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# Taxonomy and biostratigraphic significance of *Icriodus orri* Klapper and Barrick and related Middle Devonian conodont species

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**Abstract.**—The present study of the Eifelian icriodid conodonts is based on collections from Belarus and the Michigan Basin (USA). It is here proposed that forms originally included in *Icriodus orri* Klapper and Barrick, 1983 can be attributed to *I. retrodepressus* Bultynck, 1970, *Icriodus orri* sensu stricto, and *Icriodus michiganus* new species, each displaying a distinct morphology, stratigraphical range, and geographic distribution. *Icriodus retrodepressus*, characterized by a triangular spindle, deep depression in its posterior part, and a well-pronounced spur and antispur, appeared in the lower *partitus* Zone of the lowermost Eifelian and disappeared in the upper Eifelian *kockelianus* Zone. *Icriodus michiganus* n. sp., distinguished by a lachrymiform spindle with a shallow posterior depression, ranges from the lower *costatus* Zone to the upper *kockelianus* Zone. *Icriodus orri* differs from the other two species by the occurrence of transverse denticle rows with lateral denticles displaying sharp edges. It ranges from the upper *kockelianus* Zone to the *ensensis* Zone of the uppermost Eifelian. *Icriodus retrodepressus* first occurred in the European part of the Euramerican continent and later migrated into the North American area. *Icriodus michiganus* n. sp. has been found in the interior part of the North American Craton and near the eastern Euramerican margin. *Icriodus orri* occurs in the North American interior, in British Columbia (Canada), and in the eastern part of Euramerica (Belarus). The introduction of *I. retrodepressus* can be related to the transgressive Choteč Event, whereas that of *I. orri* to a transgressive stage of the Ie eustatic cycle.

## Introduction

The conodont species *Icriodus orri* was erected by Klapper and Barrick (1983) for $P_1$ elements differing from *I. retrodepressus* Bultynck, 1970 by a wider posterior part of the basal cavity. Its large intraspecific variability was indicated by the authors by defining two morphotypes. The illustrated material was obtained from the lower part of the Spillville Formation exposed in Iowa and southern Minnesota (USA). The age of the studied sections was estimated approximately as the *kockelianus* Zone of the upper Eifelian.

Preliminary study of the original material included in *Icriodus orri* confirms its morphological inhomogeneity. The $P_1$ elements differ not only in the presence or absence of the depression but also in the outline of the spindle, course of its axis, size, and shape of the denticles. Even the size and shape of the basal cavity, important criteria for distinction of the species from *I. retrodepressus*, are variable. This suggests that *I. orri* sensu Klapper and Barrick (1983) comprises forms that can be attributed to more than a single species.

The aim of the present study is a taxonomic revision of the material presented by Klapper and Barrick (1983), aided by the authors' own collections from the Michigan Basin (USA) and Pripyat Graben (Belarus), together with relevant published data. In addition to morphological features, stratigraphical ranges and geographic distributions are also discussed in detail.

## Studied materials and their regional background

The Belarussian material was obtained from the drill cores from the wells Zhitkovichi 2 and Pinsk 54 situated in the western part of the Pripyat Graben (Fig. 1; Golubtsov et al., 2000, fig. 1; Narkiewicz and Kruchek, 2008, fig. 2). During the Middle Devonian, this area formed a part of the intracontinental basin with a prevailing terrestrial and restricted shallow-marine sedimentation in a tropical climatic belt of the eastern part of the Euramerican continent. Studied material came from the basal parts of the dolomitic-shaly succession of the Kostyukovichi Horizon (Golubtsov et al., 2000, fig. 2; Kruchek et al., 2001, fig. 5.23). This lithostratigraphic unit represents an important correlative level due to its unique open-marine aspect contrasting with enclosing terrigeneous nearshore and/or terrestrial facies. Numerous fossil remains, including conodonts, fishes, and miospores, permit correlation of this horizon with the *ensensis* Zone of the uppermost Eifelian (Narkiewicz and Kruchek, 2008, p. 190).

The collection from the Michigan Basin (USA) was obtained from the United States Steel Corporation Quarry located southeast of Rogers City, Michigan, USA (Orr, 1971, p. 105, section 15-IU10711; Bultynck, 1976, p. 134, fig. 2, Locality 1). The Middle Devonian Michigan Basin was an intracontinental shallow-marine basin near the southwestern margin of Euramerica in a tropical paleoclimatic zone. The samples were taken in 1972 from the Dundee and Rogers City

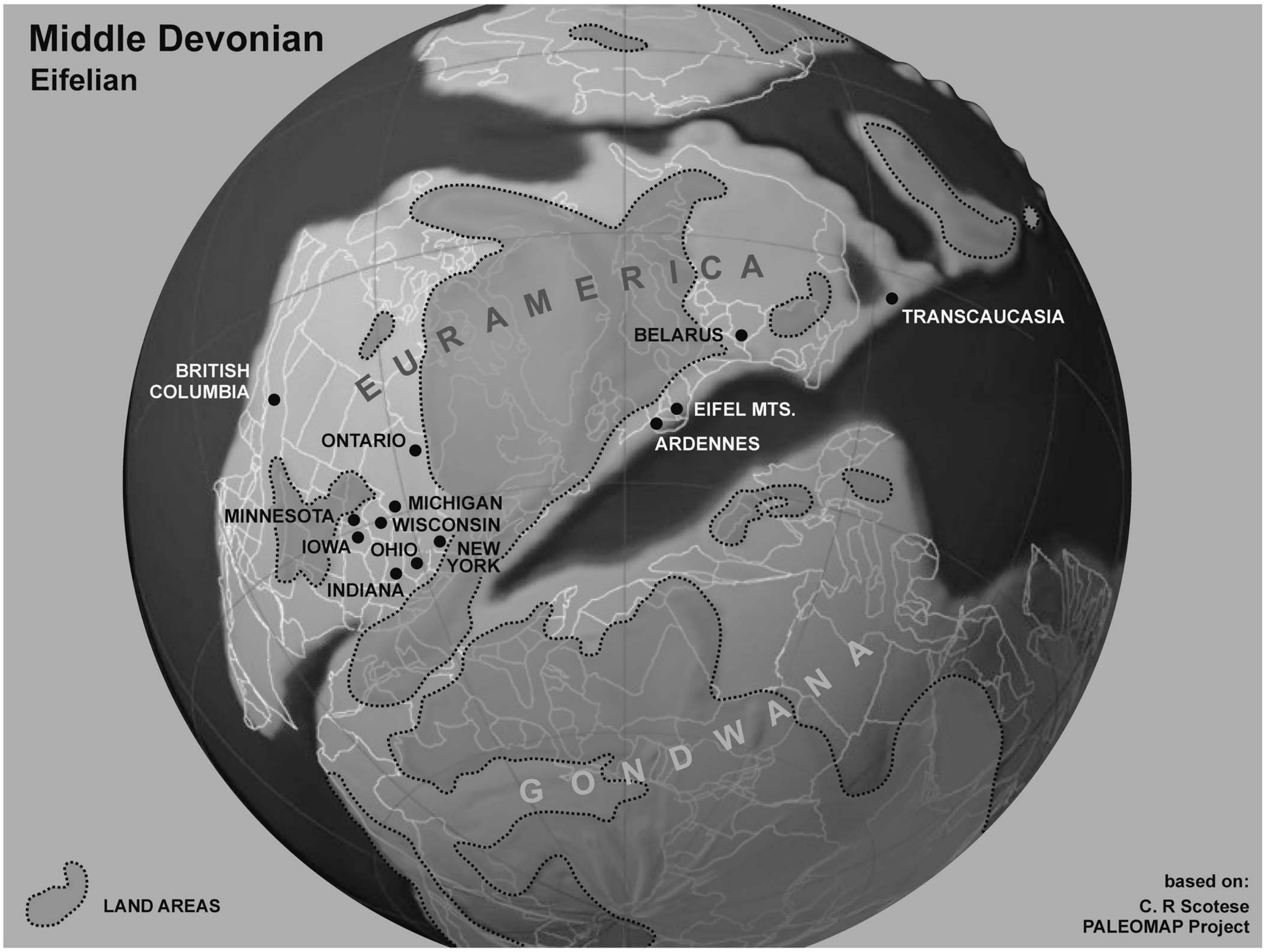


**Figure 1.** Eifelian palaeogeographic map of Euramerica and northern Gondwana (after Scotese, 2002) showing locations of the studied Eifelian conodont fauna. Approximate location of Transcaucasia after Tolokonnikova and Ernst (2010).

formations, and from the lowermost part of the Bell Shale Formation. The distribution and frequency of particular taxa was given by Bultynck (1976, table 1) without, however, any photographic documentation. Some specimens from the Dundee Formation, including two identified as *Icriodus orri*, were illustrated in a later paper by Bultynck (2003, pl. 2, figs. 34, 35).

The studied material, illustrated in Figures 2–4, is generally well preserved. In the Belarussian collection, small, most probably juvenile, specimens prevail. The specimens have smooth lustrous surfaces and their amber color points to a low thermal maturity (conodont CAI 1). The Michigan Basin specimens display a porous and rough surface texture that could indicate activity of subsurface fluids. The conodont CAI attains a value between 2.5 for medium-sized specimens and 3 for the large ones.

In addition to the study of our own collections, we analyzed literature data from North America, Europe, and Asia (Fig. 1). North American data are from the USA, from Indiana (Klapper and Johnson, 1980; Klug, 1983), Ohio (Klapper and Johnson, 1980; Sparling, 1983), Iowa (Klapper and Barrick, 1983), Minnesota (Klapper and Barrick, 1983), and Wisconsin (Schumacher, 1971); and from Canada, from the provinces of Ontario (Orr, 1971; Uyeno et al., 1982), and British Columbia (Chatterton, 1978). The discussed European data are from the Ardennes in Belgium (Bultynck, 1970; Klapper and Barrick, 1983, fig. 9.V, W) and the Eifel Mountains in Germany (Weddige, 1977; Werner and Ziegler, 1982), and those from Asia come from Transcaucasus in Azerbaijan (Khalymbadzha, 1990).

