Acanthodian Jaw Bones from Lower Devonian Marine Deposits of Podolia, Ukraine

Authors: Voichyshyn, Victor, and Szaniawski, Hubert

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Acanthodian jaw bones from Lower Devonian marine deposits of Podolia, Ukraine

VICTOR VOICHYSHYN and HUBERT SZANIAWSKI

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Ischnacanthiform acanthodian dentigerous jaw bones from the Lower Devonian (Late Lochkovian) of Podolia are described for the first time. One new genus and one new species are established. *Podoliacanthus* gen. nov. is diagnosed as having small-sized jaw bones, the presence of specific accessory cusps/denticles on the medial side of teeth of the lateral tooth row, and groups of denticles forming the lingual tooth row. *Podoliacanthus zychi* sp. nov. is distinguished in having elongated slender jaw bones and lateral teeth with one medial side denticle. Besides, three species are described in open nomenclature: *Podoliacanthus* sp. 1, while similar to *Podoliacanthus zychi* sp. nov., differs in having stronger posterior inclination of the teeth tips and presence of well developed flanges of the teeth, *P.* sp. 2 has quite robust jaw bones and teeth with two medial side denticles, and *Podoliacanthus* sp. 3 has small narrow jaw bones and teeth with three medial side denticles. Morphology of the lingual tooth row is considered to be a diagnostic feature of generic and higher taxonomic levels, while accessory medial cusps/denticles of the teeth are regarded as diagnostic features at species level. The new genus also occurs in Upper Silurian or Lower Devonian deposits of North Greenland. Preservation of the jaw bones possibly depends on their secondary mineralization.

Key words: Acanthodii, Ischnacanthiformes, dentigerous jaw bone, Devonian, Lochkovian, Podolia.

Victor Voichyshyn [victor@museum.lviv.net], State Museum of Natural History NASU, Teatralna Str. 18, 79008, L'viv, Ukraine;
Hubert Szaniawski [szaniaw@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

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Introduction

Acanthodians are probably the earliest gnathostome fishes known (Märss 1992; Janvier 1996). They lived in Palaeozoic seas and fresh waters from the Silurian (or even Late Ordovician; see Smith and Sansom 1997) to Permian (Denison 1979). Their fossils, mainly microscopic scales, are widely distributed in mid-Palaeozoic deposits. The most recognizable remains of ischnacanthiform acanthodians are dentigerous dermal jaw bones, recorded from many localities around the world, from Silurian (?Wenlock; Hanke et al. 2001b) to latest Devonian (Long et al. 2004), reflecting the high dispersal capability of the group (Denison 1979). However, they were not known previously from Podolia (Ukraine), a region with many important sites yielding well preserved middle Paleozoic fish fossils.

Fish remains from the Podolian Lower Devonian have a long history of investigation, beginning with the work of Kner (1847) and Alth (1874), although agnathans have dominated these studies (Voichyshyn 2011). Brotzen (1934) established four acanthodian genera and 59 species based on scales from the Baltic States, but did not work on similar fossils from Podolia. He intensively examined Early Devonian fish fauna from the region, but focused exclusively on agnathan heterostracans and Arthrodira (Brotzen 1933; Voichyshyn 2011). Nevertheless, acanthodians are represented in Podolian marine deposits by abundant scales, tooth whorls, single teeth, jaw bones, ossified fragments of shoulder girdles, fin spines, and probably dermal bone platelets. Perhaps because of their mostly microscopic size, Podolian acanthodian remains were ignored until the late 1960s. Obruchev and Karatajūtė-Talimaa (1968), listing the taxonomic diversity of the Podolian Early Devonian fish fauna, noted the presence of *Nostolepis*- and *Gomphodus*-like scales, *Onchus*-like spines and "head plates" of Acanthodii in the stratigraphical interval from Chortkiv Horizon to Brotzen's (1933) first Old Red Zone (= Ustechko Member of the Dniester Series) inclusive (Fig. 1). Valiukevičius (2000) reported 18 forms of acanthodians based on scales collected from the Tyver Series up to the first Old Red zone. These included the genera *Nostolepis* (to which half of the recognized forms were assigned), *Gomphonchus*,

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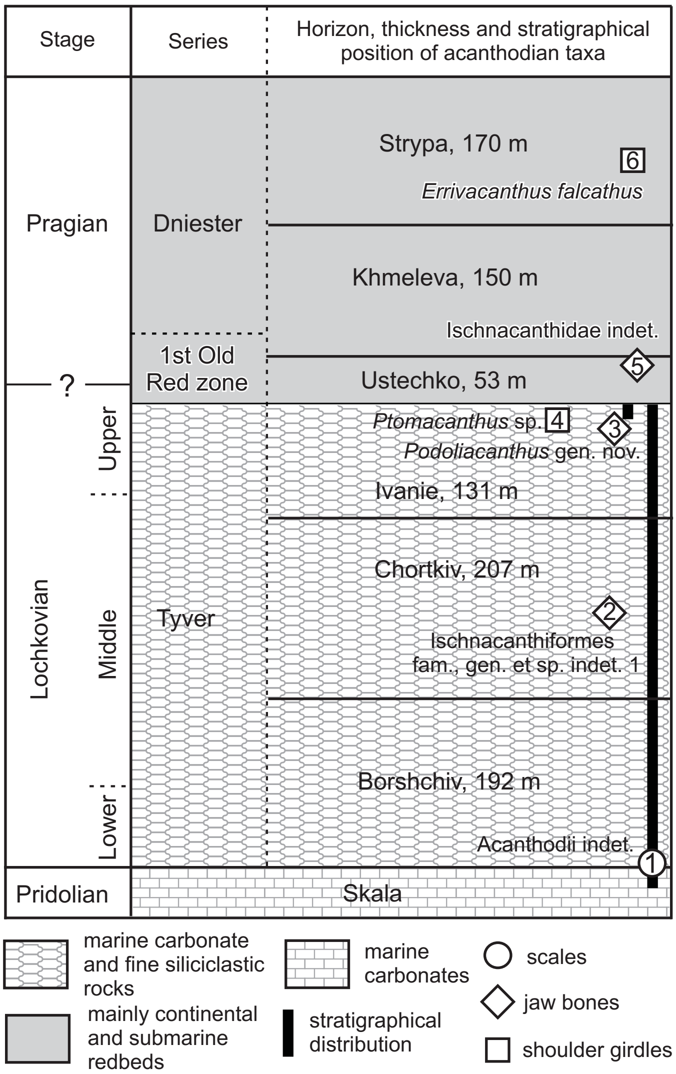

Fig. 1. Stratigraphy of the Silurian–Devonian boundary beds in Podolia (after Drygant 2003; Małkowski et al. 2009) and stratigraphical distribution of acanthodian taxa.

Pruemolepis, *Cheiracanthoides*, ?*Acanthodes*, *Canadalepis*, *Lietuvacanthus*, *Tareyacanthus*, and *Ectopacanthus*. Among them only three genera, *Gomphonchus*, *Lietuvacanthus*, and *Ectopacanthus* were regarded as ischnacanthiform acanthodians (Valiukevičius 1979, 1998).

In other publications, acanthodian microremains from Podolia were only mentioned. Novitskaya and Obruchev (1964) noted scales of *Gomphodus* from the "Upper Silurian" (in present understanding Nikiforova et al. 1972; Lower Devonian) and spines of *Onchus* from the Lower Devonian. Karatajūtė-Talimaa (1978) pointed out that in the Chortkiv and Ivanie limestones numerous thelodont scales are second in quantity after acanthodian ones. Acanthodian scales from the Upper Silurian (Skala Horizon) are considered to be the earliest vertebrate remains found in Podolia (and in the Ukraine) (Fig. 1: point 1; Voichyshyn 2001, 2010, 2011).

Except for the microremains, rare macrofragments of rather large climatiid acanthodians have been recorded from marine and continental deposits of the Lower Devonian of Podolia. *Ptomacanthus* sp. is represented by a shoulder girdle from the upper part of the Ivanie Horizon in Zalishchyky (Fig. 1: point 4; Miles 1973; Denison 1979). Also a shoulder girdle, the type specimen of *Erriwacanthus falcatus* Ørvig, 1967, has been described from the Strypa Member of the Dniester Series in Zvenygorod (Fig. 1: point 6; Ørvig 1967; Denison 1979). Thus, the majority of acanthodian remains identified to date in Podolian Lower Devonian deposits belong to the climatiids, although this group could be an artificial assemblage (Hanke and Wilson 2004).

Ischnacanthiform jaw bones from Podolia still remained undescribed, although Ørvig (1967: 145) mentioned two specimens from Horodnytsia (Fig. 1: point 5). These specimens were grouped together with jaw bones of *Ischnacanthus* species (being 14–90 mm in length, or even more) in contrast with the largest ischnacanthiform known to date, *Xylacanthus grandis* Ørvig, 1967, with jaw bone length estimated at 350 mm. Here we describe small ischnacanthiform jaw bones discovered by the second author in residues of Lower Devonian limestone samples dissolved in acetic acid while searching for conodonts. The fossils were picked from the residues without earlier treatment with heavy liquid or magnetic separator, as is usually applied by conodont investigators. The jaw bones co-occur with numerous taxonomically differentiated and well preserved acanthodian and agnathan microremains. The present paper is devoted to the description of a new genus and several new forms based on isolated ischnacanthiform jaw bones.

Institutional abbreviations.—MGUH, Geological Museum, Copenhagen, Denmark; MMMC, Collection of Mineralogical and Mining Museum, Sydney, Australia; NMC, National Museum of Canada, Ottawa; SMNH, Swedish Museum of Natural History, Stockholm, Sweden; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviation.—EDS, Energy Dispersive X-ray Spectroscopy.

Material, methods, and terminology

The samples were collected during fieldwork in 2008–2010. All of the samples came from the carbonate layers of the Lower Devonian marine sections. The sampled outcrops are located on escarpments of the Dniester valley in the vicinities of the villages Dobrivliany, Doroshivtsi, Ivanie Zolote, Ustechko, and the town Zalishchyky (Fig. 2). All the samples, except for those from Doroshivtsi, which were taken from the Chortkiv Horizon, are from the Ivanie Horizon (Fig. 1). Most of the jaw bones were found in the uppermost marine, shallow water sediments occurring a few metres below

