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Late Famennian pelagic shark assemblages

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ABSTRACT:

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Chondrichthyan microremains from a section at Soureillé d'Izarne (Montagne Noire, southern France), with a new species, *Thrinacodus tranquillus* sp. n., are described and compared to several other late Famennian pelagic chondrichthyan assemblages. Three general chondrichthyan biofacies are distinguished: shallow water *Protacrodus* biofacies; intermediate *Phoebodus-Thrinacodus* biofacies, characteristic of moderately deep, open shelves; and deep water *Jalodus* biofacies. The intermediate biofacies is the most widely distributed and usually yields the richest and most diverse assemblages.

Key words: Chondrichthyes, Late Famennian, Palaeogeography, Biofacies.

INTRODUCTION

During the past decade chondrichthyan microfossils from quite a few late Famennian sites all over the world have been described. Most of them come from various pelagic environments (*e.g.* Holy Cross Mts, GINTER 1990; South Urals, IVANOV 1996; Thailand, LONG 1990; Thuringia, GINTER 1999). The term "pelagic" is applied here to the distant from land, deeper basins and to drowned continental margins below the tidal zone, with well oxygenated waters and an open connection with the ocean. The main goal of this paper is to present the diversity and distribution of late Famennian elasmobranch communities from such areas, based on published records, the detailed description of a new microvertebrate fauna from the Montagne Noire in southern France, and the preliminary results of new studies on samples from Tafilalt in Morocco. Of relevance to discussion, but outside the main scope of this paper are such regions as the Cleveland Shale Basin or the Main Devonian Field. The former was a restricted basin with a thick anoxic bottom water layer, which favoured extremely good preservation of shark skeletons. The latter constituted a late Famennian shallow gulf characterised by mainly clastic and evaporite sedimentation. Elasmobranch assemblages from these areas will be treated only in passing.

The currently informal term "late Famennian" will shortly be formally defined by the Subcomission on Devonian Stratigraphy (SDS). The future unit will probably span the interval from the base of the Early *Palmatolepis expansa* through the Late *P. praesulcata* conodont Zone, i.e. up to the end of the Devonian (BECKER 1998). However, in most cases when the expression "late Famennian assemblages" is used here, it concerns chondrichthyans that lived during the *Phoebodus limpidus* ichthyolith Zone (GINTER & IVANOV 1995), i.e. from the basal Early *expansa* transgression up to the Hangenberg shallowing event in the Middle *praesulcata* Zone. Many important Famennian shark and other fish species and even higher rank groups (phoebodonts, placoderms) apparently died out during that event, so the ichthyofauna of the Late *praesulcata* Zone must have been incomparable to that of the earlier zones.

The late Famennian was chosen as the basis for the first global comparison of Devonian shark communities because of the relatively large number of samples, their richness, and their global distribution. The only other comparable Late Devonian microvertebrate fauna is that of the late Frasnian *rhenana* Zone (GINTER & IVANOV 2000, TURNER & YOUNGQUIST 1995). This is probably due to the substantial increase in pelagic, often condensed limestone facies in many areas during marine transgressions taking place in the Early *marginifera* and Early *expansa* Zones, related to the final reconstruction of chondrichthyan diversity after the Kellwasser (Frasnian/ Famennian boundary) crisis (GINTER & TURNER 1999). The relative abundance of late Famennian samples is also a result of the recent search for conodonts from Devonian – Carboniferous boundary beds, undertaken during last few decades by many teams for the purpose of establishing a global boundary stratotype. Whatever the reason, the abundance of shark microfossils from late Famennian rocks of pelagic origin now available makes it possible to show not only which species were present in a given region at a given time, but also to prepare a quantitative, comparative analysis of the whole assemblages.

Abbreviations used in the text: IGPUW – Institute of Geology, University of Warsaw, Warsaw; ZPAL – Institute of Palaeobiology, Polish Academy of Sciences, Warsaw; MB – Institut für Paläontologie, Museum für Naturkunde, Humboldt-Universität, Berlin.

SOUREILLÉ D'IZARNE, MONTAGNE NOIRE, SOUTHERN FRANCE

Geological setting

The Montagne Noire material studied comes from the samples collected by Dr. D. KORN and Dr. D. WEYER in 1992 and 1995 from the cephalopod limestone exposed on the SSE slope of Soureillé d'Izarne peak, about 0.5 km NWW from the famous and thoroughly studied La Serre section, a global stratotype for the Devonian – Carboniferous boundary (Text-fig. 1; WEYER 1997, FLAJS & FEIST 1988, Fig. 3). The limestone represents the Middle Member of the Griotte Limestone Formation (FEIST 1985); it is rich in goniatites and clymeniids, conodonts, crinoids, trilobites (mainly phacopids with large eyes), rugose and tabulate corals, brachiopod fragments, shells of the pseudoplanktonic bivalve *Guerichia*, and agglutinating foraminifer tests. The samples were taken *in situ* and from loose blocks. The accompanying ammonoids indicate the *Gonioclymenia* level of the *Clymenia* genozone, which corresponds to the Early or Middle *expansa* conodont Zones. Conodonts, although abundant, did not permit further refinement of the date.

The lithology and invertebrate fauna of the samples indicate their rather shallow water, but probably far offshore origin. It is not easy to determine precisely the palaeobathymetric conditions in the *expansa* Zone of the Montagne Noire sections because, by that time, the Griotte Limestone was developed uniformly over a vast area. However, in spite of the deformation and translation which took place in the area, some conclusions as to the situation at Soureillé d'Izarne can be drawn by analogy with the nearby La Serre section which is more complete and intensively studied. Water depth at La Serre during the *expansa* Zone times can be inferred from the position it occupied, in relation to the other areas of Montagne Noire, during the slightly later shallowing event of the *praesulcata* Zone. At La Serre the latter zone is represented by an intermediate oolitic facies, while deeper water Hangenberg shale crops out in nappe sections (e.g. Pic de Bissous situated to the north), while the section at Touriere (NW of La Serre) displays a stratigraphic gap, due to emersion and erosion (FLAJS & FEIST 1988). This may show, unless considerable synsed-

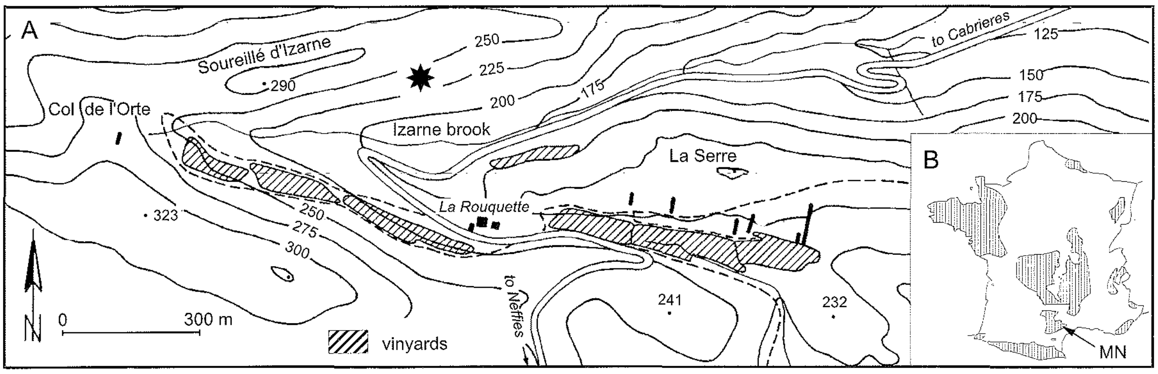

Fig. 1. A – Location of Soureillé d'Izarne (after FLAJS & FEIST 1988, modified); the studied outcrop marked with an asterisk; B – Sketch map of France to show the position of Montagne Noire (MN)

imentary block faulting has changed the relative conditions, that in the *expansa* Zone, La Serre (and, perhaps, Soureillé d'Izarne) also lay intermediately in this case between submarine heights and the epicontinental basin.

The palaeogeographic reconstruction for the latest Devonian (363 mya.) by GOLONKA & *al.* (1994) shows the Montagne Noire area in the middle of a large epicontinental sea which covered North-West Gondwana and a few adjacent terranes (Text-fig. 10). The sea extended towards the ocean, opening to the north-east. The early Variscan ridge partly separated the area from the closing oceanic strait of the Saxo-Thuringian Zone.

Material

The collection of ichthyoliths extracted from the Soureillé d'Izarne samples consists of 87 shark teeth and five unidentified tooth fragments, three chondrichthyan scales (Text-fig. 9A-B), more than 100 palaeoniscoid conical teeth, and a dozen palaeoniscoid scales. Specimens are black to very dark brown (except for two light brown cladodonts); conodonts from the same samples are dark brown, but brighter than most ichthyoliths. Shark teeth are generally well preserved, fairly complete, retaining the tips of the cusps. However, some specimens are covered with dust or small crystals; enameloid and cusp ornamentation are often missing.

All specimens are housed at the Institute of Geology, University of Warsaw (IGPUW).

SYSTEMATIC ACCOUNT

Class Chondrichthyes HUXLEY, 1880
Subclass Elasmobranchii BONAPARTE, 1838
Order indet.
Family Phoebodontidae WILLIAMS, 1985

Genus *Jalodus* GINTER, 1999

TYPE SPECIES: *Phoebodus australiensis* LONG, 1990

Jalodus australiensis (LONG, 1990)
(Text-figs 4D, 5A, 6D-F)

1999. *Jalodus australiensis* (LONG); GINTER, p. 30, Pl. 1, Figs 1-11. [see for older synonymy]
2000. *Phoebodus? australiensis* LONG; GINTER & IVANOV, Fig. 3E.

MATERIAL: 13 specimens from Soureillé d'Izarne, Famennian, Early or Middle *expansa* Zones.

DESCRIPTION: Most specimens of *Jalodus* are typical and belong to Morphotype 1 *sensu* GINTER (1990). However, there is a single larger tooth (Text-fig. 6D-F) with a lingually narrowing base and an unusually large lingual foramen; this specimen can only tentatively be referred to as *J. australiensis.* The lack of enameloid, typical of this material, and therefore the absence of characteristic ornamentation of the cusps makes the correct identification even more difficult.

OCCURRENCE: see Table 1.

Genus *Phoebodus* ST. JOHN & WORTHEN, 1875

TYPE SPECIES: *Phoebodus sophiae* ST. JOHN & WORTHEN, 1875

Phoebodus gothicus GINTER, 1990
(Text-figs 2G, M, 5E-G)

2000. *Phoebodus gothicus* GINTER; GINTER & IVANOV, Pl. 2C. [see for older synonymy]

MATERIAL: 11 specimens from Soureillé d'Izarne, Famennian, Early or Middle *expansa* Zones.

REMARKS: Specimens of *Ph. gothicus* from Soureillé d'Izarne are typical, all variations of the base shape known from the type material (from the Ostrówka Quarry, GINTER 1990) and the Maple Mill Shale (GROSS 1973) are represented here. As usual, the number of cusps in the tooth crowns varies from three to five.

