglu 1984: fig. 4G–R) differ from typical representatives of the genera *Icriodus* Branson and Mehl, 1938 and *Latericriodus* Müller, 1962 (e.g., type species *Icriodus latericrescens* Branson and Mehl, 1938) but is close to *Caudicriodus* Bullynck, 1976.

**Stratigraphic and geographic range.**—Uppermost Lochkovian to lower Pragian (*Caudicriodus* *steinachensis* Zone) in Frankenwald (Germany), Barrandian (Czech Republic), Carnic Alps (Austria), central Pirenees, Victoria (Australia), central Nevada.

**Genus *Pelekysgnathus* Thomas, 1949**

*Type species:* *Pelekysgnathus inclinata* Thomas, 1949; southeast Iowa, Devonian.

**Pelekysgnathus csakyi** (Chatterton and Perry, 1977) Fig. 10V.

1990 *Pelekysgnathus csakyi* (Chatterton and Perry, 1977); Uyeno 1990: 59, pl. 20: 4–9, 13–15.
2010 *Pelekysgnathus* sp. (?*Pelekysgnathus csakyi* [Chatterton and Perry, 1977]); Drygant 2010: pl. 4: 12.

**Material.**—Two Pa elements from the upper part of the Ivanye Formation. Samples 2A/7 and 52/500 m.

**Remarks.**—Podolian specimens are closest in morphology to the holotype and other illustrated specimens from the type locality. They are of similar length and height, and have similar subtriangular outline of the basal cavity, and backwardly directed primary cusp with its tip broken of. Other denticles on the thin longitudinal ridge are lower and slightly flattened. One of the specimens bears small supplementary cusp on the outer side of that ridge.

**Geologic and geographic range.**—Anycyrodelloides delta Zone in Hyde Parker Island and Delorme Formation, Lochkovian of northwestern Canada.

**Genus *Pedavis* Klapper and Philip, 1971**

*Type species:* *Icriodus pesavis* Bischoff and Sannemann, 1958; Frankenwald, Lochkovian.

**Pedavis cf. *breviramus*** Murphy and Matti, 1982 Fig. 10W.

**Material.**—One specimen from the Ivanye Formation, sample 52/500 m.

**Remarks.**—Small specimen, representing probably juvenile form, do not allow for certain specific determination.

**Family Spathognathodontidae Hass, 1959**

**Genus *Zieglerodina* Murphy, Valenzuela-Ríos, and Carls, 2004**

*Type species:* *Spathognathodus remschaeidensis* Ziegler, 1960; Rhenish Slate Mountains, Hünghaus Beds, lower Lochkovian.

Zieglerodina remscheidensis (Ziegler, 1960)

Figs. 8N, O, 12A–G.

For synonymy see Drygant (2010) and include:
1960 Spathognathodus remscheidensis n. sp.; Ziegler 1960: 194, pl. 13: 1, 2, 4, 5, 7 [non pl. 13: 8, 10, 14].
1972 Ozarkodina steinhornensis remscheidensis (Ziegler, 1960); Mashkova 1972: 83, pl. 2: 19–21, 23, 24 [non pl. 2: 22].
1984 Spathognathodus eosteinhornensis Walliser; Drygant 1984: 123, pl. 13: 5–8, 11, 12, 15 [only].
1990 Ozarkodina remscheidensis Walliser, 1964; Olivieri and Serpagli 1990: pl. 4: 10 [only].
Non 2005 Ozarkodina remscheidensis (Ziegler, 1960); Barrick et al. 2005: 120, pl. 1: 1 (= ?), 2 (= Z. planilingua [Murphy and Valenzuela-Rios, 1999]), 9, 10 (= ?); pl. 2, fig. 8 (= Zieglerodina prosoplatus Mawson, Talent, Molloy, and Simpson, 2003).
2010 Zieglerodina remscheidensis (Ziegler, 1960); Drygant 2010: 49, pl. 1: 1–10, 12.

Material.—About 460 of the Pa and about 100 of other elements (Pb–Sc) from the Dzvenyhorod, Khudykivtsi, Mytkiv, and lower part of the Chortkiv Formation. Sections and samples: 33/2, 14D/1, 14/4, 4b, 5a, 5v, 6, 7, 37/1, 1a, 1b, 2, 37A/1, 2, 37B/1, 16/1, 2, 3, 4, 5, 16B/1b, 15/1a, 17/3, 4v, 12/2, 18A/5, 45/170 m.