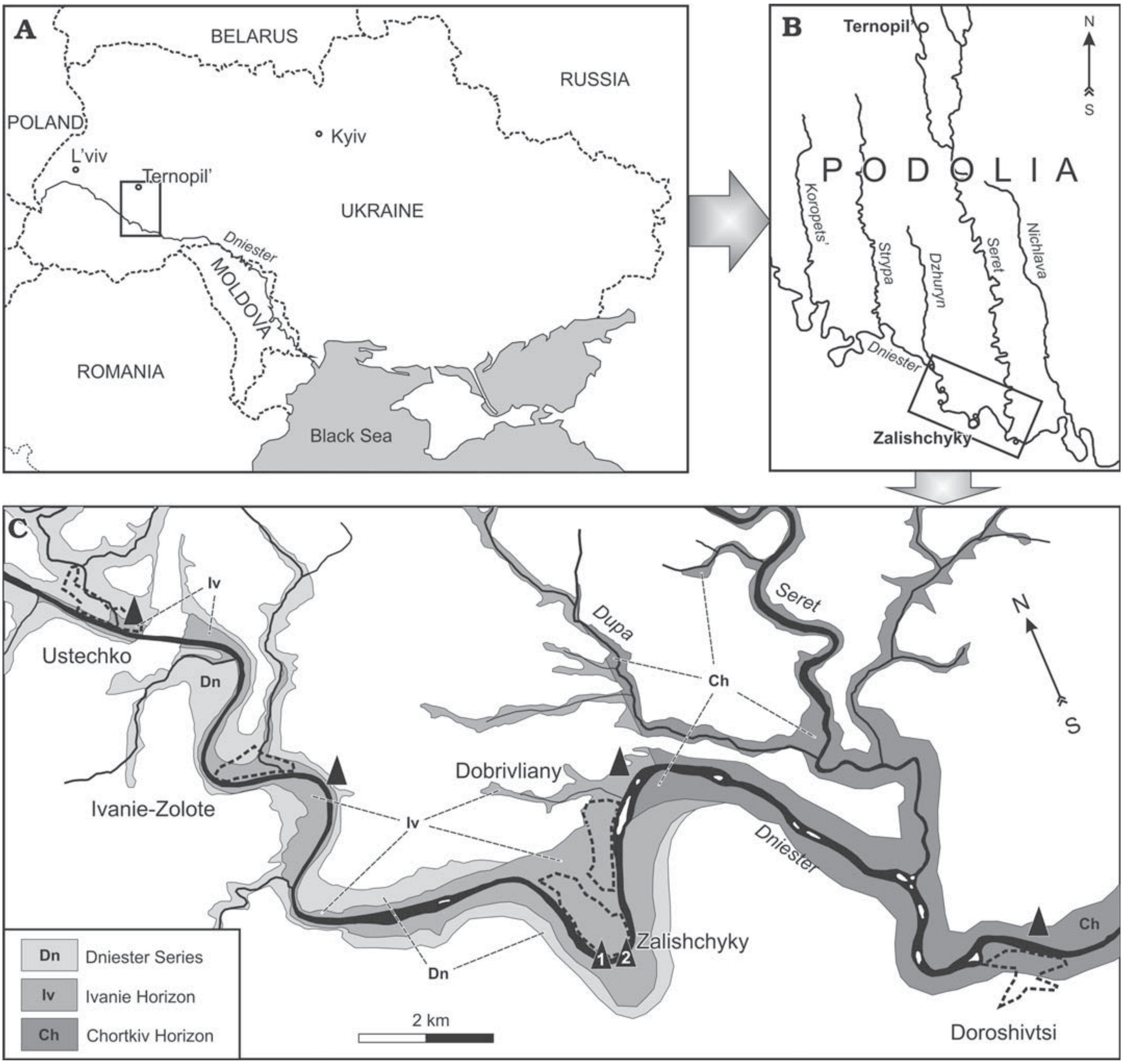

Fig. 2. Location of the study area. **A**. Contours of Ukraine with position of Podolia. **B**. Studied region within Podolia. **C**. Lower Devonian exposures (after Voichyshyn 2011) with points of sampling of studied material (indicated by black triangle).

the Old Red Formation, in outcrops located near Ivanie Zolote and Zalishchyky.

There are 95 specimens in the collection; 63 of them were photographed and investigated under SEM (Scanning Electron Microscopy). The photos and EDS analyses were made in the laboratory of the Institute of Paleobiology PAS, Warsaw, using a Philips XL-20 microscope (SEM) and EDAX analyzer (instrument providing EDS). The specimens (jaw bones, their fragments and isolated teeth, sized 1–5 mm) were mounted on SEM stubs and coated with platinum. Three of the stubs previously had been coated with carbon only for the EDS analyzes of the specimens. All the photographs were recorded as high-resolution TIFFs (Tagged Image File Format), which were used to prepare the figures using Adobe Photoshop 7.0, CorelDraw 11, and PhotoZoomPro 2 software.

Terminology used in the paper follows mainly that of Denison (1979), Lindley (2000), and Burrow (2002). The term "multicuspidate teeth" is understood here in the meaning of Ørvig (1967: 147). Nevertheless, since in the material from Podolia there are no visible limits between "secondary cusps" of the lateral tooth row indicating separate denticle groups around the "main cusp", we use the terms "teeth" and "inter-tooth denticles" rather than "main cusp" and "anterior and posterior cusps" which together formed the "multicuspi-

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date teeth". In all jaws described here the lateral tooth row equates to the main tooth row. Therefore only the first of the terms is used. "Mesial tooth row" being accepted earlier has been termed here as "lingual tooth row" (Burrow 2004a, b; Long et al. 2004). The posterior end of the jaw bone in the material examined bears some features that are recognized here as diagnostic. These are the postero-lateral process (Figs. 5E, $7C_1$, D_1; see also Lindley 2002: fig. 5C) and postero-medial process (Figs. $3A_2$, 7A, B, D). In some specimens there is a small posterior projection between them (Figs. $3A_2$, A_5, 5E). Since the jaw bones described here do not have the articulation areas of ossified cartilage preserved, it is not possible to recognize if they represent the upper or lower jaw (see Long et al. 2004).

All the material presented in the paper is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland. The last two numerals after the individual museum numbers indicate the SEM stub number and specimen number on the stub.

Preservation of the described material

None of the jaw bones collected is complete. Probably most of the specimens in the collection were fractured during the sedimentation process, which took place in near shore, not quiet environments. Some of the jaws were fractured as a result of the laboratory processing of the residues, as in some cases two fragments of the same jaw were found in the residues of the same sample, e.g., the specimen illustrated in Fig. 3.

The elemental compositions of 10 jaw bone specimens were examined with EDS analyzer combined with SEM to determine whether chemistry of the preserved material explains why the fossils were so fragile. For comparison, three co-occuring acanthodian scales, three spines and one phosphatised coprolite were investigated. As expected for fish fossils, the jaw bones are composed mainly of Ca and P (calcium phosphate). However the jaws differ from the other remains (mainly scales and spines) by having a much larger admixture of Si, Al, and Fe (alumino-silicates). One of the jaws examined even has a greater amount of these "admixtures" than of the calcium phosphate. Specimens were analyzed at several points along the bone, but no significant differences were found within each specimen. The "admixtures" indicate diagenetic mineralization of the jaw bones, which probably could be more easily infiltrated by different components than other fish remains because of their greater porosity: well preserved scales and spines are shiny because of their dentinous tissues, while the jaw bones are matt except for the dentinous teeth and denticles. The quantity of "admixtures" in the specimens obtained from the same sample is similar, but the teeth are usually less mineralized than the bones. The degree of secondary mineralization can differ significantly in specimens obtained from the different layers. Also, fossils from some of the uppermost marine layers of the Ivanie Horizon contain very little Si and Al but are secondarily phosphatized: in one of the samples with such fossils, taken from the outcrop Ivanie Zolote, ostracods with phosphatized soft parts were found (Olempska et al. 2012) and in another sample from the same outcrop microscopic phosphatised coprolites are present. Jaw bones occurring in those layers are comparatively well preserved.

Most, if not all, of the collected jaw bones are secondarily mineralized with alumino-silicates or phosphate and as a result, they are comparatively well preserved. Without the mineralization or in the case of calcium carbonate mineralization only they probably would be much more fragile, especially after the treatment with acetic acid. This explains why the jaws are not commonly found in the search for conodonts and other microfossils by dissolution of the limestone matrix.

Geological setting

Early Devonian deposits in Podolia are formed of genetically and facially two different series, composed of: (i) marine, siliciclastic, and carbonate deposits, and (ii) continental, reddish, terrigenous deposits (Fig. 1; see also Drygant 2010). The lower, marine series is stratigraphically divided into the Borshchiv, Chortkiv and Ivanie horizons of the Tyver Superhorizon. The upper, continental Dniester Series (= Old Red Formation) is subdivided into several lithological units (members), the lowermost being the Ustechko Beds. Ischnacanthiform jaw bone fragments have been recorded from the upper half of the Chortkiv and the whole Ivanie Horizon, while the oldest acanthodian scales in Podolia are known from the Upper Silurian (Voichyshyn 2001). Most of the jaw bone material is from the upper 20 metres of the Ivanie Horizon.

The Chortkiv Horizon, more than 200 m thick (Figs. 1, 2C), is represented by alternating dark grey argillaceous shale and thin-bedded fine-grained limestone. The fossil assemblages are very diverse in the limestone but not in the shale. In addition to abundant invertebrate fossils (brachiopods, nautiloids, bryozoans, bivalves, ostracods, tentaculitids, graptolites, corals, trilobites, crinoids, conodonts, scolecodonts, chitinozoans), numerous fish remains occur, including scales of thelodonts, acanthodians, and chondrichthyans, scales and carapace fragments of heterostracans, and scales and tesserae of placoderms (Obruchev and Karatajūtė-Talimaa 1968; Nikiforova et al. 1972; Karatajūtė-Talimaa 1978; Paris and Grahn 1996; Karatajūtė-Talimaa and Märss 2004; Drygant 2010; Voichyshyn 2011).

The Ivanie Horizon, up to 131 m thick (Fig. 1), outcrops along the Dniester River, in the vicinities of Dobrivliany, Zalishchyky, Ivanie Zolote, and Ustechko (Fig. 2C). Its rocks comprise dark, variably silty shales, with interlaminations of thin-bedded, often nodular or biodetrital limestone. Except for the ostracods, the faunal assemblages are similar to those of the underlying Chortkiv Horizon. The fossils are often represented by endemic species dominated by brachiopod *Muta-*

tionella podolica and ostracod *Leperditia tyraica*, shells of which locally form coquinas associated with corals, bivalves, nautiloids, tentaculitids, crinoids, and fish remains (Nikiforova et al. 1972). Fish fossils consist of micro- and macroremains of all major agnathan and gnathostome groups known to date from the Podolian Lower Devonian section (Obruchev and Karatajūtė-Talimaa 1968; Karatajūtė-Talimaa and Märss 2004; Voichyshyn 2011). The upper part of the horizon (about 70 m) is dominated by siltstone beds containing fossil assemblages with ostracods, brachiopods, eurypterids plus a range of abundant fish microremains (Nikiforova et al. 1972; Voichyshyn 2001, 2010; Drygant 2010). Stratigraphically important conodonts *Pandorinellina praeoptima*, *Zieglerodina serrula*, *Caudicriodus serus* are not common but occur in the whole unit (Drygant and Szaniawski 2012).

The boundary between the Ivanie Horizon and the Old Red Sandstone (the Dniester Series) is marked by the disappearance of grey carbonate and siliciclastic rocks with marine fossils and their gradual replacement by monotonous red sandstone beds.

Systematic palaeontology

Class Acanthodii Owen, 1846

Order Ischnacanthiformes Berg, 1940

Family Ischnacanthidae Woodward, 1891

Genus *Podoliacanthus* nov.

Type species: *Podoliacanthus zychi* sp. nov.; see below.

Etymology: Referring to Podolia, where fossils were first found, and Latin *acanthus*, thorn.

Species included.—Besides the type species, *Podoliacanthus* sp. 1, *P*. sp. 2, and *P*. sp. 3, all are from Early Devonian of Podolia.

Diagnosis.—Small ischnacanthiforms with jaw bones from about 3 mm to 7 mm long. Conical teeth of the lateral tooth row are generally subcircular-triangular in parabasal section. The teeth, which increase in size anteriorly, have narrow posterior flanges and variable additional dentiform structures attached to their base or lower third of the tooth on the medial side. These structures look as small robust denticle(s) and/or short vertical ridge. Lingual ridge of jaw bone is sloped down anteriorly and bears a tooth row or tooth field which terminates posterior to the lingual ridge end. The lingual tooth row consists of groups of denticles, with one principal (central) denticle and usually two (or rarely more) smaller ones. The denticle groups of the lingual row have a common elongate base that is surrounded by several small pores of vascular canal system. Inter-tooth pits of the lateral tooth row are quite clearly defined, rather deep and posses or not pores of vascular canals on their surface. Inter-tooth flanges comprise three to seven denticles that decrease in height/number posteriorly. Posterior part of the jaw bone has either postero-lateral and postero-medial processes, or only a postero-lateral process.

