Lochkovian conodonts from Podolia, Ukraine, and their stratigraphic significance

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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 phyletic 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; Kozłowski 1929; Nikiforova and Priedtiechiensky 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 Republik, 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 stratigraphically significant conodont species described from Podolia, and insufficient knowledge of their distribution in sections, the whole Lochovian 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

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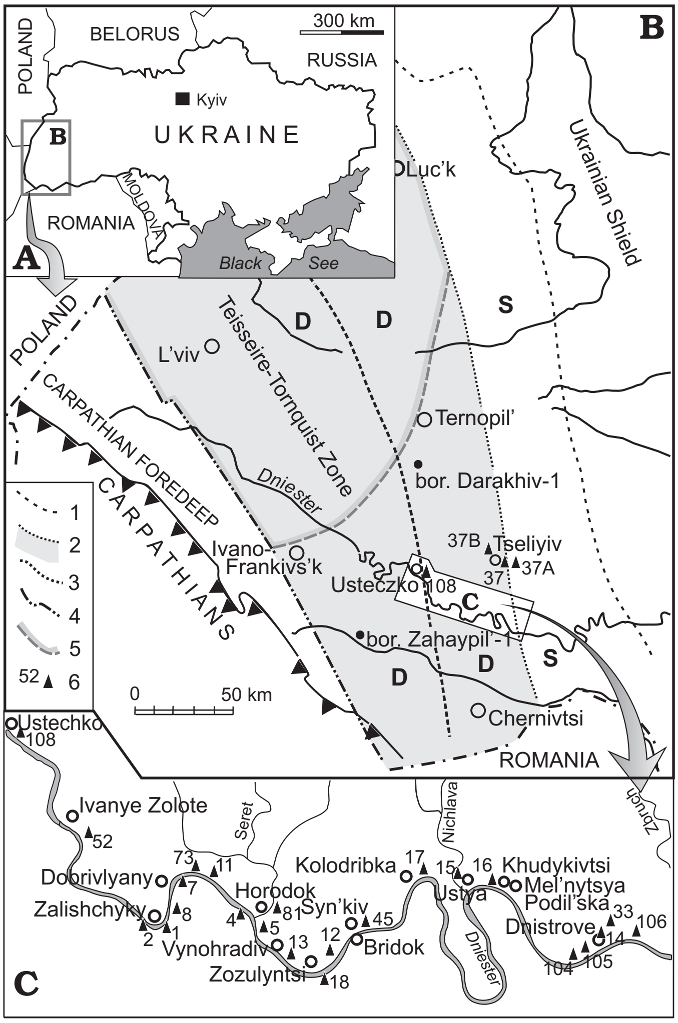

Fig. 1. **A**. General location of the study area. **B**. Distribution of the subsurface Silurian and Devonian deposits in Podolia and geological setting of the area. 1, Eastern extent of the Silurian deposits; 2, Eastern extent of the Devonian Tyver Group (see Fig. 2); 3, Eastern extent of Dniester Member (Old Red Formation); 4, Western extent of the Devonian deposits. 5. Extent of the Middle Devonian deposits (area of the Lviv Depression); 6, Location of the studied borings. **C**. Location and numbers of the studied outcrops (see also Table 1).

the results have been already published in Ukrainian (Drygant 2010); 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 extensive field investigations of both authors of the present paper. The new investigations have been undertaken for better recognition of the conodont species occurring in the region, their evolutionary development and stratigraphic ranges. We also confirm and better document some earlier observations on the great differentiation of the conodont assemblages in different facies. Their provincialism in distribution and sensitivity to facial fluctuations greatly complicate stratigraphic 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 results of the project (see Małkowski et al. 2009; Baliński 2010, 2012; Olempska et al. 2011; Filipiak at al. 2012; Olempska 2012; Racki et al. 2012; Voichyshyn and Szaniawski 2012). Some preliminary results of the new conodont investigations have been published earlier in the abstract volumes of international conferences (Drygant and Szaniawski 2008, 2009).

Institutional abbreviations.—SMNH, State Museum of Natural History, National Academy of Sciences of Ukraine, Lviv, Ukraine; ZPAL, Institute of Paleobiology, Polish Academy 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.20/7.28: 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

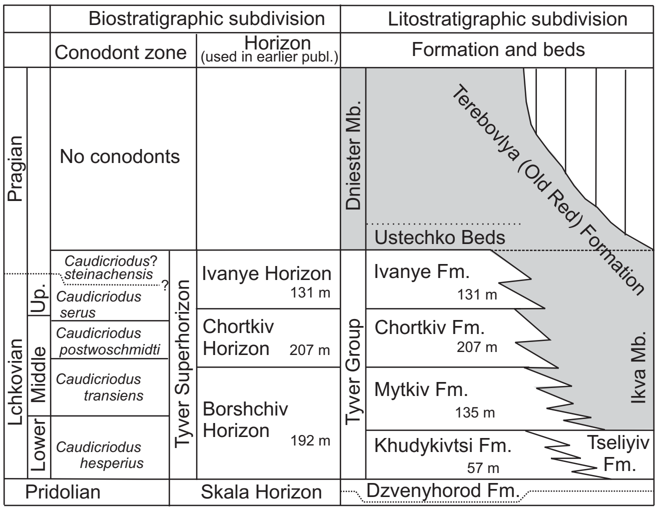

Fig. 2. Genaral stratigraphy of the Lower Devonian strata in Podolia (modified after Drygant 2010). Traditional, local division terms are used.Abbreviations: Fm., Formation; Mb., Member.

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; Voichyshyn 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 interbedding layers of shale and limestone, where *Monograptus uniformis angustidens* Přibyl, 1940, *Acastella heberti* (Gosselet, 1888), *Clorinda pseudolinguifera* Kozłowski, 1929, *Glossoleptaena 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 *Pristiograptus 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 Borshchiv, Chortkiv, and Ivanye horizons and Khudykivtsi, Mytkiv, Chortkiv, and Ivanye formations (Fig. 2) (see Nikiforova et al. 1972).

Borshchiv 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 Dnistrove in the east to the Nichlava 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* Přibyl, 1940), trilobites (*Warburgella rugulosa* Alth, 1874, *Acastella heberti elsana* R. and E. Richter, 1954, *A. tiro* R. and E. Richter, 1954), brachiopods (*Resserella elegantuloides* Kozłowski, 1929, *Clorinda pseudolinguifera* Kozłowski, 1929, *Glossoleptaena emarginata* [Havlíček, 1967], *Cyrtina praecedens* Kozłowski, 1929), and conodonts (*Zieglerodina remscheidensis* [Ziegler, 1960], *Caudicriodus woschmidti* [Ziegler, 1960], *C. hesperius* [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 Khudykivtsi 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 gray shale with thin interbeds and lenses of gray clayey limestone, partially detrital. Frequent agglomerations of the brachiopod shells form thin coquina layers and lenses. Most of the limestone beds are fossiliferous and contain numerous assemblages of brachiopods (*Lanceomyonia borealiformis* [Siemiradzki, 1906], *Plectodonta maria* Kozłowski, 1929, *Cyrtina praecedens* Kozłowski, 1929), trilobites (*Warburgella rugulosa* Alth, 1874, *Homalonatus roemeri* Comte, 1959), ostracods (*Opistoplax gyratus* Abushik, 1968, *Ochescapha podolica* [Abushik, 1968]), conodonts (*Zieglerodina remscheidensis* [Ziegler, 1960], *Caudicriodus transiens* [Carls and Gandl, 1969], *Caudicriodus hadnagyi* [Chatterton and Perry, 1977]), crinoids, 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 Dniester 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 interbedded 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 commonly occuring brachiopods (*Mutationella podolica* Kozłowski, 1929, *Howelella zaleszczykiensis* Kozłowski, 1929), ostracods (*Cornikloedenia inornata* [Alth, 1874], *C. binata* Abushik, 1971, *Evlanella rubeli* Krandijevsky, 1963), conodonts (*Caudicriodus postwoschmidti* [Mashkova, 1968], *Zieglerodina mashkovae* [Drygant, 1984]), also remnants of the agnathan fishes (*Thelodus oervigi* Talimaa, 1966 and *Podolaspis lerichei* [Zych, 1927]) are abundant (see Nikiforova 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 sediments in Podolia. Total thickness of the Formation is about 130 m. Its lower boundary is established at the first appearance 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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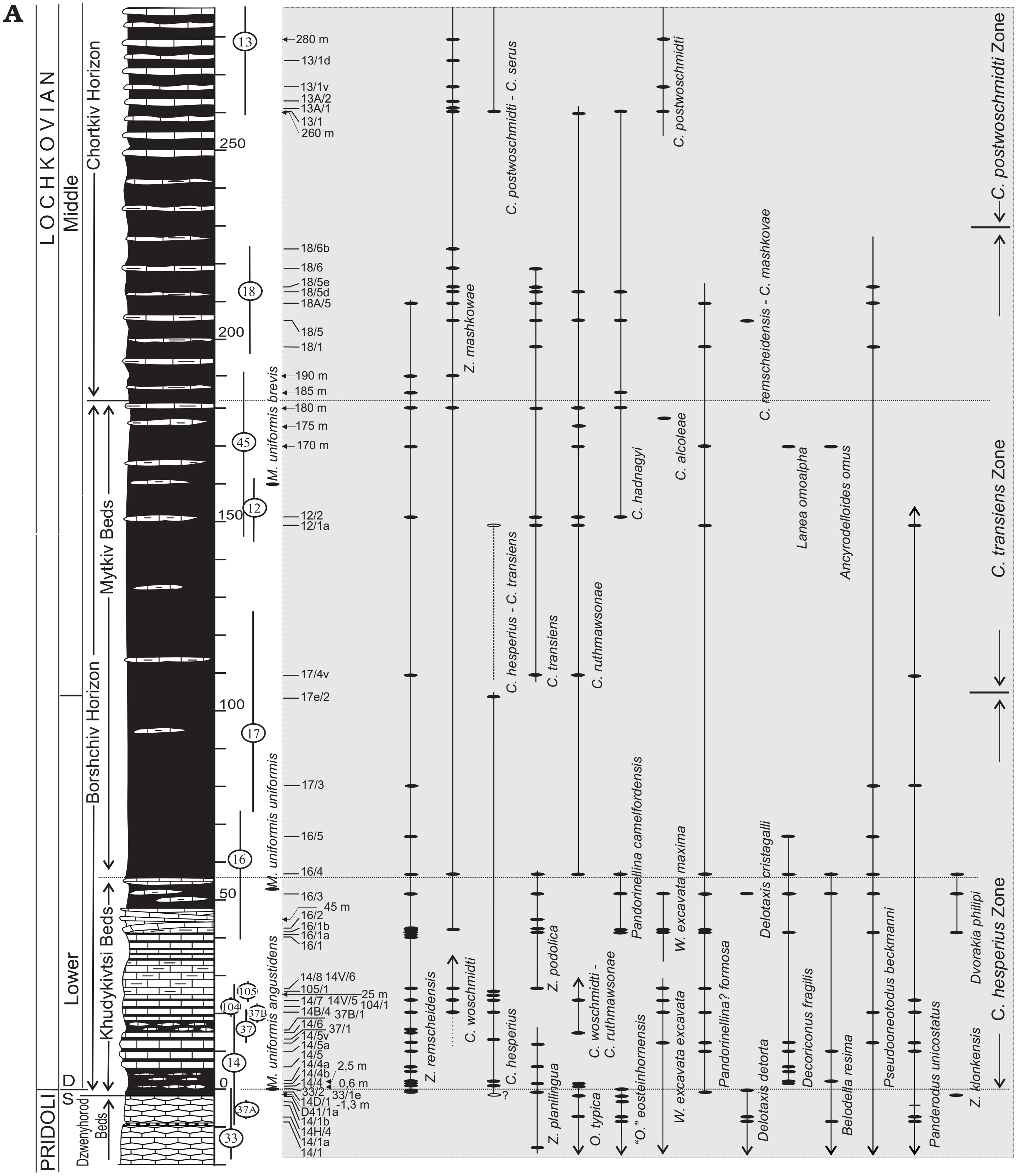
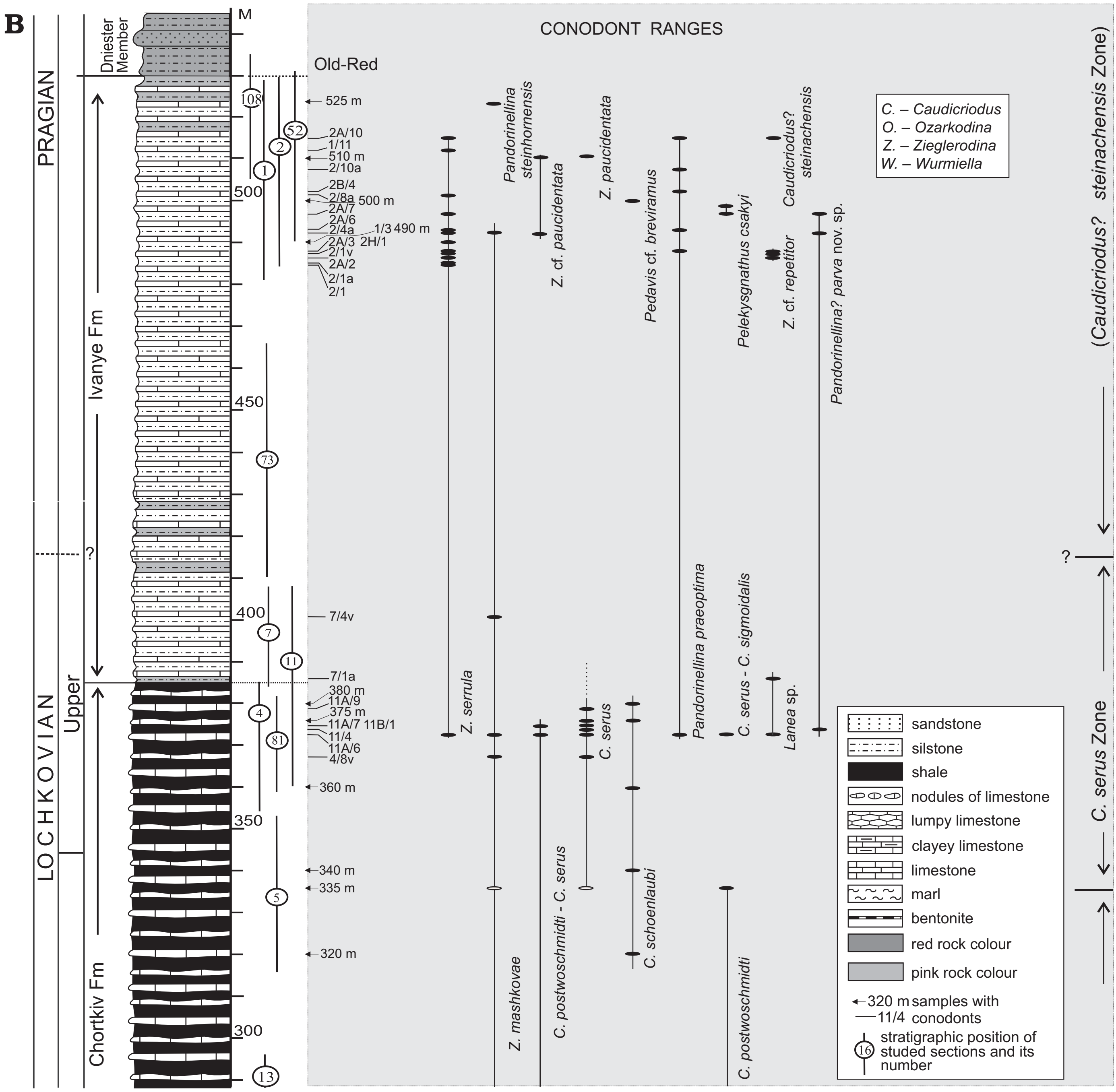