Remarks.—Typical Pa elements of the species (stratigraphically later forms from the upper part of Khudykivtsi Formation) have long (0.95–1.3 mm) and high (0.2–0.33 mm) blade with straight lower margin. A denticle above the basal cavity (cusp) comparatively high. Also 2–3 anterior denticles, especially the third, higher than others. Basal cavity closer to the posterior end. In specimens of the stratigraphically earlier forms (Silurian/Devonian boundary beds and lower part of the Khudykivtsi Formation) height of the anterior denticles and that above the basal cavity do not differ significantly from the rest (Fig. 6).

It is worthy to mention that “Spathognathodus eosteinhornensis” Walliser, 1964° has been considered as an ancestor species of the “Spathognathodus remscheidensis” Ziegler, 1960” (Walliser 1964). Material from Podolia shows that typical specimens of “Spathognathodus eosteinhornensis” do not occur above the Silurian/Devonian boundary. Its uppermost occurrence has been stated in the bed with Monograptus uniformis angustidens (Fig. 3). That means Zieglerodina remscheidensis (sensu stricto) do not replace the discussed species but appears independently, already in Prirodina brocki (Farrell, 2004) but it has shorter and higher blade, higher anterior denticles and smaller basal cavity lips.

Stratigraphic and geographic range.—Uppermost part of “Ozarkodina” eosteinhornensis and Caudicriodus hesperius Zone in Podolia, lower Lochkovian in Barrandian.

Zieglerodina planilingua (Murphy and Valenzuela-Rios, 1999)

Fig. 13A–D.

1971 Spathognathodus steinhornensis remscheidensis Ziegler; Mashkova 1971: pl. 2: 11 [only].
1984 Spathognathodus remscheidensis Ziegler; Drygant 1984: pl. 13: 18 [only].
2003 Ozarkodina remscheidensis remscheidensis (Ziegler); Farrell 2003: 137, pl. 8: 17, 18 [only].
2003 Ozarkodina martinsonsi auriformis n. ssp.; Simpson 2003: 76, pl. 1: 1–13 [only].
2005 Ozarkodina remscheidensis (Ziegler); Barrick et al. 2005: 120, pl. 1: 2 [non pl. 1: 9, 10].
2005 Ozarkodina? planilingua Murphy and Valenzuela-Rios; Barrick et al. 2005: 120, pl. 1: 11, 12; non pl. 1: 3, 4 [= Z. remscheidensis (Ziegler, 1960)].
2010 Zieglerodina planilingua (Murphy and Valenzuela-Rios); Drygant 2010: 52, pl. 1: 9.

Material.—16 Pa elements from the Dzvenyhorod, Khudykivtsi and Tseliyiv Formations. Sections and samples 14/1, 13 m, 14D/1, 37/1, 1a, 37A/2, 37B/1.

Remarks.—Zieglerodina planilingua is distinguished from Z. remscheidensis by contrasting lower and raised posterior section of the blade with low slightly backwardly inclined denticles. Just behind the cusp these denticles are very small but became higher towards the posterior end of the blade.

Stratigraphic and geographic range.—Uppermost part of “Ozarkodina” eosteinhornensis Zone and lower part of Caudicriodus hesperius Zone in Podolia. Uppermost Pridoli to mid-
Zieglerodina prosoplatys (Mawson, Talent, Molloy, and Simpson, 2003)

Fig. 13E, F, J.

1977 Ozarkodina remscheidensis remscheidensis n. form beta; Chaterton and Perry 1977: pl. 4: 26 [only].
1982 Ozarkodina remscheidensis (Ziegler); Savage 1982: 986, pl. 2: 21–23 [only].
1992 Ozarkodina remscheidensis remscheidensis (Ziegler); Barrick and Klapper 1992: pls. 4: 8, 9, 6: 8, 9 [only].
2005 Ozarkodina sp. 1; Barrick et al. 2005: pl. 2: 7 [only].

Material.—Three Pa elements from the lower part of Khudykivtsi Formation and Ivanye Formation. Sections and samples: 14/0,6 and 2.5 m, 52/500 m.

Remarks.—Blade elongated (0.8–1.0 mm), comparatively high (about 0.22 mm), with the anterior end downcurved, forming a beard-like process. The upper edge nearly straight. Denticles sharp, comparatively low, uneven in height. Denticle above the basal cavity (cusp) little enlarged. Basal cavity located at the posterior half of the blade and has comparatively wide lips. Podolian specimens differ from the typical material by more elongated and beard-like anterior end of the blade.

Stratigraphic and geographic range.—Lower part of Caudicriodus hesperius Zone in Podolia, Nowshera Limestone in Pakistan, Road River Formation in Northwestern Canada, Frame Formation in Texas, Lochkovian in Alaska.