Remarks.—If we assume that we are dealing with adult remains, dentigerous jaw bones from other genera differ in being significantly larger in size. Most also lack the additional denticles medially placed at the tooth base. No other genera with jaw bones having a lingual tooth row show the same denticle groupings as in *Podoliacanthus* gen. nov. In contrast, *Atopacanthus* (Middle Devonian of Russia, Spitsbergen, and USA) differs in having circular teeth (in parabasal section) in the lateral tooth row, with striated lingual face and smooth labial face, and by lacking inter-tooth denticles; length of the jaw bone of the genus is estimated at 30–80 mm (Burrow 2004b). *Cacheacanthus* (Early Devonian of USA) differs in having monocuspid teeth with a D-shaped parabasal section in the lateral tooth row; the jaw bone is up to 50 mm long (Burrow 2007). *Gomphonchus* (Late Silurian to Early Devonian of England, Estonia, Greenland, Lithuania, Nova Scotia, Podolia, Severnaya Zemlya, Spitsbergen, Sweden, and Timan-Pechora) differs in having a single row of teeth that are typically circular in parabasal section (Denison 1979; Burrow 2004a: fig. 2B); the genus was originally based on isolated scales, and there is no certainty that jaws, teeth and scales attributed to this genus are from related fishes (see Hanke et al. 2001b). *Grenfellacanthus* (Late Devonian of Australia) differs in having large, broad-based teeth in the lateral row with a lunate parabasal section, a wide lingual field of parallel longitudinal rows of regularly spaced small denticles and a separate lingual row of small equidimensional teeth along the posterior half of the bone, and in lacking inter-tooth denticles; the jaw bone is estimated at 90–100 mm of length and is probably the second largest ischnacanthiform after *Xylacanthus grandis* (Long et al. 2004). *Ischnacanthus* (Late Silurian to Early Devonian of Canada, Great Britain, and USA) differs in having large teeth of the lateral tooth row with subcircular or oval parabasal section, in lacking additional denticles at the base of tooth and a lingual tooth row; the jaw bone length is 14–90 (up to 150?) mm; assuming all specimens are adults total body length is 4 to 16 cm (Ørvig 1967; Denison 1979; Long 1986; Hanke et al. 2001b; Burrow 2002, 2004a, 2007). *Persacanthus* (Late Devonian of Canada, Iran, and USA) differs in having subpyramidal teeth, ornamented on their lingual faces with vertical sharp crests; estimated jaw bone length for fishes in this genus is 30–50 mm (Denison 1979; Reed 1986; Valiukevičius 1992; Hermus and Hanke 2002; Burrow 2004b). *Plectrodus* (Late Silurian of England) differs by the lack of denticles attached to each tooth of the lateral tooth row (Denison 1979). *Rockycampacanthus* (Early Devonian of Australia) differs in having large teeth in both the lateral and lingual tooth rows, and in teeth of the lateral tooth row having two rows of secondary cusps on their lingual face; jaw bone is about 14 mm long (Long 1986). *Taemasacanthus* (Early Devonian of Australia) differs in having two rows of large teeth separated by a longitudinal ridge, and teeth (circular in parabasal section) with up to 10 vertical noded ridges; the jaw bone length in different species ranges between 15–36 mm (Long 1986); Burrow (2002) conditionally referred to this genus jaw bone fragments which are similar in size to *Podoliacanthus* gen.

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nov. *Xylacanthus* (Late Silurian to Early Devonian of Canada and Spitsbergen) differs in having coarsely striated monocuspid teeth that are (sub)circular in parabasal section, and low densely spaced denticles forming the lingual tooth row; estimated length of the lower jaw is from 57 to 350 mm (Ørvig 1967; Denison 1979; Long 1986; Gagnier and Goujet 1997; Hanke et al. 2001b; Long et al. 2004). *X. minutus* from the Late Lochkovian (or Pragian according to Hanke et al. 2001b) of Spitsbergen has additional medial denticles on the tooth base comprising one or two very small denticles situated behind the principal medial vertical stria of the teeth in the lateral tooth row (Gagnier and Goujet 1997: fig. 2). These denticles, in comparison with those of *Podoliacanthus* gen. nov., are very small (1/9 of the teeth height) and probably of different shape, appearing to be tiny tubercles rather than denticles. *Youngacanthus* (Lochkovian of China) differs in having teeth in the lateral tooth row of triangular parabasal section formed by three well developed ridges at their anterior, posterior and medial margins; the teeth lack medially attached denticles; the lingual field is randomly covered with small blunt tubercles; estimated total length of jaw bone is about 10 mm (Wang 1984; Long 1986; Burrow 2004a). *Zemlyacanthus* (Lochkovian of Severnaya Zemlya) differs in having thick tricuspidate teeth with 2–3 sharp vertical keels; the numerous tiny low denticles (rather tubercles) of the lingual row are randomly and densely distributed and appear to have more numerous vertical ridges than the teeth (Valiukevičius 1992: fig. 5D, pls. 4: 3, 9: 1a, b); the jaw bone is about 30 mm long (Valiukevičius 1992).

The genera *Cambaracanthus* and *Cavanacanthus* from the Lower Devonian of Australia are considered synonyms of *Taemasacanthus* since their species are based on probably incomplete jaw bones which are similar to the jaws of *Taemasacanthus erroli* (Burrow 2002). In contrast with *Podoliacanthus* gen. nov., these forms possess vertical denticle rows surrounding each tooth of the lateral tooth row. Length of their jaw bones is about 15–22 mm (Lindley 2000) corresponding to of the size in *Taemasacanthus* (Long 1986).

An isolated jaw bone SMNH P4229 (Ørvig 1967: pl. 3: 1, 2) from the Upper Silurian of Oesel (Estonia) was assigned to *Nostolepis* sp. following Gross (1957), but Denison (1976) determined that it must derive from an ischnacanthid acanthodian. It bears some resemblance to the material described here in having medial "side-cusps" which, according to Ørvig (1967: 147), are "not infrequently found in *Nostolepis*". However, this medial cusps comprises three or four denticles arranged in a vertical row (Ørvig 1973: text-fig. 1A, B) resembling such (more numerous) rows in *Taemasacanthus*. Also the specimen SMNH P4229 has a lingual row of denticles that are thick, low, randomly arranged, with vertical striations and not grouped as in the lingual tooth row of *Podoliacanthus* gen. nov. All the denticles of the specimen from Oesel, independent of their position, seem to have blunt, probably, worn tips. The teeth, at least the biggest and non-broken one, have vertical keels (three keels form a triangular parabasal section of the tooth) and a similar size to those of *Zemlyacanthus menneri* (Valiukevičius, 1992). The SMNH P4229 specimen is also much longer than the jaw bones of *Podoliacanthus* gen. nov., being 9.5 mm with six teeth in the lateral row what is at least three times as much as in Podolian material. Another ischnacanthiform jaw bone fragment, SMNH P596 from Scania (Sweden), also has a medial additional denticle on at least one tooth (Ørvig 1967: pl. 2: 3). This specimen has three teeth preserved and is 7.3 mm long. Its other features cannot be compared because of poor preservation.

Burrow (1995) described as "Ischnacanthid fam., gen. et sp. indet." a jaw bone fragment (MMMC02279; Burrow 1995: fig. 3C) from the Trundle beds (now Connemarra Formation; Lochkovian–Pragian) of central New South Wales (Australia). Subsequently she conditionally referred the specimen to *Trundlelepis cervicostulata* (Burrow 2002: fig. 29E, F). This specimen is, in some morphological features, similar to the material described here. The jaw bone fragment is 4 mm long with five teeth of the lateral tooth row preserved. The anterior teeth ("main cusps" in Burrow's terminology) of this fragment have "one medial cusp". Judging from an enlarged photograph (Burrow 1995: fig. 3D) the position of small additional medial denticle is the same as in *Podoliacanthus zychi* gen. et sp. nov. However, in contrast to the Podolian material the lingual tooth row bears "irregularly clustered tubercles varying from less than 0.1 mm wide to 0.5 mm wide at the base, and with from five to 13 or more radiating ribs". The lingual tooth row of this specimen has its largest tubercles concentrated near the lateral tooth row, while the smallest ones are situated more medially (Burrow 2002: fig. 29E, F).

Microfossils assigned to *Gomphonchus*? *turnerae* Burrow and Simpson, 1995 from the Late Silurian of Australia include a 1 mm long fragment of dentigerous jaw bone. The specimen is figured in non-occlusal (basal) view showing concavity of its base (Burrow and Simpson 1995: fig. 6D). "Mesial ridge and a higher lateral ridge, separated by a shallow groove" as well as one preserved "cusp" are mentioned in the description of its occlusal surface. However, its morphological details are not known.

A dentigerous jaw bone from the Early Devonian of the Northwest Territories of Canada, (specimen NMC 22728) was described by Bernacsek and Dineley (1977: text-fig. 11) as an "atypical" *Ischnacanthus* sp. The specimen, less than 10 mm long, has nine teeth in the lateral tooth row (the foremost one is completely broken). Usually two or three additional denticles are situated near the tooth lingual side. These denticles are of irregular size and shape. There are also single denticles on inter-tooth pits between 6th and 7th teeth, and 7th and 8th ones. The lingual ridge bears "two rows of blunt denticles" which are densely set. Referring to the specimen as "atypical" *Ischnacanthus* sp. Bernacsek and Dineley (1977) noted its resemblance to *Nostolepis* (sensu Ørvig 1973). Now there is consensus that *Ischnacanthus* lacks of lingual tooth row (Denison 1979; Burrow 2004a), and near consensus concerning the lack of dentigerous jaw bones in *Nostolepis* (Gagnier and Wilson 1995; Gagnier and Goujet

1997; Hanke et al. 2001b). Thus the specimen should not be recognized as belonging to these taxa (see also Burrow 2004a, 2007). It differs from *Podoliacanthus* gen. nov. in morphological details of the medial side denticles and lingual tooth row. Another jaw bone fragment, specimen NMC 22708 (Bernacsek and Dineley 1977: text-fig. 16C) from the same locality is about 4.5 mm long and has six teeth in the lateral tooth row. Each of the teeth has a small denticle at its base, as in *Podoliacanthus* gen. nov., but it differs in the morphology of the lingual row which has long-based "laterally compressed cusps" surrounded by numerous small denticles. Preservation and/or illustration of the specimen does not allow determination of its affinity.

Only one jaw bone fragment from outside Podolia almost certainly belonging to the new genus is MGUH VP 3617 from the Late Silurian or Early Devonian of North Greenland (Blom 1999: fig. 41K). Its features indicate that it should be assigned to the type species of the new genus (see Remarks in the description of *Podoliacanthus zychi* gen. et sp. nov. below).

The new genus is provisionally assigned to the Ischnacanthidae, but there is not enough data to be sure in this opinion. Diversified scales and fin spines, which were found in examined samples, could belong to any other acanthodian taxon. Moreover there are insufficient family diagnostic criteria concerning jaw bones within the ischnacanthiforms.

Acritolepis (Early Lochkovian, Severnaya Zemlya) was referred by Valiukevičius (2003) to the Order Climatiiformes fam. indet. based on the morphology and histology of its scales, although its type species, *A. ushakovi*, has typical ischnacanthiform jaw bones (Valiukevičius 2003: fig. 3A). Valiukevičius (2003: 134) stated that jaw bones of the type species "bear ankylosed teeth (main cusps with intercusps) which are close to *Nostolepis* Pander, 1856 (Gross 1957), but this occur in other genera (*Parexus*, *Vernicomacanthus*, *Ptomacanthus*, *Climatius* and *Brochoadmones*) supplied with tooth whorls, which have not been observed in *Acritolepis*". However, none of the genera in this list (based on articulated fish) has dentigerous jaw bones. It is worth noting that generic determination of the jaw bones referred by Gross (1957) and Ørvig (1967) to *Nostolepis* is questionable (Denison 1976). This genus is characterized (concerning dentition) by having tooth whorls (Denison 1979). The cartilaginous jaws of *Parexus*, *Vernicomacanthus*, *Climatius*, and *Brochoadmones* bear tooth whorls, but not ankylosed teeth (Denison 1979). In *Ptomacanthus* "the dentition comprises both upper and lower jaw teeth in the form of spirals …; there are no dentigerous jaw bones" (Miles 1973), and "the upper and lower jaws bear tooth whorls" (Denison 1979). Presence of dentigerous jaw bones in *Acritolepis*, whatever the affinities of the genus (see, for example, Burrow 2004a), obliges comparison with *Podoliacanthus* gen. nov. In contrast with the new genus, *Acritolepis* dentigerous jaw bones have teeth which "have a triangular longitudinal and stretched rhombic transverse basal form with a rounded outer line" and bear "an emerged inner keel". The intercusps of *Acritolepis* are striated. Jaw bones of *Acritolepis* are 13–32 mm long, and teeth of the lateral tooth row are 2.1–3.5 mm height, far higher than in *Podoliacanthus* gen. nov.