Fig. 3. Stratigraphic range of conodonts in the Lochkovian sequence of Podolia. **A**. Lower part. **B**. Upper part (see next page). D., Devonian; S., Silurian.

detrital or bioclastic (mainly ostracod) limestone. In the upper part, named Zalishchyky 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* Kozłowski, 1929 and *Leper-*



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 red 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

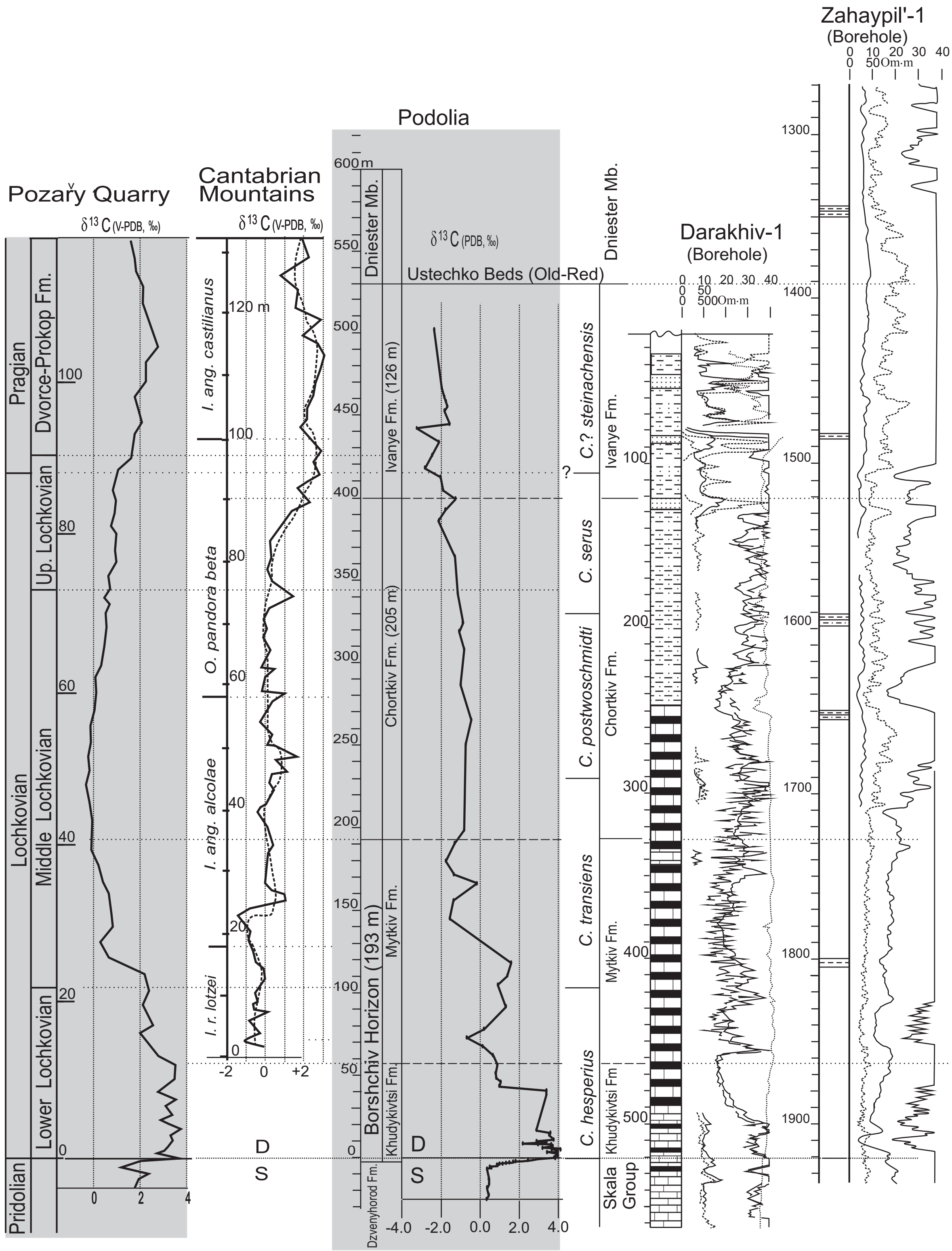


Fig. 4. Carbon isotope ($\delta^{13}C$) trends in the Lochkovian sections of Barrandian (Požáry Quarry), Cantabrian Mountais and Podolia. Subdivision of the Lochkovian after Slavík et al. (in press). Isotope curves, from Barrandian and Cantabrian Mountain after Buggisch and Mann (2004), from Podolia after Małkowski 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.

(= lower Lochkovian). 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 sedimentation 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 (Małkowski 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 boudary 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 Silurian/Devonian boundary is established directly beneath the first appearance of the graptolites *Monograptus uniformis angustidens* Přibyl, 1940 and *M. u. uniformis* Přibyl, 1940. Conodont species characteristic for the Lochkovian, mistakenly identified by J. Zikmundová (see Schönlaub 1980a: 178, 179) as *Icriodus* cf. *postwoschmidti* Mashkova, 1968, occurs there in one layer only, 4 m above the boundary. In other sections in the stratotype area (Barrandian) conodonts *Caudicriodus hesperius* (Klapper and Murphy, 1975) and *C.* ex. gr. *woschmidti* (Ziegler, 1960) were obtained from samples in lowest 6–8 m of the Lochkovian (Carls et al. 2007; Slavík et al. in press).