Zieglerodina mashkovae (Drygant, 1984)

Figs. 12, 13G, K.

1979 Ozarkodina remscheidensis remscheidensis (Ziegler); Lane and Ormiston 1979: pl. 1: 18, 34 [only].
1984 Spathognathodus mashkovae sp. n.; Drygant 1984: 125, pl. 14: 10, 11, 13–21 [non 12 = Pandorinellina? formosa Drygant].

Material.—About 290 complete Pa elements from Khudykivtsi, Chortkiv and lower part of Ivanye Formation. Sections and samples: 16/1v, 18/5, 5d, 6e, 6b, 13/1, 1v, 1d, 13A/1, 2, 11/4, 11A/6, 7/4v, 13, 4/8v, 2/4a, 45/180 and 190 m.

Remarks.—Pa elements of the species characterize short (0.6–0.7 mm) and low (about 0.2 mm) blade with straight lower and upper margins. Basal cavity with circular, symmetrical lips located approximately at mid-length or slightly closer to the posterior end of the lower margin. Each section of the blade possesses 5–7 low, nearly equal in height, denticles which on the posterior blade get wider and slightly inclined backwardly. The denticle above the basal cavity (cusp) is considerably bigger, inclined backwardly or erect.

Pa elements differ from the ancestral species Zieglerodina remscheidensis (Ziegler, 1960), Z. repetitor (Carls and Gandl, 1969), and Z. serrula (Drygant, 1984) by short, but high blade, bigger size of cusp, different width of denticles of the anterior and posterior section of the blade and location of the basal cavity at the mid-length.

Specimens described by Valenzuela-Rios (1994: 59, pl. 1: 5–35) as the new species Ozarkodina eladioi do not differ significantly in morphology and stratigraphic range from Zieglerodina mashkovae (Drygant, 1984) and are, in our opinion, conspecific with the latter.

Stratigraphic and geographic range.—From upper part of Caudicriodus hesperius Zone to C. serus Zone in Podolia, lower to middle Lochkovian in Pyrenees, Iberian Chains, Guadarrama Mountains (Spain).

Zieglerodina serrula (Drygant, 1984)

Fig. 12W, Z, AA.

2010 Zieglerodina serrula (Drygant); Drygant 2010: 53, pl. 1: 23, 24, 26, 27.

Material.—More than 90 complete Pa elements from the Ivanye Formation. Sections and samples: 11A/6, 1/3, 11, 2/1, 1b, 1v, 4a, 8a, 2A/7, 10, 52/525 m.

Remarks.—The elements are small in size (about 0.5–0.7 mm long and 0.17–0.27 mm wide), with straight upper margin of the blade which bears low and equal in size denticles. The lower margin of the blade straight or slightly sloping from its ends towards basal cavity. Basal cavity approximately at the mid-length or closer to the posterior end of the blade. Both lips of the basal cavity rounded and nearly symmetrical.

The elements are closest to Zieglerodina mashkovae (Drygant, 1984), but distinctly differ from it by the regularly arranged denticles, their nearly equal size and lack of the cusp.

Stratigraphic and geographic range.—Upper part of Caudicriodus serus Zone and Caudicriodus? steinachensis Zone in Podolia.

Zieglerodina paucidentata (Murphy and Matti, 1982)

Fig. 11R.

http://dx.doi.org/10.4202/app.2011.0124
1975 *Ozarkodina* sp. nov. E; Klapper and Murphy 1975: 44, pl. 7: 6, 9, 10.
1982 *Ozarkodina paucidentata* n. sp.; Murphy and Matti 1982: 9, pl. 1: 25–32, 39, 40.

**Material.**—Three complete Pa elements from upper part of the Ivanye Formation. Section and samples: 52/490 and 510 m.

**Remarks.**—The specimens from Podolia do not differ significantly from the holotype. They have comparatively small size, high cusp and differentiated height of the blade sections, of which the anterior one is much higher.

**Stratigraphic and geographic range.**—Pragian? in Podolia. Uppermost Silurian and lower Lochkovian, to the top of *Ozarkodina eurekaensis* Zone in North America.

**Genus Pandorinellina** Müller and Müller, 1957

*Type species:* *Pandorina insita* Stauffer, 1940; Cedar Valley limestone, Minnesota, Middle Devonian.

**Pandorinellina praecoptima** (Mashkova, 1972)

**Fig. 13R. S.**


1979 *Pandorinellina steinhornensis praecoptima* (Mashkova); Lane and Ormiston 1979: pl. 3: 1, 3.

1984 *Spathognathodus repetitor praecoptimus* (Mashkova); Drygant 1984: 126, pl. 14: 22, 23.

