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Late Viséan pelagic chondrichthyans from northern Europe

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The relatively rich assemblages of shark teeth from pelagic limestone (Mississippian, late Viséan, late Asbian–middle Brigantian) of three northern European regions: the Rhenish Mountains (Westenfeld Quarry, Germany), the Holy Cross Mountains (Todowa Grząba at the edge of Ostrówka Quarry, Poland), and Derbyshire (Cawdor Quarry, Matlock, England, UK) display certain similarities, with the absolute predominance of the teeth of Falcatidae (small Symmoriiformes) and the constant presence of *Thrinacodus* spp. The largest and most diverse assemblage from Todowa Grząba contains at least three species of a falcatid *Denaea*, a xenacanthimorph *Bransonella nebraskensis*, a newly described phoebodontid *Thrinacodus dziki* sp. nov., a few ctenacanthiform and euselachian teeth, and two abraded euchondrocephalan dental elements. Anachronistidae, common in the most of late Viséan pelagic faunas, are absent from Todowa Grząba and Westenfeld. The material under study differs from the shallow-water chondrichthyan fauna, hitherto described from the Mississippian carbonate platform facies, by its taxonomic content (particularly almost total absence of Euchondrocephali), generally lower diversity, and higher frequency of small teeth.

Key words: Chondrichthyes, teeth, Carboniferous, Mississippian, England, Germany, Poland.

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Introduction

The Viséan and Serpukhovian sea in northern Europe, from Ireland through Scotland, England, Belgium, northern Germany, Poland, to the areas north of Moscow, can be imagined as a patchwork of carbonate platforms separated by relatively deeper basins. Both on the platforms and between them carbonate sedimentation predominated (although in certain areas the siliciclastic Kulm facies also occurred), but the limestone developing there differed in type and composition. Thick masses of crinoid limestone accumulated in the shallower areas, replaced mainly by biomicritic limestone in the intervening basins. In several places the material from the platforms slumped down the slopes, disturbing the quiet basinal sedimentation and forming distinct bodies of calcirudite within the sequence of deeper water shale and biomicrite (Bełka and Skompski 1988, Szulczewski et al. 1996). Carbonate turbidites have also been recorded (Korn 2008).

Scientific interest in Viséan chondrichthyans began in the first half of the XIX century; most specimens were collected as macrofossils, found by surface picking in various calcirudite facies. The most famous source of such fossils was the Mountain Limestone in the area of Armagh (now in Northern Ireland). This formation yielded the type specimens of such famous tooth-based taxa as *Cladodus mirabilis* and *C.* (now *Saivodus*) *striatus*, described by Agassiz (1833–1843) in his classic monograph on fossil fishes. Also, the bulk of the materials described by Davis (1883; from the British Isles), De Koninck (1878; from Belgium), and the American classical authors (e.g., Newberry and Worthen 1866, St. John and Worthen 1875; USA, southern Illinois and adjacent areas) come from the shallower water limestone.

During the 1960s it was realised that conodonts had enormous potential as biostratigraphic tools. As a consequence, conodont researchers began to systematically sample Viséan rocks, especially biomicritic limestone, throughout the north-

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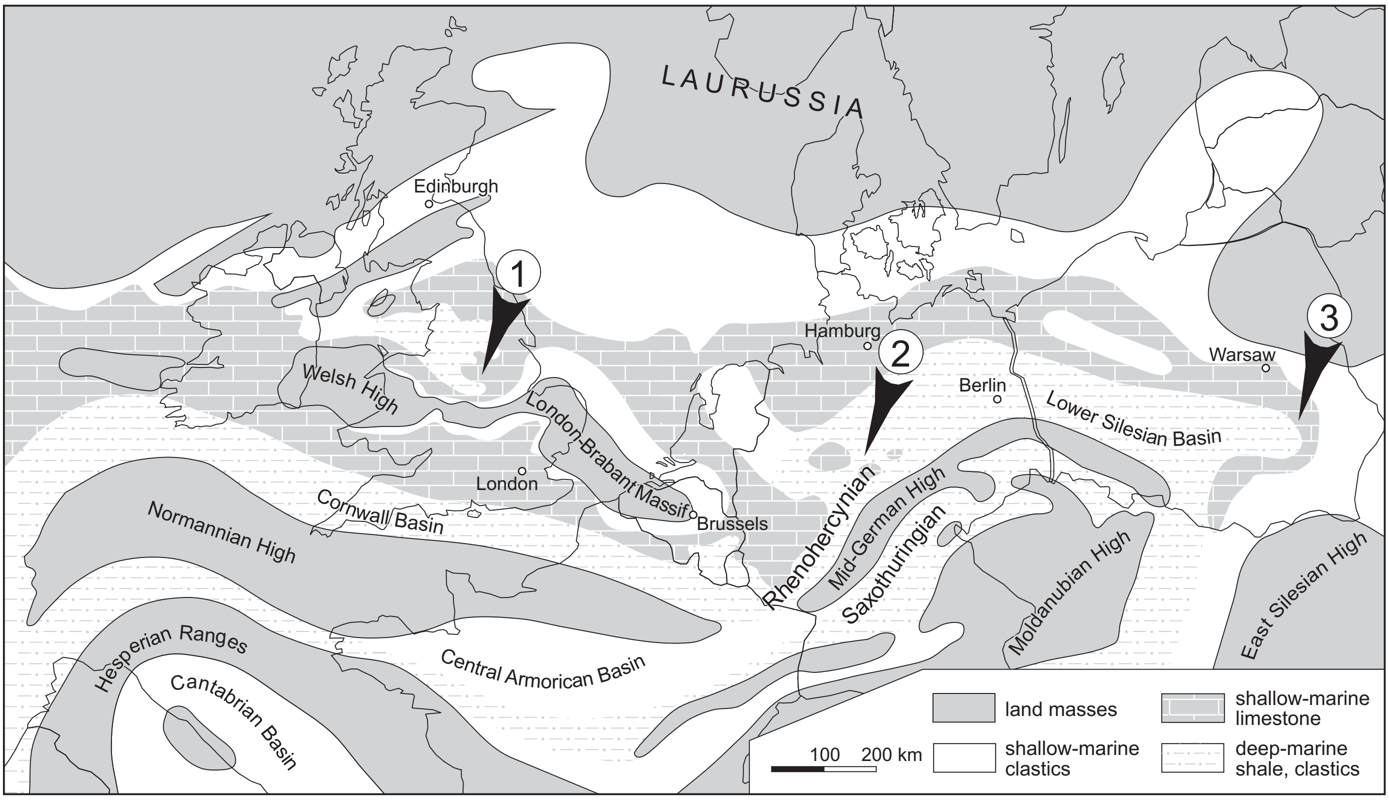

Fig. 1. Palaeogeographic reconstruction of northern Europe in the Viséan, showing positions of the areas which yielded pelagic chondrichthyan microfossils described in this paper. 1, Derbyshire, England, UK (Cawdor, Steeplehouse, and Ticknall Quarries); 2, Rhenish Mountains, Germany (Westenfeld Quarry); 3, Holy Cross Mountains, Poland (Todowa Grząba). Modified from Ziegler (1989).

ern European successions. In addition to conodonts, the acid dissolution of many of these limestone samples yielded microvertebrate remains including chondrichthyan teeth and scales, albeit in relatively small numbers, as a by-product of the sampling technique.

Thus far, however, these collections have been presented either in scattered publications of local significance or in papers concentrating on the descriptions and taxonomic significance of particular genera (e.g., Duffin and Ward 1983, Duffin and Ivanov 2008, Ginter et al. 2010). The only study which has attempted a comparison of chondrichthyan faunas from the deeper-water Viséan facies in several localities of Eurasia is that of Rodina and Ivanov (2002). These authors noted a pattern repeated in the most of the localities which they analysed: cladodont teeth of *Denaea* almost invariably occur together with the phoebodontid *Thrinacodus* and the xenacanthiform *Bransonella*. To this triplet of genera, certain anachronistids (such as *Cooleyella*), ctenacanthiforms, and rare crushing teeth of the Euselachii or Euchondrocephali could be added.

Here we present and compare the relatively rich upper Viséan assemblages of vertebrate (mainly chondrichthyan) microremains from the biomicritic parts of three sections in northern Europe (Fig. 1): Cawdor Quarry at Matlock, Derbyshire, England, UK; Westenfeld Quarry in the Rhenish Mountains, Germany; and Todowa Grząba at the edge of Ostrówka Quarry, Holy Cross Mountains, Poland. Although these assemblages are not coeval, the age range which they collectively sample is quite short, from the late Asbian through the late Brigantian. For the sake of the description of a new species of *Thrinacodus* we also illustrate a few well preserved specimens from a poorly dated (but undoubtedly Viséan) assemblage obtained from a disused quarry at Ticknall, Derbyshire, England (UK). The general observations made by Rodina and Ivanov (2002) are confirmed in the current study, but several important differences between the assemblages under consideration are also noted.

Institutional abbreviations.—MWGUW, Museum of the Faculty of Geology, University of Warsaw, Poland; NHMUK, The Natural History Museum, London, UK; ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

Geological setting and overview of the material

Derbyshire, England, UK

Cawdor Quarry.—Most of the British material comes from a series of samples originally collected in 1983 for conodont analysis by MTD, at that time a student at the Department of Geology, University of Nottingham. The samples were taken from the succession at the western end of Cawdor Quarry on the West bank of the River Derwent as it runs through

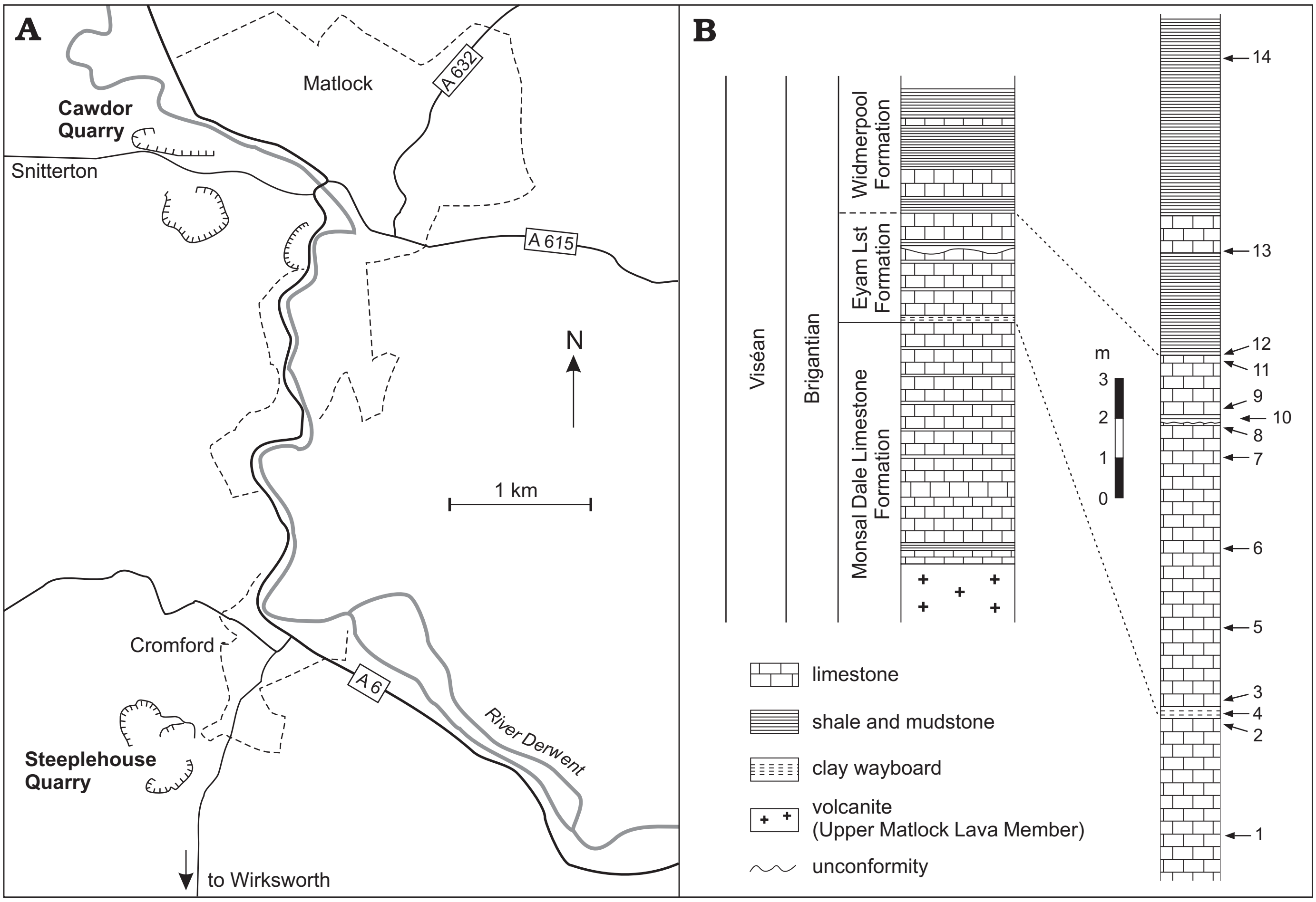

Fig. 2. **A**. Sketch map showing Viséan limestone quarries in the area of Matlock, Derbyshire, England, UK. **B**. Stratigraphic column of the rocks exposed in Cawdor Quarry. Numbered arrows, positions of the studied samples (Cawdor 1–14).

Matlock, Derbyshire (Fig. 2). This quarry, ca. SK 287606, is now disused and exposes mostly the Monsal Dale Limestone Formation (probably P1b–P1d, early Brigantian, *Gnathodus bilineatus* Conodont Zone) and the succeeding highly fossiliferous Eyam Limestone Formation (P2a, possibly P2b, middle part of Brigantian, *G. bilineatus*, and possibly *Lochriea mononodosa* conodont zones). In the uppermost (extreme west) part of the quarry the Widmerpool Formation is present (P2b–P2c, late Brigantian, *L. mononodosa*–*G. girtyi collinsoni* conodont zones). Of the studied samples, Cawdor 1 and 2 were collected from the Monsal Dale Limestone Formation, Cawdor 3–11 from the grey micrites and dark shale of the Eyam Limestone Formation, and Cawdor 12–14 apparently from the Widmerpool Formation. The stratigraphic information was updated based on Waters et al. (2009) and Colin N. Waters personal communication (2013).

The vertebrate microfossils from this collection were first studied and identified by CJD and later (in 2003) by MG. The notes from these two examinations differ in certain points, so the number of specimens shown in the Appendix 1 is a compromise. However, the main characteristics of the material and the conclusions reached are identical. The samples are generally poor, the average number of chondrichthyan teeth per sample is about 3. They are usually associated with a few chondrichthyan scales or branchial/mucous membrane denticles, actinopterygian teeth and scales, and sometimes with acanthodian scales. The only richer samples are Cawdor 5 (14 teeth) and Cawdor 11 (10 teeth), of which sample Cawdor 5 is definitely the more diverse.