OCCURRENCE: see Table 1.

Phoebodus limpidus GINTER, 1990
(Text-figs 4E, F, 5B-D, 6A-C)

1998. *Phoebodus* sp. A; LELIÈVRE & DERYCKE, p. 301-302, Fig. 4A-C.
1999. *Phoebodus limpidus* GINTER; GINTER, p. 32, Pl. 2, Figs 1-3. [see for older synonymy]
2000. *Phoebodus limpidus* GINTER; GINTER & IVANOV, Pl. 2F.

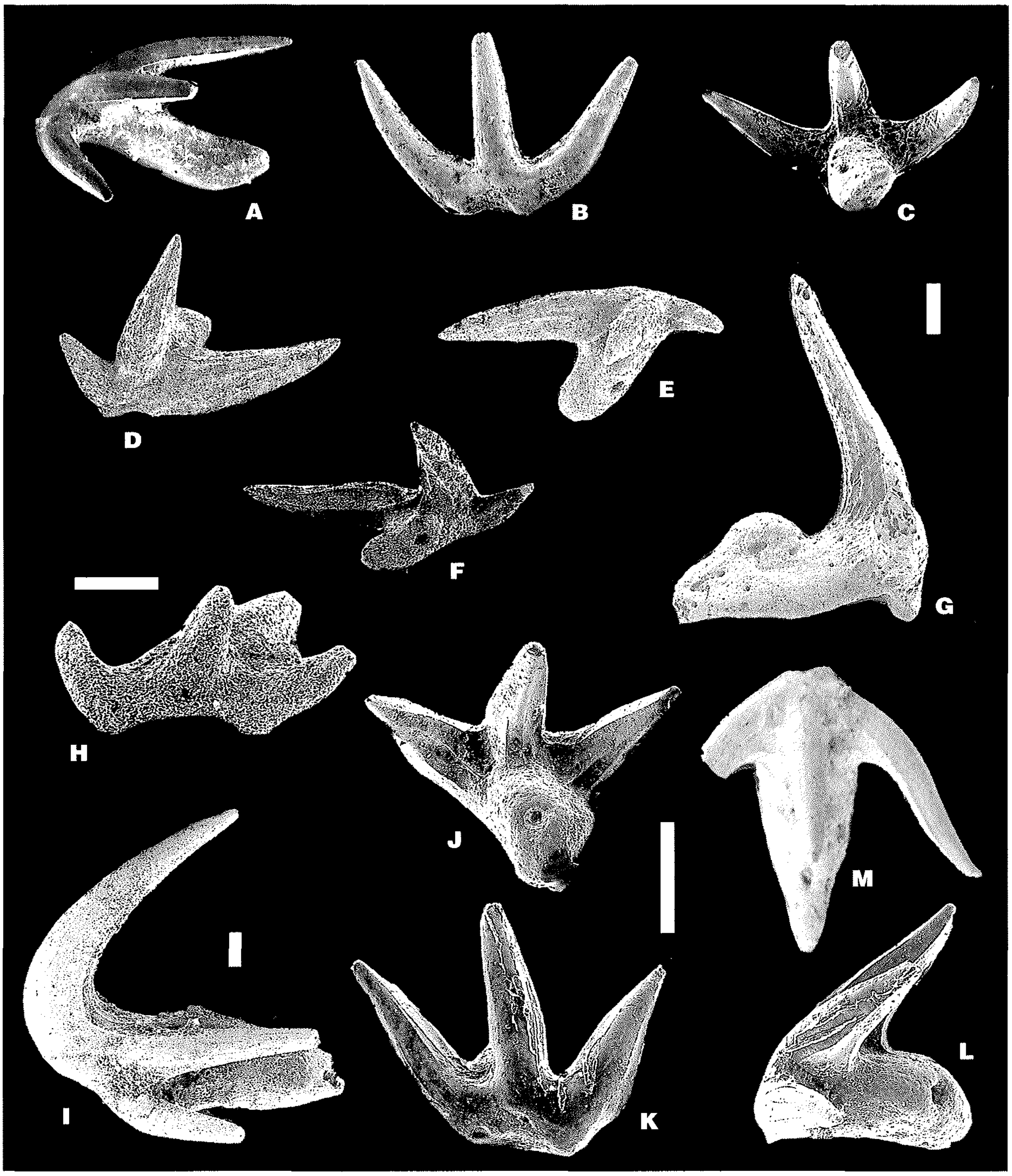

Fig. 2. A-C – *Thrinacodus tranquillus* sp. n. from the Holy Cross Mts, Ostrówka Quarry, sample F-14, middle Famennian, Late *trachytera* conodont Zone, **holotype**, IGPUW/Ps/1/47, × 42. D-F - *Thrinacodus* cf. *Th. ferox* (TURNER) from Soureillé d'Izarne, late Famennian, Early or Middle *expansa* conodont Zone, IGPUW/Ps/2/1, × 42; G - *Phoebodus gothicus* GINTER from Soureillé d'Izarne, late Famennian, Early or Middle *expansa* conodont Zone, IGPUW/Ps/2/2, × 42; H-M - comparative specimens; H - *Thrinacodus* sp. from the East Thuringian Slate Mts, Buschteich Quarry, sample Bu-20, late Famennian, Early or Middle *expansa* Zone, tooth with a large labio-basal depression, MB.f.8011, × 65; I-L - *Th. ferox* (TURNER); I - From Sudetes, Dzikowiec, sample Eb-N, Tournaisian, Late *duplicata* or *sandbergi* Zone; tooth from a lateral row, IGPUW/Ps/1/211, × 30; J-L - From Cracow Upland, sample Czatkowice A, Tournaisian, *delicatus-cuneiformis* Zone; tooth from a symphysial (?) row, IGPUW/Ps/1/212, × 90; M - *Phoebodus gothicus* GINTER, from the Holy Cross Mts, Ostrówka Quarry, sample Ost-5, late Famennian, *expansa* Zone; very small specimen with a long and narrow base, ZPAL P.IV/77, × 90; Scale bars = 0.2 mm

MATERIAL: 11 specimens from Soureillé d'Izarne, Famennian, Early or Middle *expansa* Zones.

REMARKS: Specimens from this collection basically conform with the original diagnosis (GINTER 1990); however, in a few teeth (Text-fig. 4E) intermediate cusps are missing. This condition, although normal in *Phoebodus*, has not been noted in *Ph. limpidus* before.

OCCURRENCE: see Table 1.

Genus *Thrinacodus* ST. JOHN & WORTHEN 1875

TYPE SPECIES: *Diplodus incurvus* NEWBERRY & WORTHEN, 1866.

REMARKS: Three *Thrinacodus* species have been defined to date, viz. *Th. incurvus* (NEWBERRY & WORTHEN, 1866), *Th. nanus* ST. JOHN & WORTHEN, 1875, and *Th. ferox* (TURNER, 1982). It is very probable that all of them are conspecific (GINTER & IVANOV 2000), and the names *ferox* and *nanus* should be treated only as the

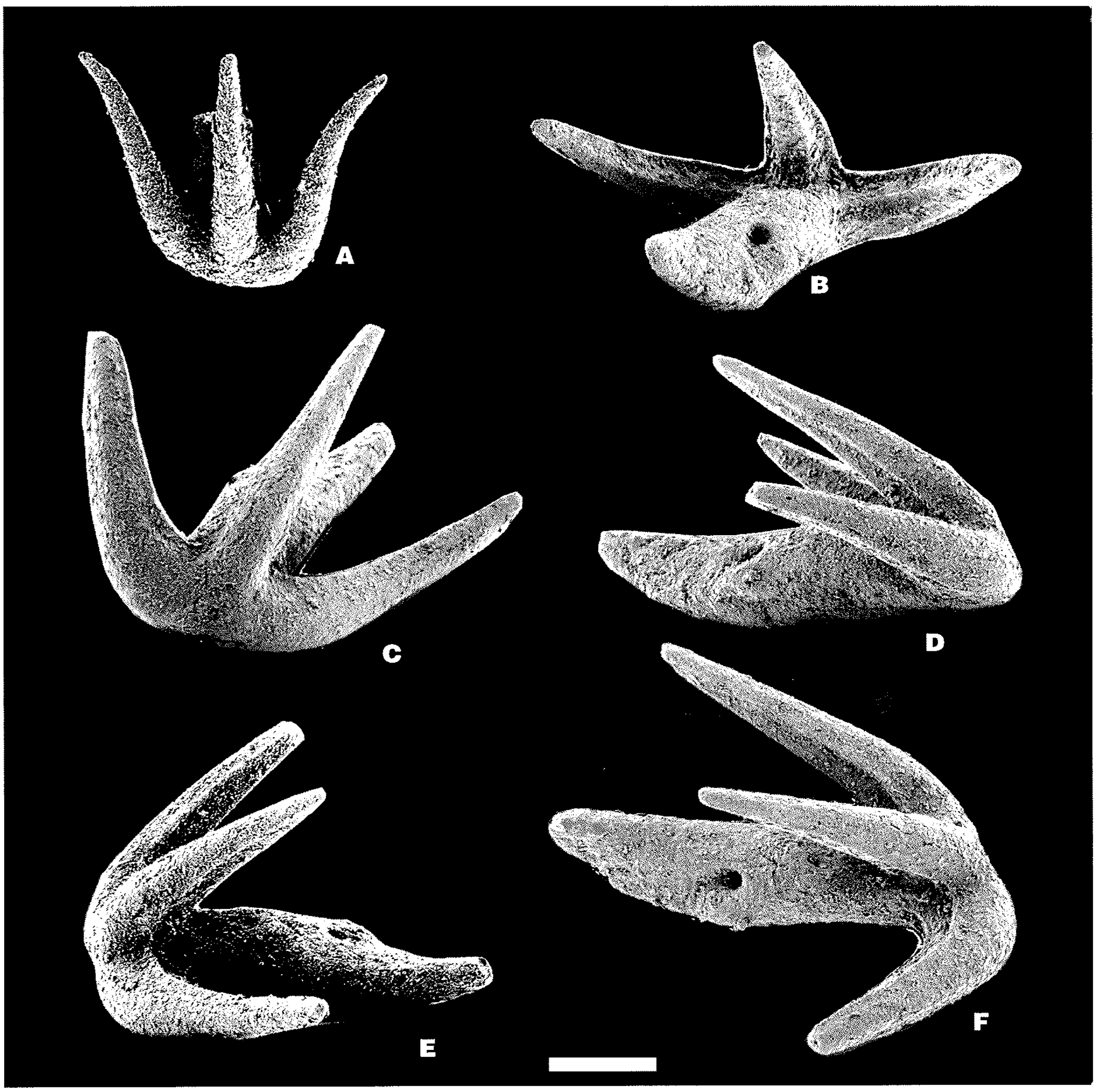

Fig. 3. *Thrinacodus tranquillus* sp. n. from Soureillé d'Izarne, late Famennian, Early or Middle *expansa* conodont Zone; A - Tooth from a symphysial (?) row, IGPUW/Ps/2/3; D-F - Tooth from a lateral row, IGPUW/Ps/2/4
All × 82; scale bar = 0.2 mm