1991 *Pandorinellina steinhornensis praecoptima* (Mashkova) sensu Lane and Ormiston; Uyeno 1991: pl. 1: 19.

2010 *Pandorinellina praecoptima* (Mashkova); Drygant 2010: 55, pl. 1: 22, 28.

**Material.**—Ten Pa elements from the Ivanye Formation. Sections and samples: 11A/6, 1/3, 4, 5, 2A/6, 10, 2V/4.

**Remarks.**—Elements comparatively long, higher in their anterior part. Denticles narrow, on the anterior section of the blade, nearly equal in height, on the posterior section decrease in size and are significantly inclined posteriorly.

**Stratigraphic and geographic range.**—*Caudicriodus serius* and *Caudicriodus? steinachensis* zones, upper Lochkovian? to Pragian in Podolia.

**Pandorinellina? formaosa** Drygant, 2010

**Fig. 12V, Y.**


**Etymology:** From Latin *formaosa*, little.

**Holotype:** Complete Pa element SMNH D1420 (Fig. 12V).

**Type locality:** Outcrop 11, the left side of the Dniester 2 km below the village Dobrivlyany (Fig. 1, Table 1).

**Type horizon:** Ivanye Formation, upper Lochkovian–Pragian.

**Material.**—Five complete Pa elements and numerous fragments from Ivanye Formation. Sections and samples: 11/4, 52/525 m. Other elements of the multielement apparatus are not known.

**Diagnosis.**—Blade short and high, faintly sigmoidaly twisted. Denticles narrow, two–three anterior slightly bigger than others. Cusp not differentiated. Basal cavity situated at the middle of the blade.

**Description.**—Blade of the Pa elements short (about 0.70–0.75 mm), high (about 0.3 mm), slightly sigmoidaly twisted, lower on the posterior end. Denticles narrow, in posterior part slightly inclined posteriorly. Two–three anterior denticles slightly bigger than others. Cusp not well differentiated. Basal cavity located at the mid-length, has small and symmetrical lips of rounded outline.

**Remarks.**—New species seems closest to *Zieglerodina serrula*, differing from it by the higher anterior denticles, characteristic for the genus *Pandorinellina* twisted blade.

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Fig. 13. SEM photographs of Pa elements of spathognathodontid conodonts, genera *Zieglerodina, Pandorinellina*, and *Lanea*, Podolia, Early Devonian.

Stratigraphic and geographic range.—Caudicriodus serus and Caudicriodus? steinachensis zones, upper Lochkovian to ?Pragian in Podolia.

Genus Wurniella Murphy, Valenzuela-Ríos, and Carls, 2004
Type species: Ozarkodina excavata tuma Murphy and Matti, 1983; central Nevada, Lower Devonian, Ancyrodelloides delta Zone.

Wurniella excavata maxima (Drygant, 1984)
Fig. 12A, B.
1968 Spathognathodus inclinatus inclinatus (Rhodes); Drygant 1968b: 51, fig. 24, 25.
1980 Ozarkodina wurmi (Bischof and Sannemann); Schönlaub 1980a: pl. 19: 17.
2005 Ozarkodina wurmi (Bischof and Sannemann); Barrick et al. 2005: pl. 2: 15.

Material.—Six Pa elements from the Khudykivtsi Formation. Sections and samples: 14V/4, 104/1, 16/1b, 1v, 3.
Remarks.—The specimens differ from the corresponding elements of other species of Wurniella by big size (blade about 1.73 mm long, 0.27 mm high and denticles 0.3 mm high) and arched blade.

Stratigraphic and geographic range.—Caudicriodus hesperius Zone in Podolia, lower Lochkovian in Barrandian, Lanea omoalpha Zone in West Texas, Southerland River Formation of Devon Island (Canadian Arctic Archipelago).

Genus Lanea Murphy and Valenzuela-Ríos, 1999
Type species: Ozarkodina eleanorae Lane and Ormiston, 1979; Salmon trout River Area, East-Central Alaska, Lochkovian.

Lanea omoalpha Murphy and Valenzuela-Ríos, 1999
Figs. 13M, P, T.
1982 Ancyrodelloides omus n. sp., alpha morph; Murphy and Matti 1982: pl. 2: 18−20 [only].
1994 Ancyrodelloides omus morphotipo δ; Valenzuela-Ríos 1994: pl. 1: 10 [only].
2005 Lanea omoalpha Murphy and Valenzuela-Ríos; Barrick et al. 2005: 117, pl. 1: 5−8, 13, 14.