The preservation of the specimens is far from perfect. The tips of the tooth cusps are rarely preserved and several teeth have broken bases which suggests that at least part of the damage could be original, due to post-mortem abrasion on the sea floor, and not the result of preparation and conservation.

Ticknall.—We present four specimens from another disused quarry at Ticknall, about 15 km south of Derby (Parsons 1917). Because the precise position and dating of the sample is unknown (it is only certain that it is from fine- to medium-grained limestone of the Ticknall Limestone Formation which is Brigantian in age; Waters et al. 2009), we do not use it in any broader analysis. However, there are present, among others, two well preserved specimens of the new species of *Thrinacodus*, described below, and a tooth very similar to those of "*Ctenacanthus*" *costellatus*, an articulated Viséan shark from Glencartholm in Scotland (Ginter et al. 2010: fig. 71). This tooth is also similar to a fragment found at Todowa Grząba (Holy Cross Mountains) which may suggest that "*C.*" *costellatus* might have occurred in the Viséan of Poland.

Rhenish Mountains, Germany

Westenfeld.—Viséan sedimentary successions in the Kulm Basin are well exposed at the northern and eastern margins of the Rhenish Mountains and include several calciturbidite-influenced areas, such as the Remscheid-Altena Anticline (Herdringen Sequence) and the Lüdenscheid Syncline (Hellefeld Sequence; Korn 2008). Calciturbidites of the Hellefeld Sequence were investigated in terms of ammonoid and conodont stratigraphy; one of the conodont samples (sample C12 from the Westenfeld section) proved to be particularly rich in shark teeth and yielded the material described in this study (Fig. 3).

The sample comes from the new large quarry of the Feldhaus Company, 800 m south-west of Westenfeld (map sheet 4614 Arnsberg; N 51°19'12,9", E 8°2'26,96"); see Nicolaus (1963), Helmkampf (1969), and Korn (2008). In this quarry, Viséan rocks of various facies are exposed, in ascending order (i) Hellefeld Formation (about 100 m thick; coarse-grained thickly bedded detrital limestone, which become thinly bedded with numerous intercalations of cherty shale and tuffitic horizons towards the top), (ii) Linnepe Formation (24 m thick; aluminous shale and cherty shale with tuffitic horizons and coarse crinoidal limestone beds up to 3 m thickness in the upper part), and (iii) Wennemen Formation (14 m exposed; succession of shale rich in *Posidonia* with intercalated calciturbidite beds as well as coarse-grained crinoidal limestone beds each up to 80 cm in thickness).

The productive sample C12 has a very distinct position in the section; it was taken from a 15 cm thick calciturbidite in the upper part of the shaly rock unit M9 (see Korn 2008; Korn and Kaufmann 2009). This is 160 cm above the *Crenistria* Limestone, which is the best index horizon within the Mississippian succession of Central Europe. In terms of ammonoid stratigraphy, rock unit M9 belongs in the *Goniatites fimbriatus* Zone, the topmost ammonoid zone of the Asbian.

Sample C12 yielded 37 chondrichthyan teeth (mainly delicate cladodonts, probably belonging to the falcatid *Denaea*, three teeth of *Thrinacodus*, and one unidentified, protacrodont-like euselachian tooth), symmoriiform branchial denticles of "*Stemmatias*" type, together with ctenacanth and hybodont scales. Shark microfossils are associated with smooth acanthodian scales (*Acanthodes*-type) and numerous actinopterygian teeth and scales. The specimens are generally well preserved with several teeth retaining even the tips of the cusps.

Holy Cross Mountains, Poland

Todowa Grząba.—On the northern edge of the huge Ostrówka Quarry (Fig. 4) situated in Middle/Upper Devonian stromatoporoid-coral limestone, there exist remnants of a small hill called Todowa Grząba (= Tod's Hill, "grząba" meaning low, rounded hill in the local dialect). The hill is mostly built of late Viséan crinoidal limestone, probably having slumped

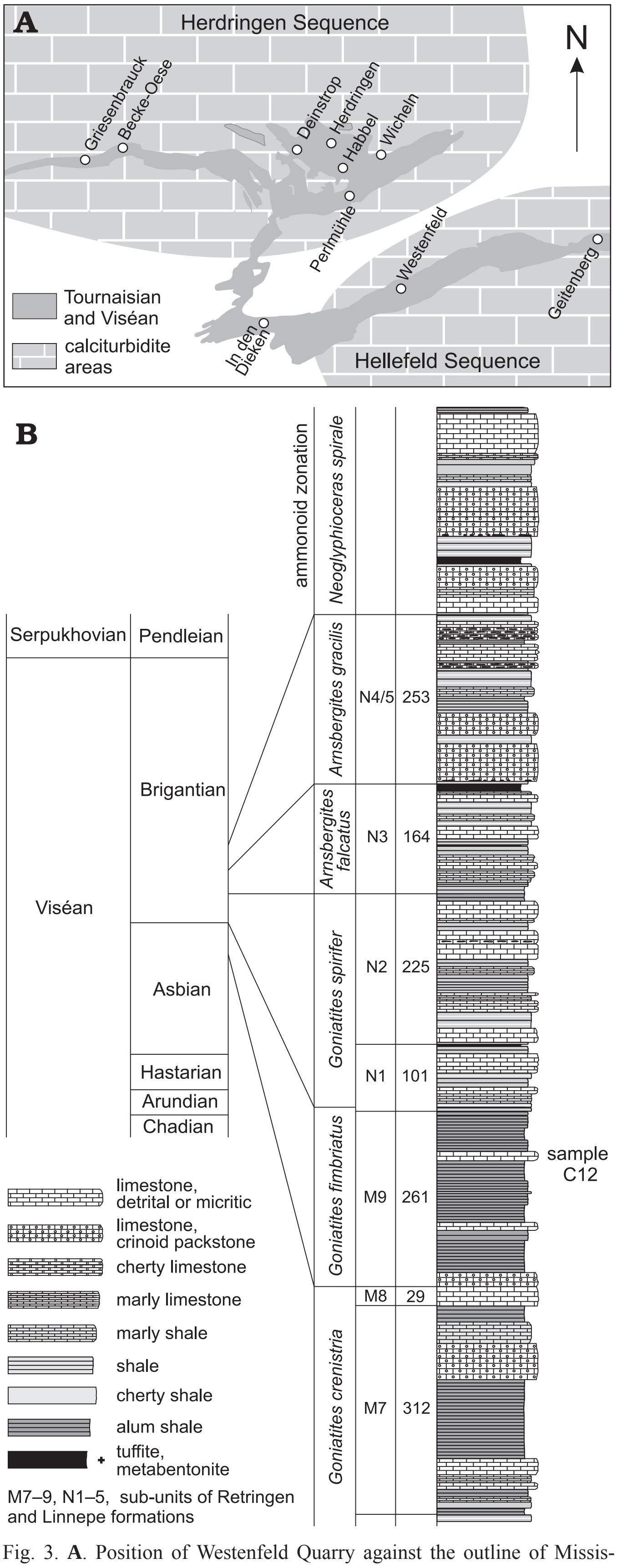

Fig. 3. **A**. Position of Westenfeld Quarry against the outline of Mississippian outcrops in the northern Rhenish Mountains. **B**. Fragment of the stratigraphic column of the Westenfeld Quarry showing position of sample C12, studied in this paper.

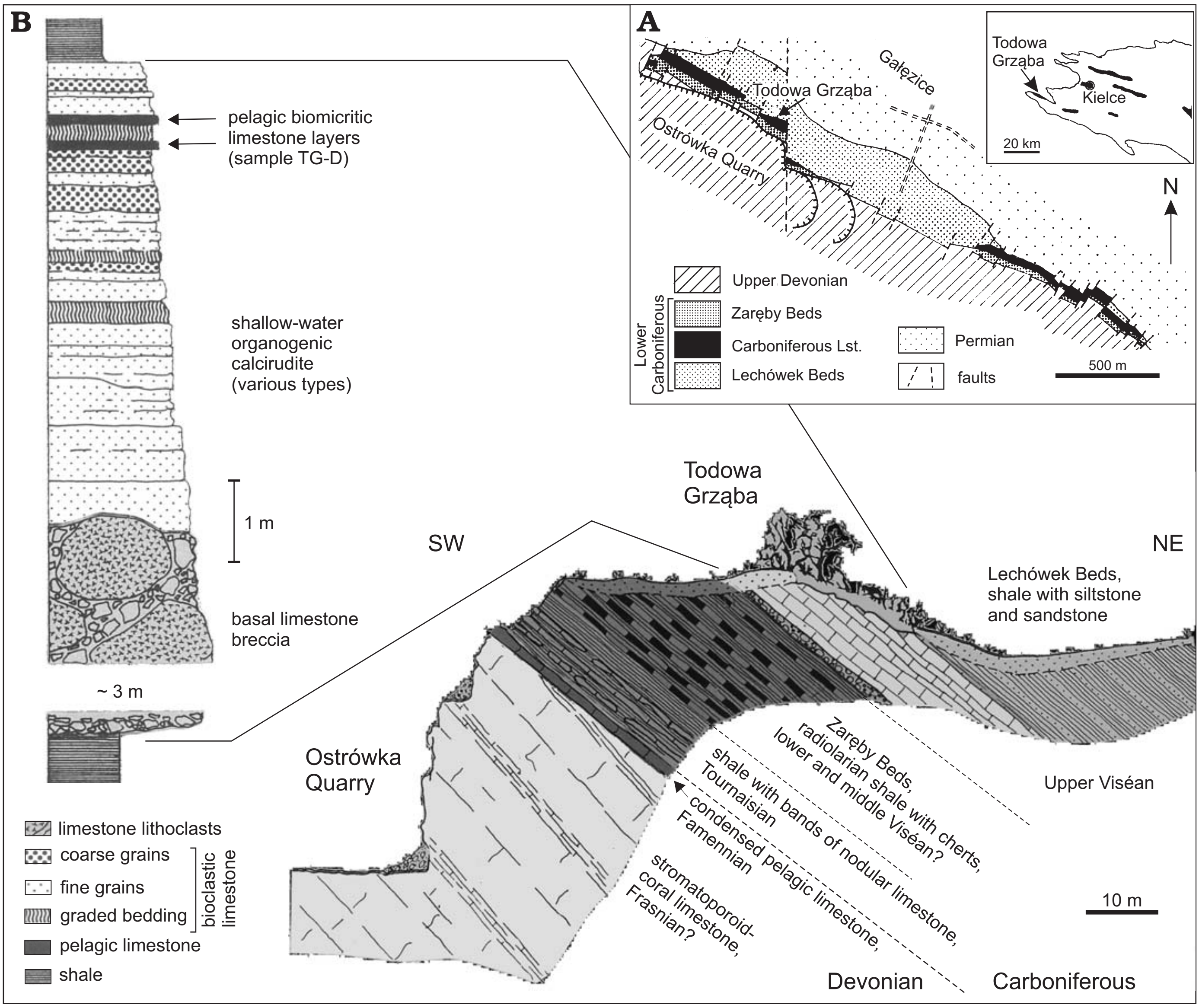

Fig. 4. **A**. Position of Todowa Grząba on the outline of Palaeozoic core of the Holy Cross Mountains (inset: solid black, Carboniferous outcrops) and on the sketch geological map of the area between the NE edge of the Ostrówka Quarry and the Gałęzice Village. **B**. Section through the NE edge of the Ostrówka Quarry and Todowa Grząba with the upper Viséan carbonate part enlarged, modified from Bełka and Skompski (1988: figs. 1, 2, 4).

from a nearby carbonate platform into the deeper parts of the basin. From these rocks, thus far only one shark tooth fragment has been recovered: a crown of a *Ctenoptychius*-like petalodont. However, within the calcirudite sequence, there occur two thin layers (no thicker than 10 cm each) of autochthonous, dark biomicritic limestone (wackestone), rich in phosphatic microfossils (e.g., several hundred conodonts per kg), juvenile goniatites, and pelagic algae. These layers were first described and interpreted by Bełka and Skompski (1988) and later briefly mentioned by Szulczewski et al. (1996: 39). Unfortunately, despite the abundance of conodonts and goniatites, precise dating has not been possible. The age of the biomicrite layers falls somewhere in the *Gnathodus bilineatus* Conodont Zone which spans the late Asbian and early Brigantian.

A large sample was taken from these layers in 1992 by Jerzy Dzik and processed for conodonts; the associated vertebrate microremains were donated to MG. In 2003, a much smaller piece of rock was dissolved by Ewa Durska, then MG's student. Both materials are designated here as a single sample TG-D. Altogether, 70 chondrichthyan teeth were recovered, and among them almost 50 *Denaea*-like falcatid cladodonts. The second most abundant is a new species of *Thrinacodus* (nine specimens) and the rest consists of the xenacanthiform *Bransonella*, non-symmoriiform cladodontomorphs, euselachians and probably two fragments of orodontiform euchondrocephalans. The shark teeth are associated with various ctenacanth, hybodont and probably neoselachian placoid scales, symmoriiform branchial denticles of "*Stemmatias*" type, as well as by acanthodian scales and actinopterygian teeth and scales.