## Rationale for the present taxonomic concepts

Analysis of the material illustrated by Klapper and Barrick (1983, fig. 9) revealed considerable morphological variability within the two morphotypes distinguished by these authors. Their Morphotype I (with a depression in the posterior part of the spindle) displays mostly oval denticles in lateral rows, and rounded and slightly smaller ones in the median row. The same form shows a fairly wide posterior part of the spindle with convex margins, contrasting with a narrow anterior part, curving inward (Klapper and Barrick, 1983, fig. 9.R, X, Y, AA, early ontogenetic stage). The single illustrated specimen shows a spindle with a triangular outline (Klappner and Barrick, 1983, fig. 9.T, intermediate ontogenetic stage).

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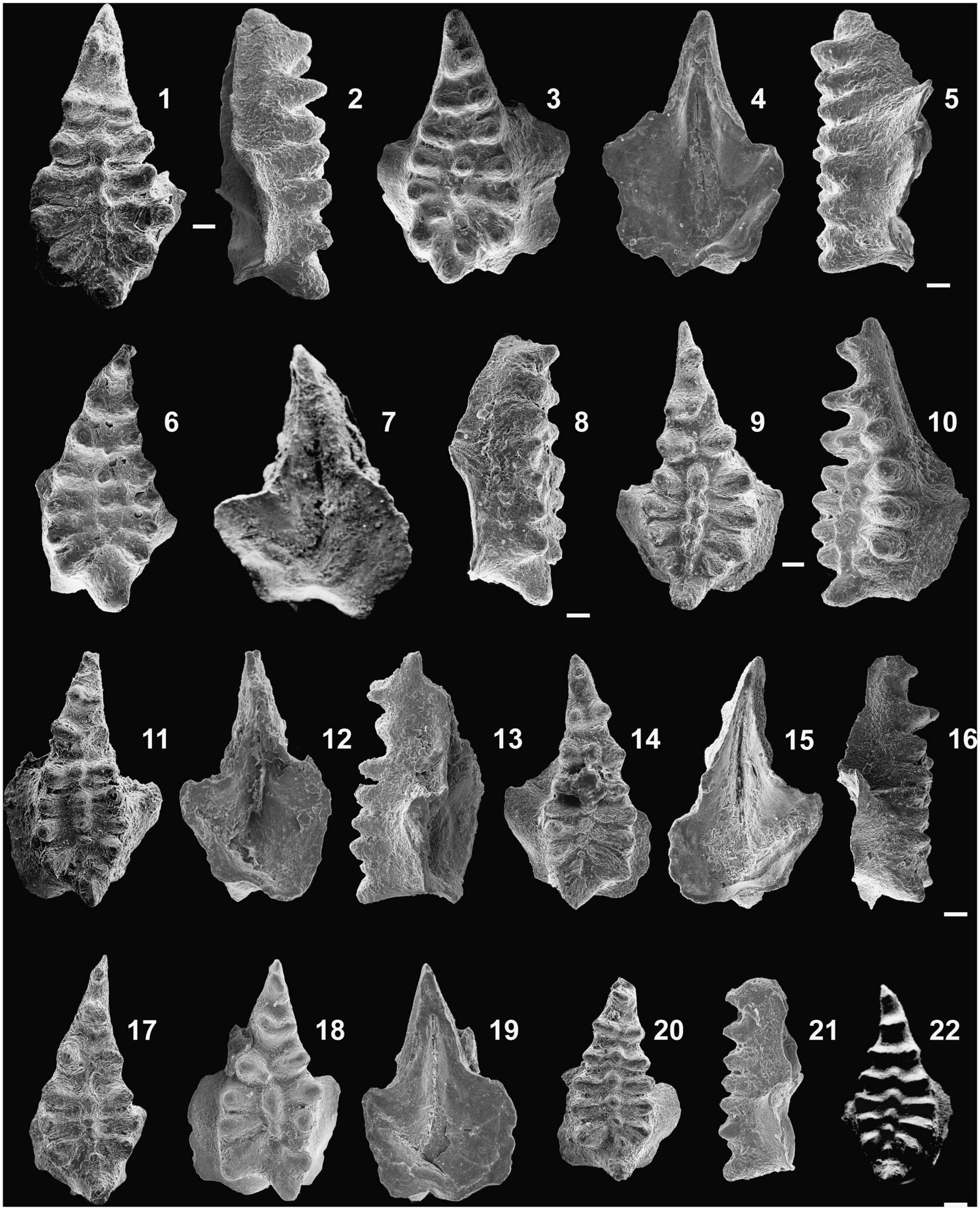


**Figure 2.** Conodont $P_1$ elements of *Icriodus michiganus* n. sp. from the Dundee Formation, the U.S. Steel Corporation Quarry section, Michigan Basin (USA). **(1, 2)** Upper and lateral views, MUZ PIG 1795.II.4, sample 29. **(3–5)** Upper, lower, and lateral (broken anterior tip of the spindle) views of holotype, MUZ PIG 1795.II.1, sample 23. **(6–8)** Upper, lower, and lateral views of paratype, MUZ PIG 1795.II.2, top of the Dundee Formation, sample 01. **(9, 10)** Upper and lateral views, MUZ PIG 1795.II.5, sample 28. **(11–13)** Upper, lower, and lateral views, MUZ PIG 1795.II.6, sample 18. **(14–16)** Upper, lower, and lateral views of paratype, MUZ PIG 1795. II.3, sample 21. **(17)** Upper view, MUZ PIG 1795.II.7, sample 23. **(18, 19)** Upper and lower views of paratype, MUZ PIG 1795.II.8, top of the Dundee Formation, sample 01. **(20, 21)** Upper and lateral views, MUZ PIG 1795.II.9, sample 31. **(22)** Upper view, MUZ PIG 1795.II.10, sample 29. Scale bars = 100 μm.

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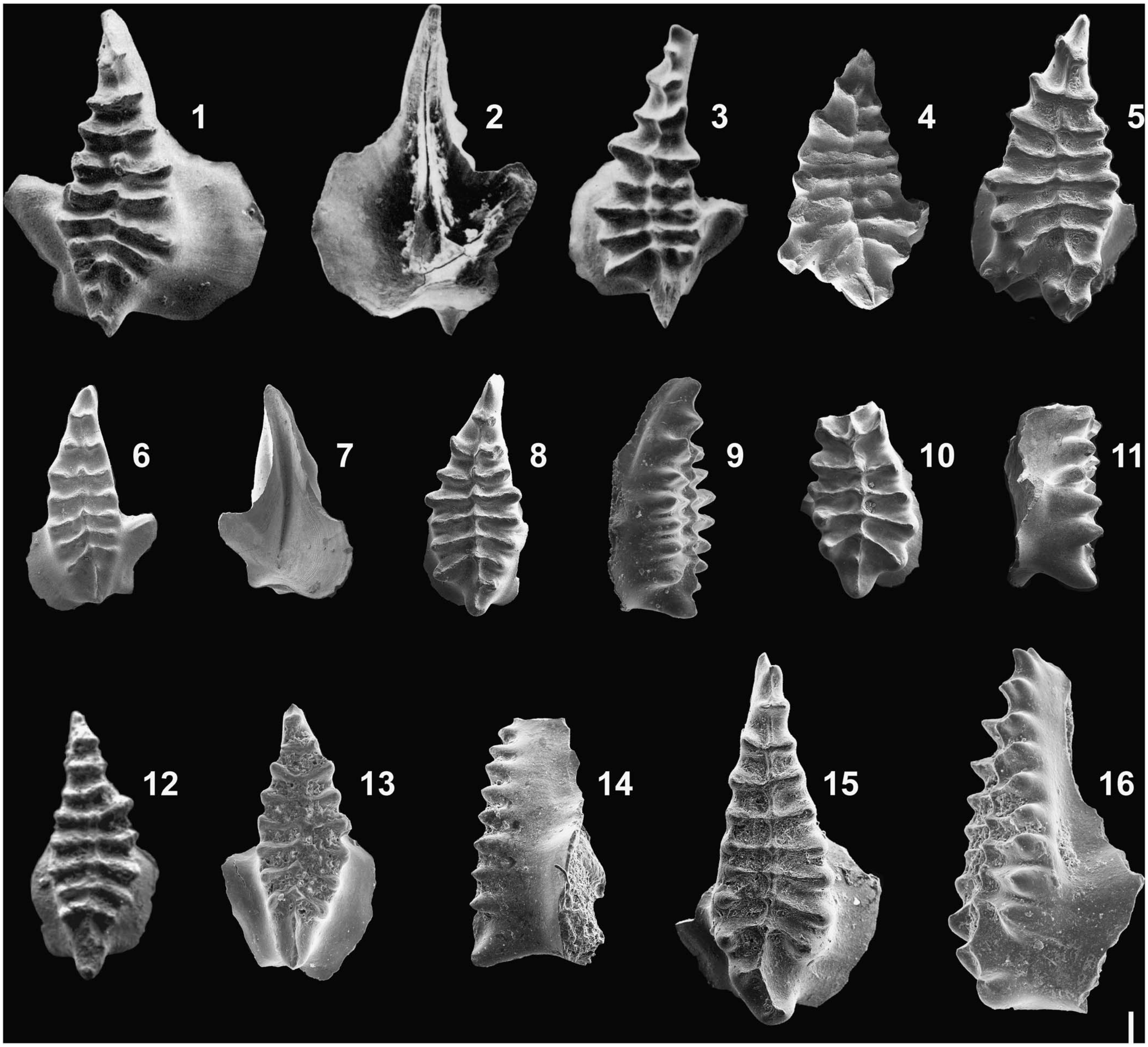
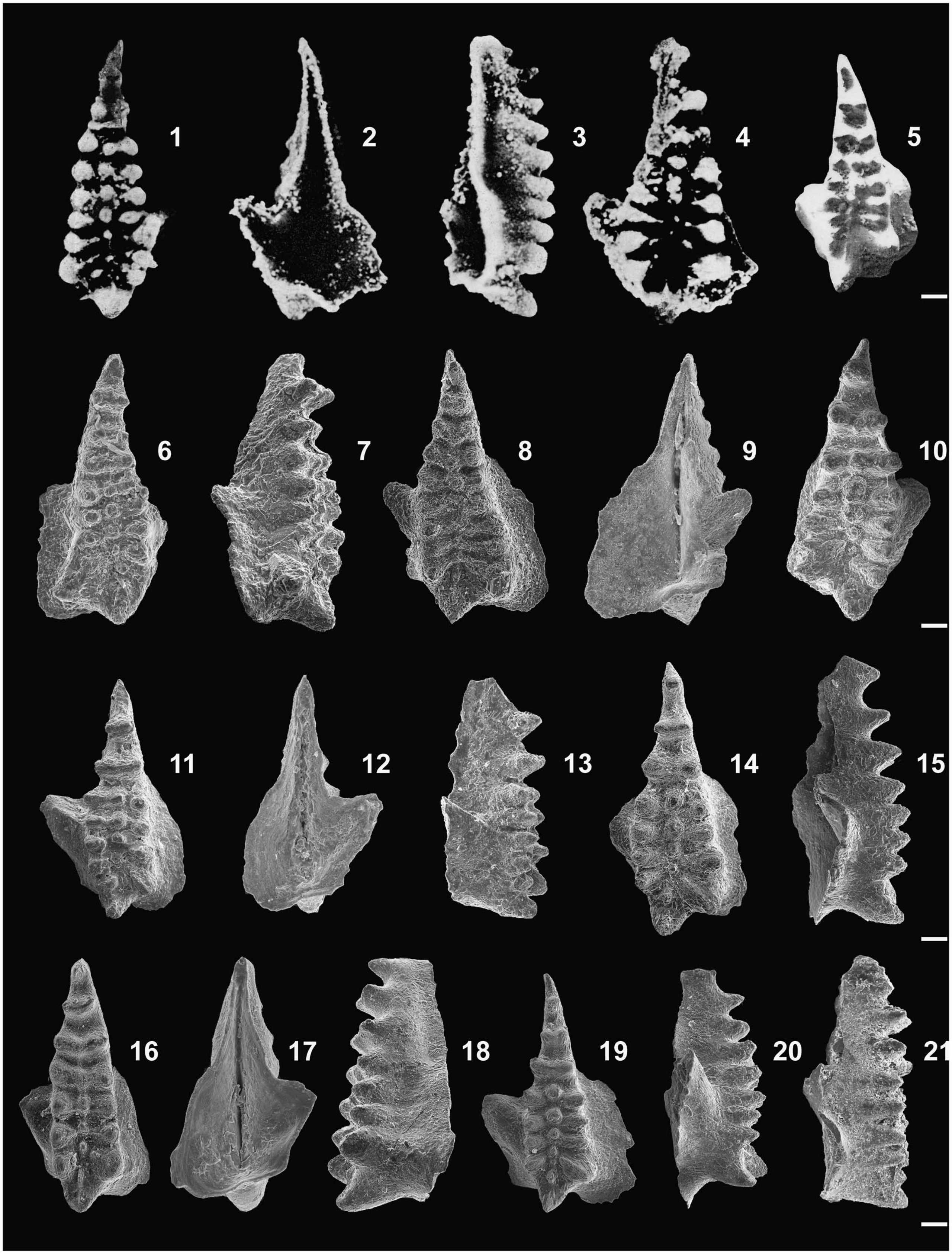