Except previous information about occurence 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 eoletericrescens* Zone became thicker, and coincides with the disapperance 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. 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* Graptolite 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-

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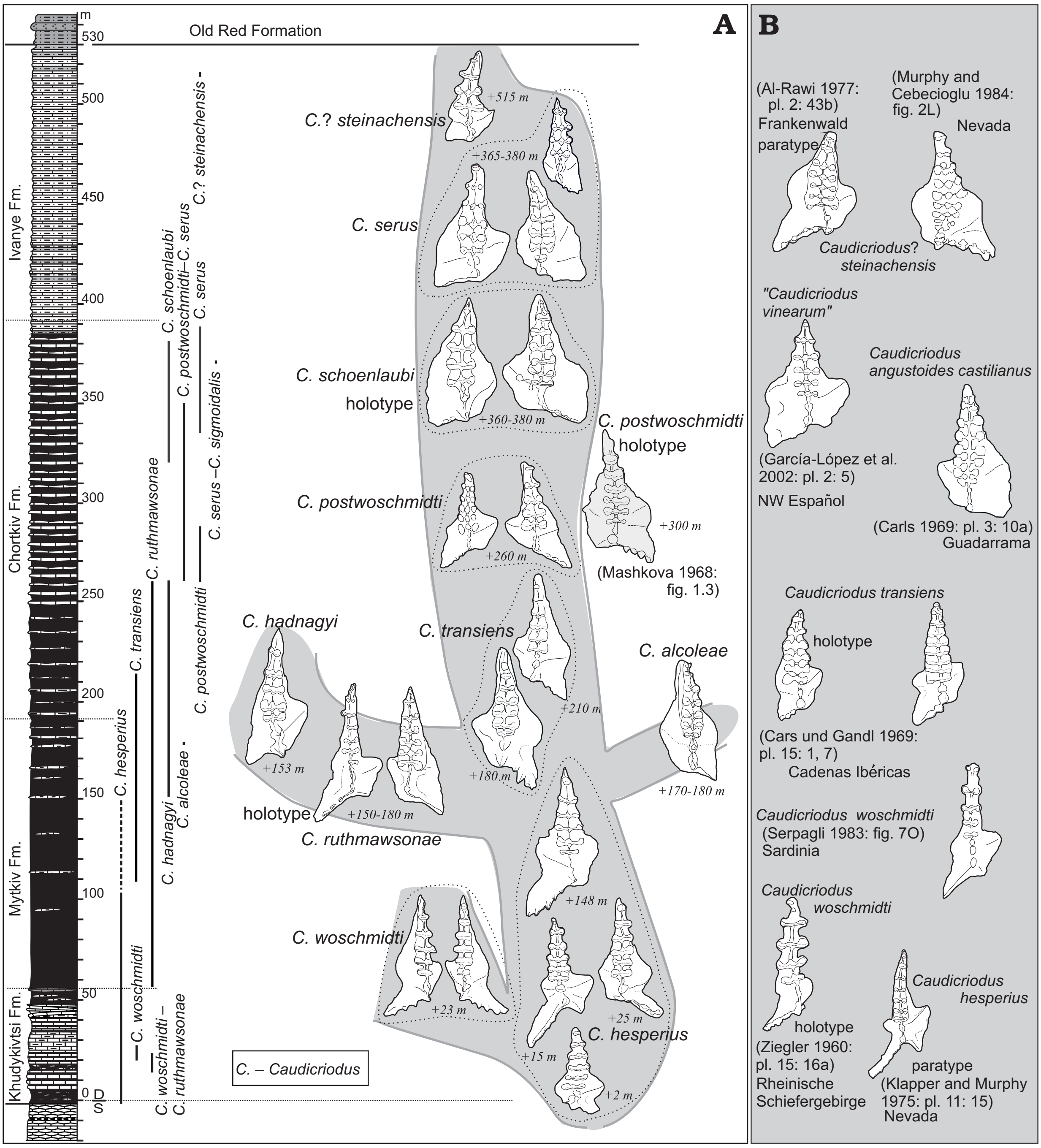

Fig. 5. **A**. Probable phyletic relationships within *Caudicriodus*, based on the evidence of the Podolian collection. **B**. Similar forms in other regions. D., Devonian; S., Silurian; Fm., Formation. For legend see Fig. 3.

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 convinced that *Icriodus eolatericrescens* 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 oher 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 occuring in the sediments are not diversified and not sufficient for precise age determination. Judging from the presence of *Caudicriodus*? *steinachensis* (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*" *eosteinhornensis* (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-Ríos, 1999), *Pseudooneotodus beckmanni* (Bischoff and Sannemann, 1958), and *Panderodus unicostatus* (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. mashkovae* (Drygant, 1984), *Z. flabellicauda* (Sorentino, 1989), *Z. planilingua* (Murphy and Valenzuela-Ríos, 1999), *Z. prosoplatys* (Mawson, Talent, Molloy, and Simpson, 2003) (Fig. 6).

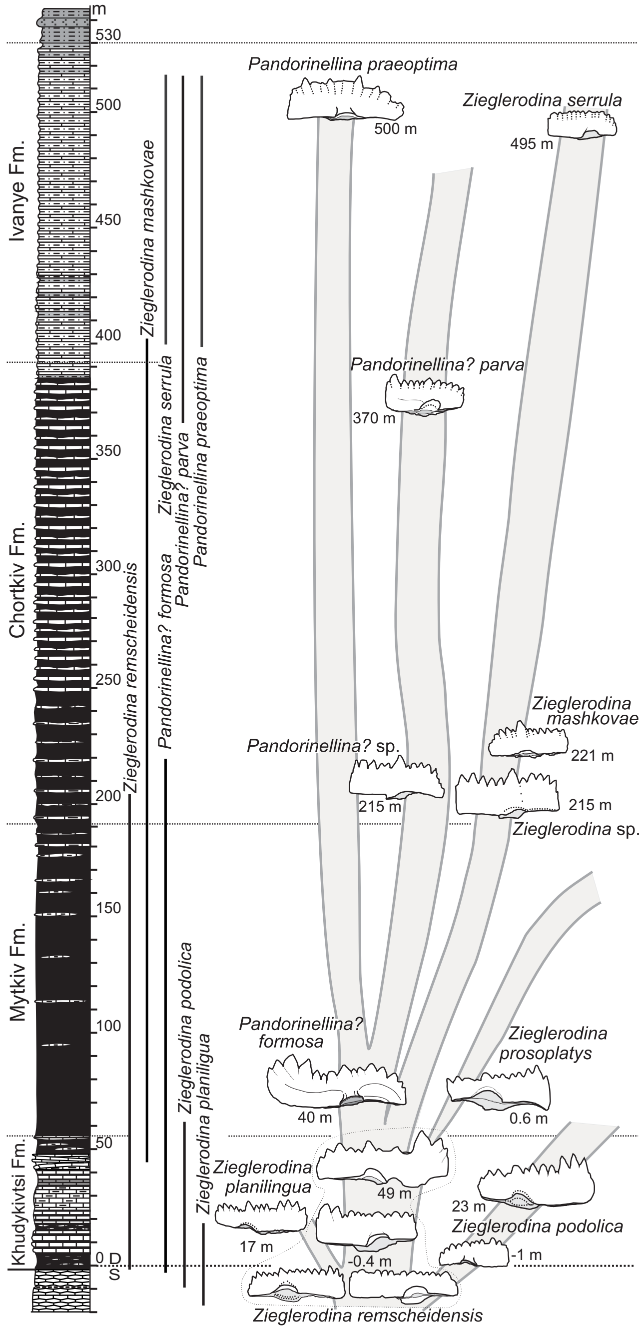

Fig. 6. Probable phyletic relationship within *Zieglerodina* and *Pandorinellina*? based on the Podolian collection. D., Devonian; S., Silurian; Fm., Formation. For legend see Fig. 3.

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

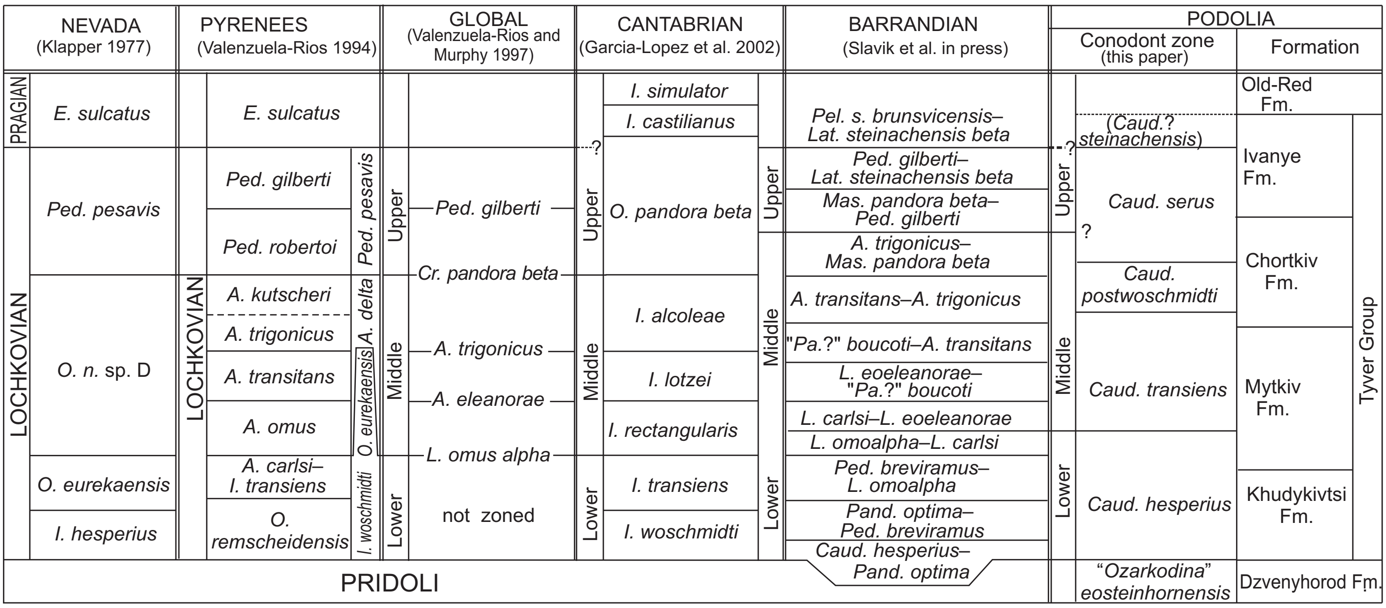

Fig. 7. Correlation of the Lochkovian conodont zonations in different regions. Abbreviations: *A.*, *Ancyrodelloides*; *Caud.*, *Caudicriodus*; *Cr.*, *Criteriognathus*; *E.*, *Eognathodus*; *I.*, *Icriodus*; *L.*, *Lanea*; *Lat.*, *Latericriodus*; *Mas.*, *Masaraella*; *Pand.*, *Pandorinellina*; "*Pa.*?", "*Pandorinellina*?"; *Ped.*, *Pedavis*; *Pel.*, *Pelekysgnathus*; *O.*, *Ozarkodina*; Fm., Formation.

of *Caudicriodus postwoschmidti* and *C. hesperius* in the lower part of the *M. uniformis* Zone (Schönlaub 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 (Mashkova 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 vinearum* Carls, 1975 (García-López 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), *Peleksygnatus csakyi* (Chatterton 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 ingression 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 hesperius*, *Caudicriodus transiens*, *Caudicriodus postwoschmidti*, *Caudicriodus serus*, and *Caudicriodus*? *steinachensis* (Fig. 7).

The *Caudicriodus hesperius* Zone corresponds in its stratigraphic range to the *Monograptus uniformis* Graptolite Zone. Its lower boundary is defined by the disappearance of "*Ozarkodina*" *eosteinhornensis* (Walliser, 1964) s. s. and *Delotaxis detorta* (Walliser, 1964). Conodonts occuring in this zone are: *Zieglerodina remscheidensis* (Ziegler, 1960), *Z. podolica* Drygant, 2010, *Z. planilingua* (Murphy and Valenzuela-Ríos, 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 morphological modifications of *Caudicriodus woschmidti,* which moving upwards gradually become more similar to *C. transiens* (Carls and Gandl, 1969) and other co-occuring 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 *Wurmiella excavata excavata* (Branson and Mehl, 1933), which gave rise to *Wurmiella 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 characteized by the comparatively common occurrence of the name giving species and *Zieglerodina mashkovae* (Drygant, 1984), the rare occurence 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 serus* 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 occurence 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.