Acanthospina (Early Lochkovian, Severnaya Zemlya) was originally designated as Acanthodii incertae sedis, with "chondrichthyan-type scales, composed of "*Nostolepis*"-type tissues, … and ischnacanthid-like (particularly *Poracanthodes*-type) teeth" (Valiukevičius 2003: 187–188). Burrow (2004a) considered the taxon ischnacanthiform. It differs from *Podoliacanthus* gen. nov. in having "slightly basally striated main cusps (up to 7 mm high)" with "stretched highpyramidal longitudinal section" (Valiukevičius 2003: fig. 46A). Position of the "lateral cusps" mentioned in original description was not indicated. Since the teeth ("main cusps') size is much bigger than the total supposed length of the jaw bones of *Podoliacanthus* gen. nov. the size difference between the compared genera is significant.

There are a number of supposed ischnacanthiform genera based on isolated scales, tooth whorls or fin spines but their jaw bones are generally not known. These are *Acanthopora* (Early Devonian [Early Lochkovian], Severnaya Zemlya). *Arcticacanthus* (Lochkovian, Severnaya Zemlya), *Arenaceacanthus* (Late Silurian, Lithuania), *Bracteatacanthus* (Late Silurian, Lithuania), *Ectopacanthus* (Early to Middle Devonian, Baltic States, Podolia, Spitsbergen), *Garralepis* (Early Devonian, Australia), *Lietuvacanthus* (Early Devonian, Baltic States, Podolia), and *Rohonilepis* (Late Silurian, Lithuania) (Valiukevičius 1979, 1998, 2000, 2003, 2004; Burrow 2002; Hairapetian et al. 2006).

Gomphonchoporus, *Radioporacanthodes* (Late Silurian to Devonian, Australia and Northern Europe), and probably, *Trundlelepis* (Early Devonian [Lochkovian to Pragian], Australia) also have been described after isolated scales and tooth whorls (Burrow 2003a; Hairapetian et al. 2006). All of these together with *Zemlyacanthus* (see above) are placed in the family Poracanthodidae (another family of the Ischnacanthiformes) based on the scale histology (Vergoossen 1997). *Poracanthodes* Brotzen, 1934, the type genus of this family, was also originally established on isolated scales, but jaw bones have since been referred to it as well. Valiukevičius (2003: fig. 28A) figured such a jaw bone fragment from Severnaya Zemlya with tooth cusps of the main row in lateral view. The teeth of this specimen are about 4 mm high, comparable to the total length of jaw bone of the new genus. Burrow (2003b: fig. 3) also figured a jaw bone fragment among dissociated remains of *Poracanthodes punctatus* Brotzen, 1934 from the Upper Silurian of Nevada. The fragment is about 10 mm long and seems to have three teeth of the lateral tooth row, probably triangular in parabasal section. However, the surface of the specimen is too eroded to discern its morphological features. A small 2.1 mm long fragment of poracanthodid dentigerous jaw bone from the Late Silurian of Scania (southern Sweden) has one tooth of the lateral tooth row with four inter-tooth denticles and strong lingual row dentition which includes densely placed, low, obtuse denticles of differentiated size (Vergoossen 2004: pl. 8: 86). The largest denticles

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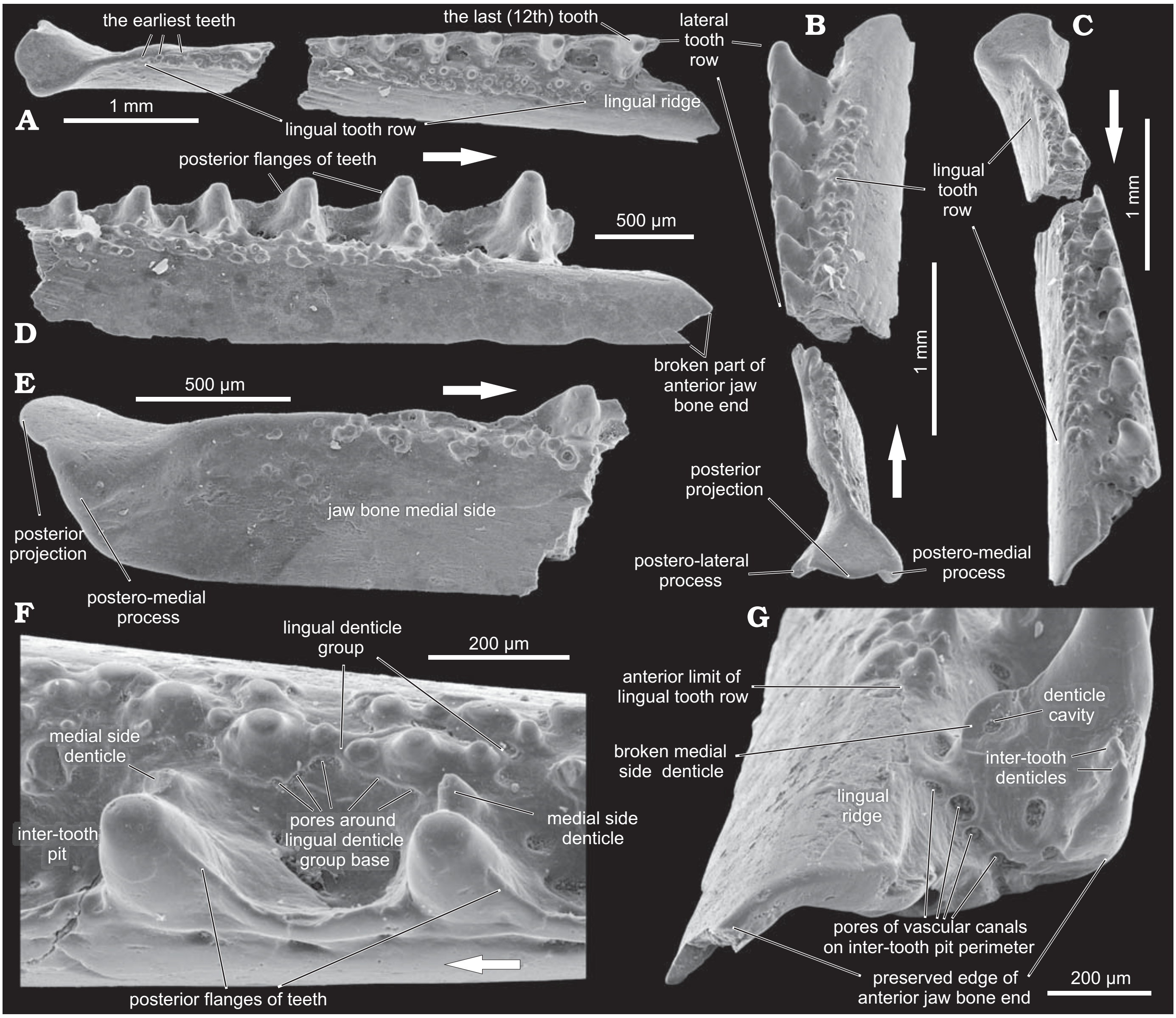

Fig. 3. Acanthodian *Podoliacanthus zychi* sp. nov. from Ivanie Zolote, Early Devonian. The holotype, ZPAL P.14/13.3, almost complete jaw bone in two pieces in occlusal (**A**), postero-occlusal (**B**), and antero-occlusal (**C**) views. Anterior (**D**) and posterior (**E**) pieces in lateral view. Enlarged region of 9th and 10th teeth from the beginning of the lateral tooth row in latero-occlusal view (**F**). Enlarged anterior part in antero-occlusal view (**G**). Arrow indicates rostral direction.

are comparable in size with the single preserved tooth. Judging from the photograph the tooth and largest denticles have ribs or striation on their sides.

Several genera which had previously been referred to ischnacanthid acanthodians are now referred elsewhere. These are *Acanthodopsis* (see Denison 1979; Burrow 2004a; Long et al. 2004), *Uraniacanthus* (see Miles 1973; Denison 1979; Hanke et al. 2001a, b; Burrow 2004a; Hanke and Wilson 2004; Hanke and Davis 2008), *Machaeracanthus* (see Lehman 1976; Denison 1979; Reed 1986; Burrow and Young 2005; Maisey and Melo 2005; Südkamp and Burrow 2007; Burrow et al. 2010), *Apatheacanthus* (see Denison 1979; Burrow 2004b), *Doliodus* (see Denison 1979; Miller et al. 2003), and *Helenacanthus* (see Denison 1979; Burrow 2004a, b).

Stratigraphic and geographic range.—Early Devonian (Late Lochkovian) of Podolia, Ukraine (Fig. 1: point 3; Late Silurian or Early Devonian of north Greenland, Denmark).

Podoliacanthus zychi sp. nov.

Figs. 3, 4, 5A–F, H, 6A, B, D, G, H, 7A, B, 8B.

1999 Acanthodii indet.: Blom 1999: 73, fig. 41K.

Etymology: In honour of the late Dr. Władyslaw Zych (1899–1981), famous researcher of Early Devonian agnathan fauna of Podolia.

Holotype: ZPAL P.14/13.3, jaw bone in two pieces, 5.1 mm long.

Type locality: Left bank of the Dniester River, east vicinity of Ivanie Zolote, Zalishchyky rayon, Ternopil oblast' (Podolia), Ukraine; Fig. 2C.

Type horizon: Upper part of Ivanie Horizon of the Tyver Series, 3–4 m below the boundary with the Dniester Series, Lower Devonian.

Material.—Except for the holotype, 26 near-complete jaw bones or their fragments: ZPAL P.14/1.1, probable juvenile jaw bone with partly preserved posterior end, 1.7 mm long, with 6 or more teeth; ZPAL P.14/2.2, jaw bone with poorly preserved posterior end, 4.5 mm long, with 9 teeth from the beginning of lateral tooth row; ZPAL P.14/3.1, fragment of rather anterior jaw bone part, 1.5 mm long, with 3 lightly worn teeth; ZPAL P.14/3.3, fragment of central to anterior part of jaw bone, 3.9 mm long, with 6 worn or broken teeth; ZPAL P.14/4.2, fragment, 1.3 mm long, with 3 teeth; ZPAL P.14/6.1, fragment of anterior part of adult jaw bone, 2.9 mm long with 2 teeth, probably the largest ones; ZPAL P.14/6.5, fragment 0.6 mm long with 2 teeth; ZPAL P.14/7.2, jaw bone with preserved posterior end and broken anterior part, 2.9 mm long, with 5 teeth; ZPAL P.14/7.5, fragment of central part of jaw bone, 2.5 mm long, with 6 very worn or broken teeth; ZPAL P.14/7.6, fragment of central part of jaw bone, 2.1 mm long with 5 worn teeth, ZPAL P.14/7.10, fragment, 1 mm long, with 2 moderately worn teeth; ZPAL P.14/8.3, fragment of possible juvenile jaw bone, 1.3 mm long, with 4 teeth; ZPAL P.14/9.2, fragment 2 mm long, with 3 teeth; ZPAL P.14/9.3, fragment of jaw bone in two pieces, together 3.1 mm long, with 5 teeth and half of the 6th one; ZPAL P.14/9.5, straight jaw bone with partly preserved posterior end, about 2.5 mm long, with 7 or more teeth (posterior part is dirty and unavailable for observation); ZPAL P.14/9.11, jaw bone with almost preserved posterior end, 2.6 mm long, with 6 teeth; ZPAL P.14/11.2, fragment, 1.2 mm long, with 3 teeth of, possibly, juvenile individual; ZPAL P.14/11.11, straight jaw bone fragment with partly broken posterior end, 2.3 mm long, with 5 teeth and sixth one broken off; ZPAL P.14/12.4, posterior part of jaw bone, 1.7 mm long, with probably 4 teeth; ZPAL P.14/12.6, fragment, 1.5 mm long, with 3 or more worn and broken teeth; ZPAL P.14/12.7, fragment, 1.4 mm long, with 3 preserved teeth; ZPAL P.14/13.1, partial jaw bone with broken posterior and anterior ends, 5 mm long, with 7 more or less preserved teeth; ZPAL P.14/13.4, fragment, 2.2 mm long, with 4 worn or broken teeth; ZPAL P.14/13.5, posterior half of jaw bone, 2.9 mm long, with 7 teeth from the beginning of lateral row; ZPAL P.14/13.6, jaw bone posterior half, about 2.1 mm long, with 5 teeth; ZPAL P.14/13.8, fragment, 2.6 mm long, with 5 teeth.