Material.—Five complete Pa elements from Mytkiv Formation. Section and sample 45/170 m.
Remarks.—Podolian specimens do not differ significantly from the type material from Spain: the elements have thick, elongated (0.9−1.1 mm) and high (about 0.2−0.35 mm) blade. Lower margin of both sections of the blade nearly straight. Basal cavity with terraced, rounded and asymmetrical lips, located approximately at mid-length or closer to the posterior end of the blade. Cusp is considerably bigger, the anterior denticles and anterior end of the blade somewhath higher.

Stratigraphic and geographic range.—Caudicriodus trignicus Zone in Podolia, Lanea omoalpha and Ancyrodelloides trigonicus zones in Spain, middle Lochkovian in central Nevada Spanish Pyrenees and Czech Republic.

Genus Ancyrodelloides Bischoff and Sannemann, 1958
Type species: Ancyrodelloides trigonica Bischoff and Sannemann, 1958; Frankenwald (Germany), Lochkovian.

Ancyrodelloides omus Murphy and Matti, 1982 beta morph
Fig. 11N.
1982 Ancyrodelloides omus n. sp. beta morph; Murphy and Matti 1982: 16, pl. 2: 14, 21−29 [only].

Material.—One Pa element from the Mytkiv Formation. Section and sample 45/170 m.
Remarks.—In morphology and denticulation the specimen does not differ significantly from the type material from Nevada. It is elongated (1.1 mm), has thick, high (0.3 mm) and sigmoidally curved blade, denticles differentiated in size, somewhat bigger cusp located at the mid-length of the blade. Basal cavity lips are unequal in size, asymmetrical and with a tubercle on the lips.

Stratigraphic and geographic range.—Caudicriodus triangles Zone in Podolia, Ancyrodelloides delta Zone in Nevada, Cooper Creek Limestone in Victoria (Australia).

Genus non satis notae “Ozarkodina” Branson and Mehl, 1933
(= Spathognathodus Branson and Mehl, 1941 [Walliser 1964, partly]; = Ozarkodina Branson and Mehl, 1933 [Jeppsson 1989, partly]; = “New Genus W” sensu Murphy et al. [2004])
Characteristic species: Spathognathodus steinhornensis eosteinhor−nensis Walliser, 1964 [Pa element]; Cellon section (Carnic Alps), Pridoli.

“Ozarkodina” eosteinhor−nensis (Walliser, 1964)
Figs. 11O, P, Q.
1964 Spathognathodus steinhornensis eosteinhor−nensis n. ssp.; Walliser 1964: 85, pls. 9: 15, 20: 19, 20, 21 upper, 22 [non pl. 20: 7−16, 23−25; text−fig. 9].
Non 1980 Ozarkodina remschiedensis eosteinhor−nensis (Walliser, 1964); Schönlaub 1980a: pl. 17: 16, 17, 18, 19 (= Zieglerodina remschiedensis [Ziegler, 1960]).
1984 Spathognathodus eosteinhor−nensis Walliser, 1964; Drygant 1984: 123, pl. 13: 9, 10 [only].
1990 Ozarkodina remschiedensis eosteinhor−nensis (Walliser, 1964); Olivieri and Serpagli 1990: 69, pl. 4: 11−15.
The level is defined as the Silurian/Devonian boundary by Mashkova (1972: pl. 2: 25–30) as the Ozarkodina stein−hornensis with wide roots.

From Cellon section in Carnic Alps (Walliser 1964: pl. 20: 19, 20, 21 upper, 22). Typical specimens distinctly differ from Zieglerodina remscheidensis (Ziegler, 1960) by presence of denticles on the basal cavity lips, straight upper and lower margins of the blade and comparatively low denticles with wide roots.

In the apparatus from Dzvenyhorod Formation illustrated by Mashkova (1972: pl. 2: 25–30) as the Ozarkodina steinhornensis eosteinhornensis (Walliser, 1964) the Pa element has the same morphology of blade and denticulation as the representatives of Zieglerodina remscheidensis (Fig. 12C) from the transitional Silurian/Devonian beds.

Stratigraphic and geographic range.—“Ozarkodina” eosteinhornensis Zone. Pridoli in Podolia, Pridoli Series in Barrandian Area (Czech Republic), Carnic Alps (Austria and Italy), Sardinia, Gotland, East Baltic, Roberts Mountains (central Nevada).

According to our investigations the uppermost occurrence of the typical specimens of “Ozarkodina” eosteinhornensis is coincident with the first occurrence of the graptole Monograptus uniformis angustidens Přihyl, 1940. The level is defined as the Silurian/Devonian boundary (Fig. 3).

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