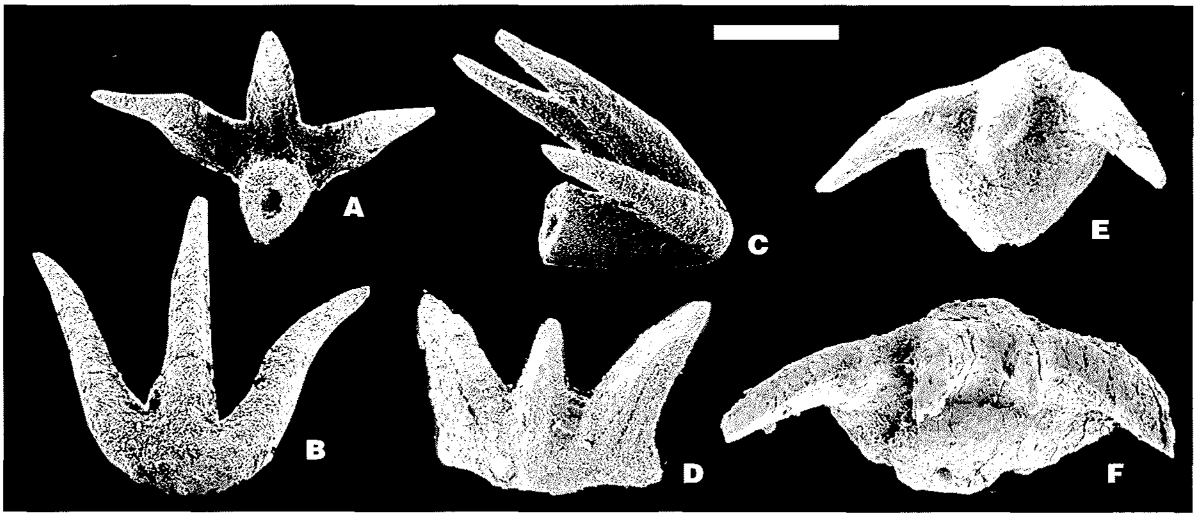

Fig. 4. Phoebodontidae from Soureillé d'Izarne, late Famennian, the Early or Middle *expansa* Zone; A-C - *Thrinacodus tranquillus* sp. n., tooth from a symphysial (?) row, IGPUW/Ps/2/x, same specimen as Text-fig. 3A; D - *Jalodus australiensis* (Long), IGPUW/Ps/2/5; E-F - *Phoebodus limpidus* Ginter; E - tricuspid specimen, IGPUW/Ps/2/x, F - IGPUW/Ps/2/6; all × 82; scale bar = 0.2 mm

names of asymmetrical and symmetrical morphotypes of *Th. incurvus* (Duncan 1999) respectively. However, for the purpose of this paper, I will use the older meaning of *Th. nanus* (= the tooth illustrated by St. John & Worthen 1875) and *Th. ferox* (= the series of teeth illustrated by Turner 1982 and specimens similar to them presented by later authors).

Thrinacodus tranquillus sp. n.
(Text-figs 2A-C, 3A-F, 4A-C, 5H-K)

1990. *Thrinacodus ferox* (Turner); Ginter, p. 76, Pl. 3, Figs 2-4.
1992. *Thrinacodus ferox* (Turner); Derycke, p. 30, Pl. 1, Fig. 3.
1995. *Thrinacodus* sp. nov.; Ginter, fig. 4G.
cf.1995. *Thrinacodus ferox* (Turner); Derycke & *al.*, p. 472, Pl. 3, Fig. B [*non* Pl. 4, Fig. A].
1996. *Thrinacodus ferox* Turner [*sic*]; Ginter & Ivanov, figs 2A-B [*non* figs 2C-D].
1996. *Thrinacodus* sp.; Ivanov, fig. 4C [*non* figs 4A-B, *non*? fig. 4D].
1998. *Thrinacodus ferox* Turner [*sic*]; Lelièvre & Derycke, p. 302-303, fig. 5.
cf. 1998. *Phoebodus gothicus* ?; Lelièvre & Derycke, p. 300, fig. 3.
1999. *Thrinacodus* sp.; Ginter, p. 34, Pl. 3, Fig. 4.
2000. *Thrinacodus* sp.; Ginter & Ivanov, Pl. 2G [*non* Pl. 2H].

HOLOTYPE: Specimen IGPUW/Ps/1/47, Ostrówka Quarry, Holy Cross Mountains, Poland; sample F-14; Famennian, Late *trachytera* Zone; Text-fig. 2A-C. Same specimen as in Ginter (1990, Pl. 3, Fig. 3) and Ginter & Ivanov (1996, fig 2A).

ETYMOLOGY: Latin *tranquillus* = quiet.

MATERIAL: 18 specimens from Soureillé d'Izarne, Famennian, Early or Middle *expansa* Zones.

DIAGNOSIS: The tooth crown is composed of three equal, slender, strongly recurved cusps, covered on both sides with gentle, subparallel cristae. The base is long (labio-lingually), very narrow, subcircular in vertical section close to the crown and flattened or concave in the lingual part; it is twisted, and its long axis is slightly curved in relation to the crown (with exception to few teeth probably of the symphysial row). The opening of the main basal canal is usually situated half-way along the base.

DESCRIPTION: Two slightly different morphotypes of *Th. tranquillus* were found in the material under study. The characteristics of the first, more numerous type (14 specimens) strictly corresponds to the diagnosis of the species: teeth of this type have lingually flattened bases, asymmetricaly situated in relation to the crown (Text-figs 2A-C, 3B-F, 5H-K). Because the base can be curved to the left or right from the midline, and both possibilities are equally common in the material, it seems most probable that such specimens represent lateral tooth rows (compare reconstructions by Turner 1982, fig. 5A-B, concerning *Th. ferox*). The other type is represented here by four very small teeth (Text-figs 3A, 4A-C), which are almost entirely symmetrical. The crown is composed of three very gentle, sigmoidal cusps, and the base is apparently rather short and tube-like, with an opening exactly at the lingual end. The base of the illustrated specimen seems broken at first sight, however, it looks exactly the same in the case of three other specimens. Such specimens apparently derive from the symphyseal tooth row of *Thrinacodus* dentition.

A slight depression can be seen in the labio-basal part of almost all specimens which suggests that the tooth bases were imbricating. These depressions are much smaller, however, than those characteristic of *Thrinacodus* teeth from Thailand (LONG 1990, fig. 5L-M) and Thuringia (Text-fig. 2H; GINTER 1999, Pl. 3, Figs 1-3, 5).

REMARKS: Teeth of *Th. tranquillus* sp. n., because of their almost symmetrical crown with long and slender cusps, sometimes more closely resemble teeth of

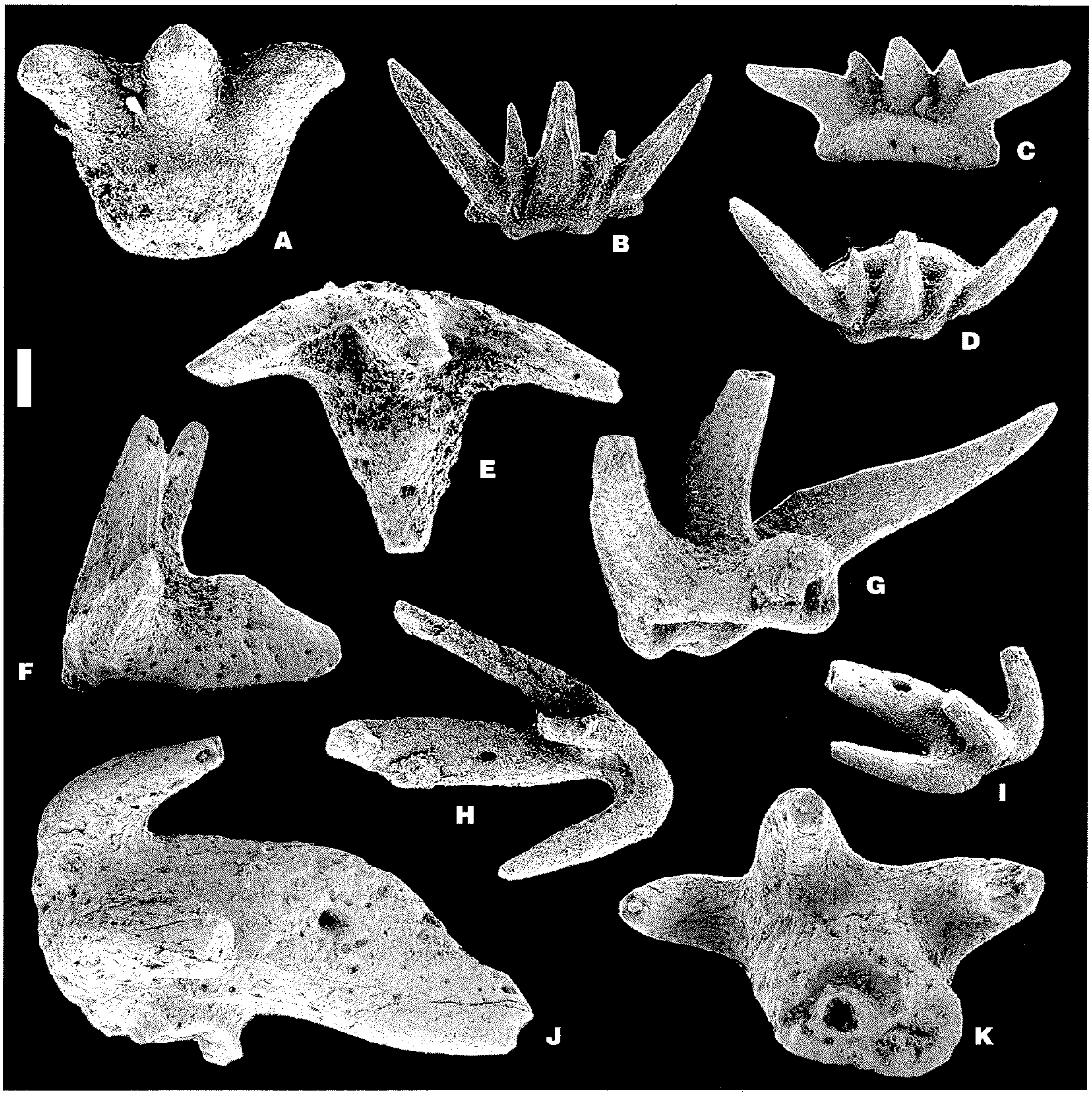

Fig. 5. Phoebodontidae from Soureillé d'Izarne, late Famennian, the Early or Middle *expansa* Zone; A - *Jalodus australiensis* (LONG), strongly abraded specimen, IGPUW/Ps/2/7; B-D - *Phoebodus limpidus* GINTER, IGPUW/Ps/2/8; E-G - *Ph. gothicus* GINTER; E-F - IGPUW/Ps/2/x, G - specimen with broken lingual base, IGPUW/Ps/2/9; H-K - *Thrinacodus tranquillus* sp. n., different tooth sizes; H - IGPUW/Ps/2/10, I - IGPUW/Ps/2/11, J - IGPUW/Ps/2/12, K - IGPUW/Ps/2/13; all × 42; scale bar = 0.2 mm