Diagnosis.—*Podoliacanthus* species with elongate slender jaw bones. The teeth of the lateral tooth row have one accessory denticle on their medial side. Pores of the vascular canal system on jaw bone medial side are very rare or lacking. The inter-tooth pits are deep and bear pores of vascular canals. The posterior part of the jaw bone has moderately developed postero-lateral and shorter postero-medial processes.

Description.—Teeth of the lateral tooth row increase in size anteriorly, in usual as a rule for the ischnacanthiforms manner. The anterior edge, preserved only in the holotype, is smooth and arcuate in shape (Fig. 3G). The foremost tooth is the largest in the lateral tooth row (Fig. 3D). The teeth are conical in shape, gradually tapering to the tip, which is worn or broken in many cases. The upper third of each tooth is slightly inclined posteriorly (Figs. 4F, 6B, D). Their width to height ratio is about 0.6–0.65. The tooth surface is smooth, but one denticle is attached medially near the tooth base or about 1/5 to 1/4 of the tooth height (Figs. 3F, 4B, E, F, 5A, B, 6A, B, G, H). There is an isthmus between each tooth and its side denticle (Figs. 5A, 6G, H). The isthmus crest sometimes is extended up the tooth side as a small short ridge (Figs. 4E, 5A). The teeth have a variably expressed narrow posterior flange (Figs. 3D, F, 4F, 6A, G), but it is often poorly preserved. The anterior flange on teeth in the lateral tooth row seems to be absent in this species, although there are two specimens in the material possessing probable remains of the flange, ZPAL P.14/3.1 and 9.2 (Figs. 4E, 5A, 6B, D). These specimens are somewhat similar to *Podoliacanthus* sp. 1 (see below). The medial side denticles are about the same shape and proportions as the teeth. Their height averages a third to a quarter of the tooth height. Both the teeth (Figs. 4A, B_1, F, 6G) and side denticles (Fig. 3G) are hollow in their lower half or third. In one specimen, ZPAL P.14/3.3, the tip of the largest tooth appears worn and is crooked medially and posteriorly (Fig. 5B).

The teeth are clearly separate in occlusal view from the medial side denticles, and are subcircular-triangular in cross section (Figs. 4E, 6G, 8B). The medial side denticles are circular-oval in cross section (Fig. 3G). In cross section, the joined tooth and side denticle is an elongate-triangular shape, and often is stretched diagonally in postero-anterior direction with the side denticle situated antero-medially (Fig. $4B_1$, C, E). This displacement of the side denticles may be observed along the entire lateral tooth row (Fig. 4C), but sometimes it is more obvious on the anterior teeth than in the posterior (smaller and older) ones (Fig. 4E). At the same time, the opposite trend in denticle position can be observed in the jaw bone of the supposed juvenile individual (Figs. 4A, 8B). Possibly these opposite trends reflect upper or lower position of jaw bones.

The inter-tooth denticles usually are poorly preserved (Figs. 3D, 4F, 6D). They form a continuous wall-like group between the teeth (Figs. 4D, 6B). Sometimes these groups lack the posterior denticle (Fig. $4B_2$, C) and, in such case, together with the tooth ("main cusp") placed anteriorly, may be considered as joined "multicuspidate tooth" in the classical understanding (see above, Material, methods and terminology). If this proves to be true, such a "tooth" in the described species consists of a "main cusp" and only posterior "secondary cusps". The number of the inter-tooth denticles ranges from 3–4 in the supposed juvenile jaw bone (Fig. 8B) up to 6–7 in mature jaws (Fig. 6A, B). The denticles of the inter-tooth groups slightly increase in size in the anterior direction (Figs. 4C, 6A, B).

The inter-tooth pits are comparatively deep and clearly defined (Figs. 3A, F, 4A, 5E, F, 6G, 8B). Fairly large pores of vascular canals are present on the inter-tooth pit surface. They concentrate mainly along the perimeter of the pit, especially at the base of the teeth (Figs. 3F, G, 4E, 6G, 8B).

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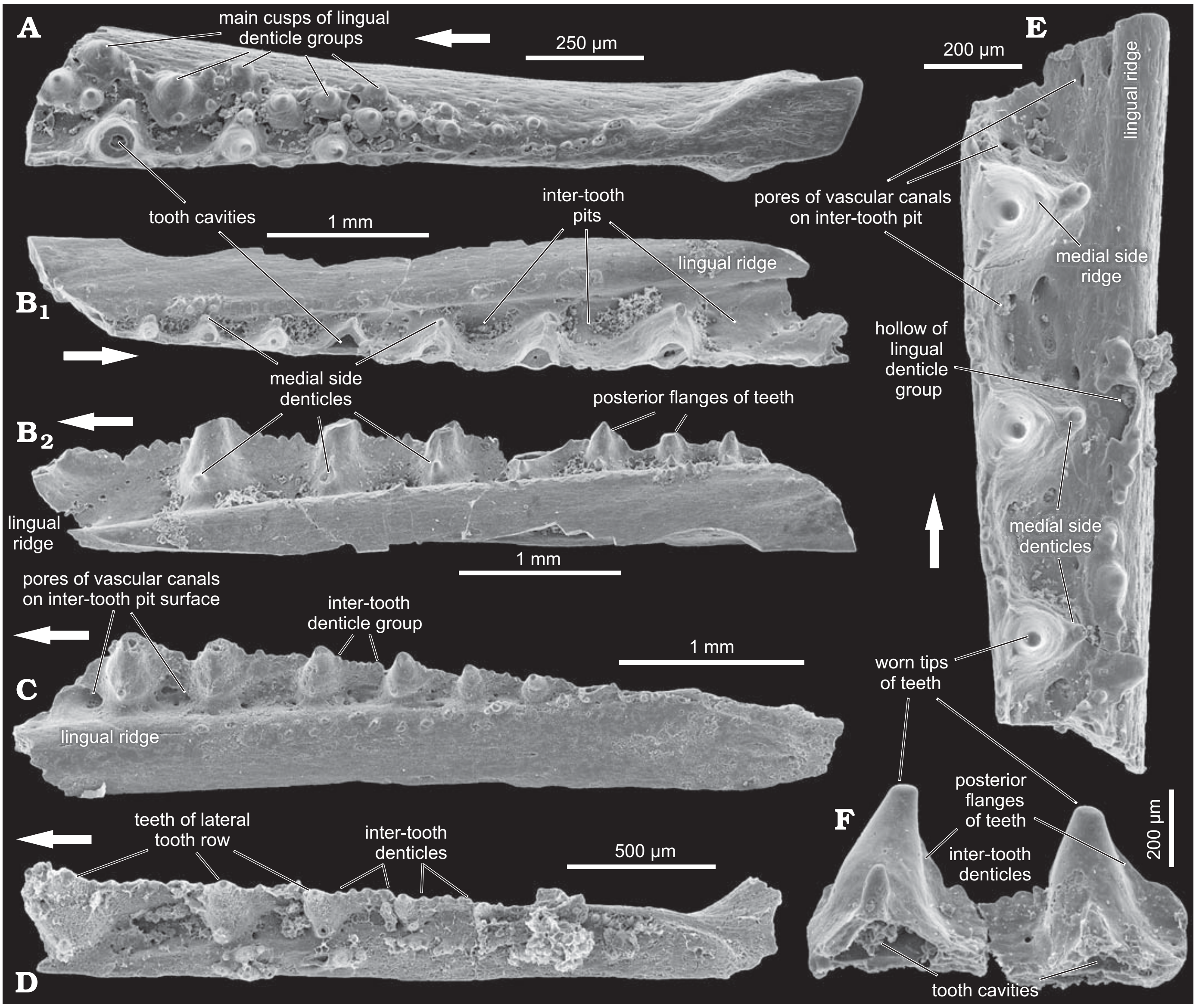

Fig. 4. Acanthodian *Podoliacanthus zychi* sp. nov. from Ivanie Zolote (all except F, Zalishchyky-1), Early Devonian. Posterior jaw bone parts (**A**–**D**). **A**. ZPAL P.14/1.1 in occlusal view. **B**. ZPAL P.14/13.1 in occlusal (B_1) and lingual (B_2) views. **C**. ZPAL P.14/2.2 in lingual view. **D**. ZPAL P.14/9.5 in occlusal view. **E**. Three-teeth jaw bone fragment, ZPAL P.14/3.1, in occlusal view. **F**. Two-teeth jaw bone fragment, ZPAL P.14/7.10, in lingual view. Arrow indicates rostral direction.

The jaw bone base (underside) forms a long trough for holding cartilage, as is typical for ischnacanthiform acanthodians (Figs. 5A, C, D, H, 6A, 7A, B). Some of the longer specimens show a certain longitudinal curvature with a slightly convex lateral jaw bone side and concave medial side (Figs. 3C, 4A, B_1, 5B), in other cases the jaw bone seems to be straight (Figs. 4D, 5C, 7B). Pores of vascular canals on the jaw bone medial side are very rare or lacking (Figs. 3D, E, $4B_2$, C, 5B, C, E, F).

The lingual ridge of the jaw bone bears a tooth row or field which consists of denticle groups. The denticle group is composed of one fairly large central denticle and two, or sometimes more, denticles of smaller size (Figs. 3F, 4A, 5F, H, 6A, H, 8B). Each group of denticles has a cavernous common base (Figs. 4E, 5A) surrounded by several pores of vascular canals, analogous with the pores in the inter-tooth pits (Fig. 3F). The arrangement of the groups and denticles within these groups is often irregular (Figs. 3F, 6H, 8B), although some appear aligned postero-lingual. In the holotype, the lingual tooth row reaches as far as inter-tooth pit between the two last teeth (Fig. 3A, B, D). In some cases, the denticle groups are situated on both the lingual ridge and the lingual slope, expanding the lingual row to a lingual field (Figs. 5D, 6H).