**Figure 3.** Conodont $P_1$ elements of *Icriodus orri* Klapper and Barrick, 1983. (**1–3**) Reillustrations of figures by Klapper and Barrick (1983, fig. 9.AF–AG,Z used with permission from SEPM): **(1, 2)** holotype, upper and lower views (fig. 9.AF–AG); (**3**) paratype, upper view (fig. 9.Z), Racine section, samples 3 and 3A, respectively, lower part of the Spillville Formation, southern Minnesota (USA). **(4–11)** Kostyukovichi Horizon, Pripyat Graben, Belarus; (**4**) upper view, MUZ PIG 1804.II.1, Pinsk 54, depth 465.0–460.0 m, sample 95w; (**5**) upper view, MUZ PIG 1804.II.2, Pinsk 54, depth 465.0–460.0 m, sample 95b; **(6, 7)** upper and lower views, MUZ PIG 1804.II.3, Zhytkovichi 2, depth 191.0–186.6 m, sample 6e; **(8, 9)** upper and lateral views, MUZ PIG 1804.II.4, Pinsk 54, depth 465.0–460.0 m, sample 95b; **(10, 11)** upper and lateral views, MUZ PIG 1804.II.5, Zhytkovichi 2, depth 191.0–186.6 m, sample 5a. **(12–16)** U.S. Steel Corporation Quarry section, Michigan Basin, USA., Bell Shale Formation, sample 16; **(12)** upper view, MUZ PIG 1795.II.11; **(13, 14)** upper and lateral views, MUZ PIG 1795.II.12; **(15, 16)** upper and lateral views, MUZ PIG 1795.II.13. Scale bars = 100 μm.

This form reveals a close similarity to the mature form identified as *Icriodus retrodepressus* by Klapper and Barrick (1983, fig. 9.W).

Their Morphotype II (lacking the previously mentioned depression) is characterized by transverse rows of denticles formed by a fusion of small circular denticles of a median row with lateral

**Figure 4.** (1–20) Conodont $P_1$ elements of *Icriodus retrodepressus* Bultynck, 1970; **(1–4)** Reillustrations of figures by Bultynck (1970; reproduced with permission); **(1–3)** holotype (Bultynck, 1970, pl. 30, fig. 1), upper, lower, and lateral views, Eau Noire section, Ardenne, Belgium, Couvin Formation, sample 75/6; **(4)** upper view (Bultynck, 1970, pl. 30, fig. 3), Eau Noire section, sample 62/2. **(5)** Reillustration of figures by Werner and Ziegler (1982, pl. 1, fig. 27, used with permission from Senckenberg Forschngsinstitut und Naturmuseum Frankfurt), upper view, Wetteldorf Richtschnitt section, assemblage V, WP. 72, Lauch Formation southern Eifelian Hills, Germany. (**6–20**) Elements from U.S. Steel Corporation Quarry section, Michigan (USA), Dundee Formation; **(6, 7)** upper and lateral views, MUZ PIG 1795.II.14, sample 17; **(8, 9)** upper and lower views, MUZ PIG 1795.II.15, sample 30; **(10)** upper view, MUZ PIG 1795.II.16, sample 28; **(11–13)** upper, lower, and lateral views, MUZ PIG 1795.II.17, sample 31; **(14, 15)** upper and lateral views, MUZ PIG 1795.II.18, sample 23; **(16–18)** upper, lower, and lateral views, MUZ PIG 1795.II.19, sample 01; **(19, 20)** upper and lateral views, MUZ PIG 1795.II.20, sample 19. (**21**) Conodont $P_1$ elements of *Icriodus* sp., lateral view of the specimen figured by Bultynck (2003, pl. 2, fig. 33) as *I. retrodepressus*, Oriskany Falls section, New York (USA), Nedrow Member, sample 2. Scale bars = 100 μm.

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denticles that are transversely elongated and display sharp edges. This morphotype has a wide spindle with convex margins (Klappner and Barrick, 1983, fig. 9.AF, Z) as well as a very narrow form, the outer margin of which is convex, whereas the inner one is concave-convex (Klappner and Barrick, 1983, fig. 9.AD).

The conodont collections from the Michigan and Belarussian basins, along with the previously illustrated specimens, were evaluated to consider the morphological similarity with the four above-mentioned varieties. It appeared that forms attributed to Morphotype I considerably differed from Morphotype II forms by the presence of a depression and the characteristic lateral rows of denticles, and for this reason, were excluded from the redefined *Icriodus orri* (see below). The latter species is typified by the holotype designated by Klapper and Barrick (1983, fig. 9.AF–AG) and was attributed to their Morphotype II. Morphotype I encompasses specimens differing not only in spindle shape and distribution of denticles on the upper surface, but also in the length and depth of the depression, and shape of the basal cavity. The differences are so conspicuous that they justify distinction of two separate species within Morphotype I. Forms with a short shallow depression, curved longitudinal axis, a spindle composed of a wide convex posterior part and narrow anterior part, and possessing a nearly circular basal cavity, have been defined here as *I. michiganus* n. sp. (Fig. 2). The forms characterized by a deeper depression, triangular spindle with a nearly straight axis, and a distinct basal cavity with a spur and antispur, have been included in the amended *I. retrodepressus* (Fig. 4).

Diagnostic differences among the species described below, and at the same time, intraspecific similarity of the specimens from various regions, are shown in Figure 5. It should be stressed