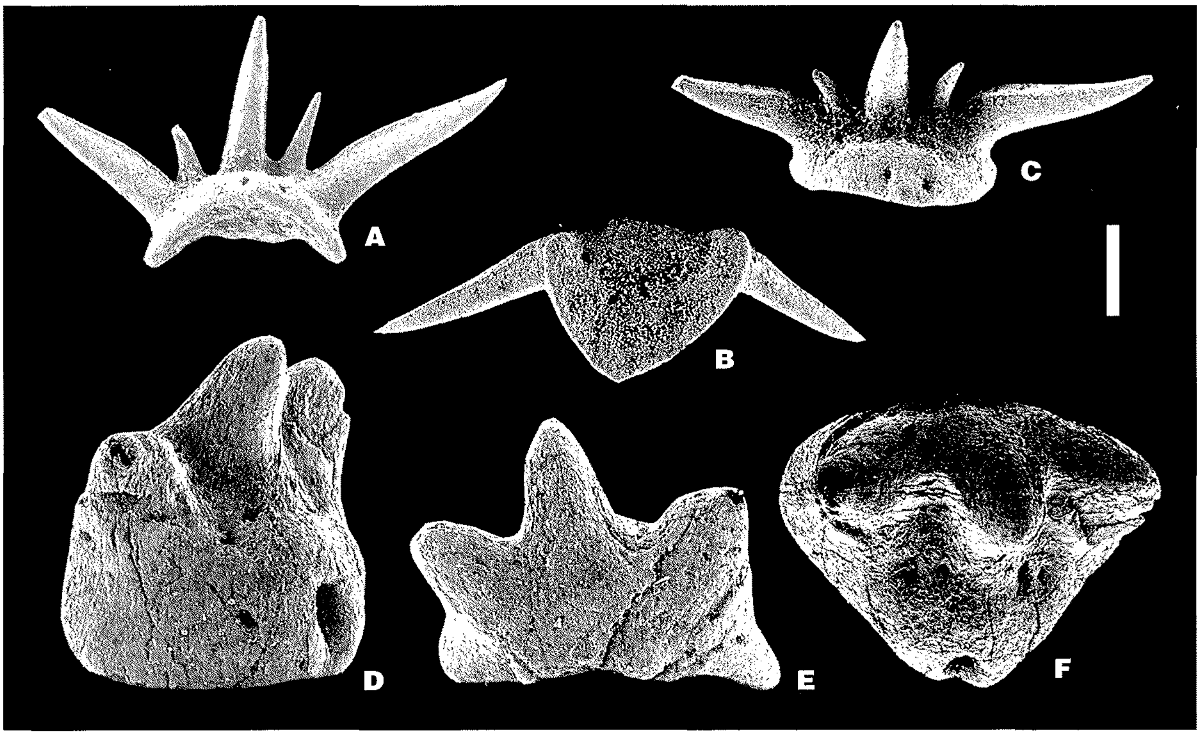

Fig. 6. Phoebodontidae from Soureillé d'Izarne, late Famennian, the Early or Middle *expansa* Zone; A-C - *Phoebodus limpidus* GINTER, a classic tooth, IGPUW/Ps/2/14; D-E - *Jalodus australiensis* ?, IGPUW/Ps/2/15; All × 62; Scale bar = 0.2 mm

Phoebodus than those of other thrinacodonts. In particular specimens of the new species with weakly twisted bases, such as the symphyseals, are similar to the teeth of *Ph. gothicus*, whose bases are often very long and narrow (Text-fig. 2M). However, *Th. tranquillus* differs from the latter by the lack of the button and the labio-basal projection. GINTER & IVANOV (1996) suggested that another difference between *Thrinacodus* and *Phoebodus* is the presence of non-sigmoidal cusps in the former. Although that statement still seems true as far as later thrinacodonts (*Th. ferox*, *Th. nanus*) are concerned, it is clear that at least some specimens of *Th. tranquillus* (Text-fig. 3A; IVANOV 1996, fig. 4c; GINTER & IVANOV 2000, Pl. 2, Fig. G) have sigmoidal cusps. This feature, possibly inherited from the phoebodonts, was probably reduced and ultimately lost during the phylogeny of *Thrinacodus*.

It must be stressed here that *Th. tranquillus* differs not only from lateral teeth of *Th. ferox* with clearly asymmetrical crowns (Text-fig. 2I; Turner 1982, fig. 3B-C, E-H), but also from certain well known Carboniferous sub-symmetrical thrinacodont forms, i.e. *Th. nanus* (ST. JOHN & WORTHEN 1875, Pl. 5, Figs 1-2) and probable symphyseal teeth of *Th. ferox* (Text-fig. 2J-L; TURNER 1982, fig. 3A; IVANOV 1996, fig. 4E). The latter forms have relatively short, labio-lingually compressed, triangular, only slightly recurved cusps, and also relatively short bases, whereas *Th. tranquillus* is characterised by long, gentle, subcircular in cross-section, strongly recurved cusps, and usually very long bases.

OCCURRENCE: see Table 1. For several years the holotype of *Th. tranquillus* sp. n., from the *trachytera* Zone of Ostrówka Quarry, was considered the oldest known specimen of *Thrinacodus* (GINTER 1990, p. 79). However, the recent study by LELIÈVRE & DERYCKE (1998) showed that *Th. tranquillus* had emerged at least as early as in the Late *marginifera* Zone: two specimens were found near the top of the Magunao Limestone (Ouijachong section, Hunan Province, South China), the range of which apparently spans the *rhomboidea* and *marginifera* Zones. It is much more difficult to determine the moment of extinction of *Th. tranquillus*. The last undoubted and numerous specimens were found thus far from the samples of the Late *expansa* through Early *praesulcata* age from Ostrówka Quarry and the South Urals, and thus it seems that *Th. tranquillus* did not persist into the Carboniferous, having died out together with the phoebodonts. However, single, incomplete specimens with apparently symmetrical crowns resembling those of *Th. tranquillus* also were found in the early Tournaisian *sulcata* Zone of La Serre (Montagne Noir, France; DERYCKE & *al.* 1995, Pl. 3, Fig. B) and in the *duplicata* Zone of Sikaza River section (South Urals, IVANOV 1996, fig. 4D). It may well transpire that, when larger collections of Tournaisian shark microfossils are thoroughly studied, *Th. tranquillus* persists to the beginning of that stage.

Thrinacodus cf. *Th. ferox* (TURNER, 1982)
(Text-figs 2D-F)

MATERIAL: 2 specimens from Soureillé d'Izarne, Famennian, Early or Middle *expansa* Zones.

DESCRIPTION: Teeth of *Thrinacodus* cf. *Th. ferox* have strongly asymmetrical crowns with three almost straight cusps, covered with a few distinct cristae. One of the lateral cusps is almost three times longer and much thicker than the other. The median cusp is of intermediate size. The base is moderately long, twisted, with an opening situated laterally, at its half-length.

REMARKS: *Thrinacodus* cf. *Th. ferox* differs from *Th. tranquillus* sp. n. and *Th. nanus* by the strong asymmetry of the crown, and from the asymmetrical forms of *Th. ferox* by only very weakly recurved cusps. However, it is still possible that it represents a variation of *Th. ferox*.

Order Symmoriida ZANGERL, 1981
Family ? Symmoriidae DEAN, 1909
Genus ? *Symmorium* COPE, 1893

"Symmorium" glabrum GINTER, 1999
(Text-fig 7A)

1989. *Symmorium* sp.; LONG & BURRETT, fig. 2D.
1990. *Symmorium* sp.; LONG, p. 65-66, fig. 7F-L, 8A-C.
1995. *Symmorium* aff. *reniforme* COPE; GINTER, fig. 4D.
1996. "symmoriid with two buttons"; GINTER & IVANOV, fig. 4D.
1996. *Symmorium* sp.; GINTER & IVANOV, fig. 5E-G.
1999. *"Symmorium" glabrum* sp. nov.; GINTER, p. 36, Pl. 4, Figs 6-11.
2000. *Symmorium* sp.; GINTER & IVANOV, Pl. 1 G-I.

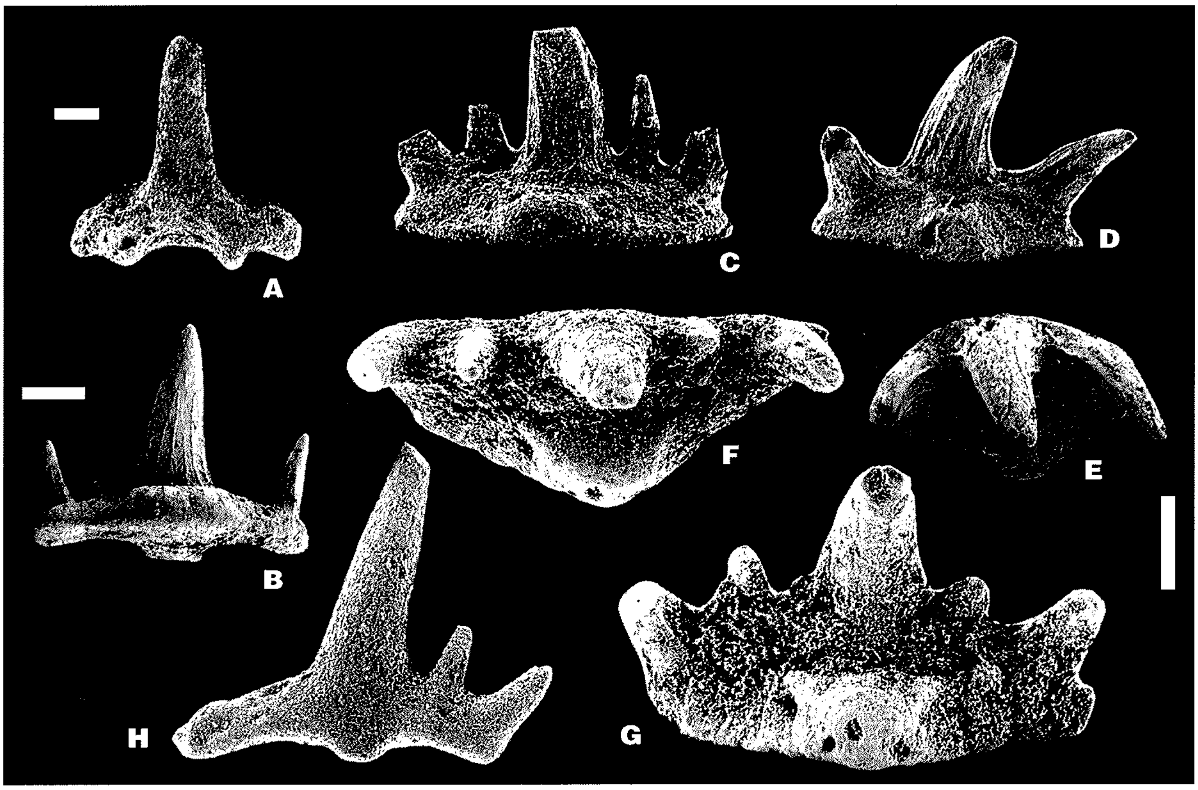

Fig. 7. Cladodonts from Soureillé d'Izarne, late Famennian, Early or Middle *expansa* conodont Zone; A - *"Symmorium" glabrum* GINTER, IGPUW/Ps/2/16, × 30; B-G - *Stethacanthus* sp; B - IGPUW/Ps/2/17, × 42; C - IGPUW/Ps/2/18, D-E - IGPUW/Ps/2/19, F-G - IGPUW/Ps/2/20, × 62. Scale bars = 0.2 mm

MATERIAL: 2 specimens from Soureillé d'Izarne, Famennian, Early or Middle *expansa* Zones.