The posterior part of the jaw bone has moderately developed postero-medial and postero-lateral processes (Figs. 3B 5E, F, 7A, B). The former is usually smaller than the latter. The posterior concavity between them is more or less expressed (Figs. 5F, 7A, B), depending on development of the

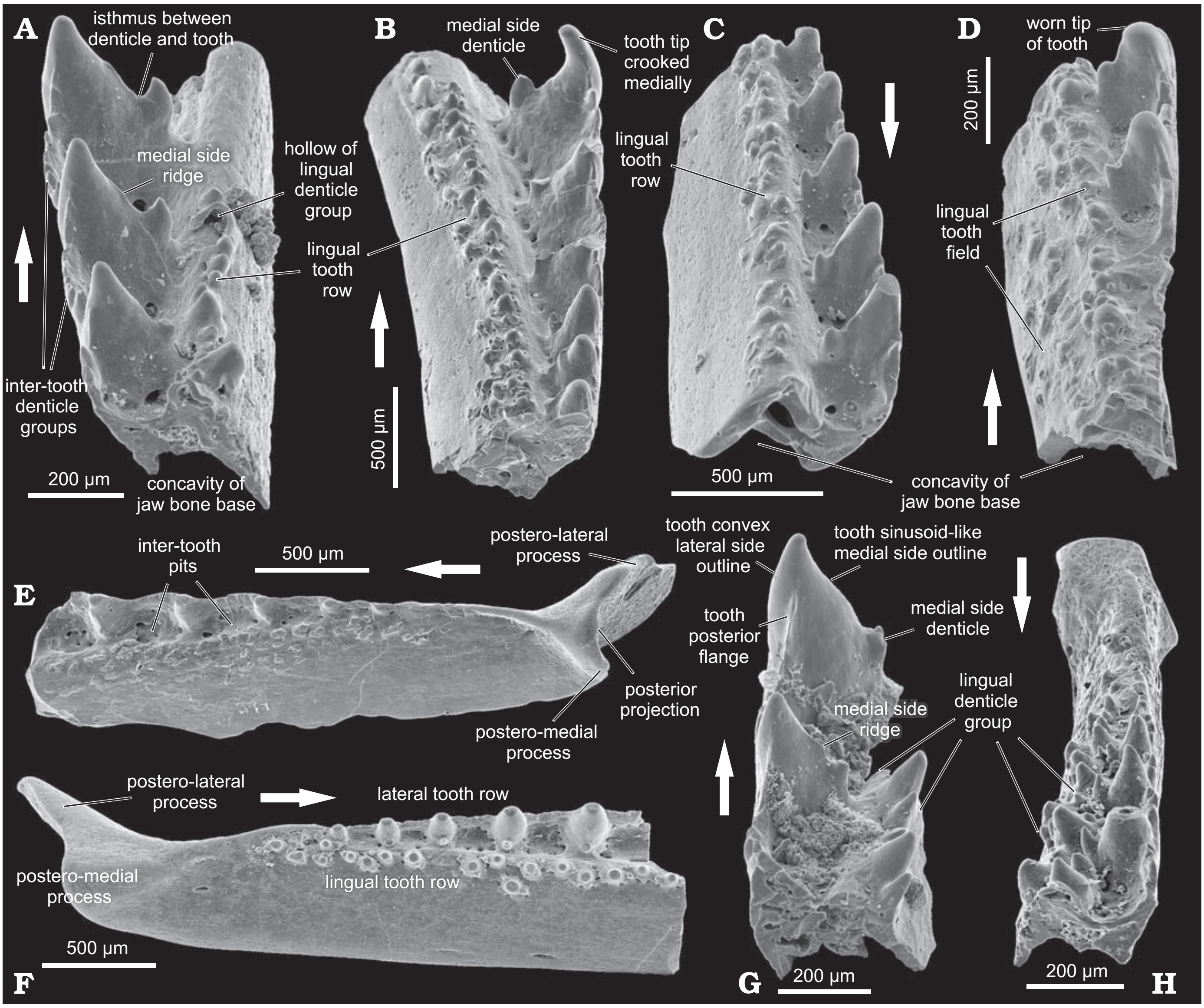

Fig. 5. Early Devonian acanthodians *Podoliacanthus zychi* sp. nov. (**A**–**F**, **H**) and *Podoliacanthus* sp. 1 (**G**) from Ivanie Zolote (A, B, D, F–H) and Zalishchyky-1 (C, E). Jaw bone parts. ZPAL P.14/3.1 (**A**), ZPAL P.14/3.3 (**B**), ZPAL P.14/12.6 (**D**) in postero-occlusal view; ZPAL P.14/7.5 (**C**), ZPAL P.14/1.1 (**H**) in antero-occlusal view; ZPAL P.14/7.2 (**E**), ZPAL P.14/13.5 (**F**) in linguo-occlusal view. **G**. Two-teeth jaw bone fragment, ZPAL P.14/11.15 in postero-occlusal view. Arrow indicates rostral direction.

posterior projection (Figs. 3A, B, 5E). Distal parts of the postero-lateral and postero-medial processes in the holotype are slightly bent downward (Fig. 3B, E).

Reconstruction of the complete holotype reveals at least 12 teeth in the lateral tooth row and the entire jaw is about 5.1 mm long (Fig. 3A). The largest specimen of *Podoliacanthus zychi* gen. et sp. nov., ZPAL P.14/3.3 (Fig. 5B), is massive and thick in cross section relative to all other specimens. We estimate the original length of this jaw bone as about 7 mm.

Remarks.—Specimen ZPAL P.14/1.1 (Figs. 4A, 5H, 8B) is 1.75 mm long, broken anteriorly, with up to five teeth from the beginning of the lateral tooth row. There are 3–4 fairly large inter-tooth denticles; the main denticles of the denticle groups in the lingual field reach almost the size of the teeth in the lateral tooth row. Estimated total length of the jaw bone is about 3 mm, or even less. Despite being much smaller in size than the others, we regard this jaw bone as from a juvenile individual rather than another species.

The jaw bone fragment MGUH VP 3617 (Blom 1999: fig. 41K) from the Upper Silurian or Lower Devonian of North Greenland is about 1.5 mm long and shows the posterior end of the lateral and lingual tooth rows, with at least two of the lateral teeth. Blom (1999) thought that the specimen was figured in postero-lateral view, but we suppose it is rather in postero-medial view. Each of the two worn teeth has one medial side denticle. The lingual tooth row on the jaw bone fragment comprises two denticle groups, recognized by Blom (1999: 73) as “two rows of two larger, separated, three-cusped teeth”, of *Podoliacanthus*-type, namely a large central denticle and two smaller ones, all arranged in-line.

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The denticles of the lingual row are of comparable size to the teeth of the lateral row, similar to the probable juvenile *Podoliacanthus* jaw bone (cf. Figs. 4A, 5H). These features are characteristic for *Podoliacanthus zychi* sp. nov., and the estimated size of the specimen is within the range for the species. The difference is in the weakly developed inter-tooth pit, but this could result from the position of this fragment along the jaw, as inter-tooth pits are not strongly developed near the origin of the main tooth row. Also the pores of the vascular canals are not observed in the Greenland specimen, neither on the inter-tooth pit surface nor around denticle groups, possibly caused by their different preservation.

Stratigraphic and geographic range.—Ivanie Zolote, Zalishchyky and Ustechko; upper part of the Ivanie Member of the Tyver Series (from 20 to 2 m below the boundary with the Dniester Series; Late Lochkovian); Monument locality, central Hall Land, North Greenland, Chester Bjerg Formation (Pridoli or Lochkovian).

Podoliacanthus sp. 1

Figs. 5G, 6C, E, F.

Material.—Three jaw bone fragments: ZPAL P.14/2.3, about 1 mm long, with 2 teeth; ZPAL P.14/9.7, 1.7 mm long, with two preserved teeth; and ZPAL P.14/11.15, 1.5 mm long, with two slightly worn but near complete teeth. All the specimens are obtained from two samples collected in 2008 and 2010 from the same locality and about the same stratigraphic level: left bank of the Dniester River, vicinity of Ivanie Zolote (Fig. 2C); upper part of Ivanie Horizon of the Tyver Series, about 11 m below the boundary with the Dniester Series, Lower Devonian.

Description.—The teeth are rather thick in the lower 2/3 of their height, and markedly tapered in their upper third. Their width to height ratio is about 0.73. In the posterior to anterior view, the largest tooth in the main row has a convex lateral outline and sinusoidal medial profile (Fig. 5G). The additional tooth denticles are represented by one medial side denticle, as in the type species. However in the specimen ZPAL P.14/11.15 this denticle is doubled, and on the smaller tooth of the jaw bone fragment there is a medial side ridge (Fig. 6C). All the teeth of the form bear quite wide anterior and posterior flanges (Fig. 6C, E, F). The lingual ridge is inclined anteriorly (Fig. 6C, F). Posterior inclination of the teeth is better expressed than in the type species (Fig. 6C, E, F). Well developed denticle groups of the lingual tooth row, including arrangement of the denticles in three lines, are typical for *Podoliacanthus* gen. nov. (Fig. 6C). The inter-tooth denticles, probably six or seven in number, are poorly preserved. Pores of vascular canals on the inter-tooth pit surface are similar to those in the type species.

Remarks.—Although not well preserved, all three specimens share several morphological features: the teeth are thick at the base and tapered in their upper third, with well expressed posterior inclination, well developed medial denticle groups of unified morphology and presence of both the posterior and anterior flanges of the teeth. Some of these features distinguish this form from the most similar *Podoliacanthus zychi* sp. nov. The form differs from the type species in having teeth thicker in parabasal section, stronger posterior inclination of the tooth tips, relatively larger and more unified morphologically lingual denticle groups, and relatively wider tooth flanges, including an anterior one that seems to be lacking in *Podoliacanthus zychi* sp. nov. The described difference cannot be regarded as intraspecific variations of *Podoliacanthus zychi* sp. nov., but may indicate a separate species, but the available material is too incomplete to permit establishment of a new species.

Podoliacanthus sp. 2

Figs. 7C, 8A.

Material.—ZPAL P.14/7.3, jaw bone fragment 2.5 mm long lacking the anterior half; right bank of Dniester River (locality Zalishchyky-1; Fig. 2), opposite to Zalishchyky, in fact, Horodenka Rayon, Ivano-Frankivs'k Oblast' (Podolia), Ukraine; upper part of Ivanie Horizon of the Tyver Series, about 5–15 m below the boundary with the Dniester Series, Lower Devonian.

Description.—The specimen is the posterior half of a jaw bone, with five teeth of the lateral tooth row. The jaw bone is rather deep. The teeth of the lateral tooth row are robust and more blunt than in *P. zychi* sp. nov., even taking into consideration that they are worn (Figs. $7C_1$, 8A). Their maximal width (diameter of the parabasal section) is almost equal to their height. The teeth are slightly inclined posteriorly and have posterior and anterior flanges. The inter-tooth denticles, probably about five in number, are poorly preserved. The first three teeth of the lateral row have one medial side denticle, but the subsequent ones have two horizontally arranged side denticles (Figs. $7C_3$, 8A). A small ridge rises up on the tooth medial side above each side denticle. The inter-tooth pits are shallow and have no vascular canal pores (Figs. $7C_2$, 8A). No lingual ridge is developed. The lateral and lingual tooth rows are closely arranged (Figs. $7C_1$, C_2, 8A). The lingual tooth row, beginning near the second tooth of the lateral row, forms a single line of relatively large denticle groups composed of three denticles with the largest central one (Fig. $7C_2$), typical for the genus. There are numerous pores of vascular canals on the surface of posterior part and medial side of the jaw bone (Figs. 7C, 8A). On the lateral jaw bone side such pores probably are lacking (Fig. $7C_4$). The posterior jaw bone part has a large postero-lateral process and barely visible posterior projection, but lacks the postero-medial process (Figs. $7C_1$, $8C_3$).

Remarks.—In contrast to *Podoliacanthus zychi* sp. nov. and *P.* sp. 1 this form has a robust (thicker in cross section) jaw bone with well developed postero-lateral process, but lacks a postero-medial one. It also differs from the type species by the presence of numerous vascular canal pores on the medial side of the jaw bone and lacks such pores in the inter-tooth pits.