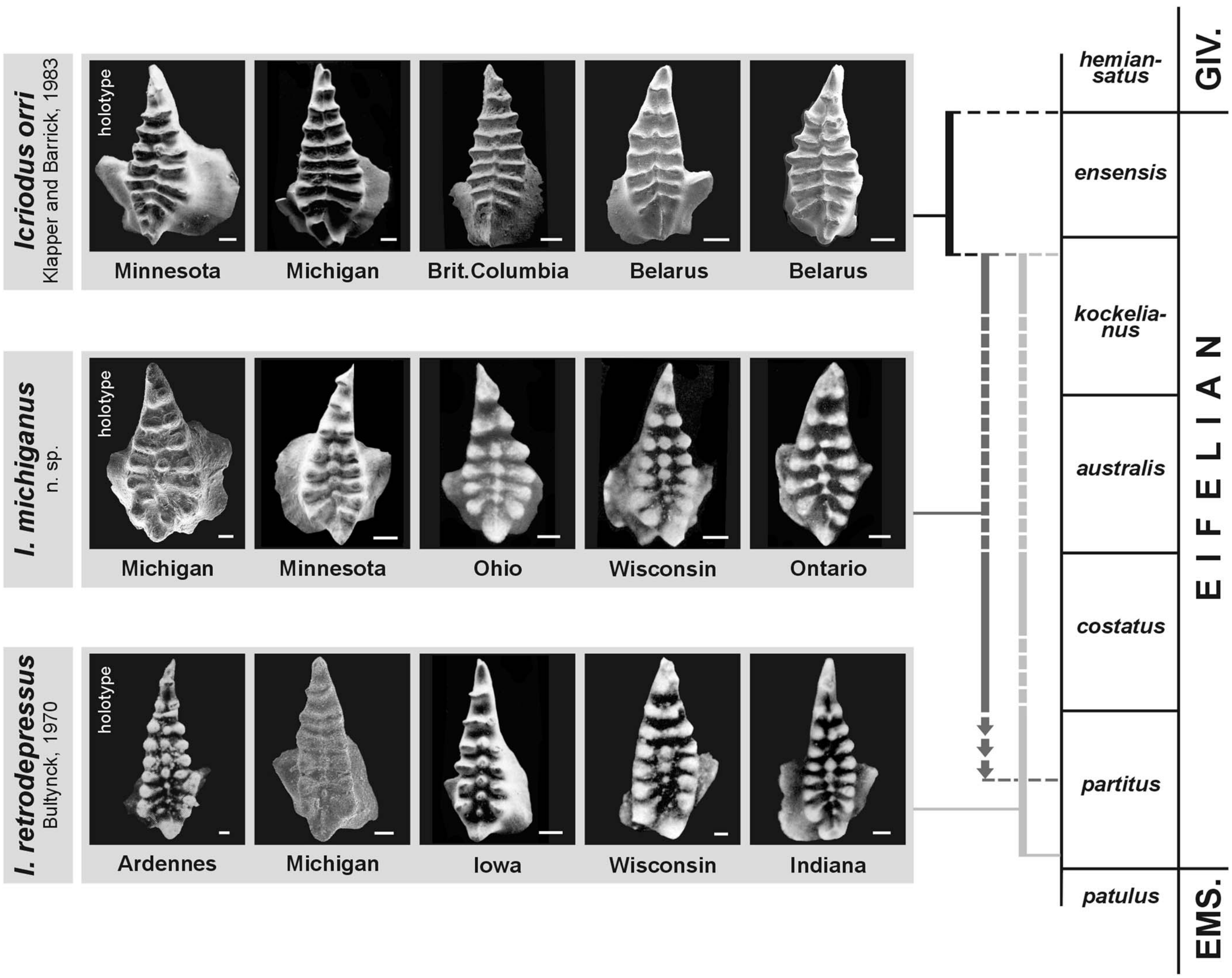


**Figure 5.** Upper views of representative specimens of the studied icriodid species and their stratigraphic ranges established by this study. Sources of illustrations: *Icriodus orri*, Minnesota (herein, Fig. 3.1); Michigan (herein, Fig. 3.15; British Columbia (Chatterton, 1978, pl. 6, fig. 1); Belarus (herein, Fig. 3.6, 3.8); *Icriodus michiganus* n. sp., Michigan (herein, Fig. 2.3); Minnesota (Klapper and Barrick, 1983, fig. 9.X, used with permission from SEPM; Ohio (Sparling, 1983, fig. 13.AS; used with permission from SEPM); Wisconsin (Schumacher, 1971, pl. 9, fig. 2, used with permission from the Wisconsin Geological and Natural History Survey); Ontario (Uyeno et al., 1982, pl. 3, fig. 16); *Icriodus retrodepressus*, Ardennes (herein, Fig. 4.1, reproduced with permission); Michigan (herein, Fig. 4.16); Iowa (Klapper and Barrick, 1983, fig. 9.T, used with permission from SEPM; Wisconsin (Schumacher, 1971, pl. 9, fig. 5, used with permission from Wisconsin Geological and Natural History Survey); Indiana (Klapper and Johnson, 1980, pl. 3, fig. 20, used with permission from SEPM). Broken horizontal lines = tentative limits of stratigraphic ranges; broken vertical lines = interval lacking documented occurrence of a species; vertical arrows = probable stratigraphic range. Scale bars = 100 μm.

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that inhomogeneity of the material analyzed by Klapper and Barrick (1983) definitely led to confusion in later taxonomic studies. Some elements included in *Icriodus orri* lack a depression, but at the same time, show variable shapes of the spindle denticles. There is only a slight tendency for development of sharp upper margins, and a basal cavity has a more or less distinct spur (e.g., Mawson and Talent, 1989; Sparling, 1995; Uyeno and Lespérance, 1997; Bultynck, 2003; Narkiewicz and Kruchek, 2008). The concept of *I. retrodepressus* was also broadly understood in previous studies. It included both triangular and distinctly biconvex forms, those with a curved axis, and having a depression of variable length and depth, but also specimens lacking the depression (e.g. Weddige, 1977; Garcia-Lopez, 1987; Khalymbadzha, 1990; Malec, 2003).

## Materials and methods

In the systematic descriptions, new synonymies for *Icriodus orri* and *I. retrodepressus* are provided, and their diagnoses have been emended with detailed descriptions and remarks highlighting differences between them and similar taxa. To better document specific diagnostic features, Figures 3 and 4 reillustrate the holotypes and specimens representing the range of intraspecific variability. The specimens are illustrated under uniform magnification to better compare different ontogenetic stages and their variability.

*Repository and institutional abbreviation*.—The described and photographed material is housed at the Geological Museum of the Polish Geological Institute-National Research Institute in Warszawa, Poland under collection numbers MUZ PIG 1804.II (Belarus collection) and MUZ PIG 1795.II (Michigan Basin collection).

## Systematic paleontology

Order Prioniodontida Dzik, 1976
Family Icriodontidae Müller and Müller, 1957
Genus *Icriodus* Branson and Mehl, 1938

*Type species*.—*Icriodus expansus* Branson and Mehl, 1938.

*Icriodus michiganus* new species
Figure 2.1–2.22

1971 *Icriodus nodosus* (Huddle); Orr, pl. 2, figs. 20–21.
1971 *Icriodus nodosus*; Schumacher, p. 93, pl. 9, figs. 1–3, 7–9.
1980 *Icriodus* sp. aff. *I. retrodepressus* Bultynck; Klapper and Johnson, pl. 3, figs. 22, 23.
1982 *Icriodus* aff. *I. retrodepressus*; Uyeno et al., p. 33, pl. 3, figs. 16, 18, 19, 25–27.
1983 *Icriodus orri* Klapper and Barrick, p. 1230, fig. 9.R, X, Y, AA.
1983 *Icriodus* sp. aff. *I. retrodepressus*; Sparling, p. 851, fig. 13.AS–AT.
1990 *Icriodus* sp. E Weddige; Khalymbadzha, table 7, figs. 6–10.
1990 *Icriodus retrodepressus*; Khalymbadzha, table 8, figs. 24–25.
2003 *Icriodus orri*; Bultynck, pl. 2, figs. 34, 35.

*Holotype*.—MUZ PIG 1795.II.1, $P_1$ element from the United States Steel Corporation Quarry, Dundee Formation, sample 23 (Fig. 2.3–2.5); paratypes, $P_1$ elements from the United States Steel Corporation Quarry: MUZ PIG 1795.II.2, top of the Dundee Formation, sample 01 (Fig. 2.6–2.8); MUZ PIG 1795.II.3, Dundee Formation, sample 21 (Fig. 2.14–2.16); MUZ PIG 1795.II.8, top of the Dundee Formation, sample 01 (Fig. 2.18–2.19).

*Diagnosis*.—The $P_1$ element is stout, with a relatively short and wide spindle. The posterior part is wide with biconvex margins and a straight axis, and is characterized by a clear short depression with one, rarely two, small middle-row denticles. The anterior part of the spindle is narrow, elongated, pointed, and more or less curved inward, and is characterized by the absence of middle-row denticles. The middle row consists of four or five rounded, isolated denticles, smaller than those of the lateral rows. One or two posterior denticles from the middle row are slightly displaced anteriorly whereas the remaining are aligned with the lateral-row denticles. The lateral rows are composed of six or seven oval, isolated denticles that are very close to each other in the posterior part of the spindle, with wider spaces in its anterior part. The cusp is large, pointed upward, and inclined posteriorly. The nearly symmetric expansion of the basal cavity starts in the middle part of the spindle or more anteriorly. The more or less pronounced spur is generally rounded.

*Occurrence*.—The new species ranges from a lower part of the *costatus* Zone or even from an upper part of the *partitus* Zone to an upper part of the *kockelianus* Zone. It occurs in the USA in Ohio (Dundee and Delaware formations), in Michigan (Dundee Formation), in Wisconsin (uppermost part of the Lake Church Formation), in Minnesota (lower part of the Spillville Formation), in Canada in Ontario (Dundee Formation and sandy facies of the Anderdon Member of the Lucas Formation), and in Asia in Transcaucasus (lower part of the Danzik Formation).

*Description*.—Denticles in the lateral rows display a tendency to develop sharp edges (Fig. 2.20, 2.22). The axes of the posteriormost lateral denticles are always directed outward and backward (V-shaped), with the outer denticle usually larger than the inner one. The cusp often bears a short, transverse lateral process on the outer side in left-curved forms (Fig. 2.11, 2.18), and on the inner side in right-curved forms (Fig. 2.3, 2.14). The basal cavity consists of a narrow anterior part and a wide posterior part. The inner margin of the expanded part of the basal cavity is more or less oblique, whereas the outer margin is more or less rounded. A distinct sinus is present on the posterior margin of the basal cavity and a shallower sinus occurs in the posterior part of the inner margin of the basal cavity.

*Etymology*.—The name of the species is derived from the Michigan Basin in the state of Michigan, USA where the taxon has been identified.

*Materials*.—MUZ PIG 1795.II.4 (Fig. 2.1, 2.2), 1795.II.5 (Fig. 2.9, 2.10), 1795.II.6 (Fig. 2.11–2.13), 1795.II.7 (Fig. 17), 1795.II.9 (Fig. 2.20, 2.21), 1795.II.10 (Fig. 2.22).

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A total of 19 specimens from the U.S. Steel Corporation Quarry, Michigan Basin, Dundee Formation, from samples 31 to 01.

*Remarks*.—The new species differs from *Icriodus orri* in the presence of a depression in the posterior median part of the spindle, and in the lack of characteristic transverse denticle ridges with sharp edges. Another difference is a smaller number of the median-row denticles that are larger than those in *I. orri*, and a more symmetrical basal cavity lacking a sharply accentuated spur. The described species differs from *I. retrodepressus* in the outline and width of the spindle and in the development of the basal cavity. The spindle of *I. retrodepressus* is narrow and triangular, whereas the depression in its posterior part is deeper and longer. Its basal cavity is asymmetric with a distinct spur and antispur, and its inner margin is more oblique than that in *I. michiganus* n. sp.