DESCRIPTION: Of the two specimens of "*S.*" *glabrum* one is fairly complete (Text-fig. 7A), and from the other only a base without cusps was found. However, teeth of this species have very characteristic, kidney-shaped bases, with two large buttons on the upper lingual side, a strong labial depression, and two hook-like labio-basal projections, so it is easy to identify them even when the cusps are broken.

REMARKS: For the discussion on the generic affinity of the species see GINTER (1999).

OCCURRENCE: see Table 1.

Genus *Stethacanthus* NEWBERRY, 1889

TYPE SPECIES: *Physonemus altonensis* ST. JOHN & WORTHEN, 1875

Stethacanthus sp.
(Text-figs 7B-G)

MATERIAL: 16 specimens from Soureillé d'Izarne, Famennian, Early or Middle *expansa* Zones.

DESCRIPTION: The main features of these cladodont teeth are a distinct, rectangular labio-basal projection (Text-fig. 7B, H); a single, lingually situated button of various shapes; and a crown composed of usually five, rarely three cusps. The cusps are subcircular in cross section and ornamented on both sides with clear, subparallel cristae. Teeth of this general form are common at least from the Frasnian through the Late Carboniferous, so it is difficult to decide if they belong to an already established stethacanthid, or to some new, typically Famennian species. The only certainty is that the number of cusps never exceeds five, so the specimens do not belong to *S. thomasi* (TURNER, 1982), whose teeth may have seven cusps in the crown.

Cohort Euselachii HAY, 1902
Superfamily Protacrodontoidea ZANGERL, 1981
Genus *Protacrodus* JAEKEL, 1921

TYPE SPECIES: *Protacrodus vetustus* JAEKEL, 1921

Protacrodus cf. *vetustus* JAEKEL, 1921
(Text-figs 8A-D)

1998. *Protacrodus* sp. A; LELIÈVRE & DERYCKE, p. 304-305, Fig. 8A.
1999. *Protacrodus* cf. *vetustus* JAEKEL; GINTER, p. 40, Pl. 3, Figs 8-10. [see for older synonymy]
2000. *Protacrodus* cf. *vetustus* JAEKEL; GINTER & IVANOV, Pl. 1F.

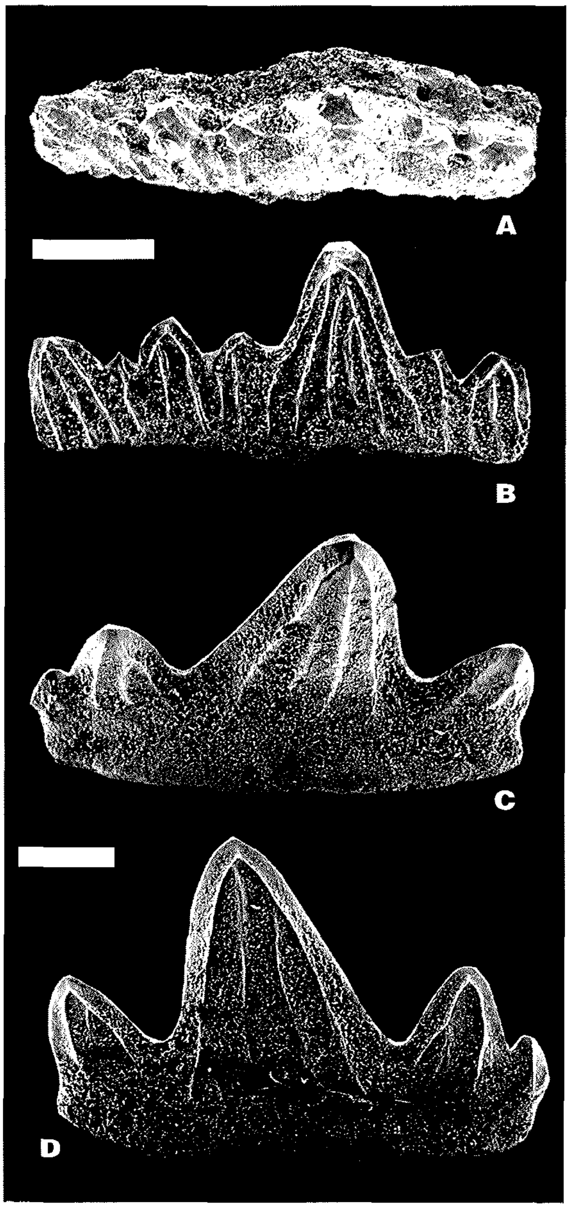

Fig. 8. *Protacrodus* cf. *vetustus* JAEKEL from Soureillé d'Izarne, late Famennian, Early or Middle *expansa* conodont Zone; A-B - IGPUW/Ps/2/21, × 82; C-D - IGPUW/Ps/2/22, × 62. Scale bars = 0.2 mm

MATERIAL: 13 specimens from Soureillé d'Izarne, Famennian, Early or Middle *expansa* Zones.

DESCRIPTION: The protacrodont material shows a wide morphological range. The found teeth are generally similar to the teeth of the holotype of *P. vetustus* JAEKEL, 1921, reillustrated by ZANGERL (1981, figs 64-65), in their laterally elongated bases, almost without lingual torus and lacking any articulation devices, and in their low, thick cusps bearing coarse ornamentation. However, teeth of the type specimen do not display labio-lingual compression of the cusps, which is common in specimens from Soureillé d'Izarne. Moreover, French protacrodonts may have from one to three pairs of lateral cusps, with the second lateral cusp usually the highest. The teeth, especially tricuspid ones, are often slightly asymmetrical, with the central cusp inclined mesio-distally (Text-fig. 8C-D). This is not the case in the holotype: all the teeth which are visible are symmetrical and have three pairs of lateral cusps which are almost identical in size. Since we know only a part of the lateral dentition of the holotype of *P. vetustus*, we may tentatively assume that teeth with a smaller number of cusps represent anterior or posterolateral tooth families or they belong to another species.

REMARKS: Protacrodonts from Soureillé d'Izarne are very similar to those from the Holy Cross Mts (GINTER 1990, pl. 4, fig. 9). All morphotypes, from three- to seven-cuspid and from symmetrical to compressed asymmetrical are present in the assemblage from the Ostrówka Quarry.

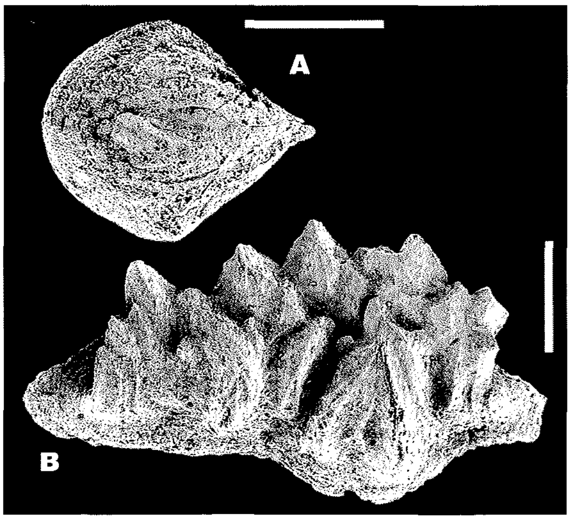

Fig. 9. Chondrichthyan scales from Soureillé d'Izarne, late Famennian, Early or Middle *expansa* conodont Zone; A - protacrodont scale, IGPUW/Ps/2/23, × 37; B - large compound scale, IGPUW/Ps/2/24, × 29; scale bars = 0.5 mm

REVIEW OF COMPARATIVE SECTIONS

Four sections were selected to compare with Soureillé d'Izarne (Text-fig. 10A). Two, Mae Sam Lap (Thailand) and Tizi Nersas (Morocco), are represented only by single, rich samples; in the remaining two, Ostrówka (Poland) and Buschteich (Germany), shark teeth were obtained from the whole interval (Early *expansa* – Early/Middle *praesulcata* Zones). In the latter two sections a few samples were dated imprecisely, as "the *postera* or Early *expansa* Zones"; such samples, although the lower possible limit of their range is below the studied interval, were also included in the study in order to increase the comparative material.

Ostrówka Quarry, Holy Cross Mountains, Poland

The Famennian of Ostrówka (westernmost part of the Holy Cross Mts, Gałęzice region) is represented by a few layers of condensed crinoid-cephalopod limestone, lying discordantly on Givetian to Frasnian peritidal, massive limestones. Famennian sedimentation started with the Late *marginifera* Zone and lasted through the Early or, in some places, Middle *praesulcata* Zone (SZULCZEWSKI & *al.* 1996a). A stratigraphic gap, spanning different intervals in different parts of the quarry, occurs on the top of Devonian rocks, which were ultimately covered by Tournaisian basinal shales and marly mudstones. In the mid to late Famennian the Holy Cross Mts area was situated on the southern Laurussian shelf which had a wide, undisturbed connection with the oceanic realm to the south-east. Because of the presence of fragmented cephalopod shells (clymeniids, goniatites and orthocone nautiloids) mixed with detached crinoid columnals, and for other sedimentological reasons, SZULCZEWSKI & *al.* (1996b) consider the depositional environment of the Ostrówka Famennian sequence as a local, intrashelf deepening. The original sediment was full of cephalopod shells, while the crinoid debris was swept from the nearby, relatively elevated areas, probably tectonically uplifted fragments of the truncated carbonate platform. After initial deposition heavy storms repeatedly stirred all the bottom elements, causing disintegration of shells.