The preservation of the material is extremely good. Most of the breakage sustained by the cusps probably occurred

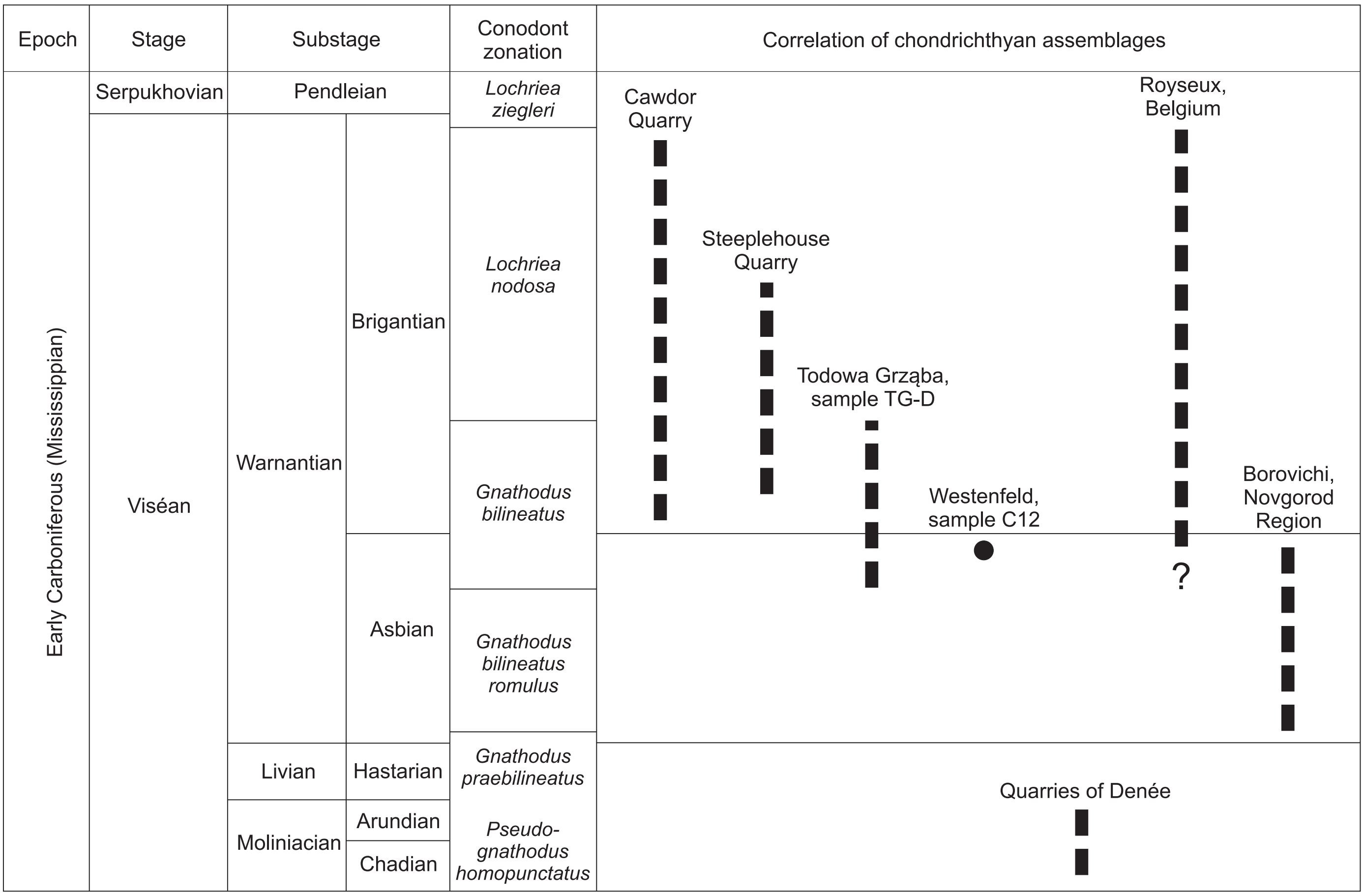

Fig. 5. Stratigraphic correlation table of Viséan chondrichthyan assemblages discussed in the text. Dashed line, dating not precise. Conodont zonation based on Korn and Kaufmann (2009).

during initial preparation or later observation. Only the broken teeth of orodonts, otherwise very resistant, were probably originally destroyed by post-mortem submarine transport.

Comparative material

The material obtained from the localities cited above will be compared with chondrichthyan faunas from four previously published (but to different levels of detail) collections of fossil chondrichthyans from the Viséan of northern Europe (Fig. 5): from Steeplehouse Quarry in Derbyshire, England, UK, situated between Matlock and Wirksworth (Fig. 2A); quarries in the area of Denée, southern Belgium (Fournier and Pruvost 1928); trenches at Royseux, south of Huy, southern Belgium (Poty et al. 2011: 121); and outcrops in the area of Borovichi, Novgorod Region, Russia (Savitskiy et al. 2000).

Parts of the very rich and fairly well preserved material from the Steeplehouse Quarry have been published several times, mainly to present individual taxa (Ford 1964; Duffin and Ward 1983; Duffin 1985, 1993; possibly also M'Coy 1848) and the whole assemblage was summarised by Duffin (in Dineley and Metcalf 1999). The fish microfossils were found in the 1 m thick crinoidal limestone unit belonging to the Eyam Limestone Formation, dated as the latest Viséan, late Brigantian, i.e., approximately coeval with the samples from Cawdor Quarry.

The sharks from the quarries around the village of Denée, mainly articulated specimens of a falcatid *Denaea fournieri* Pruvost, 1922, and several isolated teeth of other taxa, were first described by Fournier and Pruvost (1928) and recently re-studied by Ivanov and Derycke (2005) and Maisey (2008). The fossils were found on the surfaces of slabs of micritic limestone, forming parts of the famous Black Marbles of Denée (Molignée Formation), dated as early Viséan (Moliniacian).

The existence of a rich assemblage of isolated pelagic fish microfossils from Royseux was announced during the conference "Devonian vertebrates of the continental margins" in Yerevan, Armenia in 2005 and a preliminary description given in the accompanying book of conference abstracts (Derycke et al. 2005; see also Ivanov and Derycke 2005). They report several hundreds of vertebrate microremains found in the dark bioclastic limestone (Anhée Formation) of mid- to late Warnantian age (late Viséan). This remarkable collection still awaits formal publication.

On the slopes of river valleys in the area of Borovichi town, Novgorod Region in north-west Russia there occur several outcrops of Viséan limestone and clay. From there, quite a few isolated chondrichthyan teeth and scales were collected. Illustrations of representative specimens were published by Alexander Ivanov (in Savitskiy et al. 2000) and the updated identifications were presented by the same author in a conference abstract a few years later (Ivanov 2008). Most of the specimens come from the Msta Formation belonging to the Aleksinian Horizon which, according to Menning et al. (2006: fig. 3), corresponds to the Asbian.

Systematic palaeontology

The photographic illustrations of chondrichthyan teeth are arranged in geographic order, from west to east: the material from England (Derbyshire, Figs. 6–9), Germany (Rhenish Mountains, Fig. 10), and Poland (Holy Cross Mountains, Figs. 11–14).

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Order Phoebodontiformes Ginter, Hairapetian, and Klug, 2002

Family Phoebodontidae Williams in Zangerl, 1981

Genus *Thrinacodus* St. John and Worthen, 1875

Type species: *Thrinacodus nanus* St. John and Worthen, 1875, Tournaisian, Burlington, Iowa, USA.

Thrinacodus dziki sp. nov.

Figs. 6, 9B, C, 11.

1993 *Thrinacodus ferox* (Turner, 1982); Duffin 1993: 2, pl. 1: 2.
2010 "Thrinacodont teeth"; Ginter and Turner 2010: fig. 4A.

Etymology: In honour of Professor Jerzy Dzik (Institute of Palaeobiology, Polish Academy of Sciences, Warsaw), one of the most famous Polish palaeontologists.

Type material: Holotype, tooth (ZPAL P.IV/212).

Type locality: Sample TG-D of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland.

Type horizon: Carboniferous, upper Viséan, upper Asbian or lower Brigantian, *Gnathodus bilineatus* Conodont Zone.

Material.—Seventeen teeth: six from upper Viséan of Cawdor Quarry, Matlock, Derbyshire, England, UK (five from sample Cawdor 5, one from sample Cawdor 11); two from upper Viséan, Ticknall, Derbyshire, England, UK; nine from upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland (sample TG-D); NHMUK PV P73271–P73275, NHMUK PV P73279, NHMUK PV P73289, MWGUW/Ps/11/8–11, ZPAL P.IV/212.

Diagnosis.—Species of *Thrinacodus* whose teeth display the following combination of features: there are three cusps in the tooth-crown, either equal to each other or the distal cusp may be slightly larger than the other two. The median cusp is offset from its normal position and displaced lingually. The basal/labial part of the crown below the median cusp forms a bulge. In this bulge, there occurs a distinct basal canal opening. The angle between the mesial and median cusps is slightly smaller than the angle between the latter and the distal cusp.

Description.—Most of the specimens of *T. dziki* sp. nov. from Cawdor Quarry are in a rather poor state of preservation, with broken cusps and bases, so this description is based mostly on the collection from Todowa Grząba and two specimens from Ticknall. The labio-lingual size of the base ranges from 0.6 to more than 1.5 mm. The lingual part of the base is usually long and thin. It seems that in larger specimens it is relatively shorter and thicker, but this may be only an illusion, as the lingual tips of the bases in such specimens are usually broken off (except for Fig. 11B). The lingual one-third of the base is flattened and the sharp lingual tip is upturned (Figs. 9B$_2$, 11B, E). The part more proximal to the crown is elevated and on the lingual side of this elevation there opens a large foramen. This foramen most probably corresponds to the basal/labial opening of the overlying tooth in a tooth family. In two specimens (Fig. 11A$_1$, D$_2$, D$_3$) it seems that there is more than one foramen in the orolingual part of the base, but this is, perhaps, due to the partial abrasion of the surface, uncovering the internal osteodentine canals.

The most characteristic features of this species are the lingually displaced median cusp of the crown and the bulge, sometimes quite distinct (Figs. 6B$_1$, D$_2$, 9C), formed at its base on the labial side. The distal cusp, which usually seems to be slightly larger than the other two, is gently sigmoidal (Fig. 9B$_1$); the mesial cusp is sigmoidal, too (Fig. 11B); the full shape of the median cusp is unknown, because in all the specimens studied so far the apical tip is broken. The greater distance (angle) between the median and distal cusps (see especially Fig. 11C$_2$, E$_2$) indicates that the latter had a somewhat different function to that of the other two cusps.

Remarks.—Hitherto, six species of *Thrinacodus* have been recognised (see Ginter and Turner 2010). In stratigraphic order they are: *T. tranquillus* Ginter, 2000 (middle–late Famennian), *T. ferox* (Turner, 1982) (latest Famennian–Tournaisian), *T. nanus* St. John and Worthen, 1875 (early Tournaisian), *T. bicuspidatus* Ginter and Sun, 2007 (middle Tournaisian), *T. incurvus* (Newberry and Worthen, 1866) (early Viséan), and *T. gracia* (Grogan and Lund, 2008) (Serpukhovian). Of these, *T. tranquillus*, *T. ferox*, and *T. bicuspidatus* were described based on reasonably large collections of teeth and recorded from more than one region in the world; *T. gracia* was described from Bear Gulch (Montana, USA) and based on complete and articulated specimens containing well preserved dentitions, and similar teeth have been found in Russia and New Mexico (Ivanov and Lucas 2011); *T. nanus,* the genotype, is known from only two specimens, of which one is atypical and the other incomplete. Based upon our knowledge of other species (Ginter and Turner 2010: fig. 1) it is possible that *T. ferox* is conspecific with *T. nanus*, but at the moment this cannot be verified. The type specimen of *T. incurvus* was apparently lost and although we do have a good drawing of it and several teeth from the same locality, any reliable comparison with this species is impossible.

This being the case, we can meaningfully compare our new species only to *T. tranquillus*, *T. ferox*, *T. bicuspidatus*, and *T. gracia*. The latter two species can be excluded at once:

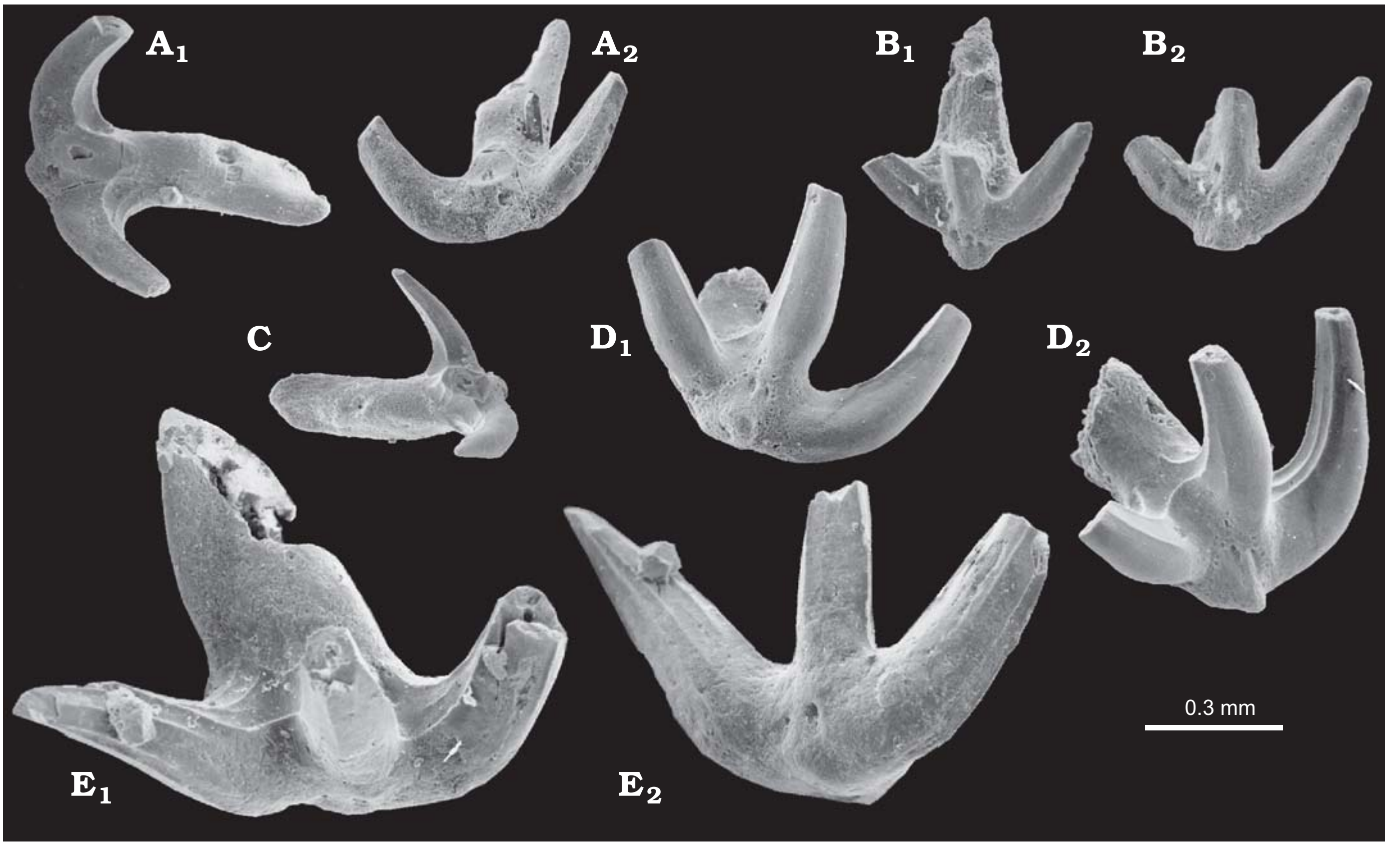

Fig. 6. Phoebodontid chondrichthyan *Thrinacodus dziki* sp. nov. from the upper Viséan of Cawdor Quarry, Matlock, Derbyshire, England, UK; sample Cawdor 5. **A**. NHMUK PV P73271, in oral (A_1) and labial (A_2) views. **B**. NHMUK PV P73272, in oral (B_1) and labial (B_2) views. **C**. NHMUK PV P73273, in lateral view. **D**. NHMUKPV P73274, in labial (D_1) and oblique labial (D_2) views. **E**. NHMUK PV P73275, in oral (E_1) and labial (E_2) views.

typical specimens of *T. bicuspidatus* have only two cusps and all the specimens of *T. dziki* sp. nov. have three; the cusps of *T. gracia* are thick and coarsely ornamented with numerous cristae, whereas the cusps of *T. dziki* are slender and the cristae on them are subtle. Moreover, the base of *T. gracia* is shorter and thicker.