*Icriodus orri* Klapper and Barrick, 1983
Figure 3.1–3.16

1978 *Icriodus* aff. *I. expansus* Branson and Mehl; Chatterton, p. 201, pl. 6, figs. 1, 2, 5.
1983 *Icriodus orri* Klapper and Barrick, p. 1230, only fig. 9.Z (paratype), 9.AF–AG (holotype).
non 1989 *Icriodus orri*; Mawson and Talent, pl. 1, figs. 13–15.
non 1995 *Icriodus orri*; Sparling, fig. 4.1–4.5.
non 1997 *Icriodus orri*; Uyeno and Lespérance, fig. 7.21–7.25, 7.31–7.32.
non 1998 *Icriodus orri*; Uyeno, pl. 11, figs. 6, 7, 12, pl. 12, figs. 22, 23.
non 2003 *Icriodus orri*; Bultynck, pl. 2, figs. 34, 35.
non 2008 *Icriodus orri*; Narkiewicz and Kruchek, pl. 1, figs. 11, 12, 14, 15, 19.

*Holotype*.—Element $P_1$ from the Racine Quarry, sample 3, Spillville Formation, southern Minnesota, USA, (Klapper and Barrick, 1983, fig. 9.AF–AG).

*Diagnosis*.—Element $P_1$ is characterized by an elongated, biconvex to lachrymiform spindle that is widest in the middle or just behind, closer to its posterior part. The spindle axis is almost straight, particularly in its posterior part, although the anterior narrow and pointed extremity of the spindle can be more or less curved inward. The small denticles of the middle row are more or less of uniform size and have circular cross sections. They can be located just opposite or slightly anterior to those of the lateral row denticles and are connected with them, forming seven or eight transverse denticle rows. The middle-row denticles are on the same level or a little higher than the lateral-row denticles. The latter are laterally elongated, with sharp upper margins, and are markedly larger than the middle-row denticles. The cusp is mostly rounded and inclined posteriorly, and its width is equal to the lateral extent of the two posteriormost denticles. The basal cavity is asymmetrical with the outer part wider and beginning more anteriorly than the inner one; on its inner side, there is a well-pronounced spur. The expanded outer part of the basal cavity is located in the middle or posterior third of the element.

*Occurrence*.—This species ranges from an uppermost part of the *kockelianus* to *ensensis* zones. It is present in the USA in Michigan (lower part of the Bell Shale Formation), in Minnesota (lower part of the Spillville Formation), in Canada in British Columbia (Dunedin Formation), and in Belarus in the Pripyat Graben (Kostyukovichi Horizon).

*Description*.—The intraspecific variability comprises elongated and fairly wide forms such as the holotype (Fig. 3.1) and narrow ones similar to that illustrated from British Columbia (Fig. 5). Ornamentation can be irregular, particularly with respect to the length of lateral row denticles. In some specimens, these can be longer than usual due to a development of additional short processes (Fig. 3.4, 3.5). Denticles in the last one or two posterior transverse rows show an inverted chevron pattern, whereas those in the anterior end of the spindle are mostly straight. The space between transverse denticle rows is much larger in the anterior part of the spindle than in the posterior part. Denticles of the middle row can be connected by thin ridges, which also continue posteriorly to the tip of the cusp. These denticles occur in the posterior and middle part of the spindle, whereas in its anterior part, they can be completely fused with the denticles of lateral rows. The size of the middle-row denticles can be variable. In the most posterior transverse rows, they are always small, whereas in the next two or three rows they can be larger. The cusp can have a short transverse process on its inner side. The width of the basal cavity is variable, from considerably expanded as seen in the holotype, to medium sized in the paratype (Fig. 3.3) or in remaining specimens from the Pripyat Graben and Michigan Basin (compare Fig. 3.5, 3.6, 3.15). Usually, sinuses are present on the inner and posterior margins of the basal cavity.

*Remarks*.—*Icriodus orri* differs from *I. michiganus* n. sp. and *I. retrodepressus* in lacking a depression in the posterior part of the spindle, and in its characteristic ornamentation. *Icriodus norfordi* Chatterton, 1978 (pl. 6, fig. 12, holotype) has a nearly triangular spindle outline, whereas in *I. orri*, the spindle is clearly biconvex. The denticulation pattern of *I. norfordi* is more irregular and its basal cavity is almost symmetrical, broadly expanded close to the anterior part of the spindle and lacking a distinct spur. *Icriodus orri* can be distinguished from *I. arkonensis arkonensis* Stauffer, 1938 (Klapper, 1975, p. 77, pl. 1, figs. 3, 4) in that the latter has thicker lateral-row denticles lacking sharp edges and almost in contact with each other. On the other hand in *I. orri*, the denticles are thin and have sharp upper margins, and the transverse rows are clearly separated, with spacing increasing toward the anterior end. In *I. a. arkonensis*, the denticles of the middle row are low and occur along the entire length of the spindle, whereas in *I. orri*, they are of the same height as the lateral denticles or even slightly higher, and they are missing in the anterior part. *Icriodus orri* has a distinct spur on the inner side of the basal cavity, which is considerably more pronounced than in *I. a. arkonensis*.

*Icriodus retrodepressus* Bultynck, 1970
Figure 4.1–4.20

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1970 *Icriodus retrodepressus* Bultynck, p. 110, pl. 30, figs. 1–4 (non figs. 5, 6).
1971 *Icriodus nodosus* (Huddle); Schumacher, pl. 9, figs. 4–6, 11–12.
1975 *Icriodus retrodepressus*; Ziegler, p. 143, pl. 8, figs. 4, 5 (refigured from Bultynck 1970, pl. 30, figs. 1, 4).
1977 *Icriodus corniger retrodepressus*; Weddige, p. 290, pl. 1, figs. 10, 12 (non fig. 11).
1980 *Icriodus* sp. aff. *I. retrodepressus*; Klapper and Johnson, pl. 3, figs. 20, 21.
1982 *Icriodus corniger retrodepressus*; Werner and Ziegler, pl. 2, figs. 26, 27.
1982 *Icriodus* aff. *I. retrodepressus*; Uyeno et al., p. 33, pl. 3, fig. 23.
1983 *Icriodus orri* Klapper and Barrick; Klapper and Barrick, fig. 9.T.
1983 *Icriodus retrodepressus*; Klapper and Barrick, fig. 9. V, W.
1983 *Icriodus retrodepressus*; Klug, fig. 9.A–F.
non 1990 *Icriodus retrodepressus*; Khalymbadzha, table 8, figs. 23, 24.
non 1987 *Icriodus retrodepressus*; Garcia-Lopez, pl. 7, figs. 9–20
non 2003 *Icriodus corniger retrodepressus*; Malec, table 343, figs. 9–13.
2003 *Icriodus orri*; Bultynck, pl. 2, figs. 27, 28 (non fig. 33)

*Holotype*.—Element $P_1$ from the Couvin Formation, Ardenne, Belgium (Bultynck, 1970, pl. 30, fig. 1a–c). The holotype has a provisional repository signature 'b168 Bultynck, 1970' in the Paleontology Collection of the Belgian Royal Institute of Natural Sciences (Brussels).

*Diagnosis*.—The $P_1$ element is characterized by an elongated, triangular spindle with a pronounced depression in its posterior part, showing one to three small middle-row denticles. In adult specimens, the lateral rows consist of six to eight oval, transversely developed denticles. In the posterior part, they can be connected with the middle-row denticles. Middle-row denticles have circular cross sections and are much smaller than those of the lateral rows. The cusp, with a fine ridge on its anterior side, is large and inclined posteriorly. The basal cavity is asymmetrical and its expanded part occupies the posterior half or even two-thirds of the element. There is a well-developed oblique spur on the inner side and a rounded posterior expansion on the outer side. The spur is rectilinear and joins the posterior margin of the cavity in that way.

*Occurrence*.—The species spans the interval from the *partitus* Zone to the upper part of the *kockelianus* Zone. It occurs in the USA in Iowa (lower part of the Spillville Formation), in Indiana (Speeds Member of the North Vernon Formation and Rocky Branch bone bed), in Michigan (Dundee Formation), in Wisconsin (uppermost part of the Lake Church Formation), in Canada in Ontario (Dundee Formation), in Europe in Belgian Ardennes (Couvin Formation), and in the Eifel Mountains of Germany (lower part of the Lauch Formation).

*Description*.—Intraspecific variability comprises forms that are narrow and thus similar to the holotype (Fig. 4.1), wider elements (Fig. 4.4), and triangular forms with a slightly convex inner margin (Fig. 4.10, 4.14; Schumacher, 1971, pl. 9, fig. 5; Klapper and Johnson, 1980, pl. 3, fig. 20; Fig. 5). Anterior spindle termination can be straight or slightly curved inward. In typical representatives of *Icriodus retrodepressus*, the strongly accentuated spur is mostly anteriorly directed, and the outer part of the basal cavity is not much expanded. In a few specimens, however, the spur does not show a distinct anterior direction, and the outer part of the basal cavity is considerably expanded outward (e.g., Klapper and Johnson, 1980, pl. 3, fig. 20; Uyeno et al., 1982, pl. 3 fig. 23; Fig. 5).

*Remarks*.—According to Klapper and Barrick (1983, p. 1231), the size of the basal cavity was the main reason to separate *Icriodus orri* from *I. retrodepressus*. These authors mentioned that *I. retrodepressus* is known mainly from the Ardennes and Eifel Mountains, from a narrow interval of the *partitus* Zone. In fact, the basal cavity of the holotype (Fig. 4.1–4.3; Bultynck, 1970, pl. 30, fig. 1) is limited mainly to the posterior part of the spindle. In the specimens illustrated from the Eifel Mountains area, however, the basal cavity can be situated either in the posterior or middle part of the spindle (Werner and Ziegler, 1982, pl. 2, figs. 26, 27 = Fig. 4.5). The younger representatives of *I. retrodepressus* from North America are characterized by a basal cavity that always expands in the anterior part of the spindle (Fig. 4.6–4.20).