The late Famennian part of the sequence yielded almost 200 shark teeth. The material was first published in part by GINTER (1990) and described in detail in a Ph.D. dissertation (GINTER 1994); several papers by GINTER & IVANOV (e.g. 1996, 1999) are based on specimens from that collection. It is composed of 36 specimens of *Phoebodus gothicus*, 15 of *Ph. limpidus*, four other phoebodonts, 20 teeth of *Thrinacodus tran-*

quillus sp. n., 47 of *Jalodus australiensis*, 17 of "*Symmorium*" *glabrum*, 33 other cladodonts and 18 various protacrodonts. In all ways, of all the chondrichthyan faunas mentioned herein, the fauna from Ostrówka is the most similar to that of Soureillé d'Izarne. However, in contrast to specimens from Montagne Noire, and especially to those from Thuringia and Thailand (GINTER 1999, LONG 1990) many teeth from Ostrówka are extremely well preserved, with entire bases and enameloid remaining on the cusps. Their colour is usually light brown, although a few were found completely black.

Species	Occurrence	Stratigraphic range	Reference
Jalodus australiensis (Long, 1990)	Thailand	late Fam., E. or M. *expansa*	Long & Burrett 1989; Long 1990
	China, Guizhou	late Fam. - early Tourn., *praesulcata* - *sulcata*	Wang & Turner 1985, 1995; Wang 1989
	? China, Xinjiang - problematic specimen	early Fam, M. *crepida*	Turner *in* Xia 1997
	Russia, South Urals	late Fam., E. *expansa* - E. *praesulcata*	Ginter & Ivanov 1992, 1999
	Poland, Holy Cross Mts	mid to late Fam., L. *marginifera* - E. *praesulcata* (Tourn., *crenulata* ?)	Ginter 1990; Ginter & Ivanov 1999
	Germany, Harz Mts	mid. or late Fam.	Gross 1973
	Germany, eastern Thuringia	mid. Fam - early Tourn., E. *marginifera* - *sulcata* (E. *duplicata*?)	Ginter 1999
	France, Montagne Noire	late Fam., E. or M. *expansa*	this paper
		early Tourn., *kockeli-dentilineatus*	Derycke *et al.* 1995
	Morocco, Tafilalt	late Fam., L. *expansa* - E. *praesulcata*	Ginter & Klug *in prep.*
Phoebodus gothicus Ginter, 1990	Poland, Holy Cross Mts	mid. to late Fam., E. *marginifera* - E. *praesulcata*	Ginter 1990; Ginter & Ivanov 1999
	Russia, South Urals	mid. to late Fam., E. *postera* - M. *expansa*	Ginter & Ivanov 1992, 1999
	France, Montagne Noire	late Fam., E. or M. *expansa*	this paper
	Morocco, Tafilalt	mid. or late Fam.	Derycke 1992
		late Fam., L. *expansa* - E. *praesulcata*	Ginter & Klug, *in prep.*
	Iran, East Azerbaijan	mid. Fam.	Hampe 2000, *this volume*
	USA, Iowa	mid. Fam, Lst *marginifera* or *trachytera* (= *velifer* according to Klapper 1971)	Gross 1973
	USA, New Mexico	Fam.	Kietzke & Lucas 1992
Ph. limpidus Ginter, 1990	Poland, Holy Cross Mts	late Fam., E. *expansa* - E. (M.?) *praesulcata*	Ginter 1990; Ginter & Ivanov 1999
	Russia, South Urals	late Fam., E. *expansa* - E. *praesulcata*	Ginter & Ivanov 1995, 1999
	Germany, eastern Thuringia	late Fam., M. *expansa* - E. *praesulcata*	Ginter 1999
	France, Montagne Noire	late Fam., E. or M. *expansa*	this paper
	Italy, Carnic Alps	late Fam., E. *praesulcata*	Blieck *et al.* 1998; M.G. *pers. obs.*
	China, Guizhou	late Fam., E. *praesulcata*	Wang & Turner 1985, 1995
	China, Xinjiang	late Fam., *expansa*	Turner *in* Xia 1997
	China, Hunan	late Fam., *praesulcata*	Lelievre & Derycke 1998
Thrinacodus tranquillus sp. n.	France, Montagne Noire	late Fam., E. or M. *expansa*	this paper
	Poland, Holy Cross Mts	mid. to late Fam., L. *trachytera* - E. (M.?) *praesulcata* (Tourn., *anchoralis* ?)	Ginter 1990
	Russia, South Urals	late Fam., E. *expansa* - E. *praesulcata* (Tourn., *duplicata* ?)	Ivanov 1996
	Germany, eastern Thuringia	late Fam., (L. *postera* ?) E. - M. *expansa*	Ginter 1999
	Morocco, Tafilalt	mid. or late Fam.	Derycke 1992
		late Fam., L. *expansa* - E. *praesulcata*	Ginter & Klug, *in prep.*
	China, Hunan	mid. Fam, *marginifera*	Lelievre & Derycke 1998
"*Symmorium*" *glabrum* Ginter, 1999	Germany, eastern Thuringia	late Fam., (L. *postera* ?) E. - L. *expansa*	Ginter 1999
	Poland, Holy Cross Mts	mid. to late Fam., L. *trachytera* - E. (M.?) *praesulcata* (Tourn., *anchoralis* ?)	Ginter 1995, Ginter & Ivanov 1999 (*in part*)
	Russia, South Urals	late Fam., E. *expansa* - E. *praesulcata* (Tourn., *duplicata* ?)	Ginter & Ivanov 1999 (*in part*)
	France, Montagne Noire	late Fam., E. or M. *expansa*	this paper
	Morocco, Tafilalt	late Fam., L. *expansa* - E. *praesulcata*	Ginter & Klug, *in prep.*
	Thailand	late Fam., E. or M. *expansa*	Long & Burrett 1989, Long 1990

Tab. 1. Stratigraphic and geographic distribution of late Famennian pelagic shark species present in Soureillé d'Izarne section. Taxa in open taxonomy (like *Stethacanthus* sp. and *Protacrodus* cf. *vetustus*) were omitted. Only the first record from each region and the most recent published revision were shown in the "Reference" column. Fam. - Famennian, Tourn. - Tournaisian, E. - Early, M. - Middle, L. - Late, Lst - Latest

Buschteich Quarry, East Thuringian Slate Mountains, Germany

Buschteich Quarry is situated in the north-western limb of Berga Anticline, about 5 km NE from Schleiz. An almost complete Upper Devonian section (lacking a few meters from the lowermost part) and a part of the Tournaisian are visible (BARTZSCH & *al.* 1993). From Frasnian Early *rhenana* through Famennian Early *praesulcata* conodont Zones the section is composed of pelagic limestones with rare nodular structures. Among scarce macrofossils goniatites and clymeniids occur, together with phacopid and proetid trilobites, rugose corals, brachiopods, bivalves and crinoids. From the microfossils only conodonts, ichthyoliths, and agglutinated foraminifer tests are present. Above the limestone sequence, after a probable sedimentary gap, the unfossiliferous grey Hangenberg Shale occurs. Carbonate sedimentation resumed in the early Tournasian *sulcata* conodont Zone and lasted through the *sandbergi* conodont Zone.

In the late Famennian the area of the East Thuringian Slate Mts belonged to the Saxo-Thuringian Zone, a narrow but possibly rather deep water channel, with a differentiated bottom relief, between the shelf of south-eastern Laurussia and North-West Gondwanan terranes (Armorican and Bohemian Massifs). GOLONKA & *al.* (1994) use a light-blue (indicating shallow water) colour for this area on their palaeogeographic map for the latest Devonian (*compare* Text-fig. 10A). However, the conditions must have been considerably deeper here than on the shelves of Laurussia or Gondwana: only 14 my. earlier a subduction zone occured in this region, and still the ocean was not completely closed. Moreover, according to some other palaeoreconstructions (e.g. LI & *al.* 1994, fig. 2.7) there was a wide oceanic strait between Armorica and the margins of Laurussia throughout the Late Devonian. The faunal paucity also suggests a deep-water environment in the eastern Thuringia, certainly deeper than that represented by Soureillé d'Izarne and Ostrówka sections.

Shark remains were found from the interval of the Late *trachytera* through *sandbergi* conodont Zones of Buschteich (GINTER 1999). From the samples representing the late Famennian, 171 shark teeth were identified. Of these, 94 belong to *J. australiensis*, three (or possibly four) to *Ph. limpidus*, six represent various thrinacodonts, 2 belong to *Siamodus janvieri* LONG, 1990, 1 to *Clairina marocensis* (DERYCKE, 1992), 39 to "*S.*" *glabrum* and 25 to other cladodonts. Not a single protacrodont was found.

Mae Sam Lap, Thailand

LONG & BURRETT (1989) and LONG (1990) described shark microremains from a single sample collected from a limestone lens within strongly deformed, apparently unfossiliferous siliciclastics along the road between the town of Mae Sariang and Mae Sam Lap village in Thailand, close to the Burmese border (LONG & BURRETT 1989, p. 811). The age of the sample was determined as the Early or Middle *expansa* Zone (M. SZULCZEWSKI, *pers. comm.* 1992). Among 31 shark teeth 14 specimens of *J. australiensis* occur in the sample, together with two specimens of *Thrinacodus* sp., seven of *S. janvieri*, four of "*S.*" *glabrum*, and four broken teeth of *Stethacanthus* sp. Several branchial denticles found there could belong to *Jalodus*. *Phoebodus* and *Protacrodus* are missing. All the teeth from Mae Sam Lap, including *Thrinacodus* sp., strongly resemble those described

Localities	Mae Sam Lap Thailand (Long 1990)		Buschteich East Thuringia (Ginter 1999)		Ostrówka Holy Cross Mts (Ginter 1994)		Soureillé d'Izarne Montagne Noir (this paper)		Tizi Nersas Anti Atlas (Ginter & Klug, in prep.)	
Taxa	specs	%	specs	%	specs	%	specs	%	specs	%
Jalodus	14	**59**	94	**57**	47	**24**	13	**15**	2	**5**
Phoebodus	0	**0**	4	**2**	55	**29**	22	**25**	4	**9**
Thrinacodus	2	**8**	6	**4**	20	**10**	20	**23**	3	**7**
Protacrodus	0	**0**	0	**0**	21	**11**	13	**15**	16	**37**
"Cladodonts"	8	**33**	60	**37**	50	**26**	19	**22**	18	**42**
Total:	24		164		197		87		43	

Tab. 2. Frequency of chondrichthyan teeth in the late Famennian of five studied sections (rare taxa omitted)

from the Early or Middle *expansa* Zone of Buschteich (GINTER 1999).

Tizi Nersas, Tafilalt, Morocco

During preparation of his M.Sc. thesis, Ch. KLUG (University of Tübingen) collected several limestone samples from the Devonian of the eastern Anti-Atlas, which yielded a few dozen shark microfossils. For the purpose of this paper the preliminary results of the observation of shark teeth from one of these samples were used. The complete fauna will be described in a separate paper (GINTER & KLUG, in prep). The sample comes from a section near Tizi Nersas, north-west of Taouz. It represents the southern part of Tafilalt Platform. It was a very shallow carbonate platform running N-S, with none or very little terrigenic contribution, contacting with two basins: Mader to the west and Tafilalt to the east. The age of the sample was determined by conodonts as the Late *expansa* or Early *praesulcata* Zones. During that time the Tafilalt Platform was restricted to an elongated shoal (WENDT 1988), and the section was possibly set high on its south-western slope.