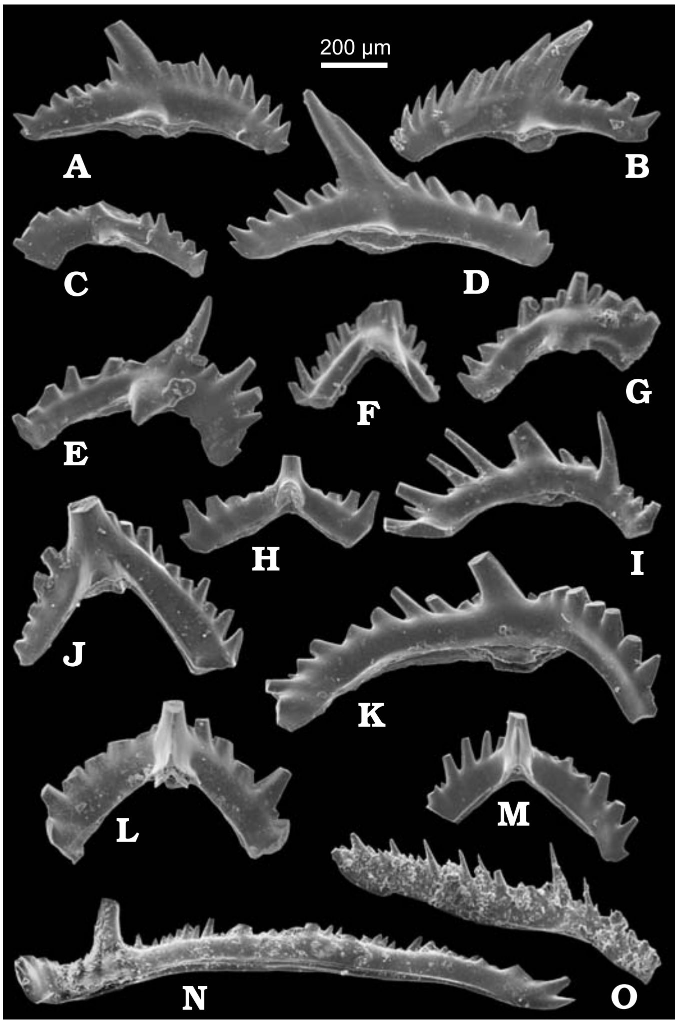

Fig. 8. Some discrete elements of the unassigned taxa from the Ivanye (**A**–**M**) and Khudykivtsi (**N**, **O**) formations, all in lateral view. **A**, **B**, **D**. Pb elements. **A**. Ivanye Zolote-52/515 m, ZPAL C.20/7.28. **B**. Zalishchyky-1/490 m, ZPAL C.20/6.5. **D**. Ivanye Zolote-52/515 m, ZPAL C.20/7.16. **C**, **E**, **G**. Sb elements. **C**. Ivanye Zolote-52/515 m, ZPAL C.20/7.17. **E**. Zalishchyky-1/490 m, ZPAL C.20/6.13. **G**. Ivanye Zolote-52/515 m, ZPAL C.20/7.29. **F**, **J**. M elements; Ivanye Zolote-52/515 m. **F**. ZPAL C.20/7.20. **J**. ZPAL C.20/7.14. **H**, **L**, **M**. Sa elements (probably genus *Pandorinellina*). **H**. Ivanye Zolote-52/515 m, ZPAL C.20/7.19. **L**. Zalishchyky-1/490 m, ZPAL C.20/6.11. **M**. Ivanye Zolote-52/515 m, ZPAL C.20/7.24. **I**, **K**. Sc elements. **I**. Zalishchyky-1/490 m, ZPAL C.20/6.10. **K**. Ivanye Zolote-52/515 m, ZPAL C.20/7.26. **N**, **O**. *Zieglerodina remscheidensis* (Ziegler, 1960); Dnistrove-14/1.3 m. **N**. Sb element, ZPAL C.20/ 1.15. **O**. Sc element, ZPAL C.20/1.14.

Material

The field investigations have been conducted in the years 2006–2010 in the natural outcrops situated on the escarp-

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Table 1. Studied sections (for locations see Fig. 1) with their GPS coordinates (when known).

Locality	Section number in this publication	Coordinates of the section		Section number in Nikiforova et al. (1972)
Dnistrove	33	N 48°32'30.5"	E 26°15'14.7"	
Dnistrove	14 (= 14A, 14B, 14V, 14D, D41)	N 48°32'16.9"	E 26°14'21.4"	64
Dnistrove	104	N 48°31'43.0"	E 26°12'32.0"	63
Dnistrove	105	N 48°32'19.6"	E 26°13'55.5"	
Dnistrove	106	N 48°32'31.3"	E 26°15'58.3"	
Khudykivtsi	16 (= 16B)	N 48°37'08.4"	E 26°07'28.4"	48
Ustya (= Mukhalkiv)	15	N 48°36'56.4"	E 26°05'19.3"	92
Kolodribka	17	N 48°38'56.9"	E 26°02'58.1"	52, 55
Syn'kiv (= Bohdanivka)	45	N 48°37'18.2"	E 25°58'53.3"	56
Zozulyntsi	13	N 48°35'44.4"	E 25°53'19.2"	70 [+77, pars]
Vynohradiv	5	N 48°36'22.3"	E 25°51'04.3"	71
Horodok	81	N 48°37'23.3"	E 25°51'48.5"	81
Dobrivlyany	11 (= 11A)	N 48°40'23.4"	E 25°47'24.7"	
Dobrivlyany	73	N 48°40'35.4"	E 25°47'04.9"	73
Zalishchyky	1	N 48°37'54.8"	E 25°44'12.9"	58
Zalishchyky	2 (= 2A, 2V)	N 48°38'00.3"	E 25°43'52.0"	
Ivanye Zolote	52	N 48°42'21.7"	E 25°39'12.5"	76
Ustechko	108	N 48°46'8.04"	E 25°36'7.07"	116
Syn'kiv	12			
Bridok	18 (= 18A)			66
Myshkivtsi	37A			88
Tseliyiv	37			105
Mazurivka	37B			106

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 cacalcareous 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 apparatuses 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 occurrence 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 (*Caudicriodus 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:

1975 *Icriodus woschmidti hesperius* subsp. nov.; Klapper and Murphy 1975: 48, pl. 11: 1–19.

1980 *Icriodus woschmidti hesperius* Klapper and Murphy; Klapper and Johnson 1980: pl. 2: 11.

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 asssigned 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 trasitional forms between the genera *Pedavis* and *Caudicriodus*.

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

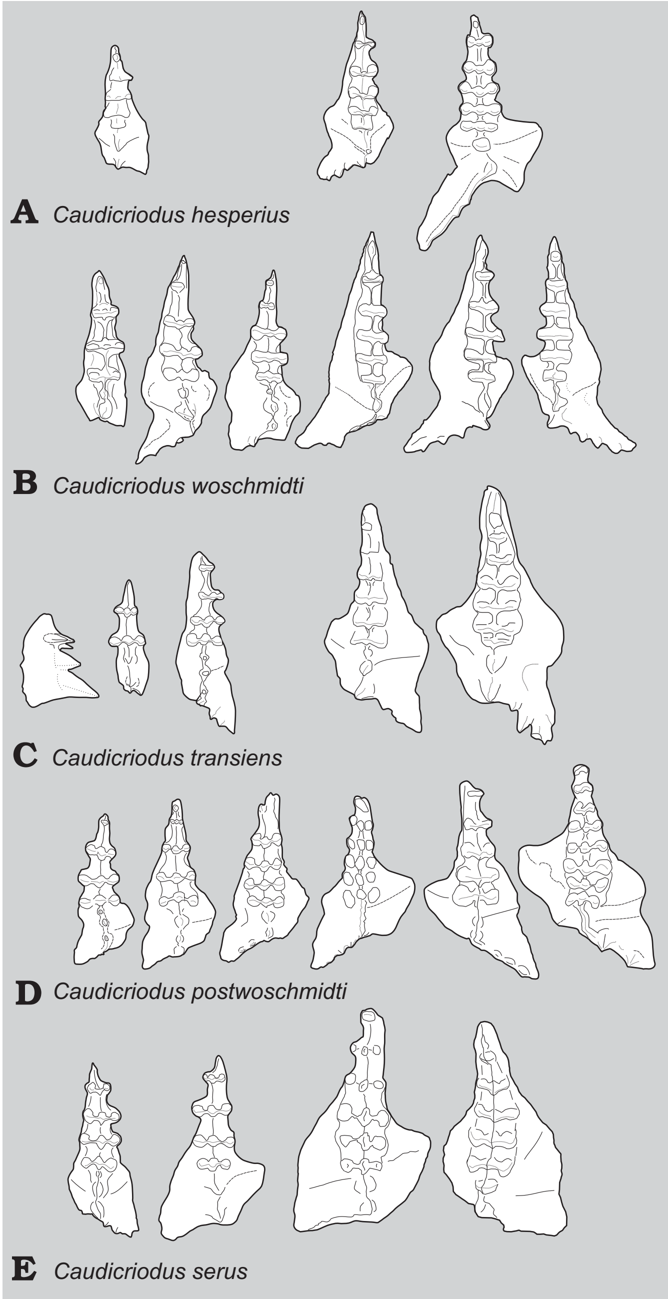

Fig. 9. Ontogenetic development and morphological comparison of Pa elements of Podolian *Caudicriodus* species.

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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)].

?1980 *Icriodus woschmidti* ssp.; Schönlaub 1980b: pl. 3: 19.

2003 *Caudicriodus woschmidti woschmidti* (Ziegler 1960); Bultynck 2003: pl. 1: 1–3.

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, especialy the outline of basal cavity and denticulation of the spindle, 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)].

1976 *Caudicriodus postwoschmidti* (Mashkova, 1968); Bultynck 1976: 26, pl. 6: 1–2.

?1980 *Icriodus woschmidti hesperius* Klapper and Murphy; Schönlaub 1980b: pl. 6: 5.

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].

2003 *Icriodus woschmidti woschmidti* Ziegler, 1960; Farrell 2003: 125, pl. 2: 4.