Analysis of the material from the Michigan Basin and literature data demonstrate that although the size of the basal cavity can differ in European and North American representatives, its asymmetry, with its well-pronounced spur and antispur, remains a constant feature, as does morphology of the upper surface of the spindle. The changing size of the basal cavity could be related to the presumed feeding functions performed by the $P_1$ elements. The latter functions could require, for example, stronger or weaker embedding in the soft tissues of an animal, depending on various types of food.

The differences between *Icriodus retrodepressus* and *I. michiganus* n. sp. are given above in the description of the latter species.

## Conodont zonation of the Eifelian stage

Verification of published stratigraphic conodont data (Table 1, Chronostratigraphy) must take into account changes that have been introduced to the Eifelian conodont zonation since its earliest proposal. In 1966, Wittkekindt (p. 627) established *Icriodus corniger*, *Spathognathodus bidentatus*, and *Polygnathus kockelianus* zones for the Rhenish Slate Mountains area. The most complete Eifelian zonation proposed by Weddige (1977, table 5) for the Eifel Mountains, Rhenish Slate Mountains, and neighboring areas comprised (in ascending order) upper *P. patulus*, *P. costatus costatus*, *Tortodus kockelianus*, and *P. ensensis* zones, and has been applied since then albeit with some modifications. Klapper and Ziegler (1979, text-figs. 3, 4) introduced the *T. kockelianus australis*

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**Table 1.** Previous taxonomic and biostratigraphic data on *Icriodus orri* and related species compared with the data from this study.

| | | | Taxonomy | | Chronostratigraphy | |
|---|---|---|---|---|---|---|
| Reference | Locality | Lithostratigraphy | Original | Revised | Original | Revised |
| Klapper and Barrick, 1983 | S Minnesota, USA | Spillville Formation, lower part | *I. orri*<br>figs. 9.Q–AG | *I. orri*<br>fig. 9.Z, AF–AG | ~*kockelianus* Zone | uppermost part of the *kockelianus* Zone (this paper) |
| | | | | *I. michiganus*<br>fig. 9.R, X, Y, AA | ~*kockelianus* Zone | upper part of the *kockelianus* Zone (Braun et al.,1988) |
| | N Iowa, USA | | | *I. retrodepressus*<br>fig. 9.T | ~*kockelianus* Zone | upper part of the *kockelianus* Zone (Braun et al., 1988) |
| Schumacher, 1971 | SE Wisconsin, USA | Lake Church Formation, uppermost part | *I. nodosus*<br>pl. 9, figs. 1–18 | *I. michiganus*<br>pl. 9, figs. 1–3<br>*I.retrodepressus*<br>pl. 9, figs. 5–6 | Late Eifelian–lowermost Givetian | upper part of the *kockelianus* Zone (equivalent of Spillville Formation after Klapper and Barrick, 1983) |
| Sparling, 1983 | NC, Ohio, USA | Delaware Formation, 12.42–12.32 m above base | *I.* sp. aff. *I. retrodepressus*<br>figs. 13.AR, AS–AT | *I. michiganus* | *kockelianus* Zone | upper part of the *kockelianus* Zone (Sparling, 1999) |
| Klug, 1983 | SC Indiana, USA | Speeds Member, North Vernon Formation | *I. retrodepressus*<br>figs. 9.A–C, D–F | *I. retrodepressus* | *Polygnathus pseudofoliatus* Zone | ~upper part of the *kockelianus* Zone (this paper) |
| Chatterton, 1978 | NE British Columbia, Canada | Dunedin Formation, 30 m below top | *I.* aff. *I. expansus*<br>pl. 6, fig. 1 | *I. orri* | early Eifelian– latest Emsian | *kockelianus-ensensis* zones (Morrow and Geldsetzer, 1988; Uyeno, 1991) |
| Orr, 1971 | SW Ontario, Canada | Dundee Formation | *I. nodosus*<br>pl. 2, figs. 20–21 | *I. michiganus* | upper part of the *angustus* Zone | upper part of the *costatus* Zone (Uyeno et al., 1982) |
| Bultynck, 1976 | N Lower Peninsula of Michigan Basin, USA | Dundee Formation | documentation lacking | *I. michiganus*<br>Fig. 2.1–22<br>*I. retrodepressus*<br>Fig. 4.6–20 | Eifelian | upper part of the *costatus* Zone (Uyeno et al., 1982) |
| Klapper and Johnson, 1980 | NW Ohio, USA | Dundee Formation, 4.4–4.7 m below top | *I.* sp. aff. *I. retrodepressus*<br>pl. 3, figs. 22–23 | *I. michiganus* | ~*kockelianus* Zone | upper part of the *costatus* Zone (Uyeno et al., 1982) |
| | SE Indiana, USA | Rocky Branch bone bed | *I.* sp. aff. *I. retrodepressus*<br>pl. 3, figs. 20–21 | *I. retrodepressus* | ~*kockelianus* Zone | ~upper part of the *kockelianus* Zone (this paper) |
| Uyeno et al., 1982 | SW Ontario, Canada | Dundee Formation 14.95–15.54 m above base | *I.* aff. *I. retrodepressus*<br>pl. 3, fig. 23 | *I. retrodepressus* | upper *costatus* Zone | upper part of the *costatus* Zone (Uyeno et al., 1982) |
| | | sandy facies of the Anderdon Member, Lucas Formation, 26.82–27.31 above quarry floor | *I.* aff. *I. retrodepressus*<br>pl. 3, figs. 16–18, 19, 25–27 | *I. michiganus* | upper part of undivided *patulus* Zone | *partitus*–lower part of the *costatus* zones (this paper) |
| Khalymbadzha, 1990 | Transcaucasia, Azerbaijan | Danzik Formation lower part | *I.* n. sp. E<br>table 7, figs. 6–10; table 8, fig. 6<br>*I. retrodepressus*<br>table 8, figs. 24-25 | *I. michiganus* | *costatus* Zone | *costatus* Zone |

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Zone below the *kockelianus* Zone, while attributing global significance to the zonation. At the same time, Weddige et al. (1979) established the *P. partitus* Zone for the lowermost Eifelian, replacing the upper part of the former *patulus* Zone. Bultynck (1987) proposed to introduce the *P. hemiansatus* Zone as an equivalent of the upper part of the *ensensis* Zone in the lowermost Givetian, although the lower part of this zone was not discussed. Consequently, the *ensensis* Zone disappeared and ceased to be used during the next decade (as e.g., in the compilation by Clausen et al., 1993 that is widely cited as the standard authority on conodont zonation). However, Walliser (2000, fig. 2) reintroduced the *ensensis* Zone in the uppermost Eifelian as an equivalent of the lower part of the former *ensensis* Zone.

The above-described biozonation is based on the first appearances of index taxa in the phylogenetic lineages of the Eifelian open and/or deeper marine genera *Polygnathus* Hinde, 1879 and *Tortodus* Weddige, 1977. For the shallower and more nearshore facies, characterized by a co-occurrence of polygnathids and pelekysgnathids, Klapper and Ziegler (1979, text-fig. 4) distinguished the informal *Pelekysgnathus pedderi*, *Polygnathus curtigladius* and *Po. pseudofoliatus* faunas above the *costatus* Zone. The *pedderi* Fauna corresponds approximately to the lower part of the *australis* Zone, the *curtigladius* Fauna to the upper part of this zone and lower part of the *kockelianus* Zone, and the *pseudofoliatus* Fauna to the upper *kockelianus* and *ensensis* zones. Later, based on data from western Canada, Braun et al. (1988, fig. 2) correlated the *curtigladius* Fauna with the upper part of the *kockelianus* Zone (without the uppermost portion), and the *pseudofoliatus* Fauna with the *ensensis* Zone.

The shallow marine and/or nearshore Eifelian conodont faunas were dominated by representatives of the genus *Icriodus* Branson and Mehl, 1938. The Eifelian zonation based mostly on icriodids was first proposed by Orr (1971) for intracratonic North American settings. He distinguished three zones (in ascending order): the *Icriodus latericrescens robustus* (= *Latericriodus l. robustus*) Zone, the *Polygnathus* '*webbi*' (= *P. costatus*) Zone, and *I. angustus* Zone. In turn, for the same time interval, Klug (1983, p. 82, fig. 3) defined the *I. l. robustus*, *I. angustus angustus* and *Po. pseudofoliatus* zones. According to Klug (1983), the *I. l. robustus* Zone is probably an equivalent of the *patulus* Zone and *I. a. angustus* Zone might correspond to the *costatus* Zone. The local *P. pseudofoliatus* Zone is correlated with the *australis-ensensis* zonal interval.

Changes in the conodont zonation have affected biostratigraphic correlation of the eustatic cycles in the Eifelian, particularly in its upper part. According to Johnson et al. (1985), the transgressive events of the cycles Ie and If correspond to the upper part of the *kockelianus* Zone and to the *ensensis* Zone, respectively. According to the recent zonation, the lower boundary of the If cycle (= *otomari* Event, = onset of black shale sedimentation marking the Kačak Event of House, 1985) is correlated with the *kockelianus*/*ensensis* zonal boundary (Walliser, 2000, p. 40).

## Regional biostratigraphic comparisons

In order to establish the stratigraphic ranges of the above-described *Icriodus* species, both new and published data on the age of the conodont-bearing strata have been reviewed and verified. Table 1 summarizes the sources of the discussed materials and compares the original interpretations with the revised results. We selected only those localities for which the taxonomic identifications could be verified based on illustrated specimens.

*Spillville Formation*.—*Icriodus orri* sensu Klapper and Barrick, 1983 has been encountered in the entire Spillville Formation. Klapper and Barrick (1983) tentatively attributed the lower part of the formation approximately to the *kockelianus* Zone, based on the presence of the *curtigladius* Fauna together with *Ozarkodina raaschi* Klapper and Barrick, 1983. The upper part was dated as the *ensensis* Zone owing to the co-occurrence of *O. raaschi* and *O. brevis* (Bischoff and Ziegler, 1957), the latter species first appearing in that zone (Klapper and Johnson, 1980). The specimens attributed to *I. orri* in this report were obtained from the lower Spillville Formation. The species has been identified in the Racine Quarry in samples 3 and 3A (Klapper and Barrick, 1983, fig. 4). *Icriodus michiganus* n. sp. has been ascertained in the Racine section in samples 2A and 3; in Spillville, in sample 1A; and in Albion, in sample 1 (Klapper and Barrick, 1983, figs. 4, 5). *Icriodus retrodepressus* has been identified in the Spillville Quarry, sample 2.