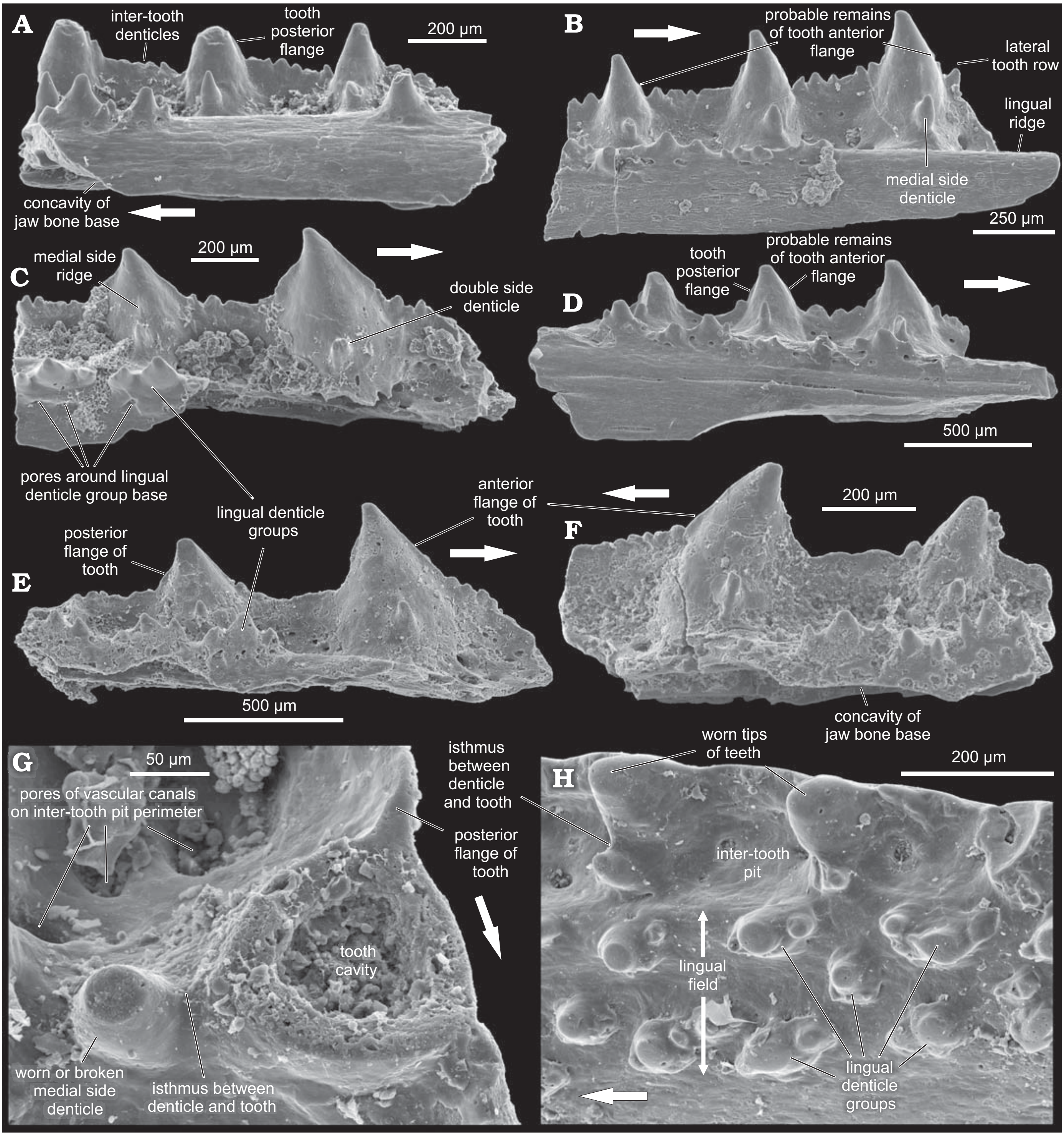

Fig. 6. Early Devonian acanthodians *Podoliacanthus zychi* sp. nov. (**A**, **B**, **D**, **G**, **H**) and *Podoliacanthus* sp. 1 (**C**, **E**, **F**) from Ivanie Zolote (all except H, Zalishchyky-1). Jaw bone fragments: ZPAL P.14/11.2 (**A**), ZPAL P.14/3.1 (**B**), ZPAL P.14/11.15 (**C**), ZPAL P.14/9.2 (**D**), ZPAL P.14/9.7 (**E**), ZPAL P.14/2.3 (**F**) in lingual view. Enlarged broken tooth ZPAL P.14/4.4 (**G**) in occlusal view. Enlarged central part of the specimen ZPAL P.14/7.5 (**H**) in postero-occlusal view. Arrow indicates rostral direction.

Moreover it differs in width/height tooth ratio (about 1.0 against 0.65 in *P. zychi* sp. nov. and 0.73 in P. sp. 1) and in having two denticles on the medial side of teeth in the main tooth row. The specimen could belong to a separate species, which can be established if additional material will be found.

Podoliacanthus sp. 3

Figs. 7D, 8C.

Material.—ZPAL P.14/12.12, jaw bone fragment lacking the anterior half, 1.8 mm long; right bank of Dniester River

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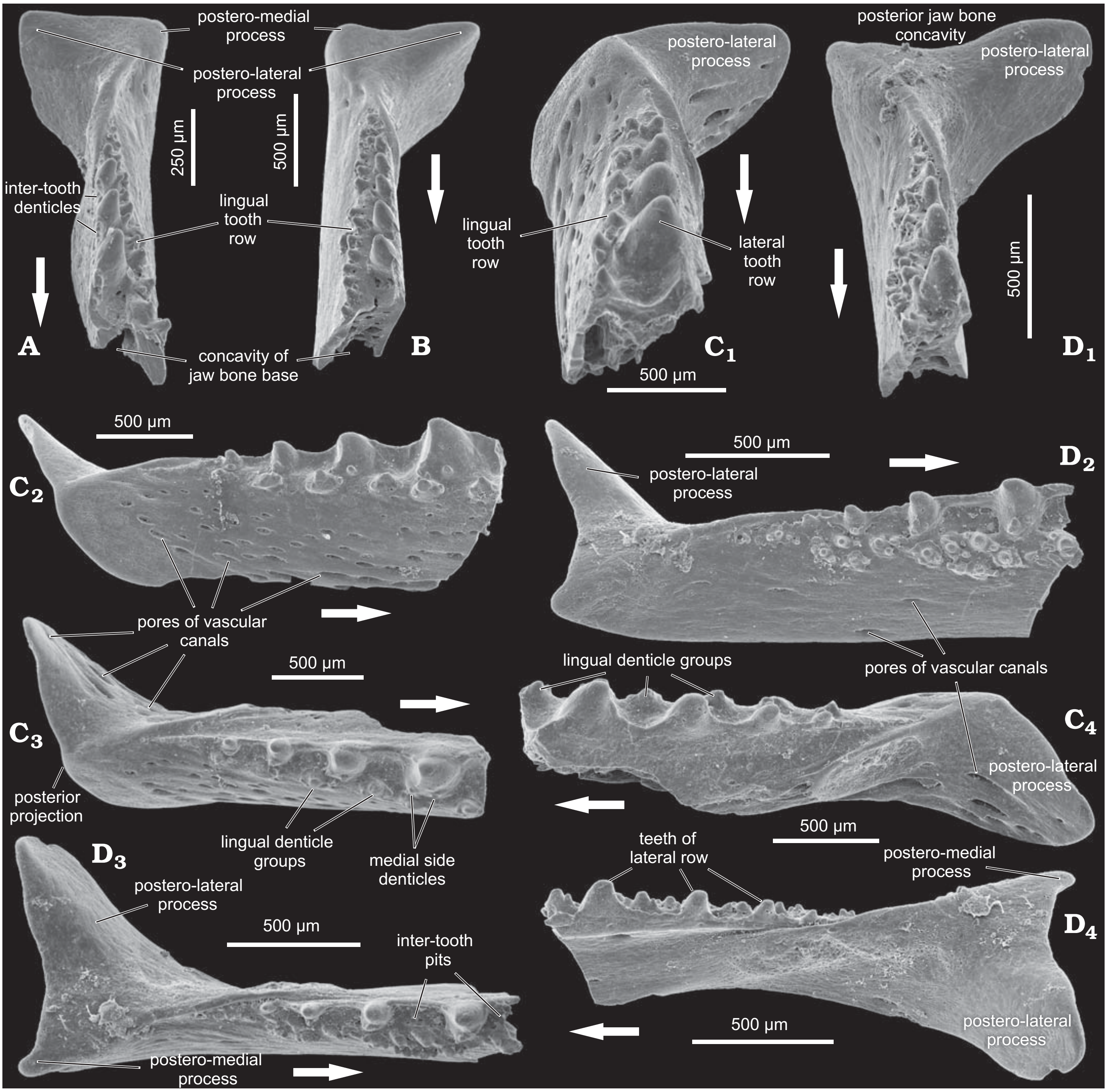

Fig. 7. Partial jaw bones of Early Devonian acanthodians from Ivanie-Zolote (A, B) and Zalishchyky-1 (C, D). **A**, **B**. *Podoliacanthus zychi* sp. nov. ZPAL P.14/12.4 (**A**) and ZPAL P.14/13.5 (**B**) in antero-occlusal view. **C**. *Podoliacanthus* sp. 2. ZPAL P.14/7.3 in antero-occlusal (C_1), linguo-occlusal (C_2), occlusal (C_3), and lateral (C_4) views. **D**. *Podoliacanthus* sp. 3. ZPAL P.14/12.12 in antero-occlusal (D_1), linguo-occlusal (D_2), occlusal (D_3), and lateral (D_4) view. Arrow indicates rostral direction.

(locality Zalishchyky-2; Fig. 2C), opposite to Zalishchyky, in fact, Horodenka Rayon, Ivano-Frankivs'k Oblast' (Podolia), Ukraine; upper part of Ivanie Horizon of the Tyver Series, about 6 m below the boundary with the Dniester Series, Lower Devonian.

Description.—The specimen is a jaw bone that lost the anterior half (or more), with five teeth in the lateral tooth row. The first tooth is broken, the second has no traces of the medial side denticle, and the third has at least one such denticle, similar to those in the type species (Fig. 7D$_2$, D$_3$). The remaining two teeth have three medial side denticles, two of them closely placed one above another, and the third situated some distance anterior to them (Fig. 8C). Perhaps, the first two denticles could be described as multiple growth of the medial side denticle. There are about six inter-tooth denticles between the two largest teeth, but the denticles are insuffi-