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

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

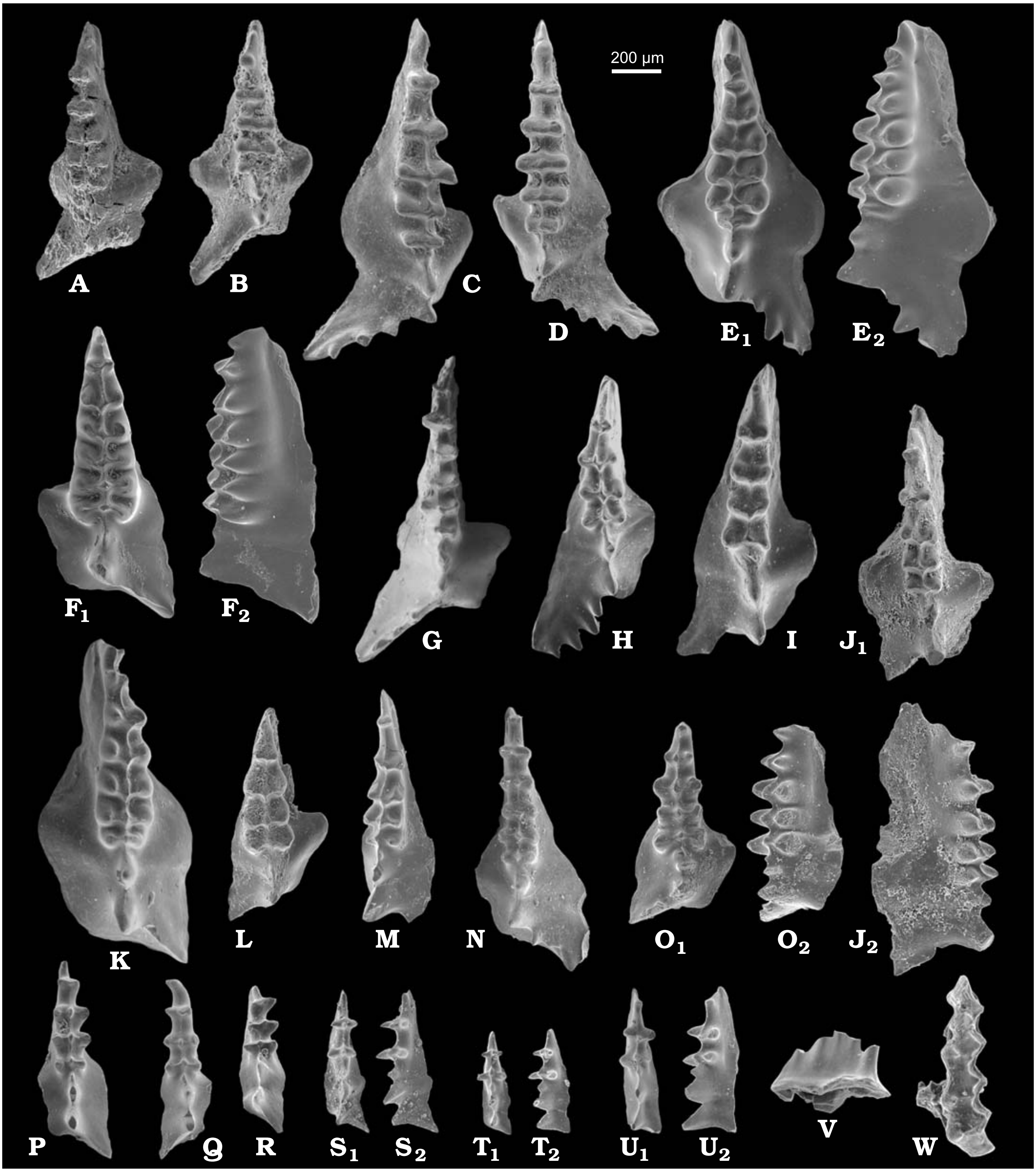
Material.—Twelve Pa elements from the Mytkiv Formation and lower part of the Chortkiv Formation. Sections and samples: 16/4, 12/1a, 2, 17/4b, 18/5, 5d, 45/170 and 180 m, 13/260 m.

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 *Caudi-*

Fig. 10. SEM photographs of Pa elements of icriodontid conodonts, Podolia, Early Devonian. **A**, **B**. *Caudicriodus hesperius* (Klapper and Murphy, 1974). **A**. Dnistrove-14/1.3 m, ZPAL C.20/1.1. **B**. Dnistrove-14/3.1 m, ZPAL C.20/3.1. **C**, **D**. *Caudicriodus woschmidti* (Ziegler, 1960); Dnistrove-105/1. **C**. SMNH D1123d. **D**. SMNH D1123e; reillustrations of the typical specimens from Drygant (2010: pl. 2: 12, 13). **E**, **I**. *Caudicriodus transiens* (Carls and Gandl, 1969). **E**. Syn'kiv-45/180 m, ZPAL C.20/2.1. I. Syn'kiv-45170–180 m, ZPAL C.20/11.10. **F–H**. *Caudicriodus ruthmawsonae* Drygant, 2010. **F**. Zozulyntsi-13/260 m, ZPAL C.20/4.18. **G**. Syn'kiv-12/1a, SMNH D1129a, reillustration of the holotype from Drygant (2010, pl. 3: 1a). **H**. Syn'kiv-45/170 m, ZPAL C.20/11.8. **J**, **L**. *Caudicriodus hadnagyi* (Chatterton and Perry, 1977). **J**. Syn'kiv-45/185 m, ZPAL C.20/4.1. **L**. Zozulyntsi-13/260 m, →



ZPAL C.20/4.20. **K**. *Caudicriodus alcoleae* (Carls, 1969); Syn'kiv-45/170–180 m, ZPAL C.20/11.9. **M**. Juvenile form of ?*Caudicriodus transiens* (Carls and Gandl, 1969); Dobrivlyany-11/380 m, ZPAL C.20/2.4. **N**, **Q**–**U**. Juvenile forms of different species of *Caudicriodus* (*Caudicriodus transiens*–*Caudicriodus serus* zones). **N**. Syn'kiv-45/180 m, ZPAL C.20/4.13. **Q**. Syn'kiv-45/185 m, ZPAL C.20/4.2. **R**. Syn'kiv-45/185 m, ZPAL C.20/ 4.7. **S**. Dnistrove-105/25 m, ZPAL C.20/3.5. **T**. Dobrivlyany-11/375 m, ZPAL C.20/2.9. **U**. Syn'kiv-45/180 m, ZPAL C.20/2.5. **O**. *Caudicriodus postwoschmidti* (Mashkova, 1968); Vynohradiv-5/335 m, ZPAL C.20/5.2. **P**. Juvenile form of *Caudicriodus postwoschmidti* (Mashkova, 1968), Zozulyntsi-13/280 m, ZPAL C.20/4.19. **V**. *Pelekysgnathus csakyi* (Chatterton and Perry, 1977); Ivanye Zolote-52/498 m, ZPAL C.20/11.24. **W**. *Pedavis* cf. *breviramus* Murphy and Matti, 1982; Ivanye Zolote-52/500 m, ZPAL C.20/9.13. A–D, E_1, F_1, G–I, J_1, K–N, O_1, P–R, S_1–U_1, W upper wiew; E_2, F_2, J_2, S_2–U_2, V lateral view.

criodus hesperius Zone and *C. transiens* Zone. Podolia, Southwestern Sardinia, Guadarrama Mountains (Spain), New South Wales (Australia), and Texas.

Caudicriodus hadnagyi (Chatterton and Perry, 1977)

Fig. 10J, L.

1977 *Icriodus hadnagyi* n. sp.; Chatterton and Perry 1977: 792, pl. 4: 10–22.

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. Platfom 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 Northwestern Canada.

Caudicriodus transiens (Carls and Gandl, 1969)

Figs. 9C, 10E, I.

Pa element

1968 *Icriodus eolatericrescens* sp. n.; Mashkova 1968b: 942 [partim].

1969 *Icriodus woschmidti transiens* n. ssp.; Carls und Gandl 1969: 174, pl. 15: 1–7.

1970 *Icriodus angustoides bidentatus* Carls and Gandl, 1969; Mashkova 1970: fig. 1: 1–6 [form juv.].

1970 *Icriodus woschmidti transiens* Carls and Gandl, 1969; Mashkova 1970: fig. 1: 7–9 [form adult.].

1975 *Icriodus postwoschmidti* Mashkova; Klapper in Ziegler 1975: 155 (partim), *Icriodus* plate 5: 5 (non 3, 4 = *Caudicriodus postwoschmidti* [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].

1984 *Icriodus eolatericrescens* Mashkova; Drygant 1984: 135, pl. 16: 17–19.

non 1994 *Icriodus woschmidti transiens* Carls and Gandl, 1969; Valenzuela-Ríos 1994: 88, pl. 8: 20.

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].

1974 *Rotundacodina noguerensis* Carls and Gandl; Drygant 1974: pl. 2: 24, 25.

1974 *Rotundacodina elegans* Carls and Gandl; Drygant 1974: pl. 2: 19–21.

1974 *Rotundacodina quadratibasis* sp. n.; Drygant 1974: 69, pl. 2: 9–11.

1974 *Drepanodus*? *curvatus* (Rhodes); Drygant 1974: pl. 2: 18.

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*? *quadratibasis* Drygant; Drygant 1984: 78, pl. 1: 43–45.

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.

1969 *Icriodus angustoides alcoleae* n. ssp.; Carls 1969: 326, pl. 1: 12; pl. 2: 1–2.

1976 *Caudicriodus angustoides alcoleae* (Carls, 1969); Bultynck 1976: 34, pl. 4: 14, 18–28; text-fig. 2.

1980 *Icriodus woschmidti hesperius* Klapper and Murphy; Schönlaub 1980a: pl. 19: 1, 12.
1994 *Icriodus angustoides alcoleae* Carls; Valenzuela-Ríos 1994: 93, pl. 8: 9–10, 12–13, 18, 27, 34.
2002 *Icriodus angustoides alcoleae* Carls; García-López et al. 2002: pl. 1: 11, 12.
2002 *Icriodus angustoides* aff. *alcoleae* Carls; García-López at al. 2002: pl. 1: 13.
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 Lebanza Formations (lower and middle Lochkovian) of Northwesern 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].
1968 *Icriodus woschmidti postwoschmidti* ssp. n.; Mashkova 1968b: 943, fig. 1: 1–3 [mature form].
1985 *Icriodus* sp. n. A; Schönlaub 1985: pl. 2: 23 [only].
2004 *Latericriodus steinachensis* (Al-Rawi) beta morph Klapper and Johnson; Slavík 2004: pl. 1: 4.
2004 *Latericriodus steinachensis* (Al-Rawi) eta morph Klapper and Johnson Slavík 2004: pl. 1: 5.
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 coniform 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 posession 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].

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2002 *Icriodus vinearum* Carls; García-López et al. 2002: pl. 2: 5.
?2007 *Icriodus steinachensis* Al-Rawi eta morphotype Klapper and Johnson; Slavík et al. 2007: fig. 3: 4 [only].
?2012 *Icriodus angustoides 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, determined as *Icriodus vinearum* Carls, 1975 (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-Raw 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.

Stratigraphic and geographic range.—*Caudicriodus postwoschmidti* Zone and lower part of *Caudicriodus serus* Zone (middle–upper Lochkovian) in Podolia, Lebanza Formation (middle Lochkovian) of Northwestern Spain, ?upper Lochkovian in Barrandian.

Caudicriodus serus (Drygant, 1984)

Figs. 9E, 11J–L.

1971 *Icriodus postwoschmidti*; Mashkova 1971: pl. 3: 1 [non 8, 9].
1984 *Icriodus serus* sp. n.; Drygant 1984: 135, pl. 16: 27–29.
?2004 *Latericriodus steinachensis* (Al-Rawi eta morph Klapper and Johnson; Slavík and Hladil 2004: 144, pl. 1: 2 [only].
2010 *Caudicriodus serus*; Drygant 2010: 62, pls. 3: 21, 4: 5, 8, 9, 11.

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 wide behind the fourth transverse ridge and is the widest approximately opposite the second transverse ridge. Outer bord of platform in all elements slighty 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 postwoschmidti* (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 angustoides 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 undenticulated edge. In our opinion its morphology is closest to *Caudicriodus serus*.

Stratigraphic and geographic range.—*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.