The Racine section is the most favorable one for estimating the age of the lower Spillville Formation. In this section, *Icriodus orri* appears above the highest occurrence of *Polygnathus curtigladius* Uyeno, 1979 (Klapper and Barrick, 1983, fig. 4). On the other hand, *I. michiganus* n. sp. appears still within the range of *P. curtigladius*. Based on the *curtigladius* Fauna, Klapper and Barrick (1983, fig. 3) correlated the lower Spillville Formation with the lower part of the Elm Point Formation in Manitoba, Canada. In turn, Braun et al. (1988, fig. 2) attributed the lower Elm Point Formation to the upper (but not uppermost) part of the *kockelianus* Zone after taking into account all available paleontological data. This age is consistent with the earlier interpretation of Johnson et al. (1985, fig. 8) who considered the Elm Point Formation as transgressive strata related to their eustatic cycle Ie.

*Lake Church Formation*.—*Icriodus michiganus* n. sp. and *I. retrodepressus* (Table 1), earlier determined as *I. nodosus* Huddle, 1934 by Schumacher (1971), have been identified in the upper part of the formation. Klapper and Barrick (1983, fig. 3) correlated these strata with the lower Spillville Formation based on a similarity of the conodont and macrofaunal assemblages. Therefore, its age is here tentatively referred to the upper but not uppermost part of the *kockelianus* Zone.

*Delaware Formation*.—In the Parkertown Quarry in north-central Ohio, Sparling (1983) found specimens that he determined as *Icriodus* sp. aff. *I. retrodepressus*, and that are here included in *I. michiganus* n. sp. (Table 1). They were encountered in the upper part of the Delaware Formation, 12.42–12.32 m above its base (sample S8OP-15). The entire formation was dated as the *kockelianus* Zone (Sparling, 1983, fig. 9).

Johnson et al. (1985, fig. 8) interpreted the Elm Point Formation (Canada) and Delaware Formation (USA) as co-eval transgressive units of the eustatic cycle Ie. Sparling (1988, fig. 9), however, regarded only the lower part of the Delaware Formation as transgressive, and the upper as regressive.

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According to his data, the entire formation corresponds to the *kockelianus* Zone except for its lowermost and uppermost part (Sparling, 1988, fig. 2). Later, Sparling (1999, fig. 2) attributed the Delaware Formation to the upper part of the *kockelianus* Zone as was earlier proposed by Johnson et al. (1985).

*North Vernon Formation, Speeds Member*.—*Icriodus retrodepressus* first appears in this unit in the sample BMQ-4 in the Berry Materials Corporation Quarry (BMQ, locality 1) in south-central Indiana (Klug, 1983, figs. 7, 9.A–F). The age of the sample was determined as a lower part of the *Polygnathus pseudofoliatus* Zone (Klug, 1983, fig. 5). *Icriodus retrodepressus* co-occurs with *I. angustus* Stewart and Sweet, 1956 (Klug, 1983, fig. 8.D–F), among other taxa. The age can be now attributed to the *kockelianus* Zone, because *I. retrodepressus* is present in sample BMQ-5, ~0.7 m above the highest occurrence of *I. latericrescens robustus* Orr, 1971 (sample BMQ-7), which disappears in the *australis* Zone (Klapper and Johnson, 1980), whereas the highest appearance of *I. angustus* is in the *kockelianus* Zone (Klapper and Johnson, 1980). Because the same age can be ascribed to sample BMQ-3, the interval between the samples BMQ-5 and BMQ-3 also belongs to the *kockelianus* Zone. Samples BMQ-1 and BMQ-2, localized at the top of the Speeds Member and slightly above it, respectively, contain a stratigraphically mixed assemblage indicating a gap spanning the *ensensis* through *timorensis* zones, and perhaps even a part of the *kockelianus* Zone. The data suggest that the analyzed BMQ-4 sample could represent an upper part of the *kockelianus* Zone (compare Brett et al., 2011, fig. 5).

*Rocky Branch bone bed*.—The specimen that was identified as *Icriodus* sp. aff. *I. retrodepressus* by Klapper (in Klapper and Johnson, 1980) in the Rocky Branch bone bed in Jennings County, southeastern Indiana, is now attributed to *I. retrodepressus* (Table 1). Because this unit is a lateral equivalent of the Speeds Member, its age should correspond approximately to the upper part of the *kockelianus* Zone (see above).

*Dunedin Formation*.—In the Mount Jane Smith locality in northeastern British Columbia, *Icriodus orri*, earlier identified by Chatterton (1978) as *I.* aff. *I. expansus* (Table 1), was found 30 m below the top of the Dunedin Formation (Chatterton, 1978, p. 162). These strata were dated as latest Emsian to early Eifelian based on the conodont fauna. The Mount Jane Smith section (situated in the area of the tectonosedimentary element labeled MacDonald Shelf by Morrow and Geldsetzer, 1988, fig. 3) is localized near the northernmost limit of the Dunedin Formation occurrence (Chatterton, 1978, p. 164). Given that the formation is ~95 m thick there (Taylor and MacKenzie, 1970, p. 12, fig. 5), it can be assumed that *I. orri* occurs in its upper part. According to Morrow and Geldsetzer (1988, fig. 4), these strata correspond approximately to the *kockelianus*-lower *ensensis* zonal interval, which was also confirmed by Uyeno (1991, fig. 4).

*Dundee Formation*.—This unit occurs in the Michigan Basin in southwestern Ontario Province in Canada (Orr, 1971; Uyeno et al., 1982), northeastern Michigan State (Bultynck, 1976), and northwestern Ohio (Klapper and Johnson, 1980). In section 14 (Brunner Quarry) from Essex County of southwestern Ontario, the present authors identified *Icriodus michiganus* n. sp., earlier determined as *I. nodosus* by Orr (1971; Table 1). However, the precise locality of the relevant sample in the section is not known.

In the northern part of Michigan's Lower Peninsula (USA), in section 15 (U.S. Steel Corporation Quarry), the age of the formation was established as Eifelian by Bultynck (1976, fig. 2) based on comparison with the Belgian Ardennes conodont succession. The present analysis and verification of the material from this section has shown that *Icriodus michiganus* n. sp. and *I. retrodepressus* occur in the entire Dundee Formation (Table 1), from sample 31 to sample 01 (sample numbers after Bultynck, 1976, table 1).

From the Medusa North Quarry in Lucas County in northwestern Ohio (Klapper and Ziegler, 1967, p. 79), Klapper (in Klapper and Johnson, 1980) illustrated a representative of *Icriodus* sp. aff. *I. retrodepressus*, now attributed to *I. michiganus* n. sp. (Table 1). It was found in the lower part of the Dundee Formation, 4.4–4.7 m below its top, in strata corresponding to the upper part of the *costatus* Zone.

The lower part of the Dundee Formation has been studied by Uyeno et al. (1982, table 8) in the United Steel Company DDH No. 1 section in southwestern Ontario. *Icriodus retrodepressus*, earlier determined by Uyeno as *I.* aff. *I. retrodepressus* (Table 1), was found 14.94–15.54 m above the base of the formation, assigned by Uyeno et al. (1982, fig. 5) to the upper part of the *costatus* Zone.

In the Michigan Basin (northern part of the Lower Peninsula of Michigan) in the lowermost sample studied by Bultynck (1976, table 1, sample 31), *Icriodus angustus* occurs in the basal part of the formation together with *I. michiganus* n. sp. (Fig. 2.20–2.21) and *I. retrodepressus* (Fig. 4.11–4.13). The first species has its entry in the *costatus* Zone (Klapper and Johnson, 1980, table 7). Another characteristic species, *Polygnathus angustipennatus* Bischoff and Ziegler, 1957, occurs in sample 1 (Bultynck, 1976, table 1) in the lower part of the Rogers City Formation overlying the Dundee Formation. The lowest stratigraphic range of the species is in the *australis* Zone (Walliser and Bultynck, 2011). The above-mentioned data indicate that the entire Dundee Formation and the lowermost part of the Rogers City Formation in Michigan belong to the *costatus* Zone.

The lower Dundee Formation in southwestern Ontario was dated by Uyeno et al. (1982, fig. 5) as an upper part of the *costatus* Zone. These authors correlated the formation with similar strata in Michigan, and, based on the data from both areas, estimated the age of the formation as the upper part of the *costatus* Zone. The same age is assumed by the present authors for the upper part of the Dundee Formation in northwestern Ohio.

*Lucas Formation, Anderdon Member*.—In southwestern Ontario, 26.82–27.31 m above the base of the calcareous-sandy Anderdon Member in section 13, Uyeno et al. (1982, fig. 3, table 4b) noted the co-occurrence of *Icriodus* aff. *I. retrodepressus* and *Polygnathus costatus patulus* → *P. cooperi cooperi* (Uyeno et al., 1982, table 4b, respectively, pl. 3, figs. 25–27, pl. 1, figs. 21–23). The first taxon is here included in *I. michiganus* n. sp. (Fig. 5, Table 1). The second one falls into the intraspecific variability range of *P. partitus* Klapper, Ziegler, and Mashkova, 1978. The affiliation to this species by the present authors is based on the narrow shape of the platform, the straight inner posterior margin, and the nearly straight outer margin, which converge to form a sagittate outline of the posterior platform. According to Uyeno et al. (1982), the age of the Anderdon Member corresponds to the upper part of the undivided *patulus* Zone (present *partitus* Zone). The presence of *P. partitus*, ranging from the *partitus* Zone to the lower *costatus* Zone (Werner and Ziegler, 1982; Berkyová, 2009), suggests the same age for the sandy Anderdon strata. Nevertheless, Brett et al. (2011, p. 29, fig. 5), based on the correlation of a shallow-marine fauna from various North American intracratonic basins, attributed the sandy Anderdon facies to the regressive phase of the Eif-1 cycle in the lower part of the *costatus* Zone.