Teeth of *T. dziki* differ from typical teeth of *T. tranquillus* in the lingual displacement of the median cusp, a character unknown in Famennian thrinacodont species. However, it has been observed in several Tournaisian specimens of *T. ferox*, particularly from the Irish collection presented by Duncan (2003: fig. 5B, 6A, B). *T. ferox* has a wide range of tooth morphotypes in a single jaw (monognathic heterodonty), varying from specialised subsymmetrical symphyseal and parasymphyseal teeth, through moderately asymmetrical anterolaterals, to the extremely asymmetrical (with an enormous distal cusp) in the lateral and posterolateral parts of the jaw. Teeth of *T. dziki* are very similar to those of the second, anterolateral morphotype, but are rather more symmetrical than that, i.e., the twist of the crown and the enlargement of the distal cusp are greater in *T. ferox* (second morphotype) than in *T. dziki*.

Thus, it is clear that the material described here as *Thrinacodus dziki* sp. nov. represents a new species, probably closely related to *T. ferox*, but with a more homodont dentition and a lesser degree of asymmetry in lateral teeth. It is not clear from the material available whether *T. dziki* has specialised, subsymmetrical (parasymphyseal?) teeth, as in *T. ferox* and *T. nanus* (see, e.g., Ginter and Turner 2010: fig. 3A–F). Such teeth are very rare (their frequency in large collections never exceeds 1:10 in relation to the other morphotypes), so their absence from the studied material may be incidental. Morphologically, the teeth of *T. dziki* which we do have in our samples, fall between morphologies of *T. tranquillus* and *T. ferox*.

There occurs a tiny collection of thrinacodont teeth from the lower Tournaisian of Armenia, designated as *Thrinacodus* aff. *tranquillus* (Ginter et al. 2011: fig. 12H–J), which appear to be intermediate forms between *T. tranquillus* and *T. dziki*. The crowns in the Armenian specimens are almost symmetrical and the median cusp is only slightly displaced lingually. The basal/labial bulge, if it exists, is only rudimentary. One might consider that such thrinacodonts gave rise to both *T. ferox*, by the increase of asymmetry and differentiation of the dentition, and *T. dziki*, by the further change of the position of the median cusp, while the asymmetry did not increase much.

Stratigraphic and geographic range.—Currently known from the upper Viséan of Derbyshire, England, UK (Duffin 1993; this paper) and the Holy Cross Mountains, Poland (Ginter and Turner 2010; this paper). The identity of similar teeth from the upper Viséan of Fife, Scotland, UK (Ginter and Turner 2010: fig. 4C) is uncertain.

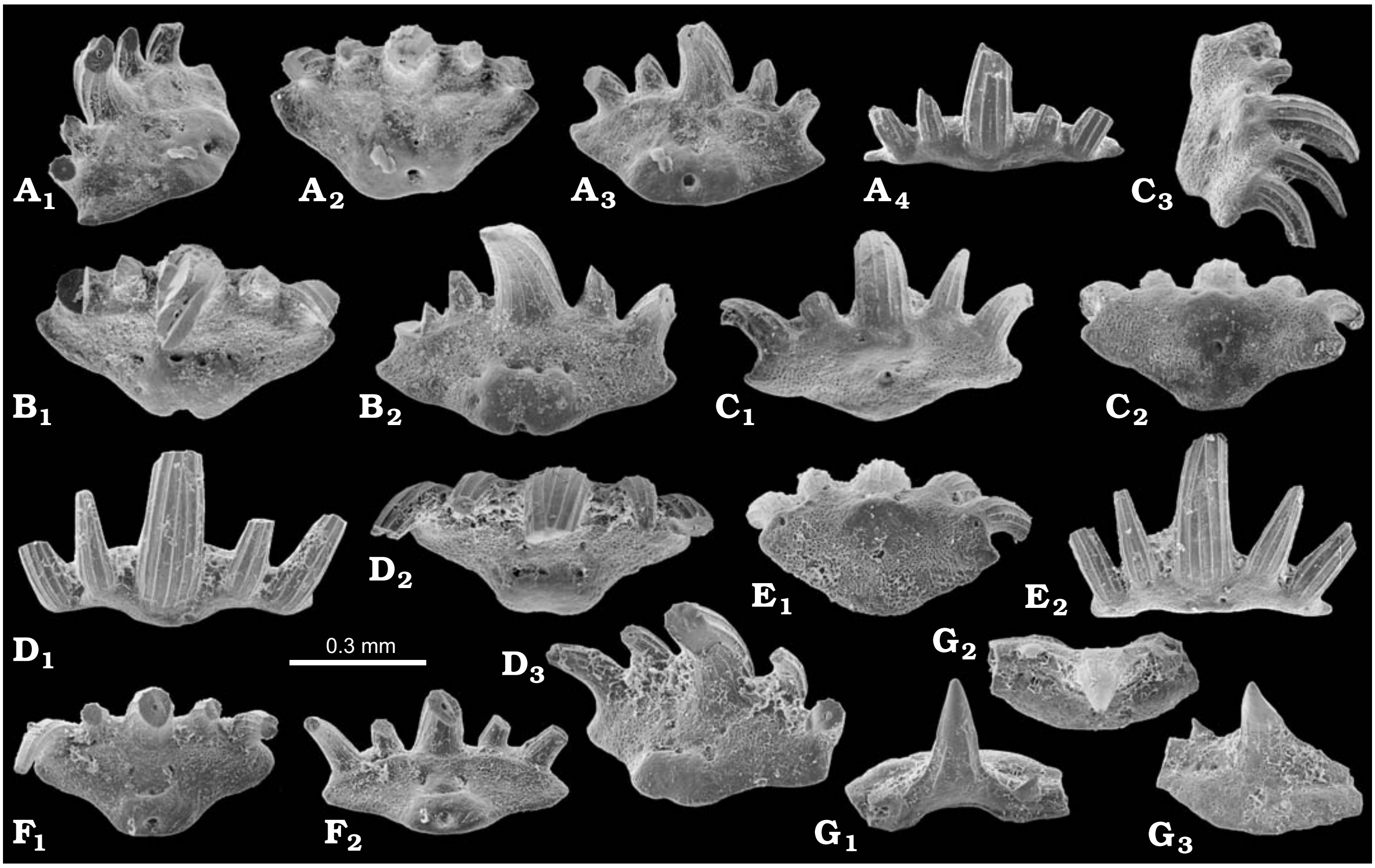

Fig. 7. Cladodont teeth from the upper Viséan of Cawdor Quarry, Matlock, Derbyshire, England, UK; sample Cawdor 9 (A–C), 11 (D–G). **A**–**F**. *Denaea* cf. *fournieri* Pruvost, 1922. **A**. NHMUK PV P73276, in lateral (A_1), oral (A_2), lingual (A_3), and labial (A_4) views. **B**. NHMUK PV P73277, in oral (B_1) and lingual (B_2) views. **C**. NHMUK PV P73278, in aboral (C_1) and aboral/labial (C_2) views. **D**. NHMUK PV P73279, in labial (D_1), oral (D_2), and oblique lingual (D_3) views. **E**. NHMUK PV P73280, in aboral (E_1) and labial (E_2) views. **F**. NHMUK PV P73281, in oral (F_1) and lingual (F_2) views. **G**. *Squatinactis caudispinatus* Lund and Zangerl, 1974, narrow tooth with broken base (NHMUK PV P73282), in labial (G_1), oral (G_2), and lingual (G_3) views.

Thrinacodus cf. *gracia* (Grogan and Lund, 2008)

Fig. 10F, G.

Material.—Three teeth from upper Asbian, *Goniatites fimbriatus* Ammonoid Zone, Westenfeld Quarry, Germany (sample C12); MWGUW/Ps/11/6–7.

Description.—In the sample from Westenfeld Quarry there occur three incomplete thrinacodont teeth, characterised by rather thick bases and thick cusps. The asymmetry of the crown is not spectacular; it is limited to the angle between the median and mesial cusps which is smaller than that between the median and distal cusp on the other side. The cusps are generally aligned, with a shallow depression in the basal/labial area below the median cusp. The cristae ornamenting the cusps are coarser than in *T. dziki*, but they look less coarse than in *T. gracia*. This, however, may be due to abrasion. Nothing can be said about the sigmoidality of the cusps, because in all three specimens the tips are broken. The same concerns the shape of the lingual part of the base which, in one of the better preserved specimens, is broken (uncovering a wide basal canal), and in the other is probably rounded by abrasion.

Remarks.—Despite the poor preservation it is evident that these teeth are more robust than those of *T. dziki* and do not display the lingually displaced median cusp and the basal/labial bulge, characteristic of the latter species. They are closer to the teeth of *T. gracia* which are known for their robustness and thickness of the base and the cusps. *T. gracia* is known thus far only from the Serpukhovian, so the teeth described here may belong to some earlier, but closely related form.

Stratigraphic and geographic range.—*Thrinacodus gracia* articulated specimens were recorded from the Serpukhovian of Bear Gulch, Montana, USA (Grogan and Lund 2008); isolated teeth designated as *T.* cf. *gracia* are known from the Serpukhovian of the Moscow Syneclise, Russia (e.g., Ginter and Turner 2010: fig. 6F, G) and the upper Viséan of Rhenish Mountains, Germany (this paper). The identity of similar teeth from the upper Viséan of Fife, Scotland, UK (Ginter and Turner 2010: fig. 4B) is uncertain.

Superorder Xenacanthimorpha Nelson, 1976

Order Bransonelliformes Hampe and Ivanov, 2007

Family indet.

Genus *Bransonella* Harlton, 1933

Type species: *Bransonella tridentata* Harlton, 1933, Lower Pennsylvanian, Ouachita Mountains, Pushmataha County, Oklahoma, USA.

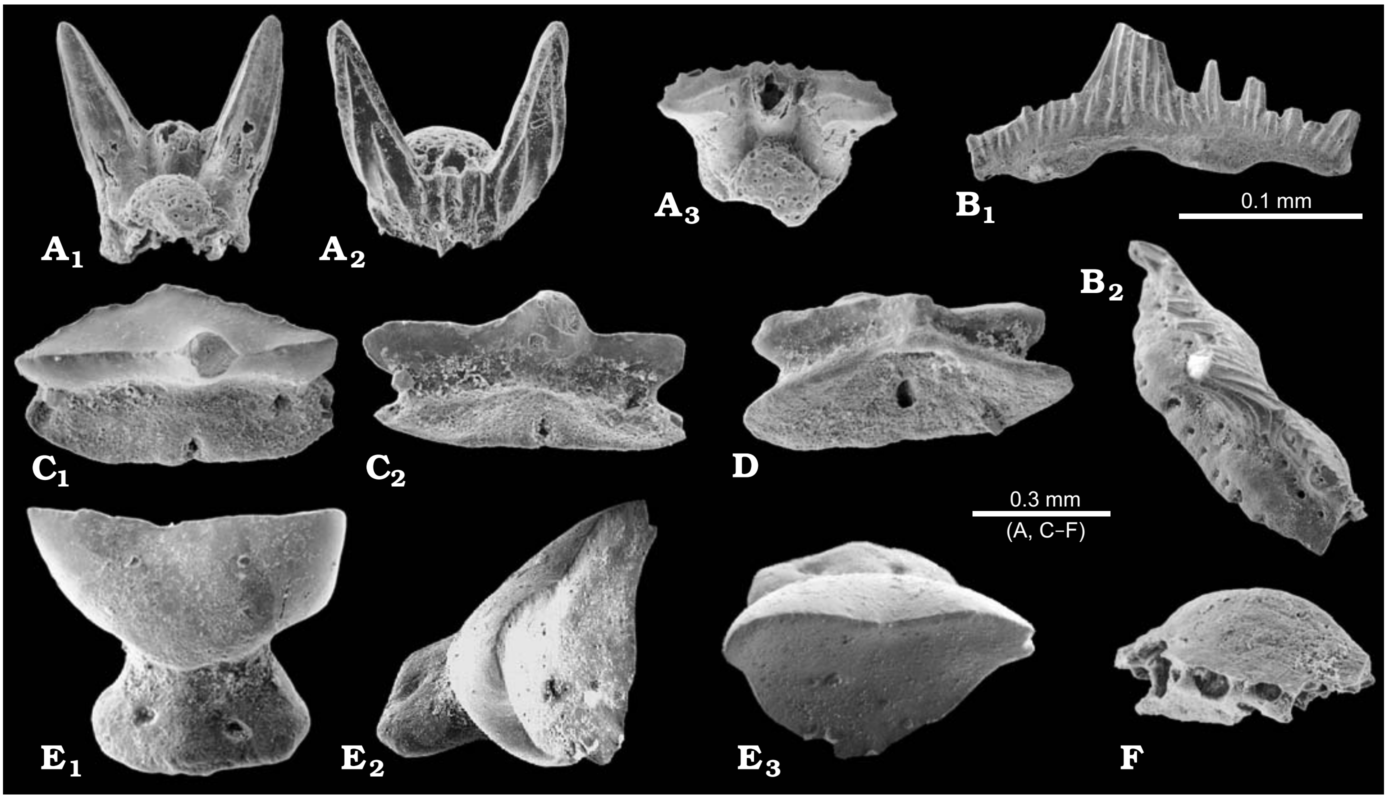

Fig. 8. Chondrichthyan teeth from the upper Viséan of Cawdor Quarry, Matlock, Derbyshire, England, UK; sample Cawdor 5 (A–E), 8 (F). **A**. *Bransonella nebraskensis* (Johnson, 1984), NHMUK PV P73283, in lingual (A_1), labial (A_2), and oral (A_3) views. **B**. *Squatinactis caudispinatus* Lund and Zangerl, 1974, NHMUK PV P73286, in labial (B_1) and oblique lateral (B_2) views. **C**, **D**. *Cooleyella fordi* (Duffin and Ward, 1983). **C**. NHMUK PV P73284, in oral (C_1) and lingual (C_2) views. **D**. NHMUK PV P73285, in aboral/labial view. **E**. *Ginteria fungiforma* Duffin and Ivanov, 2008, NHMUK PV P66676, in oral (E_1), lateral (E_2), and lingual (E_3) views. **F**. Tip of a helodontid holocephalian tooth, NHMUK PV P73287, in lateral view.

Bransonella nebraskensis (Johnson, 1984)

Figs. 8A, 9A, 14C.

Material.—Three teeth from upper Viséan of Cawdor Quarry, Matlock, Derbyshire, England, UK (sample Cawdor 5), one from upper Viséan, Ticknall, Derbyshire, England, UK, and four from upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland (sample TG-D); NHMUK PV P73283, NHMUK PV P73288, ZPAL P.IV/215.