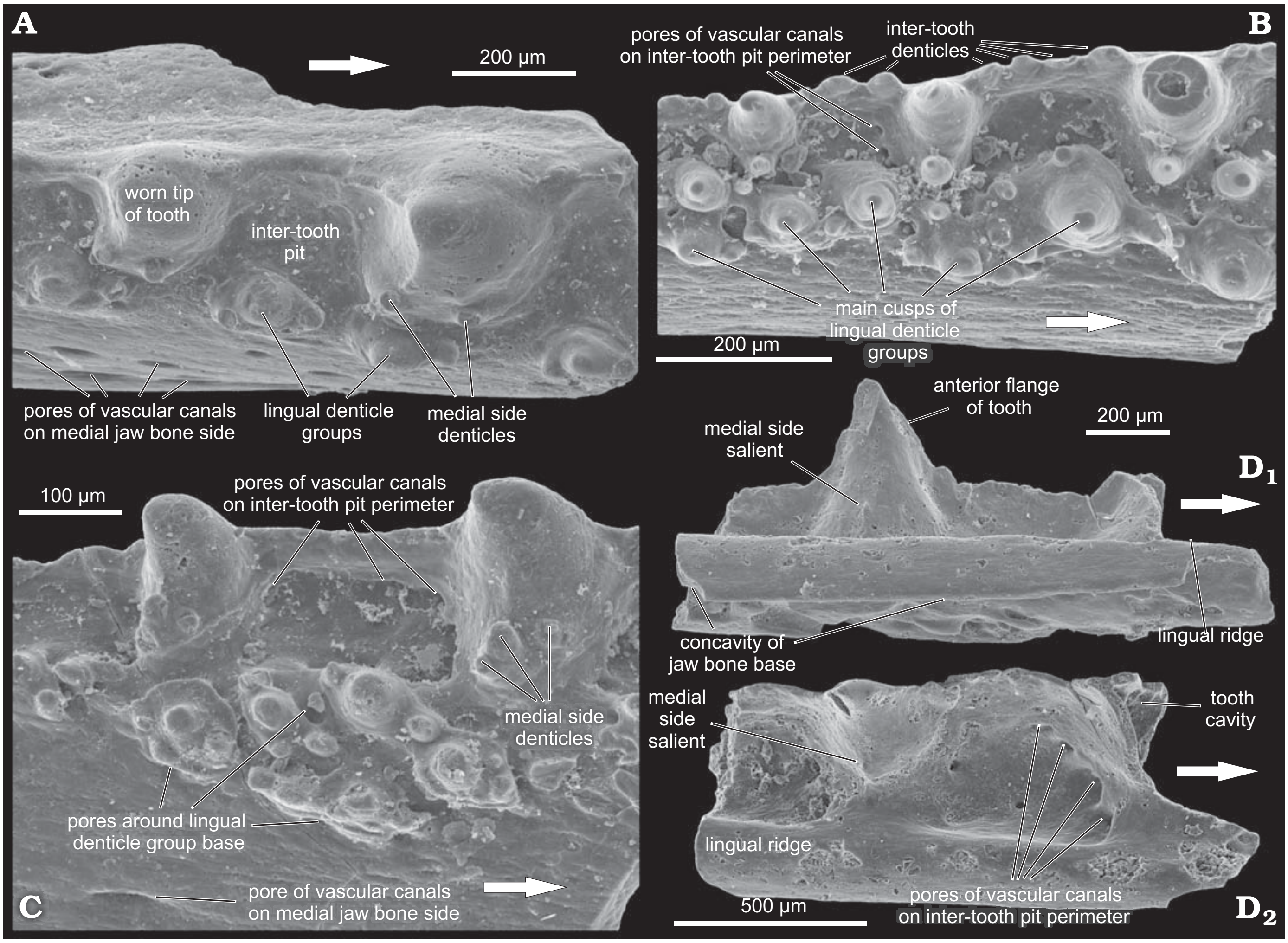

Fig. 8. Jaw bones of the Early Devonian acanthodians from Zalishchyky-1 (A, C), Iwanie Zolote (B) and Doroshivitsi (D). **A**. *Podoliacanthus* sp. 2. ZPAL P.14/7.3, enlarged anterior part of the jaw bone in occlusal view. **B**. *Podoliacanthus zychi* sp. nov. ZPAL P.14/1.1, enlarged anterior part of the juvenile jaw bone in occlusal view. **C**. *Podoliacanthus* sp. 3. ZPAL P.14/12.12, enlarged anterior part of the jaw bone in occlusal view. **D**. Ischnacanthiformes fam., gen. et sp. indet. 1, jaw bone fragment, ZPAL P.14/10.7, in lingual (D_1) and occlusal (D_2) in views. Arrow indicates rostral direction.

ciently preserved (Fig. 8C). The inter-tooth pits are quite deep and clearly defined. Pores of vascular canals concentrate along the pit perimeter but probably are lacking on the rest of the pit surface (Fig. 8C). The lingual tooth row resembles that in *Podoliacanthus zychi* sp. nov. The denticle groups are arranged diagonally and sometimes extend onto the lingual slope of the jaw bone (Fig. 8C). The posterior end of the jaw bone has a clearly expressed small postero-medial process, very large postero-lateral one, and a wide concavity in the posterior-most profile of the bone (Fig. 7D). Posterior projection is practically invisible. Total jaw bone length of the species is estimated at 3–4 mm.

Remarks.—In comparison with the other *Podoliacanthus* forms, *P*. sp. 3 has a smaller jaw bone possessing both the posterior processes (with smallest postero-medial one and a well developed postero-lateral one) and three denticles attached to the medial side of the tooth. The paucity of pores of the vascular canal system along the medial and lateral sides of the jaw, and well defined inter-tooth pits with surrounding pores distinguishes *P*. sp. 3 from *P*. sp. 2. As before, we leave this form in open nomenclature as only one jaw bone fragment is known.

Ischnacanthiformes fam., gen. et sp. indet. 1

Fig. 8D.

Material.—ZPAL P.14/10.7, a jaw bone fragment, 1.4 mm long, with two teeth of the lateral tooth row preserved (one tooth with broken tip and one tooth almost completely destroyed); left bank of the Dniester River, opposite to Doroshivtsi, Zastavna Rayon, Chernivtsi Oblast' (Podolia), Ukraine (Fig. 2C); upper part of the Chortkiv Horizon of the Tyver Series, about 240 m below the lower boundary of the Dniester Series (Middle Lochkovian), Lower Devonian (Fig. 1: point 2).

Description.—The teeth are conical in shape, hollow, and have posterior and anterior flanges which seem wider than in

Podoliacanthus gen. nov. The tooth with broken tip is 0.5 mm high, and has a smooth surface. A small salient (not developed into a denticle or ridge) is situated on the medial side of the tooth (Fig. 8D). The lingual ridge, which is quite distinct from the teeth of the lateral row, is devoid of any denticles. Inter-tooth denticles are damaged. Inter-tooth pits are deep and clearly defined. Large pores of vascular canals are situated at the anterior border of the inter-tooth pits, while elsewhere around the pit the pores are small (Fig. 8D_2). On the pit surface the pores are also small and very rare.

Remarks.—The specimen is the oldest known ischnacanthiform dentigerous jaw bone from Podolia. Because of its incompleteness, diagnostic features cannot be recognized. Additional specimens are needed to be sure whether the described medial salient of the tooth and lack of the lingual tooth row are its real characteristic features and not an artefact or atypical growth.

Discussion

The small size of the described jaw bones is noteworthy. We estimate the length of complete jaw bones of *Podoliacanthus* gen. nov. as about 3–7 mm while total body is estimated at about 5–7 cm at most. Other small acanthodians have been described. For example, the diplacanthiform acanthodian *Tetanopsyrus* has lower jaws 3.8–4.4 mm long and a total body length of about 4 cm (Hanke et al. 2001a). Burrow (2004a) has defined ischnacanthiform jaw bones as small ones when they are less than 5 mm and medium-sized if they are less than 40 mm. The forms described in this paper are among the smallest known ischnacanthiform acanthodians. But it is not inconceivable that these specimens are early ontogenetic stages of the new forms described in this paper, and these forms could be of larger size.

We think that specimen ZPAL P.14/1.1 belongs to *Podoliacanthus zychi* gen. et sp. nov. despite being significantly smaller than typical for the species. The supposition is based on the presence of one additional medial denticle and long slender jaw bone in both forms. Also, the posterior part of the jaw bone seems to be incompletely formed, suggesting the jaw represents a juvenile individual. Body length of *Ischnacanthus gracilis* is in the range from 4 to 16 cm (Burrow 2002) so a similar size differentiation is possible in other ischnacanthiform species (see also Hermus and Wilson 2001). The development of the dentition of the lingual tooth row in most specimens of *Podoliacanthus zychi* gen. et sp. nov. and specimen ZPAL P.14/1.1 (Figs. 4A, 5H) also bears comparison. Morphologically this dentition is the same as in all specimens, but the denticles of the denticle groups are much larger in ZPAL P. 14/1.1 compared with the other specimens of the species. Probably, this could be explained as a juvenile feature of the jaw bone developing when the prominent lingual row dentition compensated for the small teeth of the lateral tooth row. This also could reflect changing diet preferences through time, although few acanthodian specimens have ever been found with identifiable stomach contents.

Additional medial denticles on the teeth, which we think are typical for specific taxonomic levels, can be poorly developed (if even present) on the smallest (oldest) tooth of the lateral tooth row. Such a condition is observed in *Podoliacanthus* sp. 2 and *P*. sp. 3 (Fig. 7C_2, D_2). Sometimes the medial denticles are not developed on teeth that develop later in ontogeny (Ørvig 1967: pl. 2: 3, 1973: text-fig. 1A, B).

Probably, the additional medial denticles of the teeth were of significant adaptive importance. They vary over a wide range in the Podolian material and possibly might appear independently in different ischnacanthiform taxa (cf. *Podoliacanthus* gen. nov., *Xylacanthus minutus* from Spitsbergen, "*Gomphodus*"? from Scania (Ørvig 1967: pl. 2: 3) and probably *Trundlelepis cervicostulata* (Burrow 2002: fig. 29F) from Australia). We presume that presence, position and morphological variety of the medial denticles on teeth in the lateral tooth row can serve as diagnostic features at the specific level, while the pattern of teeth and associated denticles of the lingual ridge should be regarded as features of generic (and higher) level(s).

The family Poracanthodidae was established based on scale histology (Vergoossen 1997). The only poracanthodid genus known from articulated fish is *Zemlyacanthus*, thus the characteristics of the jaw bones of the family are based on those in *Zemlyacanthus menneri*. The original description of this species has no illustrations of its jaw bones in occlusal view; all the material was preserved in lateral aspect (Valiukevičius 1992: text-figs. 3A, 4A, 5D, 6A, 7A, pl. 1, pl. 2: 1, pl. 3: 1a, 3, pl. 4). The genus *Trundlelepis* was tentatively referred to the Poracanthodidae (Burrow 2003a). A jaw bone fragment which with probability was attributed to *Trundlelepis cervicostulata* (Burrow 2002: fig. 29F) seems to be the one known poracanthodid specimen that shows an occlusal view of poracanthodid-type dentition, as defined by Burrow (2004a: fig. 2C), in contrast to the *Gomphonchus* type. Valiukevičius (1992: 199) in his description of *Poracanthodes* (= *Zemlyacanthus*) *menneri* noted "slightly roundish-triangular or oval form" of the tooth parabasal section, while Burrow (2004a) noted a triangular form for the poracanthodid-type dentition. Vergoossen (1999) also listed a triangular parabasal section of the lateral teeth as a diagnostic character for the family Poracanthodidae (see Burrow 2003b). The classical triangular parabasal section is accentuated in *Youngacanthus* by three vertical ridges (Wang 1984: fig. 4B, C, D). However, the presence of denticles at the tooth base can significantly change the tooth parabasal section (Fig. 8A).

In possessing the lingual tooth row and rather roundish-triangular teeth in parabasal section, the jaw bones of *Podoliacanthus* gen. nov. evidently have the "poracanthodid-type" dentition. If this proves to be a distinctive feature of Poracanthodidae, the Podolian genus might be referred to this family. However, taking all the above into consideration, we provisionally prefer to keep it in Ischnacanthidae which is diagnosed in the jaw bones as having "powerful jaws bearing upper and lower dentigerous bones of dermal origin" (Burrow 2004b). At the same time we do not exclude possibility of another affinity. Among the Silurian–Early Devonian and Middle–Late Devonian types of ischnacanthiform jaw occlusion, noted by Burrow (2004a: fig. 3A, B), the jaw bones of the described genus, bearing narrow tooth flanges, occupy a rather transitional position, although closer to the first type.

Teeth of the lateral tooth row and denticles of the lingual tooth row of the same ischnacanthiform specimen/species often show similarities in sculpture. Examples are striation of the teeth and denticles in *Xylacanthus kenstewarti* (Hanke et al. 2001b), vertical keels in *Zemlyacanthus menneri* (Valiukevicus 1992: pl. 4: 2, 3, pl. 9: 1b), ribs in *Trundlelepis*? (Burrow 2002: fig. 29E), and possibly also, vertical striae in *Grenfellacanthus* (Long et al. 2004: fig. 3D) and "*Nostolepis*" (Ørvig 1967: pl. 3: 1, 2, 1973: text-fig. 1A). The surface of the teeth and denticles in *Podoliacanthus* gen. nov. is smooth, but the dentition of the lateral row, which comprises a tooth and its medial side denticlees, corresponds morphologically to the lingual denticle group with main denticle and its side denticles (see for example, Figs. 6C, 8B).

Silurian acanthodians are thought to be the earliest known predatory gnathostome fishes (Brett and Walker 2002). Among the acanthodians, the climatiids and ischnacanthids were predators possessing variable tooth apparatus (Denison 1979; Janvier 1996). Both these groups predominated in "typical" Euramerican Early Devonian (Lochkovian) assemblages (Burrow 2007). In the Middle Devonian they were cosmopolitan and apparently had good dispersal capabilities (Lukševičs et al. 2010). The Podolian acanthodians, including the new taxa described in this paper, are part of a Lochkovian acanthodian fauna similar in composition to that in other regions (Burrow 2004), but jaws of these new species are noteworthy for their size.

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