In the material of 44 shark teeth, four specimens of *Ph. gothicus*, three of *Th. tranquillus*, two of *J. australiensis*, 1 of *C. marocensis*, 18 various cladodonts (among them "*S.*" *glabrum*), and 16 protacrodonts occur.

DISCUSSION

Main categories of late Famennian chondrichthyans and their modes of life

The following comparison of chondrichthyan assemblages is based only on the relative abundance of teeth. Devonian shark scales have not yet been sufficiently studied and differentiated to be used seriously in any taxonomic, stratigraphic or palaeogeographic analysis. Fin spines are absent from the collections described above. To make the discussion and the accompanying diagrams clearer I decided to group the taxa into four categories:

- cladodonts, i.e. "*Symmorium*" *glabrum*, stethacanthids, and some other tooth forms possessing the central cusp higher than the rest of cusps;
- protacrodonts, i.e. *Protacrodus* cf. *vetustus* and similar crushing teeth, with thick and low cusps;
- *Phoebodus* + *Thrinacodus*;
- and *Jalodus*.

Very rare species which do not fit into any category, e.g. *Clairina marocensis* or *Siamodus janvieri* were not taken into consideration.

It seems that sharks belonging to the above categories differ in their mode of life and feeding habits. From publications on the better known sharks with cladodont dentition, viz. *Cladoselache*, Symmoriida and Ctenacanthoidea (e.g. BENDIX-ALMGREEN 1975, WILLIAMS 1985, ZANGERL 1981), we know that they probably were very good swimmers and fast hunters. They fed on fish like palaeoniscoids (*Kentuckia*; WILLIAMS 1992), but they also were capable in piercing a goniatite shell (MAPES & HANSEN 1984). Cladodonts were the dominant sharks in the late Famennian Cleveland Shale Basin, an environment characterised by a thick layer of soft bottom sediment, rich in organic matter, whose decay probably resulted in creation of anoxic conditions in deeper parts of the basin. They also are very common in Pennsylvanian black shales of Illinois and adjacent states. This shows that they certainly were not bottom feeders, but they probably used to hunt close to the surface, and therefore they could enter many different environments, including shallow, restricted epicratonic gulfs of the Main Devonian Field (IVANOV & LUKŠEVIČS 1994).

Protacrodonts had teeth with low and thick cusps which might have been used for crushing of shells of benthic fauna like gastropods or brachiopods. Their teeth did not form a typical pavement dentition (ZANGERL 1981). However, the teeth were strongly connected with each other (GINTER 1995, Text-fig. 4B) and tooth replacement seems to have been rather slow. Possibly, protacrodonts evolved into orodonts by further coalescence of the cusps and reducing height differences between them. Chondrichthyans of this category probably trawled close to the bottom, searching for attached or slowly moving prey, and therefore they needed rather shallow waters, well oxygenated down to the bottom. The complete absence of protacrodonts from the Cleveland Shales and, on the other hand, their presence in clastic sediments of the Main Devonian Field (IVANOV & LUKŠEVIČS 1994) confirm that assumption.

The feeding habits of *Phoebodus* and *Thrinacodus* can be inferred from those observed in the recent Filled Shark, *Chlamydoselachus*, because their tooth crowns are very similar to each other. Their three main cusps are rather long, delicate, and almost equal. Tooth families are widely spaced, with quite a few (five to six) functional teeth in each. All the teeth together form a kind of a sharp grater, with which the shark catches small, soft prey, which is subsequently swallowed whole, without cutting or tearing. For more than a hundred years

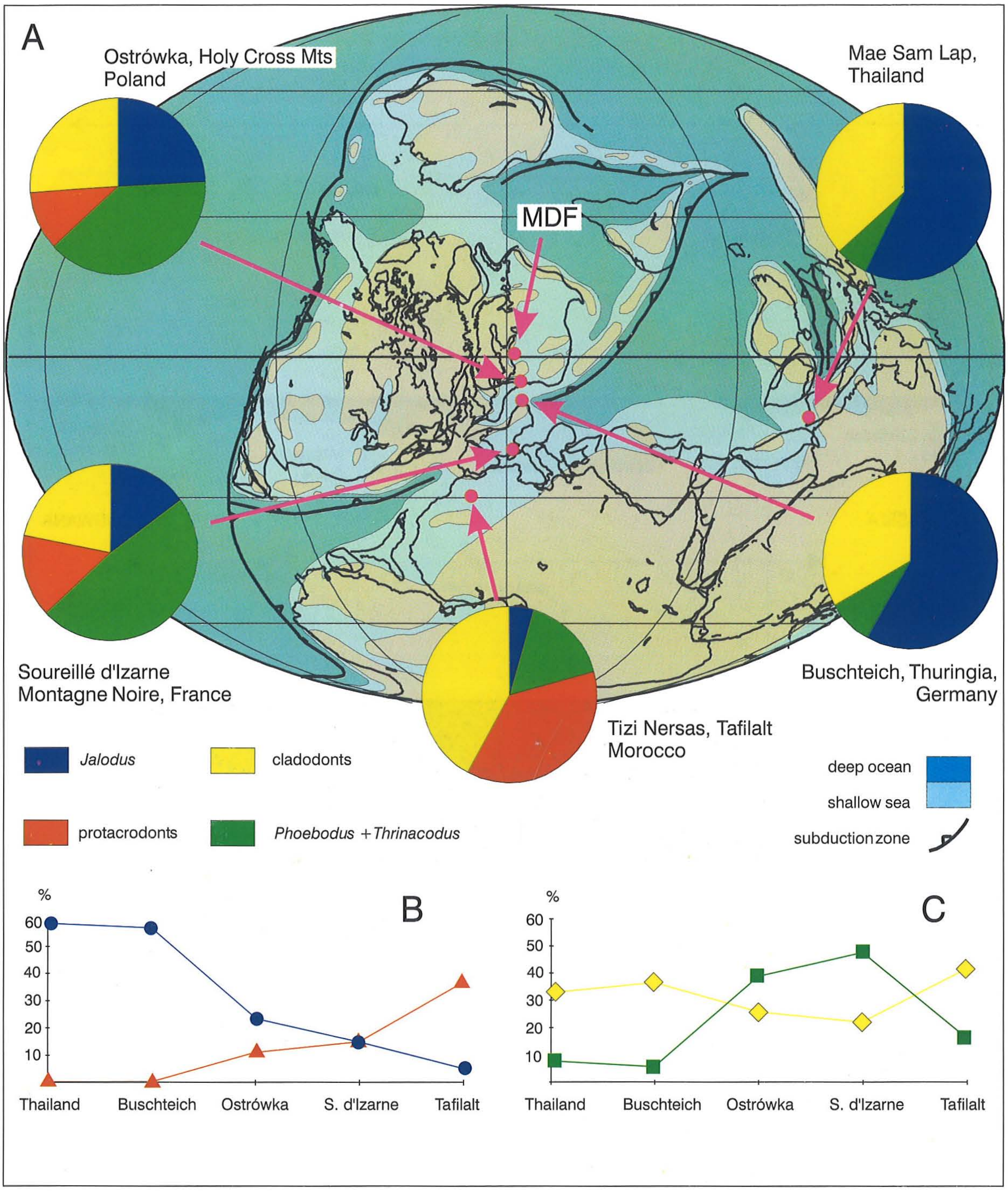

Fig. 10. A – Location of studied sections and the Main Devonian Field (MDF) on the palaeogeographic map of the latest Devonian (after GOLONKA & *al.* 1994, modified); pie-diagrams show taxonomic composition of chondrichthyan faunas in the sections; several rare taxa were omitted; B-C – Frequencies of late Famennian sharks from the studied sections; localities presumably representing the deepest facies are on the left, the most shallow on the right; B – protacrodonts and *Jalodus*, C – cladodonts and *Phoebodus* + *Thrinacodus*

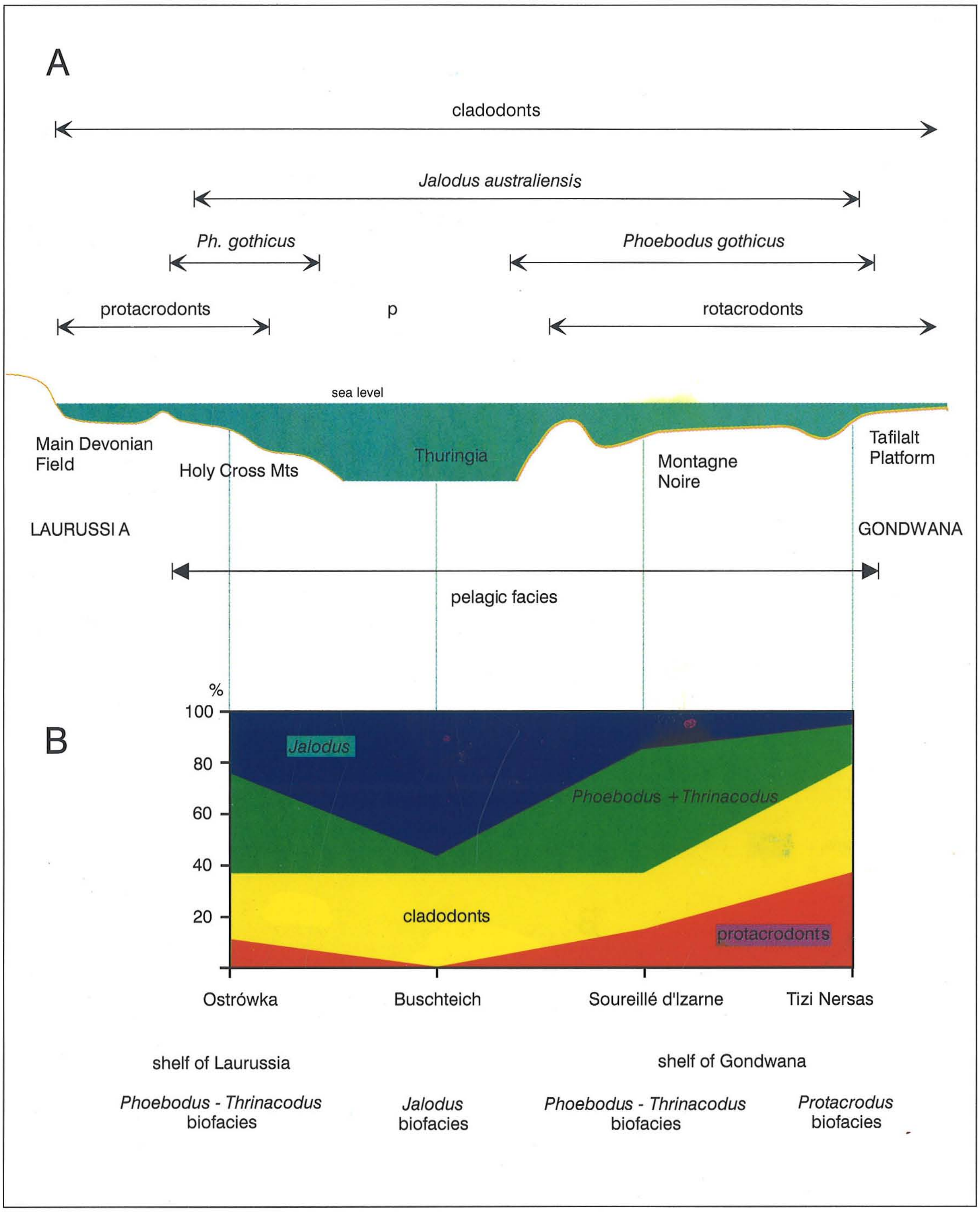

Fig. 11. A - Possible distribution of selected late Famennian chondrichthyans, in relation to palaeobathymetry and distance from land, between Laurussia and North-West Gondwana; the sea-bottom profile hypothetical, not to scale; B - Area diagram illustrating chondrichthyan biofacies from the localities situated between Laurussia and Gondwana in the late Famennian; dotted lines show possible position of each section in diagram A