Description.—The teeth of *Bransonella* from all three localities look almost exactly the same. The crown is composed of three short, straight cusps, covered on the labial faces with coarse cristae, partly straight and partly wavy, joining upwards, forming a lanceolate pattern. The lateral cusps are twice as large as the median cusp. The base is thick and compact, with a button covering almost all the orolingual side. The basolabial tubercle is heel-like, straight and thin.

The specimens of *Bransonella* from Todowa Grząba have been illustrated several times before (e.g., Ivanov and Ginter 1996), because of their good preservation.

Stratigraphic and geographic range.—*Bransonella nebraskensis* is a cosmopolitan species; it is known from the upper Viséan of Poland and Russia, Pennsylvanian and Cisuralian of USA (Oklahoma, Nebraska, Kansas; see Hampe and Ivanov 2007 for references), and the upper Viséan of Belgium (Ivanov and Derycke 2005) and England (this paper). It also probably occurs in the Upper Pennsylvanian of the Amazon Basin (Duffin et al. 1996) and in the Mississippian of Gansu, China (Wang et al. 2004).

Superorder Cladodontomorphi Ginter, Hampe, and Duffin, 2010

Order Symmoriiformes Zangerl, 1981

Family Falcatidae Zangerl, 1990

Genus *Denaea* Pruvost, 1922

Type species: *Denaea fournieri* Pruvost, 1922, early Viséan, Denée, Belgium.

Remarks.—Since the establishment of the name *Denaea* (*D. fournieri*) by Pruvost (1922) for the articulated specimens of sharks from the Viséan of Denée, Belgium, several tooth-based species from all over the world have been attributed to this genus. These are as follows: *Denaea meccaensis* Williams, 1985, *D. decora* Ivanov, 1999, *D. wangi* Wang, Jin, and Wang, 2004, *D. saltsmani* Ginter and Hansen, 2010, and *D. williamsi* Ginter and Hansen, 2010. *D. meccaensis* and *D. decora* were subsequently removed to *Stethacanthulus* Zangerl, 1990, based on the shared very special form of base. All of the species that remain in *Denaea* are characterised by

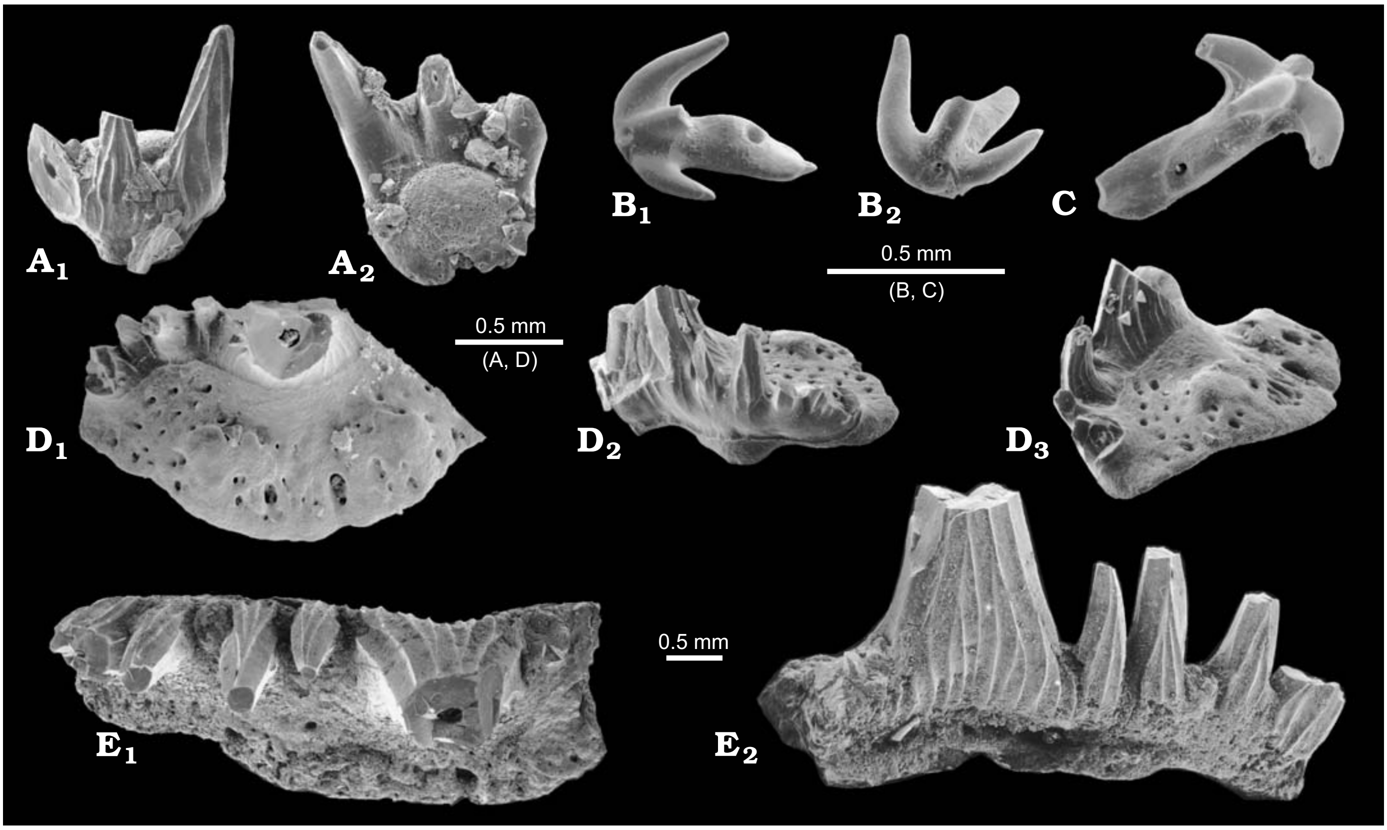

Fig. 9. Chondrichthyan teeth from the upper Viséan of Ticknall, Derbyshire, England, UK (A–D) and Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland (E). **A**. *Bransonella nebraskensis* (Johnson, 1984), NHMUK PV P73288, in labial (A_1) and lingual (A_2) views. **B**, **C**. *Thrinacodus dziki* sp. nov. **B**. NHMUK PV P66779, in lateral (B_1) and labial (B_2) views. **C**. NHMUK PV P73289, in oral view. **D**, **E**. Teeth similar to "*Ctenacanthus*" *costellatus* Traquair, 1875. **D**. NHMUK PV P73290, in oral (D_1), lateral/labial (D_2), and lateral/lingual (D_3) views. **E**. ZPAL P.IV/256, in oral (E_1) and labial (E_2) views.

cladodont crowns possessing delicate cusps and thin bases with rather weakly developed articulation devices.

It appears, however, that the teeth of two articulated falcatids from the Serpukhovian of Bear Gulch in Montana, USA (*Damocles* and *Falcatus*) closely examined by MG in 2003, are very similar to those of *Denaea*. One might even say that the five-cusped teeth of *D. fournieri* and the teeth of those falcatids are indistinguishable when seen from the labial side (which in most cases is the only visible surface of the tooth exposed on the matrix surface). Because the teeth of *D. fournieri* are poorly preserved and appear to be natural casts of original elements, they cannot be extracted chemically and observed from all sides. The teeth of *Falcatus* and *Damocles* have not, so far, been extracted from the enclosing matrix either, but in this case such a possibility, although technically challenging because of the small size of the teeth, probably exists. This being the case, it is difficult to determine which of the tooth-based putative species of *Denaea* or other *Denaea*-like isolated shark teeth really belong to this genus and which, perhaps, represent *Falcatus* or *Damocles*. There are several other taxonomic problems concerning *Denaea*, but they will be discussed in the sections dedicated to particular species.

Denaea cf. *fournieri* Pruvost, 1922

Figs. 7A–F, 10A–E, 12.

Material.—Twenty three teeth from upper Viséan of Cawdor Quarry, Matlock, Derbyshire, England, UK (samples Cawdor 1, 2, 4, 7–14); 33 from upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland (sample TG-D); 33 from upper Asbian, *Goniatites fimbriatus* Ammonoid Zone, Westenfeld Quarry, Germany (sample C12); NHMUK PV P73276–81, MWGUW/Ps/11/1–5, MWGUW/Ps/11/12–17, MWGUW/Ps/7/5, ZPAL P.IV/219–221.

Description.—The tooth crown usually consists of five or seven cusps (the prominent median cusp and two or three lateral cusps on each side, e.g., Fig. 12F and A, respectively), but in the material from Westenfeld a few teeth were found with nine cusps (four lateral cusps on each side; Fig. 10B, E). There are also specimens with an additional lateral cusp on one side (Fig. 12C). In five- and seven-cusped teeth the outer lateral cusps are the highest. In nine-cusped teeth the third pair from the median cusp is the highest.

The median cusp is long and slender, sigmoidal in lateral view, often slightly inclined laterally (distally?), and sub-circular in cross section. The whole cusp, except for the uppermost fifth, is ornamented with dense sub-parallel cristae (e.g., Fig. 12F). In some rare cases the cristae coalesce (Fig. 12B, C), and sometimes disappear earlier than the others

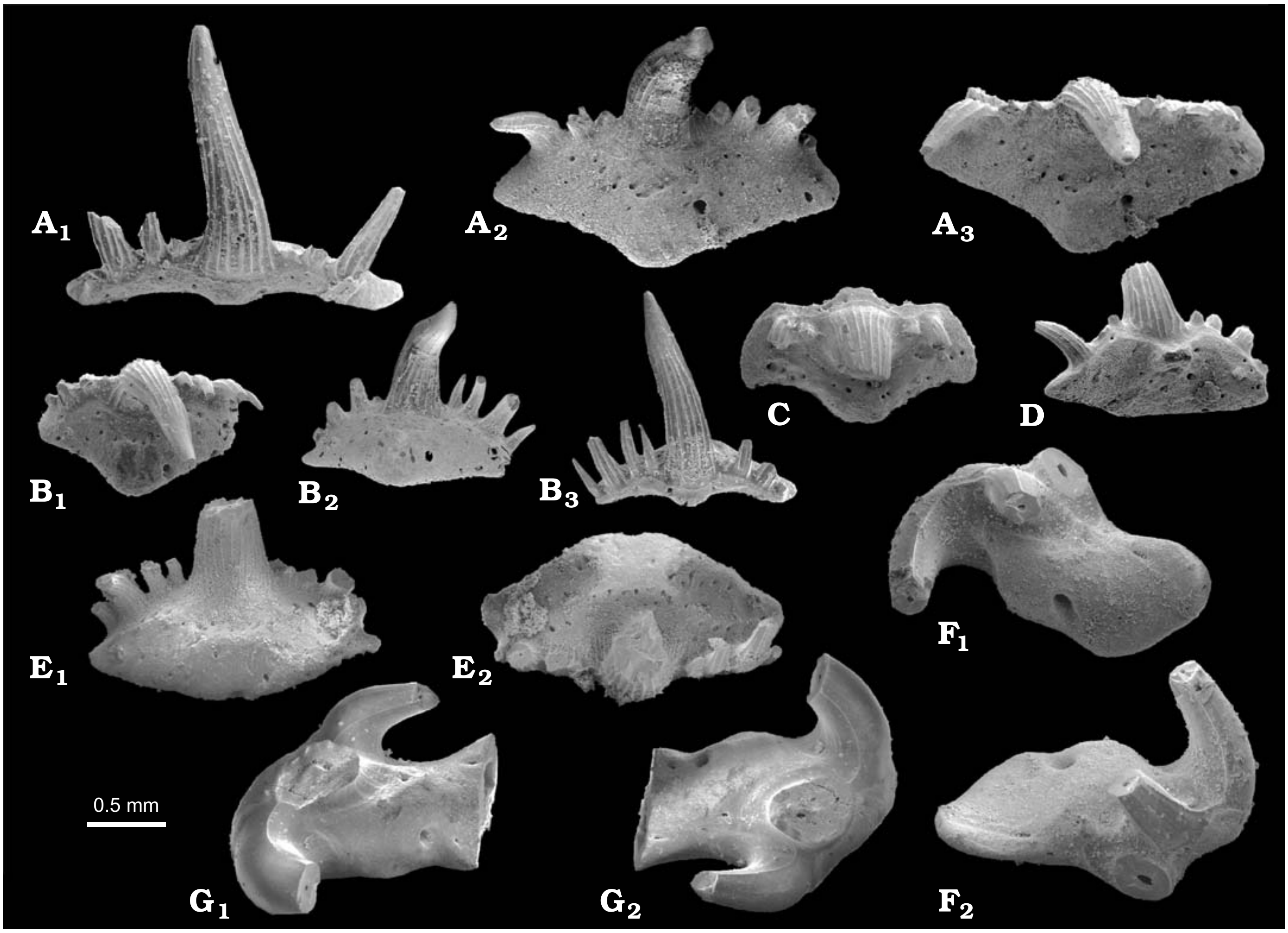

Fig. 10. Chondrichthyan teeth from the upper Viséan of the Westenfeld Quarry, Rhenish Mountains, Germany. **A**–**E**. *Denaea* cf. *fournieri* Pruvost, 1922. **A**. MWGUW/Ps/11/1, in labial (A_1), lingual (A_2), and oral (A_3) views. **B**. MWGUW/Ps/11/2, in oral (B_1), lingual (B_2), and labial (B_3) views. **C**. MWGUW/Ps/11/3, in oral view. **D**. MWGUW/Ps/11/4, in labial/aboral view. **E**. MWGUW/Ps/11/5, in lingual (E_1) and oral (E_2) views. **F**, **G**. *Thrinacodus* cf. *gracia* (Grogan and Lund, 2008). **F**. MWGUW/Ps/11/6, in oral (F_1) and lateral (F_2) views. **G**. MWGUW/Ps/11/7, in lateral (G_1) and oral (G_2) views.

(Fig. 12I). There is no distinct lateral carina; only the lateral cristae run continuously to the cusp apex. The ornamentation of the lateral cusps is similar, but usually there is no uppermost unornamented area.

The base is roughly pentagonal (in oral/aboral view), with rounded angles (Fig. 12G_3, H, J_2). Sometimes, especially in the material from Westenfeld, the lateral angles form "wings" directed lingually (Fig. 10C). The orolingual button is oval, sometimes almost split in two by the openings of the main basal canal which are situated on the lingual and labial sides of the button (Fig. 7F). It appears to be a rule that the lingual foramen in symmetrical specimens lies exactly in the midline (Fig. 12G_1), whilst in those with the median cusp inclined distally, the foramen is slightly displaced towards the distal side (Fig. 12A_3, A_4, F_2, F_3). In the smaller specimens (such as Fig. 12G) the button seems to be more compact and distinct and in the larger ones its boundaries are rather vague.