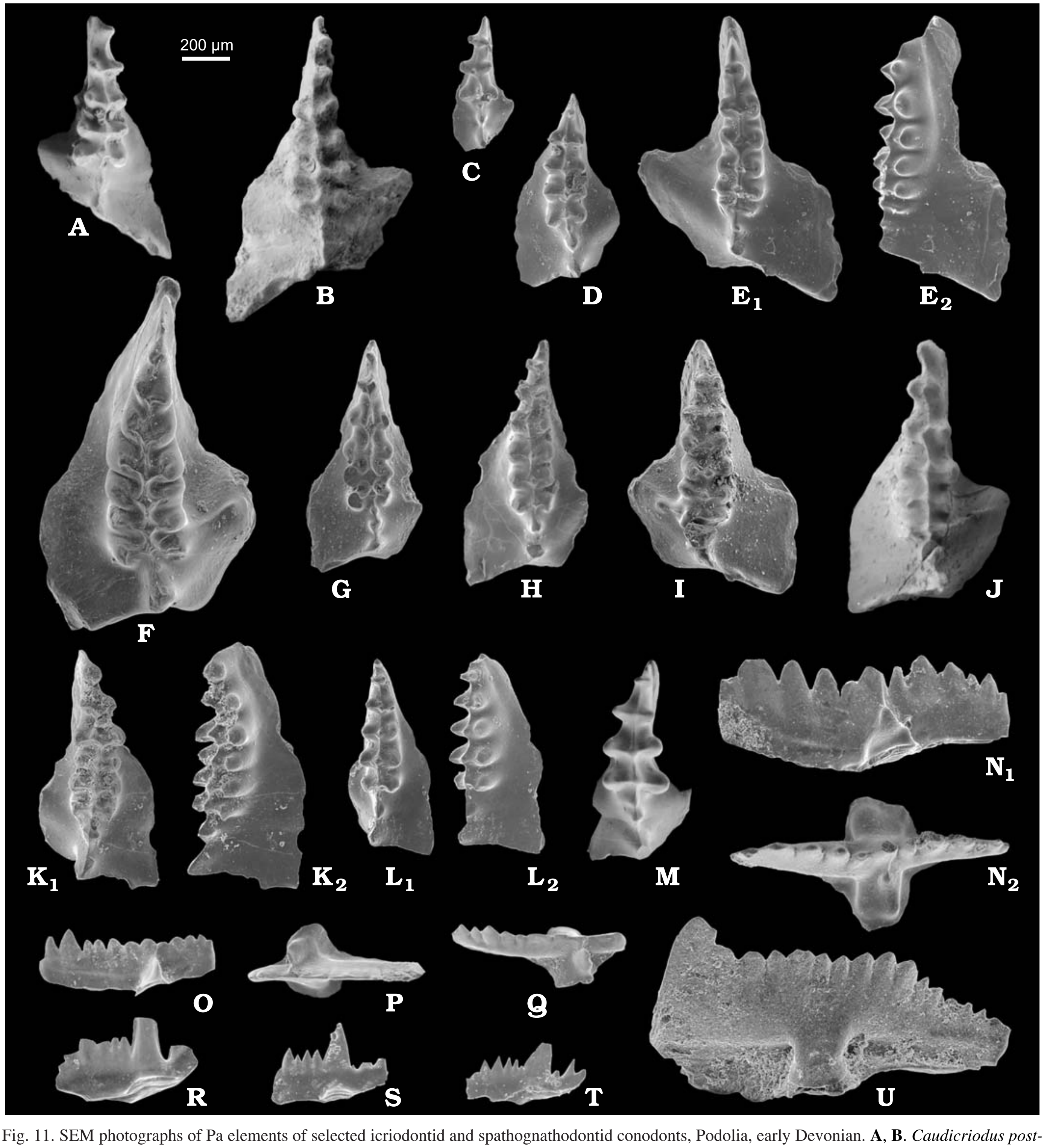

Fig. 11. SEM photographs of Pa elements of selected icriodontid and spathognathodontid conodonts, Podolia, early Devonian. **A**, **B**. *Caudicriodus postwoschmidti* (Mashkova, 1968); Zozulyntsi-13/1. **A**. SMNH D1139b. **B**. SMNH D1139v. Reillustration of specimens from the locus typicus after Drygant (2010: pl. 4: 2, 6). **C**–**I**. *Caudicriodus schoenlaubi* sp. nov. **C**. Dobrivlyany-11/375 m, ZPAL C.20/5.13. **D**. Horodok-81/380 m, ZPAL C.20/8.5, holotype. **E**. Horodok-81/380 m, ZPAL C.20/5.1. **F**, **G**. Vynohradiv-5/340 m. **F**. ZPAL C.20/8.6. **G**. ZPAL C.20/8.8. **H**. Dobrivlyany-11/375 m, ZPAL C.20/2.7. **I**. Vynohradiv-5/320 m, ZPAL C.20/8.7. **J**–**L**. *Caudicriodus serus* (Drygant, 1984). **J**. Dobrivlyany-11A/9, SMNH D1142, paratype from the type locality, after Drygant (2010, pl. 4: 8). **K**, **L**. Dobrivlyany-11/400 m. **K**. ZPAL C.20/2.8. **L**. ZPAL C.20/2.6. **M**. *Caudicriodus*? *steinachensis* (Al-Rawi, 1977); Zalishchyky-2A/10, SMNH D1146a. **N**. *Ancyrodelloides omus* Murphy and Matti, 1982; Syn'kiv-45/170 m, ZPAL C.20/11.13. **O**, **P**, **Q**. "*Ozarkodina*" *eosteinhornensis* (Walliser, 1964); Dnistrove-33/1e. **O**. SMNH D1422a. **P**. SMNH D1422b. **Q**. SMNH D1422v. **R**. *Zieglerodina paucidentata* (Murphy and Matti, 1982); Ivanye Zolote-52/510 m, ZPAL C.20/9.12. **S**, **T**. *Zieglerodina* cf. *paucidentata* (Murphy and Matti, 1982); Ivanye Zolote-52/490 m. **S**. ZPAL C.20/11.22. **T**. ZPAL C.20/11.23. **U**. ?*Ozarkodina typica* Branson and Mehl, 1933. Dnistrove-14/0.5 m, ZPAL C.20/11.5. A–D, E_1, F–J, K_1, L_1, M, N_2, P, Q upper view; E_2, K_2, L_2, N_1, O, R–U lateral view.

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1965 *Icriodus bilatericrescens* Ziegler; Philip 1965: 103, pl. 9: 30–32.
1969 *Icriodus latericrescens* n. ssp. B; Klapper 1969: 8, pl. 2: 6–9.
1977 *Icriodus steinachensis* n. sp.; Al-Rawi 1977: 55, pl. 5: 42–43.
1979 *Icriodus steinachensis* Al-Rawi, 1979; Lane and Ormiston 1979: pl. 4: 28, 29.
1980 *Icriodus steinachensis* Al-Rawi, 1980a; Schönlaub: pl. 6: 14–17; pl. 7: 20, 21.
1980 *Icriodus steinachensis* Al-Rawi eta morphotype; Klapper and Johnson 1980: pl. 2: 25–27.
1981 *Icriodus steinachensis* Al-Raw eta morphotype; Johnson and Klapper 1981: pl. 1: 13–16, 18, 19.
1982 *Icriodus steinachensis* Al-Rawi eta morph; Murphy and Matti 1982: 58, pl. 5: 31, 36.
1984 *Icriodus steinachensis* Al-Rawi; Murphy and Cebecioglu 1984: fig. 2A–R, Z–HH, 5G–Q.
1985 *Icriodus steinachensis* Al-Rawi eta morphotype; Schönlaub 1985: pl. 2: 13–16.
1994 *Icriodus steinachensis* Al-Rawi; Valenzuela-Ríos 1994: 89, pl. 8: 1–3, 5–8, 11.
1994 *Icriodus steinachensis* (Al-Rawi) eta morph Klapper and Johnson; Mawson and Talent 1994: 47, fig. 9K–N.
non 2004 *Latericriodus steinachensis* (Al-Rawi) eta morph Klapper and Johnson; Slavík 2004: pl. 1: 5 [= *Caudicriodus. postwoschmidti* (Mashkova, 1968)].
2004 *Latericriodus steinachensis* (Al-Raw) eta morph Klapper and Johnson; Slavík and Hladil 2004: 144, pl. 1: 3 [non pl. 1: 2 = ?*Caudicriodus serus* (Drygant, 1984) and pl. 1: 4 = *C. postwoschmidti* (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; Slavík et al. 2007: fig. 3: 2, 3 [?non fig. 2: 4 = *Caudicriodus schoenlaubi* sp. nov.].
2010 *Caudicriodus* sp. [?*C. serus* (Drygant, 1984)]; Drygant 2010: pl. 4: 13.

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 a little curved, transverse ridges flattened, spur short but well-developed. Postero-lateral process short, undenticulated. 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, undenticulated postero-lateral process and bigger space between the transverse ridges.

The taxon "*I. steinachensis* eta morphotype" is reffered 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* Bultynck, 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.

1977 *Icriodus csakyi* n. sp.; Chatterton and Perry 1977: 793, pl. 4: 4–6.
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 lenth 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.

Stratigraphic and geographic range.—*Ancyrodelloides 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 remscheidensis* Ziegler, 1960; Rhenish Slate Mountains, Hüinghaus Beds, lower Lochkovian.

Remarks.—All elements constructing apparatus of the *Zieglerodina remscheidensis* were described by Ziegler (1960) as discrete species *Spathognathodus remscheidensis* Ziegler, 1960, *Ozarkodina denckmanni* Ziegler, 1960, *Prioniodina bicurvata pronoides* Walliser, 1960, "*Trichonodella* n. sp. aff. *symmetrica*" (Branson and Mehl, 1933) (= *T. alternata* Drygant, 1984), *Plectospathodus* cf. *extensus* Rhodes, 1953 (= *P. alternatus* Walliser, 1964), "*Hindeodella* n. sp." of Walliser 1960 (= *H. alternata* Drygant, 1984). All these form species were described also from Podolia (Mashkova 1972: pl. 2: 19–21, 23, 24 [non 22]; Drygant 1984).

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); Mashkova1972: 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 remscheidensis* (Ziegler, 1960); 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-Ríos, 1999]), 9, 10 (= ?); pl. 2, fig. 8 (= *Zieglerodina prosoplatys* 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, 5, 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 ohers. 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 Pridoli, similarly as in Estonia (Viira 1999).

Stratigraphic and geographic range.—From the "*Ozarkodina*" *eosteinhornensis* Zone (uppermost Pridoli) to lower part of *Caudicriodus transiens* Zone in Podolia (Figs. 3, 6), Hüinghaus Beds of Rhenish Slate Mountains, Haragan Formation of Oklahoma, Road River Formation of Canadian Cordillera, Lochkovian of Barrandian Area (Czech Republic) and Poland, Elmside Formation of New Sout Wales (Australia).

Zieglerodina podolica Drygant, 2010

Fig. 12H, I, J.

?1980 *Pandorinellina* cf. *praeoptima* (Mashkova); Schönlaub 1980a: pl. 19: 8 [only].

1984 *Spathognathodus remscheidensis* Ziegler; Drygant: pl. 13: 17, 21 [only].

2010 *Zieglerodina podolica* nov. sp.; Drygant 2010: 52, pl. 1: 11, 12.

Material.—25 Pa specimens from the uppermost part of Dzvenyhorod, Khudykivtsi, and Tseliyiv formations. Sections and samples: 33/1e, 105/1, 37/A, 37B/1, 16/1, 1b, 2, 3, 4, 16/45 m.

Remarks.—The species is related to *Zieglerodina remscheidensis* (Ziegler, 1960) and *Z. klonkensis* Carls, Slavík, and Valenzuela-Ríos, 2007. It differs from the typical representatives of the first by comparatively long (0.6–1.0 mm) and high (0.3 mm) anterior part and lower (0.1–0.22 mm) posterior part of the blade, slightly convex anterior margin and narrower anterior denticles. Second of the species characterize arched lower margin of the blade, as well as more regularly and tightly arranged denticles which continue to the anterior end of the blade. Somewhat similar is also *Zieglerodina 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-Ríos, 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].

1999 "*Ozarkodina*" *planilingua* n. sp.; Murphy; Valenzuela-Ríos 1999: 326, pl. 1: 1–9.

2003 "*Ozarkodina*" *planilingua* Murphy and Valenzuela-Ríos; Farrell 2003: 136, pl. 7: 20–23.