since the first description of *Ch. anguineus* by GARMAN (1884) the prey species was unknown, because stomachs of captured individuals were always empty. Now we know (KUBOTA & *al.* 1991) that its main prey are squids, especially those exhausted and slowly swimming after spawning, and sometimes small fish. Today, *Chlamydoselachus* lives mainly at a depth of 50 to 200 metres, near continental slopes. As far as the phoebodonts and thrinacodonts are concerned, it is clear that they did not enter the shallow waters of the Main Devonian Field, and were very rare in the Cleveland Shale Basin. Only very few teeth of a single endemic phoebodont species, *Ph. politus* NEWBERRY, 1889, and no thrinacodonts at all were found in Cleveland Shales. This may suggest that *Phoebodus* and *Thrinacodus* were in some way affected by the conditions at the bottom and above.

It is difficult to determine the mode of life of *Jalodus*, which is the only representative of the fourth category. It is known only from teeth and, probably, branchial denticles. Its teeth, moreover, are unlike those of any shark known from articulated skeletons. The only similar teeth belong to the probable xenacanthid, *Bransonella* (IVANOV & GINTER 1996), also known only from isolated microremains. The resemblance does not help much in this case, because the only thing that we know about *Bransonella* is that it certainly was not a typical, freshwater xenacanthid species, but was found in marine facies. Thus, before pelagic shark assemblages were analysed, we can only say that *Jalodus* occurs neither in Cleveland Shales, nor in the deposits of the Main Devonian Field, and it apparently represents open marine fauna.

The relative abundances of shark teeth from the four above categories in the selected late Famennian pelagic assemblages are presented in Text-figure 10B-C. The arrangement of the localities corresponds to the growing protacrodont rate (from left to right). It was mentioned above that protacrodonts were probably shallow water, bottom dwelling sharks. By this arrangement, deeper environments should appear on the left, and shallower on the right. Indeed, Buschteich section representing a closing ocean and the confidently deep water Mae Sam Lap (Thailand) assemblage occur on the left; Soureillé d'Izarne and Ostrówka, situated on continental shelves, are in the middle, and the assemblage characteristic of the slope of the peritidal Tafilalt Platform occupies the far right position. It is interesting to observe what happens to sharks of the other categories when we move from deeper to shallower facies. The most spectacular event is a drop in the frequency of *Jalodus*, from 59% in Thailand to only 5% (in fact, only two specimens, Table 2) in Morocco. The relative number of *Phoebodus* and *Thrinacodus* specimens is low on the left and on the right, but it grows considerably in the intermediate, shelf assemblages. The line representing cladodonts is roughly horizontal, with only a shallow concavity in the middle; all points of the line are confined to the interval of 22-42%. This distribution is to be expected of a facies independent predatory hunter.

These results generally conform with the earlier arguments on possible modes of life of chondrichthyans under study. The stable quantity of cladodonts in different environments confirms the assumption that they were the most cosmopolitan and flexible elasmobranchs of the time. Future studies must show if there is any pattern in distribution of different species which constitute this artificial group. Based on the data used in this paper it is difficult to find any such rule; for instance both identifiable late Famennian cladodont taxa (i.e. "*S.*" *glabrum* and *Stethacanthus* sp.) were found from all the localities studied.

Phoebodus and *Thrinacodus* appeared to be a typically pelagic, open shelf group of sharks. Representatives of this group occur in all pelagic environments (Text-fig. 11), but in the deep sea and on the shallow platform they become marginal; in the former case they are outnumbered by *Jalodus*, and in the latter by the protacrodonts. Moreover, there are some differences in distribution of particular species. All of them are numerous at Ostrówka and Soureillé d'Izarne, but while *Th. tranquillus* was found everywhere from Tafilalt to Buschteich, *Ph. gothicus* seems to be restricted to shallower areas. On the other hand, the other late Famennian phoebodont, *Ph. limpidus*, possibly preferred slightly deeper waters, since it is absent from Tafilalt, and a few specimens of that species were found at Buschteich.

In a paper describing the East Thuringian assemblage I have suggested (GINTER 1999) that *Jalodus* had high adaptive potential to different environments, but probably preferred open marine conditions. This statement seems to be justified by the current study: *J. australiensis* occurs in all the studied sections, even in Tafilalt, but it is the most common in the environments treated here as representative of deep water. Unfortunately, still we cannot say anything about its habits. If it was so resistant, why did not it enter such areas as the Cleveland Shale Basin, restricted but open to cladodonts? The answer might be that it pursued a specialised, unknown prey whose lifestyle limited *Jalodus* to pelagic waters.

Chondrichthyan biofacies

Three provisional types of late Famennian pelagic chondrichthyan assemblages, or biofacies, may be proposed here: *Protacrodus* biofacies, *Phoebodus – Thrinacodus* biofacies, and *Jalodus* biofacies.

1. *Protacrodus* biofacies represents shallow water conditions of the peritidal to shallow subtidal zones. It is defined by a protacrodont frequency higher than 25% and a phoebodont+thrinacodont frequency lower than 25%. In this biofacies *Jalodus* plays only an accessory role. This biofacies is known thus far only from the Tizi Nersas section on the slope of Tafilalt Platform.
2. *Phoebodus-Thrinacodus* biofacies represents environments situated on open shelves, of intermediate bathymetric conditions, mainly below the shallow subtidal zone. In this biofacies the phoebodont + thrinacodont frequency is higher than 25%; *Jalodus* may be an important factor here. It is the most diverse and widely distributed biofacies, best known from Ostrówka (Holy Cross Mts), Soureillé d'Izarne (Montagne Noire), and South Urals sections (Ginter & Ivanov 2000).
3. *Jalodus* biofacies represents deep water areas. The main constituent of this biofacies is *J. australiensis* (from 25% up), whereas the phoebodont+thrinacodont frequency does not exceed 25%, and protacrodonts form less than 10%. It was recorded from Buschteich (East Thuringian Slate Mts) and Mae Sam Lap (Thailand).

Cladodonts were not used in defining the biofacies because their abundance is very similar in all the assemblages studied, as noted above.

The relatively extensive distribution of the second biofacies in the late Famennian can be explained by the widespread, moderately deep epicontinental seas which were very common on the margins of all the continents. Preservation of sediments from such areas was very probable, especially when compared to those from the elevated submarine areas or subduction zones. The intermediate position of this biofacies results in the large species diversity which occurs here. If a sample is rich, usually almost all known late Famennian phoebodonts and thrinacodonts can be found in it, together with at least two cladodont species, *J. australiensis*, some protacrodonts and a few teeth of less common, "accessory" chondrichthyans. However, that does not mean that the *Phoebodus-Thrinacodus* biofacies is uniform all over the world. New records (Hampe 2000, this volume; M.G. *pers. obs.*) show that *Ph. gothicus* is apparently the only phoebodont present in the late Famennian Iranian sections, whereas *Ph. limpidus* strongly predominates in the late Famennian of Nevada and Utah (C.A. Sandberg's collection, M.G. *pers. obs.*).

Shark assemblages similar to those typical of the late Famennian *Phoebodus-Thrinacodus* biofacies were recorded from slightly earlier times as well. One of the best known is the collection from the Maple Mill Shale (Iowa), described by Gross (1973); its age was tentatively determined by Klapper & *al.* (1971) as the *S. velifer* (Latest *marginifera* through *trachytera*) conodont Zone. Gross (1973) did not provide the exact numbers of specimens. However, we see from his descriptions that the collection was composed of "far more than 100 specimens" of *Ph. gothicus* (incorrectly assigned as *Ph. politus*, see Ginter 1990), allegedly "even more numerous" teeth of *Protacrodus* sp., and about six specimens of (stethacanthid ?) cladodonts (only five were figured, and the author stated that these were "almost all available specimens"). If we apply the above definitions of biofacies to this assemblage, it is clearly visible that it belongs to the *Phoebodus-Thrinacodus* biofacies (more than 25%, in fact probably even more than 40%, of phoebodonts), and possibly to its shallower part (very high protacrodont frequency). The absence of *Thrinacodus* from such a rich assemblage seems to be rather strange, since it is almost always found together with *Ph. gothicus* in the upper Famennian. One reasonable solution is that the Maple Mill assemblage is actually older than the first appearance of *Th. tranquillus* sp. n. However, Lelièvre & Derycke (1998) presented specimens of the latter species from Hunan (China), where it was found from the alleged *marginifera* Zone. That means that either one of the datings was incorrect (the dating of Maple Mill Shale by Klapper & *al.* 1971 or of the Hunan sample by Lelièvre & Derycke 1998), or the distribution of *Th. tranquillus* was restricted for some time to Chinese realms.

CONCLUSIONS

Although our knowledge on Devonian chondrichthyan assemblages is still very poor and based on irregularly dispersed records, the analysis presented in preceding sections clearly shows that shark microremains can be useful for reconstruction of pelagic palaeoenvironments. The proposed feeding categories of sharks and therefore the chondrichthyan biofacies are easy to recognise if samples are rich enough, even for a non-specialist. However, the data discussed above give only a rough picture of chondrichthyan distribution in late Famennian seas and their meaning as facies indicators. Lumping of taxa into categories, although useful for general comparison, obscures to some extent the real distribution of particular species. The next step, when further collections of shark microremains are described, should be the refinement of chondrichthyan biofacies based on the most sensitive, environmentally dependant taxa. It is important that future authors, when describing sharks from other localities, always present precise data on the frequency of every species from each horizon, as conodont students do. Only then can new material be used to make detailed comparisons of assemblages.

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