On the aboral side of the base there is a third opening of the main basal canal, situated roughly in the centre (Figs. 7C, 12H), and probably yet another, small perforation close to the basolabial projection. The latter foramen is rarely seen, but was revealed in thin section. The basolabial projection is tubercle-like, squarish in cross-section, and not wider than the basal part of the median cusp (Fig. 12J).

The size of the teeth of *D.* cf. *fournieri* from Todowa Grząba and Westenfeld is usually confined to the interval 0.6–1.5 mm (mesio-distal dimension of the base), the five-cusped specimens being smaller than the seven-cusped ones. However, in the material from Westenfeld there occurs a seven-cusped tooth whose size reaches 2 mm. It is interesting that all the specimens from Cawdor Quarry (Fig. 7A–F) are similar to the smaller teeth from Todowa Grząba. Their size is about 0.6–0.7 mm, all of them are five-cusped, symmetrical, and have relatively compact buttons situated at the lingual rim of the base. Such morphological uniformity, and especially the lack of seven-cusped specimens (please note that the illustrated specimens come from two different horizons), leads to the suspicion that the material from Cawdor Quarry might actually represent a different species to that present in Todowa Grząba and Westenfeld.

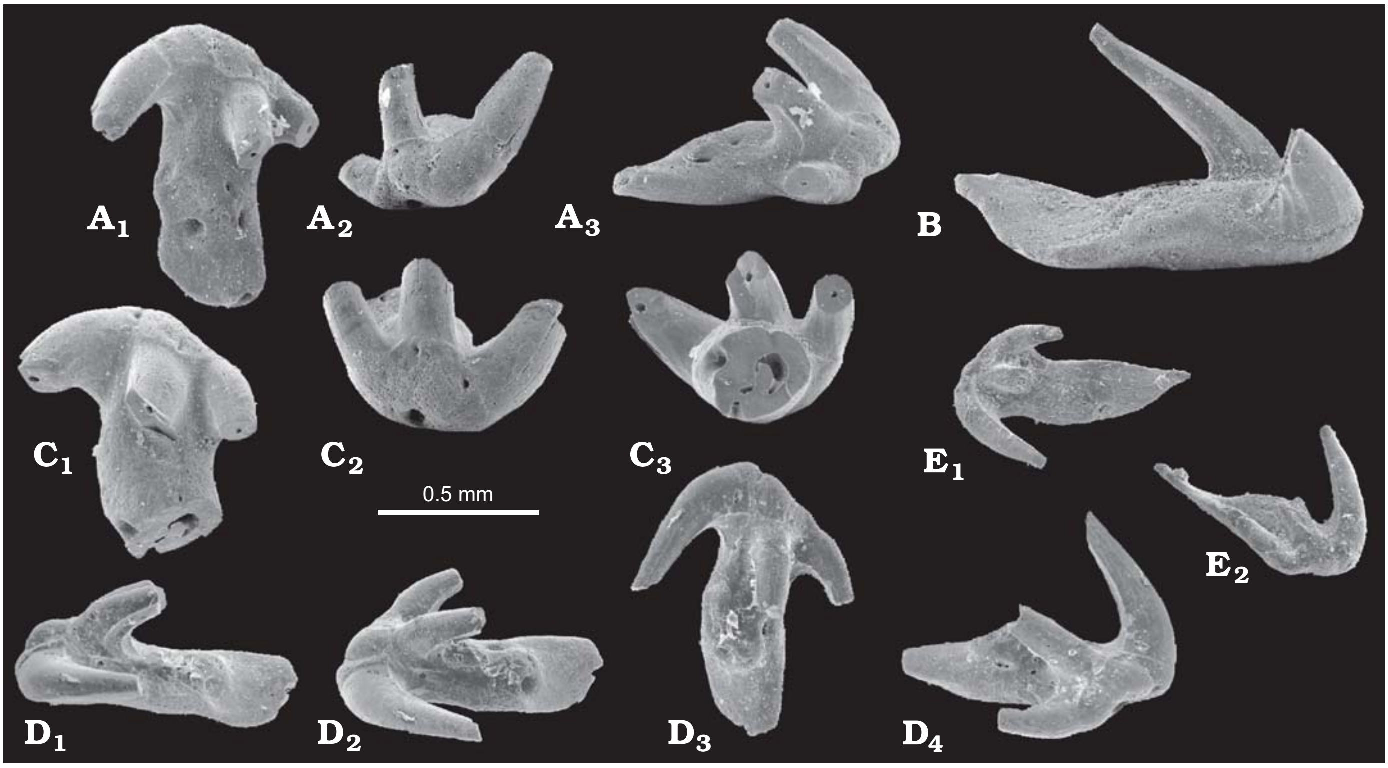

Fig. 11. Teeth of phoebodontid chondrichthyan *Thrinacodus dziki* sp. nov. from the upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland. **A**. MWGUW/Ps/11/8, in oral (A_1), labial (A_2), and lateral (A_3) views. **B**. Large tooth, MWGUW/Ps/11/9, in lateral view. **C**. MWGUW/Ps/11/10, in oral (C_1), labial (C_2), and lingual (C_3) views, broken lingual part shows the internal structure of the base. **D**. Holotype, ZPAL P.IV/212, in lateral (D_1), oral/lateral (D_2), oral (D_3), and oblique labial (D_4) views. **E**. Small tooth, MWGUW/Ps/11/11, in oral (E_1) and labial (E_2) views.

Remarks.—Despite the problems listed in the remarks concerning the genus, quite a few morphological features of the teeth of *D. fournieri* can be determined from the photograph provided by Fournier and Pruvost (1928: figs. 8, 9) and the recent re-examinations of the material (MG personal observation 1998; Ivanov 1999; Ivanov and Derycke 2005: fig. 1A–I). These features were summarised by Ginter and Hansen (2010: 29) and Ginter et al. (2010: 65). The comparative analysis suggests that of all known Viséan *Denaea*-like teeth, the series of *Denaea* cf. *fournieri* found at Todowa Grząba and at the Westenfeld Quarry are morphologically the closest to the type material and we believe that they actually represent the type species.

Stratigraphic and geographic range.—*Denaea fournieri* articulated specimens were described from the lower Viséan (Moliniacian) of Denée, Belgium (Fournier and Pruvost 1928); isolated teeth similar to those of *D. fournieri*, here referred to as *D.* cf. *fournieri*, were noted from the upper Viséan of the Holy Cross Mountains, Poland; Derbyshire, England, UK; and the Rhenish Mountains, Germany (this paper). Unexpectedly, Derycke et al. (2005) and Ivanov and Derycke (2005) do not mention any species of *Denaea*, except the specialised *D. wangi*, from the upper Viséan of Royseux, Belgium.

Denaea wangi Wang, Jin, and Wang, 2004

Fig. 13A–D.

Material.—Seven teeth from upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland (sample TG-D); ZPAL P.IV/222–224, MWGUW/Ps/7/6.

Description.—In the sample from Todowa Grząba there are rare finds of minute (0.4–0.7 mm mesio-distally), multicuspid asymmetrical teeth, identical to those named by Wang et al. (2004) as *Denaea wangi* based on their material from the Qilian Mountain in Gansu, China. The cusps (up to 11 in a row) are very delicate and smooth. The number of cusps present on either side of the median cusp differs (e.g., 2 and 5), and on the longer (distal?) side there is usually an accessory, smaller cusplet in the outermost position, toward which the median cusp is inclined (Fig. 13A). The base is very thin, lacking articulation devices. A shallow concavity usually occurs in place of the orolingual button (Fig. 13B).

Remarks.—Because of the small size and delicate construction of the teeth of *D. wangi* from Todowa Grząba and their much lower numbers in the sample than those of *D.* cf. *fournieri*, Ginter (2005) proposed that *D. wangi* might represent the juvenile teeth of *D.* cf. *fournieri*. This idea was strengthened by the observation made by Ginter in 2003 (personal observation) that the larger specimens of *Damocles serratus* (a falcatid from the Bear Gulch, Montana, USA) have simple, pentacuspid cladodont teeth, whereas the smaller, putative juvenile specimens of the same species have teeth of *D. wangi* morphotype (Ginter et al. 2010: fig. 59). The identification of the specimens of *Damocles serratus* was based on information from Rich-

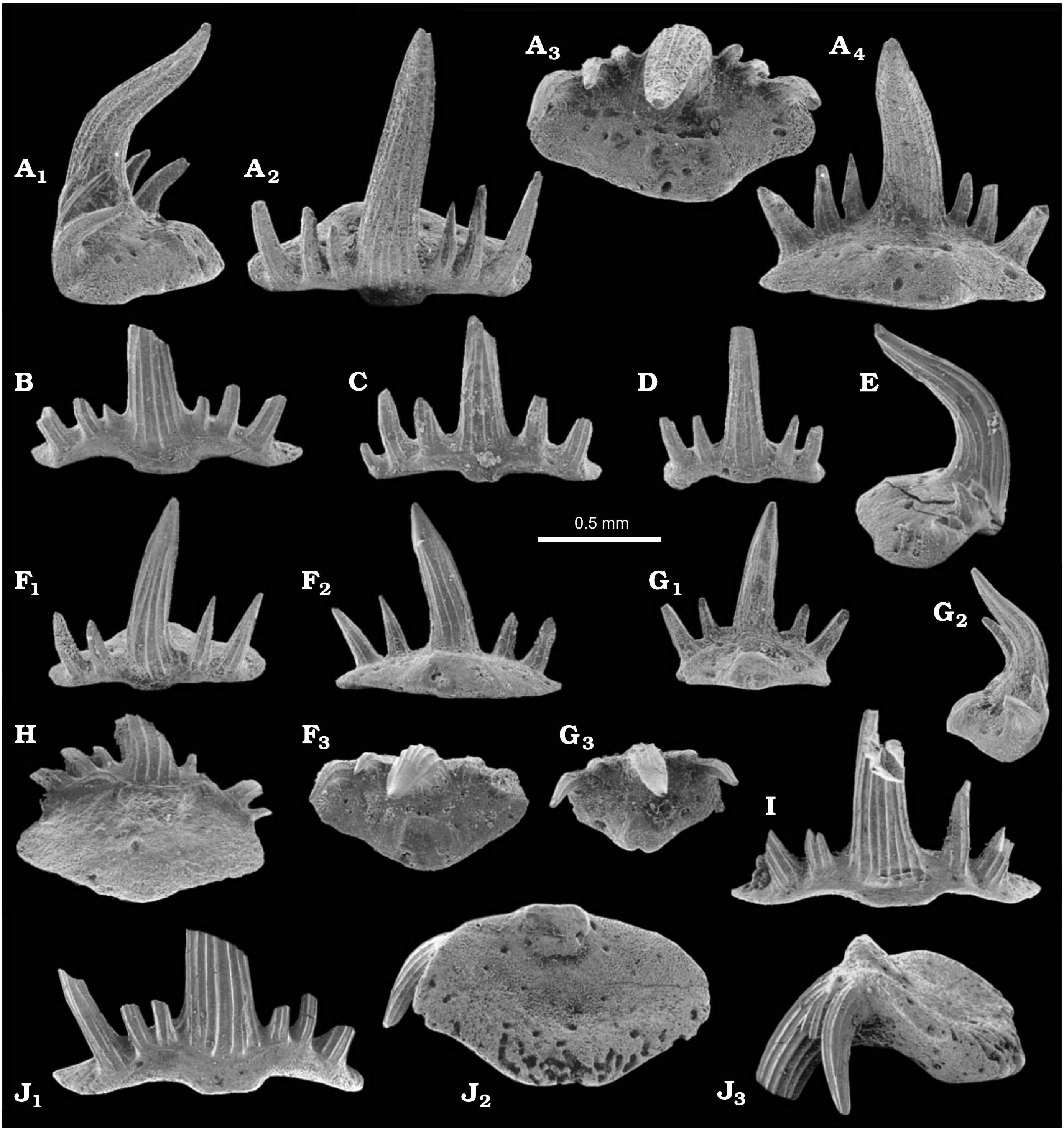

Fig. 12. Teeth of phoebodontid chondrichthyan *Denaea* cf. *fournieri* Pruvost, 1922, from the upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland. **A**. ZPAL P.IV/221, in lateral (A_1), labial (A_2), oral (A_3), and lingual (A_4) views. **B**–**D**. MWGUW/Ps/11/12, MWGUW/Ps/11/13, and MWGUW/Ps/11/14, respectively, in labial views. **E**. MWGUW/Ps/11/15, in lateral view. **F**. MWGUW/Ps/11/16, in labial (F_1), lingual (F_2), and oral (F_3) views. **G**. ZPAL P.IV/219, in lingual (G_1), lateral (G_2), and oral (G_3) views. **H**. ZPAL P.IV/220, in aboral/labial view. **I**. MWGUW/Ps/11/17, in labial view. **J**. MWGUW/Ps/7/5, in labial (J_1), aboral (J_2), and aboral/lateral (J_3) views.

ard Lund and Eileen Grogan (personal communication 2003). However, two new facts seem to undermine Ginter's concept. Firstly, in the rich collection from Royseux (Derycke et al. 2005; Ivanov and Derycke 2005) there are numerous teeth of *D. wangi* and apparently no tooth of *D.* cf. *fournieri*. Secondly, R. Lund and E. Grogan (personal communication 2008) no longer consider the smaller individuals from Montana to be juveniles and conspecific with larger *Damocles serratus*: the claspers are fully grown in the smaller specimens and the head spine morphology differs substantially in the two species.