2003 *Ozarkodina remscheidensis remscheidensis* (Ziegler); Farrell 2003: 137, pl. 8: 17, 18 [only].

2003 *Ozarkodina martinssoni 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-Ríos; Barrick et al. 2005: 120, pl. 1: 11, 12; non pl. 1: 3, 4 [= *Z. remscheidensis* (Ziegler, 1960)].

2010 *Zieglerodina planilingua* (Murphy and Valenzuela-Ríos); Drygant 2010: 52, pl. 1: 9.

Material.—16 Pa elements from the Dzvenyhorod, Khudykivtsi and Tseliyiv Formations. Sections and samples 14/1,3 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 middle Lochkovian in central Nevada and Spanish Pyrenees, New South Wales (Australia), Frame Formation in Texas.

Zieglerodina prosoplatys (Mawson, Talent, Molloy, and Simpson, 2003)

Fig. 13E, F, J.

1977 *Ozarkodina remscheidensis remscheidensis* n. form beta; Chatterton 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].
2003 *Ozarkodina remscheidensis prosoplatys* n. subsp.; Mawsonet al. 2003: 92, pl. 1: 4–23.
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. 12U, 13G, K.

1971 *Spathognathodus* sp. nov.; Mashkova 1971: pl. 3: 11, 14.
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].
1994 *Ozarkodina eladioi* n. sp; Valenzuela-Ríos 1994: 59, pl. 5: 1–35.
2010 *Zieglerodina mashkovae* (Drygant); Drygant 2010: 53, pl. 1: 18–20.

Material.—About 290 complete Pa elements from Khudykivtsi, Chortkiv and lower part of Ivanye Formation. Sections and samples: 16/1v, 18/5, 5d, 5e, 6, 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-Ríos (1994: 59, pl. 5: 1–35) 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 Pirenees, Iberian Chains, Guadarrama Mountains (Spain).

Zieglerodina serrula (Drygant, 1984)

Fig. 12W, Z, AA.

1984 *Spathognathodus serrula* sp. n.; Drygant 1984: 126, pl. 14: 24, 25.

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.

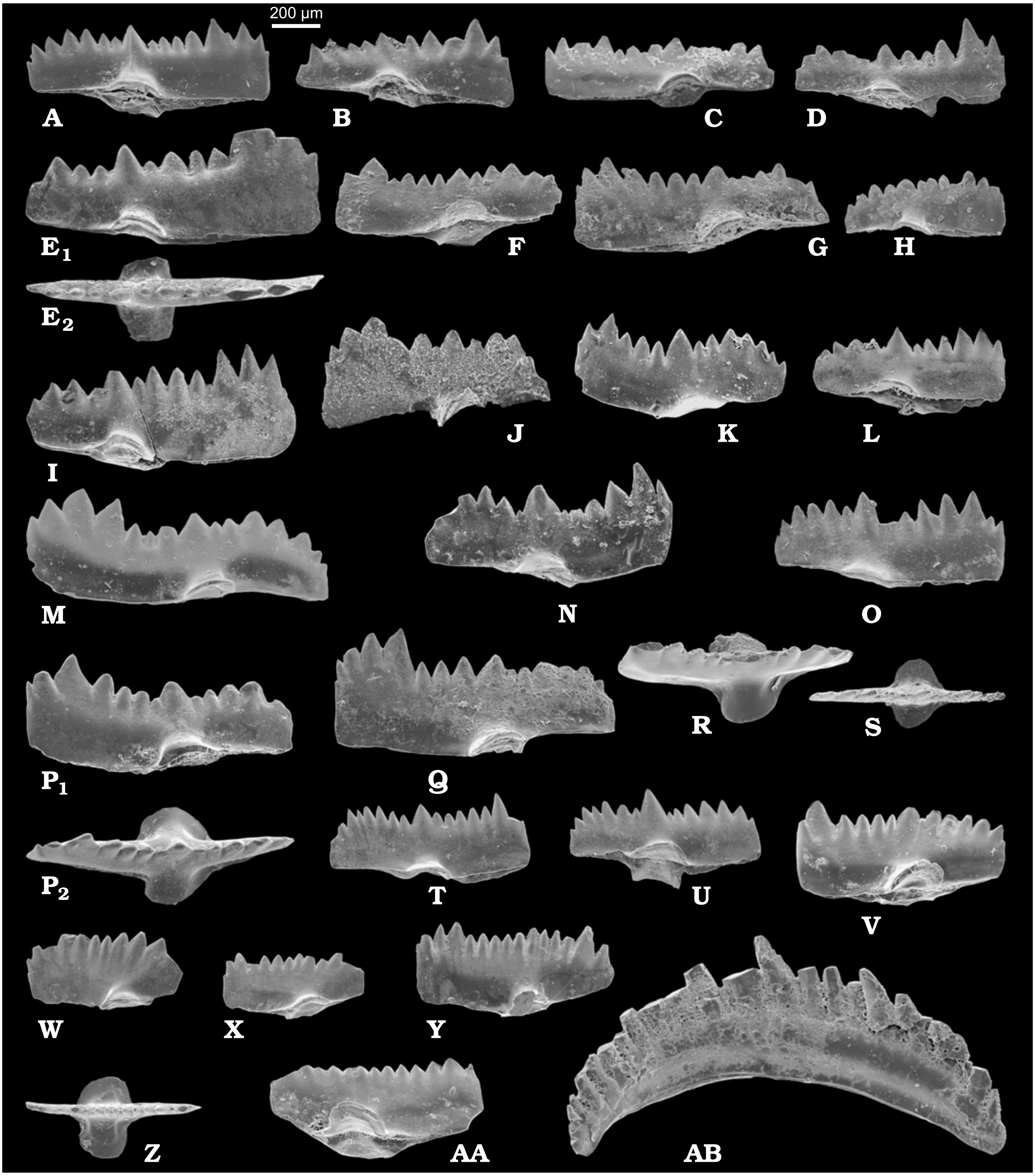
The elements are closest to *Zieglerodina mashkovae* (Drygant, 1984), but distinctly differ from it by the regularly arranged denticles, their nearly equal size and lack of the cusp.

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

Zieglerodina paucidentata (Murphy and Matti, 1982)

Fig. 11R.

Fig. 12. SEM photographs of Pa elements of spathognathodontid conodonts, genera *Zieglerodina*, *Pandorinellina*, and *Wurmiella*, family Spathognathodontidae, Podolia, Early Devonian. **A**–**G**. *Zieglerodina remscheidensis* (Ziegler, 1960). **A**. Dnistrove-14V/5, SMNH D 1423. **B**. Khudykivtsi-16/3, SMNH D 1430. **C**. Dnistrove-14/0.3 m, ZPAL C.20/1.16. **D**. Dnistrove-14/2 m, ZPAL C.20/9.29. **E**. Syn'kiv-45/170 m, ZPAL C.20/11.2. **F**. Khudykivtsi-16/47 m, ZPAL C.20/11.17. **G**. Dnistrove-106/10 m, ZPAL C.20/12.1. **H**, **I**, **J**. *Zieglerodina podolica* Drygant, 2010. **H**. Dnistrove-33/1e, SMNH D1424. **I**. Dnistrove-105/1, SMNH D1109, reillustration of the holotype from Drygant (2010: pl. 1: 12). **J**. Khudykivtsi-16/45 m, ZPAL C.20/11.3. **K**, **M**, **N**, **P**–**R**. *Pandorinellina*? *formosa* Drygant, 2010. **K**. Khudykivtsi-16/3, SMNH D1432. **M**. Khudykivtsi-16/1v, SMNH D 1419, reillustration of the holotype from Drygant (2010: pl. 1: 25). **N**. Dnistrove-14/1.3 m, ZPAL C.20/11.12. **P**. Syn'kiv-45/170 m, ZPAL C.20/11.21. →



Q. Mazurivka-37B/1, SMNH D1431. **R**. Khudykivtsi-16/1v, SMNH D1427. **L**, **O**, **S**, **T**. Transitional forms between *Zieglerodina remscheidensis* (Ziegler, 1960) and *Z. mashkovae* (Drygant, 1984). **L**. Khudykivtsi-16/3, SMNH D 1428. **O**. Tseliyiv-37/1b, SMNH D 1425. **S**. Khudykivtsi-16/3, SMNH D 1426. **T**. Syn'kiv-45/190 m, ZPAL C.20/10.19. **U**. *Zieglerodina mashkovae* (Drygant 1984); Syn'kiv-45/190 m, ZPAL C.20/10.22. **V**, **Y**. *Pandorinellina*? *parva* sp. nov. **V**. Dobrivlyany-11/4, SMNH D1420, holotype. **Y**. Ivanye Zolote-52/525 m, ZPAL C.20/9.5. **W**, **Z**, **AA**. *Zieglerodina serrula* (Drygant, 1984). **W**. Ivanye Zolote-52/525 m, ZPAL C.20/9.2. **Z**. Zalishchyky-1/1, SMNH D1433. **AA**. Zalishchyky-2/1v, SMNH D1434. **X**. Transitional form between *Zieglerodina serrula* (Drygant, 1984) and *Pandorinellina*? *parva* sp. nov.; Ivanye Zolote-52/525 m, ZPAL C.20/9.16. **AB**. *Wurmiella excavata maxima* (Drygant, 1984); Khudykivtsi-16/1v, SMNH D1436. A–D, E_1, F–O, P_1, Q, T–Y, AA, AB lateral view; E_2, P_2, R, S, Z upper view.

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 praeoptima (Mashkova, 1972)

Fig. 13R, S.

1972 *Ozarkodina steinhornensis praeoptima* n. subsp.; Mashkova 1972: 84, pl. 2: 13–18.

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

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

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

2010 *Pandorinellina praeoptima* (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 serus* and *Caudicriodus*? *steinachensis* zones, upper Lochkovian? to Pragian in Podolia.

Pandorinellina? *formosa* Drygant, 2010

Fig. 12K, M, N, P–R.

1971 *Spathognathodus steinhornensis* subsp. nov. aff. *Sp. steinhornensis remscheidensis* Ziegler; Mashkova 1971: pl. 3: 10.

1984 *Spathognathodus remscheidensis* Ziegler; Drygant 1984: pl. 13: 28, pl. 14: 4 [only].

1984 *Spathognathodus mashkovae* sp. n.; Drygant 1984: pl. 14: 12 [only].

2010 *Pandorinellina formosa* nov. sp.; Drygant 2010: 54, pl. 1: 25.

Material.—Above 20 Pa elements from Khudykivtsi and Mytkiv Formations. Sections and samples: 14/5v, 6, 7, 14V/5, 105/1, 16/1b, 1v, 2, 3, 4, 37/1, 1a, 1b, 2, 37A/2, 37B/1, 12/1a,18/1, 18A/5, 14/1,3 m, 45/170 m. Other elements of the multielement apparatus are still unknown.

Remarks.—Pa elements have intermediate shape between *Ozarkodina typica* Branson and Mehl, 1933 and *Zieglerodina remscheidensis* (Ziegler, 1960) (for comparisons of this species see also Chatterton and Perry 1977: 791). Comparatively long (0.8–1.1 mm) blade twisted up in the anterior part and down in the posterior. The denticles are low, with wide basis; the one above the basal cavity slightly bigger. Also 3–4 anterior denticles higher than others, slightly bowed backwardly or (rarely) increasing rapidly and erect. Basal cavity located closer to the posterior end or approximately at mid-length.