*Danzik Formation*.—This unit has been recognized in the upper part of the Mount Kara-Burun section and in the lower part of the Arpachay River section near Danzik village in the Autonomous Republic of Nakhichevan (Azerbaijan, Transcaucasus) (Khalymbadzha, 1990, figs. 6, 7). The formation is composed predominantly of terrigenous deposits, shales, and siltstones with rare intercalations of dark bituminous limestones containing conodonts. Among these are specimens identified by Khalymbadzha (1990) as *Icriodus* n. sp. E of Weddige (1977) and *I. retrodepressus* (Table 1). All these elements are here attributed to *I. michiganus* n. sp., and the age of the strata is constrained to the *costatus* Zone.

*European localities*.—Verification of *Icriodus orri* reported earlier from the lower part of the Kostyukovichi Horizon in the Pripyat Graben of Belarus (Narkiewicz and Kruchek, 2008, pl. 1) confirmed the earlier taxonomic and biostratigraphic determinations (Table 1). Also, earlier data from the Belgian Ardennes and Eifel Mountains strata containing *I. retrodepressus* were confirmed, their age being attributed to the *partitus* Zone (Weddige, 1977; Werner and Ziegler, 1982; Bultynck et al., 2000).

## Biostratigraphic importance of the results

The above-discussed biostratigraphic data have been used to establish total stratigraphic ranges for the described *Icriodus* species (Fig. 5), and to evaluate their applicability for chronostratigraphic correlations.

*Icriodus retrodepressus* has the widest stratigraphic range, covering the interval from the *partitus* Zone to the upper but not uppermost part of the *kockelianus* Zone. It first appears slightly above the base of the *partitus* Zone in Europe. In the Lower-Middle Devonian boundary stratotype in the Wetteldorf Richtschnitt section of Germany, it occurs in the lower part of the Lauch Formation in the Bed WP 37, ~2 m above the entry of the zonal species *Polygnathus partitus* (Werner and Ziegler, 1982; Ziegler, 2000), and thus in the lower *partitus* Zone. In the Belgian Ardennes, the first representatives of the species were found in the Couvin Eau Noire section (Couvin Formation) in sample 62/2 and thus ~7 m above the lowest occurrence of *P. partitus* in sample 54, in the highest part of the Eau Noire Formation (sample numbers from Bultynck, 1970, pl. 30; section from Bultynck and Godefroid, 1974, p. 5, 6; compare with Bultynck et al., 2000, fig. 5). Bultynck (2003) suggested occurrence of the species in the *partitus* Zone in the Nedrow Member (New York State, USA), but this seems doubtful because the specimen illustrated by Bultynck (2003, pl. 2, fig. 33) does not possess a depression in the posterior part of the spindle (Fig. 4.21, showing lateral view), and thus cannot be included in *I. retrodepressus*. The first representatives of this species in North America were reported from an upper part of the *costatus* Zone at the base of the Dundee Formation in the Michigan Basin. The uppermost range of *I. retrodepressus* has been recognized in the Spillville section, in sample 2 from the lower part of the Spillville Formation (Klapper and Barrick, 1983). The age of the sediments is attributed to the upper (but not uppermost) part of the *kockelianus* Zone (see Regional biostratigraphic comparisons; Table 1). So far, *I. retrodepressus* has not been recognized in the lower part of the *costatus* Zone, in the *australis* Zone, or in the lower part of the *kockelianus* Zone.

The earliest occurrence of *Icriodus michiganus* n. sp. has been noted in the sandy facies of the Anderdon Member, Lucas Formation (Uyeno et al., 1982). This unit was attributed to the interval comprising the *partitus* Zone to a lower part of the *costatus* Zone (see above; Table 1). The lower boundaries of both zones have not been recognized in the investigated strata. The present authors suggest that *I. michiganus* n. sp. first appears in the lower part of the *costatus* Zone, and possibly even earlier, in the *partitus* Zone. The latest occurrence of the species has been noted in the lower Spillville Formation dated as the upper (but not uppermost) part of the *kockelianus* Zone (Racine section, samples 2A, 3, and Albion locality, sample 1; Klapper and Barrick, 1983, figs. 4, 5). So far, *I. michiganus* n. sp. has not been found in the *australis* and lower part of the *kockelianus* zones.

*Icriodus orri* first appears in the lower Spillville Formation above the last occurrence of *P. curtigladius* (Racine section, sample 3, Klapper and Barrick, 1983, fig. 4). These strata were dated as the uppermost part of the *kockelianus* Zone. The last occurrence is in the *ensensis* Zone based on data from the Pripyat Graben of Belarus (Narkiewicz and Kruchek, 2008).

## Paleogeographic controls on species distribution

When projected on the paleogeographic map of Scotese (2002), the distributions of *Icriodus retrodepressus*, *I. michiganus* n. sp., and *I. orri* appear concentrated mainly in shallow epicontinental marine areas along the southern margin of the Euramerican continent (Fig. 1). None of the three species has been found in Gondwana, e.g., in the well-studied Devonian sections of the Moroccan Anti-Atlas.

It can be noticed that particular species have a characteristic distribution in time and space. The earliest occurrences of *Icriodus retrodepressus*, in the lowermost Eifelian, have been noted only in the European part of Euramerica, in the Ardennes (Bultynck, 1970) and in the Eifel Mountains (Weddige, 1977; Werner and Ziegler, 1982). The relatively high number of the species in the Eifel Mountains area (Weddige, 1977, p. 291) suggests that this was the region where the species evolved and from which it expanded into other basins. It can be assumed that the most favorable habitats for the species were the neritic facies with some pelagic influences, as represented by the crinoidal limestones with brachiopods, trilobites, and rugose corals, occurring in the lower part of the Lauch Formation (Werner and

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Ziegler, 1982, p. 27; Weddige, 1988, p. 114). The disappearance of the species corresponds to a deepening of the basin and introduction of numerous representatives of *I. corniger corniger* Wittekindt, 1966 known from the goniatite-bearing pelagic facies (Wittekindt, 1966).

In the Ardennes, rare specimens of *Icriodus retrodepressus* (see Bultynck, 1970, pl. 30) have been found in the alternating calcareous and shaly beds with brachiopods and tabulate corals. The shaly interbeds disappear upward, replaced by a biostromal facies with domal and platy stromatoporoids and corals (Bultynck, 1970, pl. 35; Bultynck and Godefroid, 1974, p. 6). The last representative of *I. retrodepressus* has been found in the basal part of these sediments. The gradual shallowing and the onset of biostromal facies are considered unfavorable for the species in question, leading to its disappearance in that area. The frequency of the species increased within the *costatus* Zone, characterized by shallow-marine, quiet-water sedimentation in the intracratonic Michigan Basin (Bultynck, 1976). Numerous representatives of the species have also been found in the shaly calcareous sediments of the Speeds Member in the upper part of the *kockelianus* Zone (Klug, 1983).

The geographic range of *Icriodus michiganus* n. sp. includes shallow-marine epeiric seas of the inner part of the North American craton (Fig. 5, Table 1) and on the eastern margin of Euramerica (Transcaucasus) (Fig. 1, Table 1). The species probably first appeared in the American part of Euramerica and thereafter migrated along the northern continental margin not reaching the European part. *Icriodus orri* has a similar distribution except that it was also found in the European part of Euramerica (Belarus) in addition to the North American area (Iowa, British Columbia).

The first appearance of *Icriodus retrodepressus* might have been related to the transgressive Choteč Event, connected to considerable global biotic changes (Walliser, 1996). The appearance of *I. michiganus* n. sp. seems to be unrelated to any known eustatic and/or global biotic event. The introduction of *I. orri* correlates approximately with the transgression of the eustatic cycle Ie (Johnson et al., 1985, 1996). The occurrence of the last species in the *ensensis* Zone indicates that its development was unaffected by the initial Kačak Event (House, 1985) corresponding to the If transgression at the *kockelianus*-*ensensis* zonal boundary. On the other hand, the If transgression could have facilitated and fostered the migration of *I. orri* through the 'northern route' around Euramerica to the European part of the continent.

## Conclusions

The comparative study of abundant Eifelian icriodid assemblages from eastern Europe (Belorussian Basin) and North America (Michigan Basin) has permitted revision of the earlier concept of *Icriodus orri* (see Klapper and Barrick, 1983) and related species. Morphological features in conjunction with stratigraphic and geographic considerations led to a more restricted definition of *I. orri* and its more rigorous separation from *I. retrodepressus*. The original concept of *I. retrodepressus* has been revised and its diagnosis emended by stressing the presence of a triangular and elongated spindle with a pronounced posterior depression and the basal cavity displaying a well-developed oblique spur on its inner side and a rounded posterior expansion on its outer side. Some forms originally included in Morphotype I of *I. orri* (of Klapper and Barrick, 1983) are described herein as *I. michiganus* n. sp. The diagnostic features of the latter are the lachrymiform spindle with a wide, biconvex posterior part showing a short, shallow depression and a narrow, elongated, pointed anterior part, more or less curved inward. The basal cavity is nearly symmetrical with a rounded spur on its inner side.

Analysis of our collections and re-evaluation of published materials has made verification of the stratigraphic ranges of the studied icriodid species possible, and, for the first time, documentation of their significance for biostratigraphic correlation of shallow-marine strata. *Icriodus retrodepressus* ranges from the lowermost Eifelian (slightly above the base of the *partitus* Zone) to the upper (but not uppermost) part of the *kockelianus* Zone. Its appearance and dispersal might have been related to the transgressive/biotic Choteč Event (Walliser, 1996). *Icriodus michiganus* n. sp. appeared in the lowermost *costatus* Zone (and perhaps earlier in the *partitus* Zone) and disappeared close to the last occurrence of *I. retrodepressus*. *Icriodus orri* has the narrowest stratigraphic range, from the uppermost part of the *kockelianus* Zone to the top of the *ensensis* Zone (= top Eifelian). Its first appearance in the Michigan Basin coincides with the eustatic Ie transgression, whereas its migration to eastern Euramerica could have been related to the If transgressive pulse (= initial Kačak Event).

This study reaffirms the need for a comprehensive approach to a conodont species definitions, including not only unequivocal diagnostic morphology but also well-established stratigraphic and geographic constraints.

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