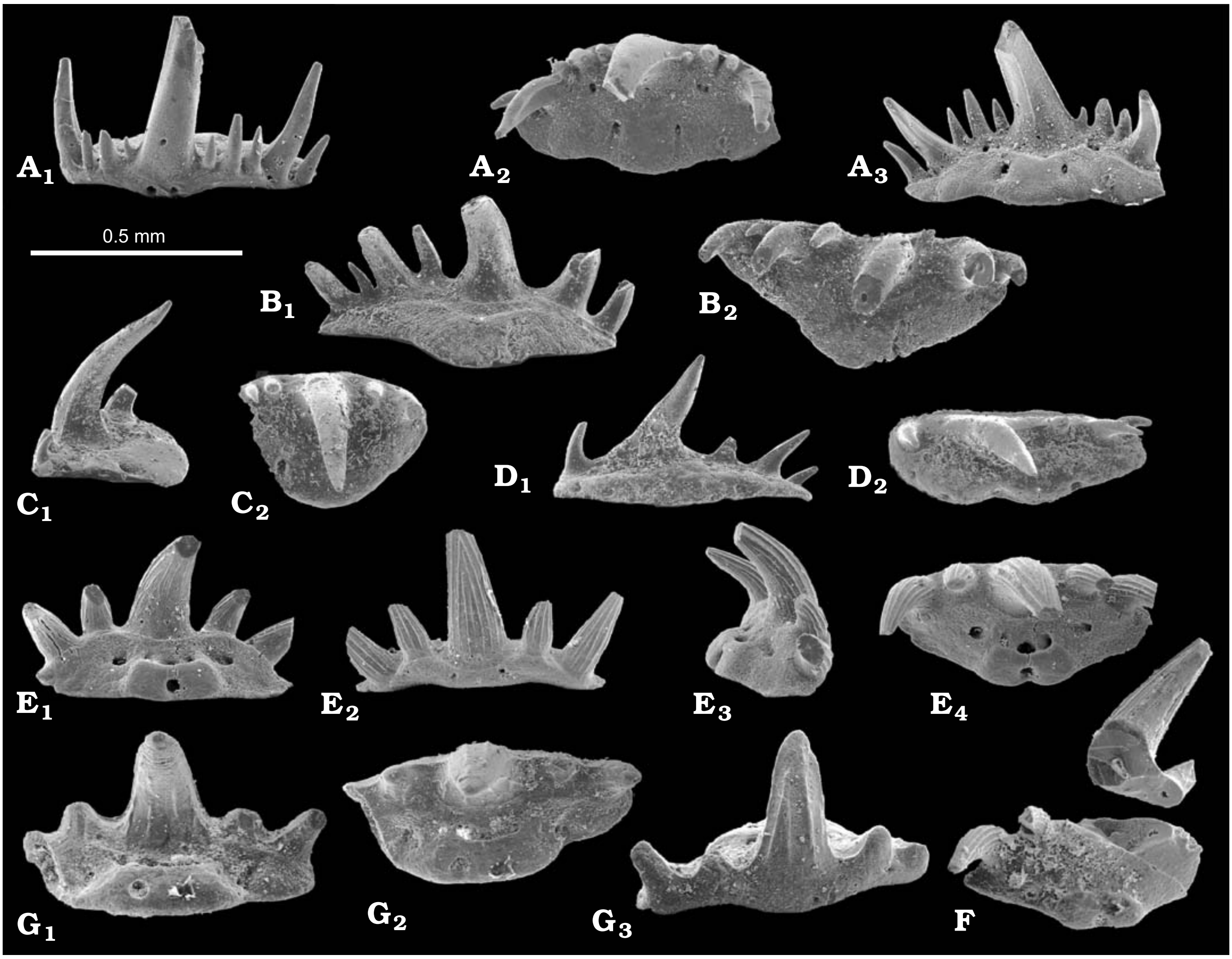

Fig. 13. Cladodont teeth from the upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland. **A**–**D**. *Denaea wangi* Wang, Jin, and Wang, 2004. **A**. MWGUW/Ps/7/6, in labial (A_1), oral (A_2), and lingual (A_3) views. **B**. ZPAL P.IV/224, in lingual (B_1) and oral (B_2) views. **C**. ZPAL P.IV/223, in lateral (C_1) and oral (C_2) views. **D**. ZPAL P.IV/222, in lingual (D_1) and oral (D_2) views. **E**, **F**. *Denaea williamsi* Ginter and Hansen, 2010. **E**. MWGUW/Ps/11/18, in lingual (E_1), labial (E_2), lateral (E_3), and oral (E_4) views. **F**. MWGUW/Ps/11/19, tooth with two cusps broken off in lingual view. **G**. Ctenacanthidae gen. et sp. indet., MWGUW/Ps/11/20, in lingual (G_1), oral (G_2), and labial (G_3) views.

At first this new information was ignored (see Ginter in Ginter et al. 2010: 65–66). However, after reconsideration, it seems possible that *D. wangi* is indeed a valid species which perhaps is conspecific, or at least closely related, to the shark formerly thought to be a young *Damocles serratus*. However, it is too early to decide the question as to which genus this species should be attributed—*Denaea*, *Damocles*, or a new one. The collection from Royseux and the specimens of the "small *Damocles*" (e.g., CM 35472) need to be formally described and published before further discussion can take place.

Stratigraphic and geographic range.—Viséan of Gansu, China (Wang et al. 2004); upper Viséan of Belgium (Ivanov and Derycke 2005), and the Holy Cross Mountains, Poland (this paper). Perhaps also Serpukhovian of Montana, USA (articulated specimens, Ginter et al. 2010).

Denaea williamsi Ginter and Hansen, 2010

Fig. 13E, F.

2000 *Denaea* sp.; Savitskiy et al. 2000: 49–50, pl. 16: 2–4.

2010 *Denaea* sp. nov B Ginter and Hansen (in press); Ginter et al. 2010: fig. 62.

2010 *Denaea williamsi* sp. nov.; Ginter and Hansen 2010: 34–36, figs. 3, 4.

Material.—Five teeth from upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland (sample TG-D); MWGUW/Ps/11/18–19.

Description and remarks.—The teeth of *D. williamsi* from Todowa Grząba are very similar to those from the type material for the genus (Serpukhovian of Illinois, USA; Ginter and Hansen 2010: figs. 3, 4). They possess the specific ornament of the median cusp, composed of cristae which, on the labial side, diverge laterally at the base and then corresponding

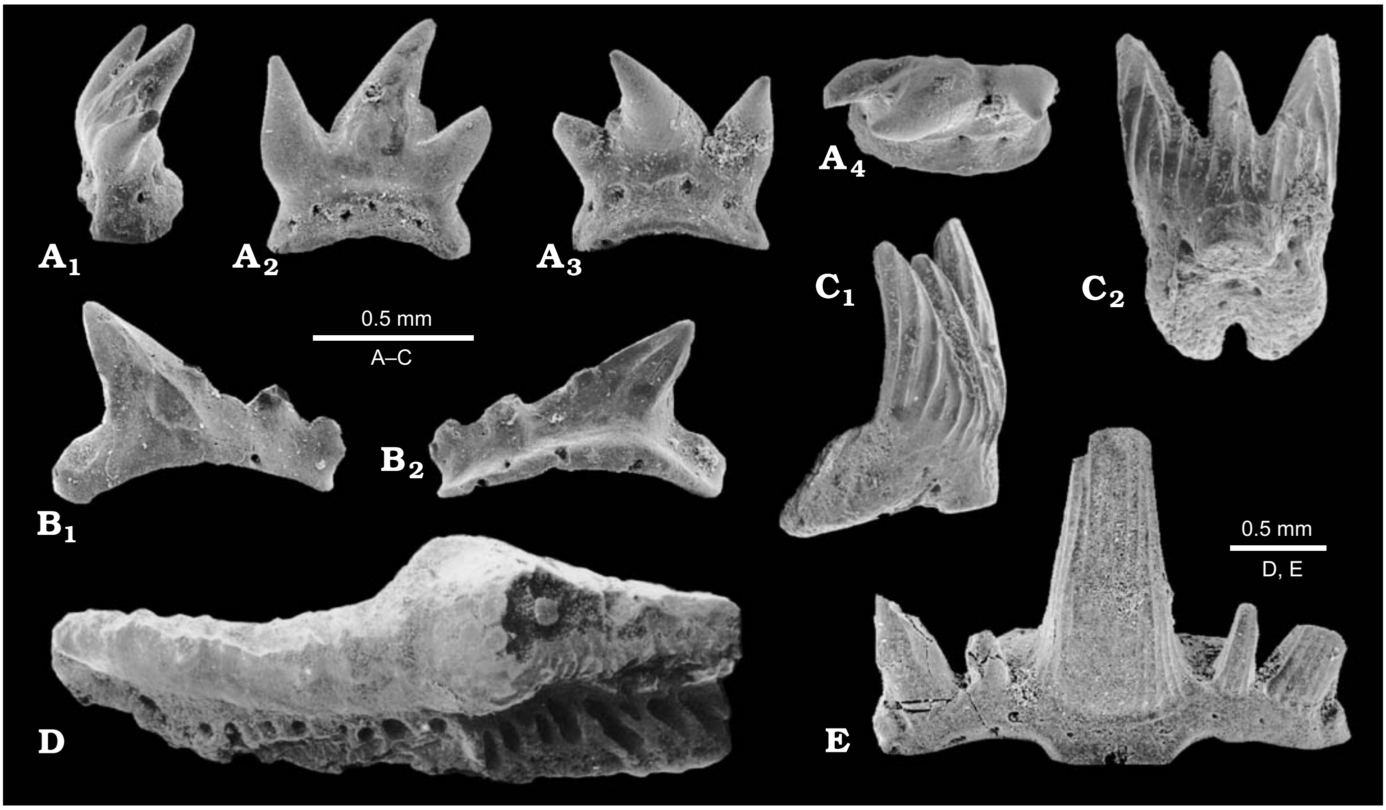

Fig. 14. Chondrichthyan teeth from the upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland. **A**. Euselachii indet. 2, MWGUW/Ps/11/21, in lateral (A_1), labial (A_2), lingual (A_3), and oral (A_4) views. **B**. Euselachii indet. 1, MWGUW/Ps/11/22, in labial (B_1) and lingual (B_2) views. **C**. *Bransonella nebraskensis* (Johnson, 1984), ZPAL P.IV/215, in lateral (C_1) and labial/aboral (C_2) views. **D**. Orodont-like crushing tooth, ZPAL P.IV/233, in oral/lingual view. **E**. *Denaea* sp., large tooth, MWGUW/Ps/11/23, in labial view.

pairs join before reaching the tip, whereas on the lingual face they converge at various heights. The outermost cusps are strongly divergent, more so than in *D.* cf. *fournieri*. The base is provided with a distinct button, in the shape of horizontal figure of 8, at the lingual rim. However, whereas in the type material there are apparently only two large openings of the main basal canal, one in the centre of the aboral surface and another on the lingual rim, in at least one specimen from Todowa Grząba (Fig. 13E) an additional foramen is located between the button and the median cusp, as in smaller specimens of *D.* cf. *fournieri* (Fig. 7F).

The teeth from Todowa Grząba are small (0.5 mm across the base) and five-cusped. It seems that the seven-cusped tooth-crown of *D. williamsi* noted from Illinois, USA (Ginter and Hansen 2010: fig. 4D) was an anomaly, probably occurring only in the largest specimens.

Stratigraphic and geographic range.—Viséan of the Moscow Syneclise (Savitskiy et al. 2000), lower Serpukhovian of Illinois, USA (Ginter and Hansen 2010), and upper Viséan of the Holy Cross Mountains, Poland (this paper). Similar, but not identical teeth from Serpukhovian/Bashkirian boundary beds of South Tien-Shan, Uzbekistan, were designated as *Denaea* cf. *D. williamsi* by Ivanov (2013),

Denaea sp.

Fig. 14E.

Material.—Four teeth from upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland (sample TG-D); MWGUW/Ps/11/23.

Description.—There are a few poorly preserved five-cusped cladodont teeth in the material from Todowa Grząba which are generally similar to *D.* cf. *fournieri*, but larger (about 2.5 mm across the base) and with more robust cusps. They may belong to a larger species of *Denaea*, some other falcatid, or an undetermined symmoriiform.

Order Ctenacanthiformes Glikman, 1964

Family indet.

Genus indet.

"*Ctenacanthus*" *costellatus* Traquair, 1884

Fig. 9D, E.

1884 *Ctenacanthus costellatus* Traquair; Traquair 1884: 3–8, pl. 2.
1936 *Ctenacanthus costellatus* Traquair, 1884; Moy-Thomas 1936: 762–771, text-figs. 1, 2, pl. 1: a, b.
2002 "*Ctenacanthus*" *costellatus* Traquair, 1884; Ginter 2002, figs. 4A, 5.
2010 "*Ctenacanthus*" *costellatus* Traquair, 1884; Ginter et al. 2010: 77–78, fig. 71.

Material.—One tooth from upper Viséan, Ticknall, Derbyshire, England, UK and one from upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy

Cross Mountains, Poland (sample TG-D); NHMUK PV P73290, ZPAL P.IV/256.

Description.—There are two relatively large but incomplete teeth in the analysed material, one (from Ticknall; Fig. 9D) with the mesio-distal dimension probably exceeding 2 mm when complete, and another (from Todowa Grząba; Fig. 9E) probably no smaller than 7 mm.

The smaller tooth has about 2/3 of the base preserved, with all of the important features available for observation. The lingual part of the base is broad and rounded, and there are two prominent, widely spaced, orolingual buttons. To these buttons correspond two separate basolabial projections, semi-circular in aboral view, with a shallow median depression lying between them. The crown in this specimen is heavily damaged, but the fragment that remains reveals that it was cladodont, with three lateral cusps on each side (if the tooth was symmetrical). The outermost cusps appear to be larger than the intermediate two. The labial side of the cusps is covered with strong cristae. On the most complete of the lateral cusps, the two cristae converge and reach the tip as one (Fig. 9D$_2$). The cristae on the lingual side are more gentle and sub-parallel.

In the larger tooth, only half of the crown is preserved; the base is completely destroyed. The crown is cladodont, with four lateral cusps on each side. Again, the outermost cusp is larger than the intermediate ones. The labial side of the crown is covered with strong cristae, converging at various heights, and the lingual side bears more delicate cristae. The shallow depression at the base of the labial side of the median cusp (Fig. 9E$_2$) suggests, that there might also have been a basolabial depression in the base, as in the smaller tooth.

Remarks.—Although incomplete, the two teeth can confidently be considered as smaller and larger morphotypes belonging to the same species, particularly because of the form and ornamentation of the crown. Moreover, the combined characters of these two specimens show similarities with the teeth associated with the articulated material of "*Ctenacanthus*" *costellatus* Traquair, 1884, from the Viséan of Glencartholm, Scotland, UK (NHMUK PV P20144-5; Ginter et al. 2010: fig. 71). The size of those teeth is from ca. 2 to 8 mm across the base. They have two orolingual buttons, two semi-circular basolabial projections (Ginter 2002: fig. 5C) separated by a shallow depression, with strong cristae converging upwards over the labial side of the cusps, and more gentle, subparallel cristae on the lingual side. The smaller teeth have only two lateral cusps on each side of a prominent medial cusp, but the largest illustrated tooth-fragment (Ginter et al. 2010: fig. 71C) displays at least three on one side (there is a space for a fourth one). Also one of the early illustrations by Moy-Thomas (1936: pl. 1b) shows strong cristae and three cusps on each side.

To us, it appears very probable that the teeth from Ticknall and Todowa Grząba actually belong to "*C.*" *costellatus*. If our reasoning is correct, this would be the first report of that important species outside of the type locality.

Stratigraphic and geographic range.—Both articulated specimens were found in the Viséan of Glencartholm, Scotland, UK (Traquair 1884; Moy-Thomas 1936); isolated teeth are known from the upper Viséan, Ticknall, Derbyshire, England, UK and Holy Cross Mountains, Poland (this paper).

Family Ctenacanthidae Dean, 1909

Ctenacanthidae gen. et sp. indet.

Fig. 13G.

Material.—Two teeth from upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland (sample TG-D); MWGUW/Ps/11/20.

Description and remarks.—This taxon is represented by two minute (0.5 mm across the base), five-cusped cladodont teeth with the crowns compressed labio-lingually and all the cusps connected with the continuous carina, in the same manner as in other ctenacanthids. There are a few cristae on each side of the median cusp. There is an orolingual ridge which is slightly wider than the base of the median cusp. All these features suggest that these are juvenile teeth of the Ctenacanthidae, but more precise identification is impossible.