Pandorinellina? *formosa* differs from the related to it *Zieglerodina remscheidensis* (Ziegler, 1960) by sigmoidaly curved blade. It differs from somewhat similar *Pandorinellina camelfordensis* (Farrell, 2004) by wider and deeper basal cavity, as well as by bigger and rounded cavity lips.

Stratigraphic and geographic range.—*Caudicriodus hesperius* and *Caudicriodus transiens* zones, lower to middle Lochkovian in Podolia.

Pandorinellina? *parva* sp. nov.

Fig. 12V, Y.

2010 *Pandorinellina* sp. nov.; Drygant 2010: pl. 1: 21.

Etymology: From Latin *parva*, 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.

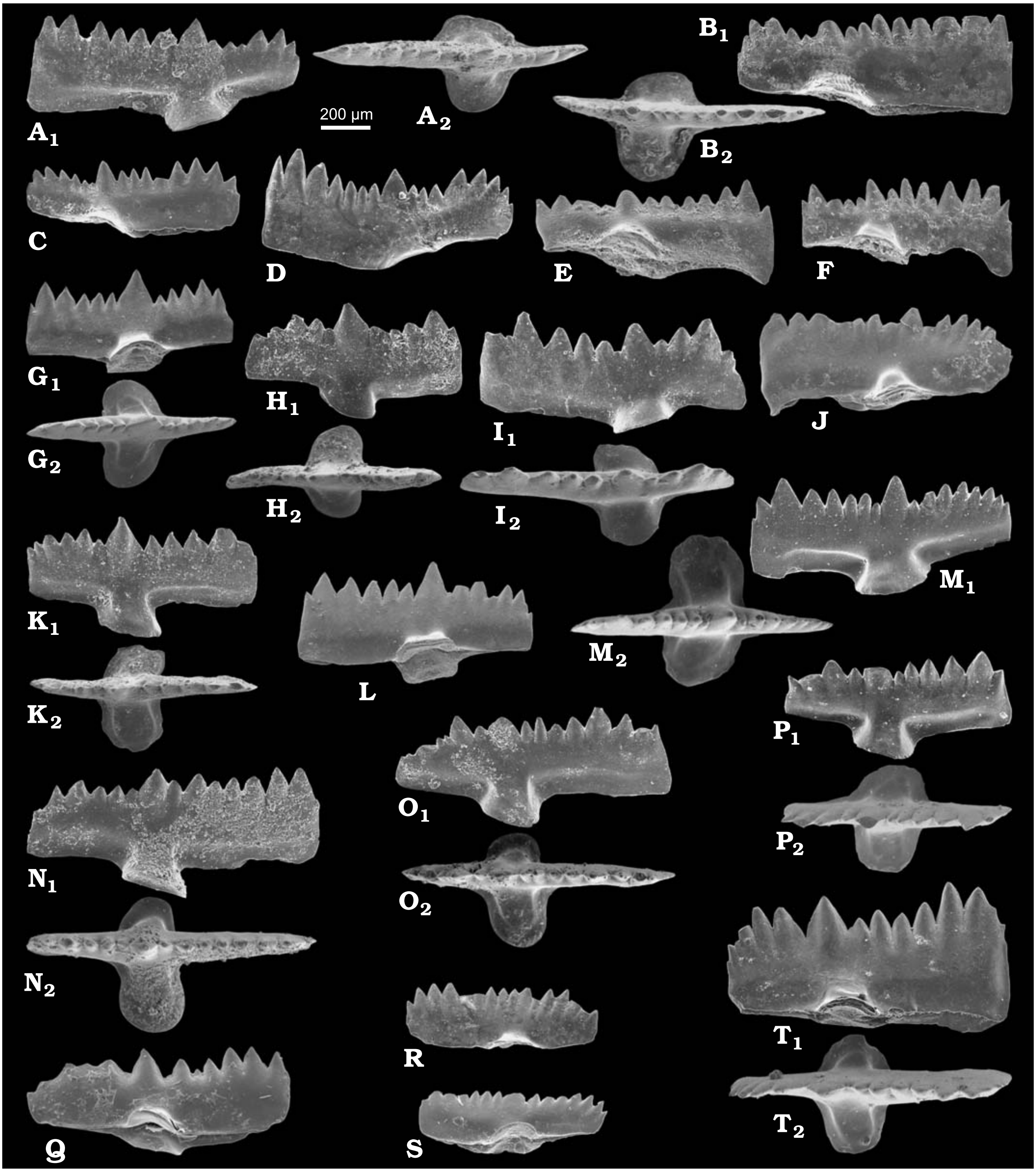
Material.—Five complete Pa elements and numerous fragments from Ivanye Formation. Sections and samples: 11/4, 52/525 m. Other elements of the multielement apparatus are not know.

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 sigmoidal 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.

Fig. 13. SEM photographs of Pa elements of spathognathodontid conodonts, genera *Zieglerodina*, *Pandorinellina*, and *Lanea*, Podolia, Early Devonian. **A–D**. *Zieglerodina planilingua* (Murphy and Valenzuela-Ríos, 1999). **A**, **B**. Dnistrove-106/15 m. **A**. ZPAL C.20/11.6. **B**. ZPAL C.20/11.7. **C**. Tseliyiv-37/1a, SMNH D1107. **D**. Dnistrove-14/1.3 m, ZPAL C.20/11.11. **E**, **F**, **J**. *Zieglerodina prosoplatys* (Mawson, Talent, Molloy, and Simpson, 2003). **E**. Dnistrove-14/0.6 m, ZPAL C.20/10.23. **F**. Dnistrove-14/2,5 m, ZPAL C.20/10.1. **J**. Ivanye Zolote-52/500 m, ZPAL C.20/9.20. **G**, **K**. *Zieglerodina mashkovae* →



(Drygant, 1984); Syn'kiv-45/180 m. **G**. ZPAL C.20/11.18. **K**. ZPAL C.20/11.19. **H**. Transitional form between *Zieglerodina mashkovae* (Drygant, 1984) and *Pandorinellina*? sp.; Syn'kiv-45/170 m, ZPAL C.20/11.20. **I**. Transitional form between *Zieglerodina remscheidensis* (Ziegler, 1960) and *Pandorinellina*? *formosa* Drygant, 2010; Khudykivtsi-16/45 m, ZPAL C.20/11.4. **L**. Transitional form between *Zieglerodina remscheidensis* (Ziegler, 1960) and *Z. mashkovae* (Drygant, 1984); Syn'kiv-45/190 m, ZPAL C.20/10.20. **M**, **P**, **T**. *Lanea omoalpha* Murphy and Valenzuela-Ríos, 1999; Syn'kiv-45/170 m. **M**. ZPAL C.20/11.14. **P**. ZPAL C.20/11.16. **T**. ZPAL C.20/11.15. **N**, **O**. *Pandorinellina steinhornensis* (Ziegler, 1956); Ustechko-108/525 m. **N**. ZPAL C.20/11.25. **O**. ZPAL C.20/11.26. **Q**. Transitional form between *Zieglerodina remscheidensis* (Ziegler, 1960) and *Pandorinellina*? sp.; Khudykivtsi-16/1v, SMNH D1429. **R**, **S**. *Pandorinellina praeoptima* (Mashkova, 1972). **R**. Zalishchyky-2/490 m, ZPAL C.20/9.21. **S**. Zalishchyky-2/1v, SMNH D1435. A_1, B_1, C–F, G_1– I_1, J, K_1, L, M_1–P_1, Q–S, T_1 lateral view; A_2, B_2, G_2–I_2, K_2, M_2–P_2, T_2 upper view.

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

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

Type species: *Ozarkodina excavata tuma* Murphy and Matti, 1983; central Nevada, Lower Devonian, *Ancyrodelloides delta* Zone.

Wurmiella excavata maxima (Drygant, 1984)

Fig. 12A, B.

1960 *Spathognathodus* n. sp.; Walliser 1960: 35, pl. 8: 7.
1968 *Spathognathodus inclinatus inclinatus* (Rhodes); Drygant 1968b: 51, fig. 24, 25.
1980 *Ozarkodina wurmi* (Bischoff and Sannemann); Schönlaub 1980a: pl. 19: 17.
1984 *Spathognathodus inclinatus maximus* ssp. n.; Drygant 1984: 122, pl. 10: 17, 18.
2005 *Ozarkodina wurmi* (Bischoff 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 *Wurmiella* 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; Salmontrout 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].
1999 *Lanea omoalpha* n. sp.; Murphy and Valenzuela-Ríos 1999: 327, pls. 1: 10–19, 23, 27–29, 2: 12–14.
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 somewath higher.

Stratigraphic and geographic range.—*Caudicriodus transiens* 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 morp; 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 transiens* Zone in Podolia, *Ancyrodelloides delta* Zone in Nevada, Coopers 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 eosteinhornensis* Walliser, 1964 [Pa element]; Cellon section (Carnic Alps), Pridoli.

"*Ozarkodina*" *eosteinhornensis* (Walliser, 1964)

Figs. 11O, P, Q.

1964 *Spathognathodus steinhornensis eosteinhornensis* 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 1972 *Ozarkodina steinhornensis eosteinhornensis* (Walliser, 1964); Mashkova 1972: 83, pl. 2: 25–30 (= *Zieglerodina remscheidensis* [Ziegler, 1960]).
Non 1980 *Ozarkodina remscheidensis eosteinhornensis* (Walliser, 1964); Schönlaub 1980a: pl. 17: 16, 17, 18, 19 (= *Zieglerodina remscheidensis* [Ziegler, 1960]).
1984 *Spathognathodus crispus* Walliser, 1964; Drygant 1984: 126, pl. 10: 12, 13.
1984 *Spathognathodus eosteinhornensis* Walliser, 1964; Drygant 1984: 123, pl. 13: 9, 10 [only].
1989 *Ozarkodina s. eosteinhornensis* (Walliser, 1964) sensu Jeppsson 1975; Jeppsson 1989: 28, pl. 2: 1–4; pl. 3: 10.
1990 *Ozarkodina remscheidensis eosteinhornensis* (Walliser, 1964); Olivieri and Serpagli 1990: 69, pl. 4: 11–15.

1992 *Ozarkodina remscheidensis remscheidensis* (Ziegler, 1960); Barrick and Klapper 1992: pl. 6: 14, 15 [only].
2004 New genus W *eosteinhornensis* (Walliser, 1964); Murphy et al. 2004: 16, fig. 2.45–2.47; 3.26–3.28; 3.33–3.35.
2007 Genus W *eosteinhornensis* (Walliser, 1964); Carls et al. 2007: fig. 8A–F.
2012 *Ozarkodina eosteinhornensis* s.s. (Walliser, 1964); Corradini and Corriga 2012: fig. 6J.

Material.—Six specimens of Pa elements from the upper part of the Dzvenyhorod Formation. Sections and samples: 32/1v, 33/1e, D14/1, D41/1a.

Remarks.—Pa elements of the species characterize straight, comparatively elongated (approximately 0.66 mm) and high blade with about 10 wide denticles, sub-equal in height and 2–3 higher at the anterior end. The denticles are nearly completely fused. The posterior process is about half the length of the anterior one or even shorter. Upper and lower margins of them are subparallel. Basal cavity well-developed, with asymmetrical lips. Outer basal cavity lip is wider and bears one flattened denticle.

Podolian Pa elements are nearly identical in morphology and size to those described by Jeppsson (1989: 28, pl. 2: 1–4) from Klonk (Czech Republic) and to the typical specimens 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 repesentatives 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 graptolite *Monograptus uniformis angustidens* Přibyl, 1940. The level is defined as the Silurian/Devonian boundary (Fig. 3).

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