Order Squatinactiformes Zangerl, 1981

Family Squatinactidae Cappetta, Duffin, and Zidek, 1993

Genus *Squatinactis* Lund and Zangerl, 1974

Type species: *Squatinactis caudispinatus* Lund and Zangerl, 1974, Serpukhovian, Bear Gulch, Montana, USA.

Squatinactis caudispinatus Lund and Zangerl, 1974

Figs. 7G, 8D.

Material.—Four teeth from upper Viséan of Cawdor Quarry, Matlock, Derbyshire, England, UK (samples Cawdor 5 and 11); NHMUK PV P73282, NHMUK PV P73286.

Description and remarks.—A few small cladodont teeth (less than 0.5 mm across the base) from Cawdor Quarry are tentatively attributed to *S. caudispinatus* because of the short base (labio-lingually) provided with two separate, oval orolingual buttons and two basolabial projections, separated by a deep basolabial depression. Some of the teeth are wide (mesio--distally) and have multicuspid crowns (up to four lateral cusps; Fig. 8B), covered on both sides with sub-parallel cristae, and the other have narrower bases (Fig. 7G), fewer cusps and apparently less well developed ornamentation. Similar differences were observed in the material of *S. caudispinatus* from the Tournaisian of Illinois, USA (Ginter et al. 2010: fig. 73A–F).

Stratigraphic and geographic range.—Articulated specimens from Serpukhovian of Bear Gulch, Montana, USA (Lund and Zangerl 1974; Lund 1988), Tournaisian of Illinois, USA (Ginter et al. 2010) and South Urals, Russia (Ivanov 1996), upper Viséan of Derbyshire, England (this paper).

Cohort Euselachii Hay, 1902

Subcohort Neoselachii Compagno, 1977

Order indet.

Family Anachronistidae Duffin and Ward, 1983

Genus *Cooleyella* Gunnell, 1933

Type species: *Cooleyella peculiaris* Gunnell, 1933, Kasimovian, Leeds, Kansas City, Missouri, USA.

Cooleyella fordi (Duffin and Ward, 1983)

Fig. 8C, D.

Material.—Three specimens from upper Viséan of Cawdor Quarry, Matlock, Derbyshire, England, UK (sample Cawdor 5), NHMUK PV P73284–5.

Description.—The teeth of *Cooleyella* from Cawdor Quarry are typical, with a crown composed of a triangular median cusp, lateral wings (connected with the median cusp by a common carina) and a labial extension of the crown ("basal flange"). The base is lenticular, with a deep pit in the aboral side. The openings of the main basal canal are situated lingual to the centre of the pit and at the lingual rim of the base.

Stratigraphic and geographic range.—Viséan (Asbian) of Novgorod Region, Russia (Savitskiy et al. 2000), upper Viséan of Derbyshire, England (Duffin and Ward 1983 and this paper) and Belgium (Ivanov and Derycke 2005); Cisuralian of the South Urals, Russia (Ivanov 2011). Ivanov (2011) also notes the presence of this species, but with no illustration or reference to particular locality, in the Viséan of Nearpolar Urals, Serpukhovian of Moscow Syneclise, and Pennsylvanian of the North Timan.

Genus *Ginteria* Duffin and Ivanov, 2008

Type species: *Ginteria fungiforma* Duffin and Ivanov, 2008, early Serpukhovian, Kalinovskie Vyselki Quarry, Moscow Region, Russia.

Ginteria fungiforma Duffin and Ivanov, 2008

Fig. 8E.

Material.—Two specimens from upper Viséan of Cawdor Quarry, Matlock, Derbyshire, England, UK (samples Cawdor 8 and 13); NHMUK PV P66676.

Remarks.—One of these mushroom-like teeth from Cawdor Quarry was thoroughly described by Duffin and Ivanov (2008).

Stratigraphic and geographic range.—Upper Viséan of Derbyshire, England and Novgorod Region, Russia; upper Viséan–lower Serpukhovian of Moscow Region, Russia (Duffin and Ivanov 2008); upper Viséan of Belgium (Ivanov and Derycke 2005).

Euselachii gen. et sp. indet.

Fig. 14A, B.

Material.—One tooth from upper Viséan of Cawdor Quarry, Matlock, Derbyshire, England, UK (sample Cawdor 5), three teeth from upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland (sample TG-D), one from upper Asbian, *Goniatites fimbriatus* Ammonoid Zone, Westenfeld Quarry, Germany (sample C12); MWGUW/Ps/11/21–22.

Description and remarks.—There are a few teeth which can be attributed to euselachians, but without a precise systematic placement. Four are characterised by a protacrodont crown, slightly compressed labio-lingually (designated here as Euselachii indet. 1; Fig. 14B). It is impossible to say whether or not all of them represent the same taxon; it is probable that numerous Mississippian sharks possessed teeth of this type, e.g., *Tristychius* and *Sphenacanthus*. One tooth from Todowa Grząba (Euselachii indet. 2; Fig. 14A) is different from the rest. Its crown is composed of three conical cusps, the median cusp being slightly larger than the laterals, and the base is deep. The specimen has a superficial resemblance to an anterior, clutching tooth of the Jurassic to Recent shark *Heterodontus* to which its function in the dentition of an undefined Viséan euselachian was probably analogous.

Subclassis Euchondrocephali Lund and Grogan, 1997

Euchondrocephali gen. et sp. indet.

Figs. 8F, 14D.

Material.—Three teeth from upper Viséan of Cawdor Quarry, Matlock, Derbyshire, England, UK (samples Cawdor 1, 3 and 5), two from upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland (sample TG-D); NHMUK PV P73287, ZPAL P.IV/233.

Description and remarks.—Several fragments of possible euchondrocephalan teeth were found in the studied material. They are seriously damaged and usually only dome-like pieces of crowns (Fig. 8F), built of tubular dentine, suggest their identity. The best preserved tooth was found at Todowa Grząba (Fig. 14D). It is orodont-like, elongated mesio-distally, with a euselachian base and a crown composed of a dome-like (at least in the present state) median cusp and lateral wings with a mesio-distal ridge and numerous ridges transversal to it on the labial and lingual sides. The tooth is somewhat similar to *Orodus minutus* Newberry and Worthen, 1866, known from the Mississippian of Iowa, USA and Bristol area, England, UK (see Ginter et al. 2010: fig. 102G, H).

Chondrichthyan scales and branchial denticles

There are several types of scales in the studied material: typical composite ctenacanth scales (sensu Reif 1978) with the odontodes directed posteriorly and arranged rather irregularly, and the convex bases showing a common pulp cavity (Fig. 15A, F, I); hybodont scales with vertically arranged odontodes (Fig. 15B, O); as well as neoselachian? (Fig. 15G) and euchondrocephalan (Fig. 15H) placoid scales. Also, symmoriiform branchial denticles of the "*Stemmatias*" type, both with a single (Fig. 15D, M; "*S. simplex*") and a

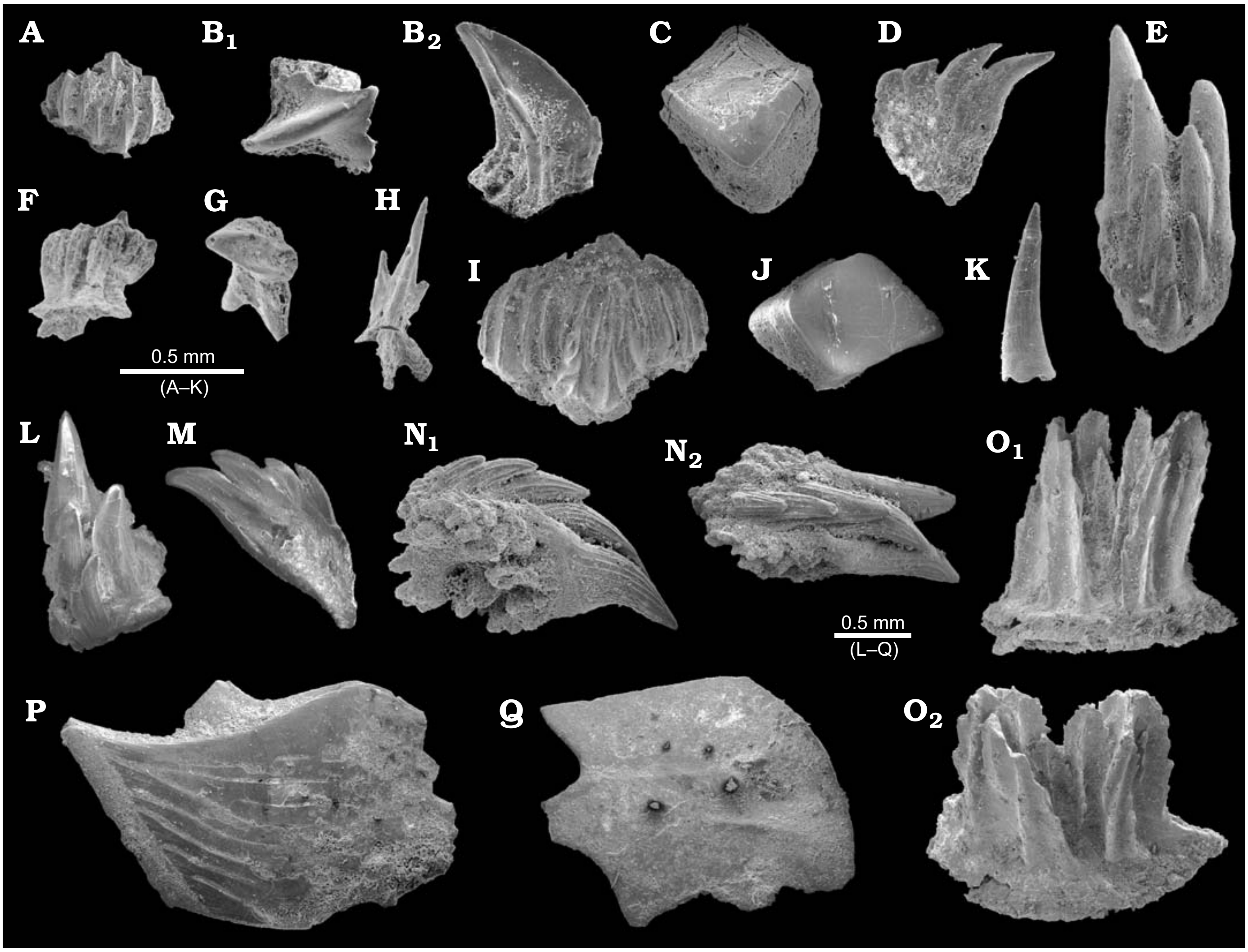

Fig. 15. Ichthyoliths from the upper Viséan of Todowa Grząba, north of Ostrówka Quarry, Gałęzice Region, Holy Cross Mountains, Poland (A–E), Cawdor Quarry, Matlock, Derbyshire, England, UK, sample Cawdor 5 (F–H), and Westenfeld Quarry, Rhenish Mountains, Germany (**I**–Q). **A**, **F**, **I**. Ctenacanth-type scales. **A**. MWGUW/Ps/11/24, in coronal view. **F**. NHMUK PV P73291, in lateral view. **I**. MWGUW/Ps/11/29, in coronal view. **B**, **O**. Hybodont-type scales. **B**. MWGUW/Ps/11/25, in coronal (B_1) and anterior/lateral (B_1) views. **O**. MWGUW/Ps/11/30, in anterior (O_1) and coronal/anterior (O_2) views. **D**, **E**, **L**–**N**. Symmoriiform branchial denticles ("*Stemmatias*"). **D**. MWGUW/Ps/11/27, in lateral view. **E**. MWGUW/Ps/11/26, in coronal view. **L**. MWGUW/Ps/11/32, in anterior view. **M**. MWGUW/Ps/11/31, in lateral view. **N**. MWGUW/Ps/11/33, in lateral (N_1) and coronal (N_2) views. **G**, **H**. Neoselachian (NHMUK PV P73292) and holocephalian (NHMUK PV P73293) placoid scales, in lateral views. **C**, **J**. *Acanthodes*-type acanthodian scales. **C**. MWGUW/Ps/11/28, in anterior/coronal view. **J**. MWGUW/Ps/11/37, in lateral/coronal view. **K**. Actinopterygian tooth, MWGUW/Ps/11/34, in lateral view. **P**, **Q**. Actinopterygian scales in external (**P**, MWGUW/Ps/11/35) and internal (**Q**, MWGUW/Ps/11/36) views.

double (Fig. 15E, L, N; "*S. bicristatus*") row of cusps, occur in the samples. They are particularly numerous at Westenfeld and Todowa Grząba.

Acanthodian scales and actinopterygian microremains

Only one type of acanthodian scales was recovered, with diamond-shaped crowns and absolutely smooth surfaces, devoid of ridges (Fig. 15C, J). A few such scales occur at Westenfeld, Todowa Grząba, and in samples 2 and 5 of Cawdor Quarry. In almost every sample there occur conical teeth with acrodine caps and/or rhomboidal scales belonging to palaeoniscoid actinopterygians (Fig. 15K, P, Q).

Discussion

The taxonomic contents of chondrichthyan assemblages from the three localities analysed here differ at the species level, but, with the exception of sample 5 from Cawdor Quarry (which will be treated separately), there are considerable similarities as far as supra-specific categories are concerned. For the sake of comparison between our assemblages (as well as with those which have been previously published) we have distinguished five such categories, based on the form of the teeth and probably also connected with the mode of life and feeding. These categories are as follows:

(i) Falcatidae, with cladodont dentition, delicate clutching teeth; probably small fast-swimming hunters, feeding on smaller fish; we know the size and shape of their bodies from the excellent whole-bodied and articulated fossils from the Serpukhovian of Bear Gulch, Montana, USA (Lund 1985, 1986), Pennsylvanian Black Shales of Indiana, USA (Williams 1985), and the Viséan of Denée, Belgium (Fournier and Pruvost 1928).

(ii) Other Cladodontomorphi, represented by only a few specimens in the whole of the studied material, mainly comprising ctenacanthids and squatinactids.

(iii) *Thrinacodus*, with specialised asymmetrical teeth, characterised by twisted phoebodont crowns and long bases; a few articulated specimens of *T. gracia* with long, eel-like bodies and extremely narrow jaws were found in Bear Gulch (Grogan and Lund 2008); they must have been slow-swimming hunters, catching small common prey items, such as conodont animals.

(iv) *Bransonella*, with ornamented diplodont teeth; it is considered to be an open-marine relative of the Xenacanthiformes but, on the other hand, its teeth share several features with *Jalodus*, a Famennian shark abundant in far offshore environments (Ginter et al. 2010: figs. 18, 34).

(v) Anachronistidae, with cutting-crushing teeth, similar to those of modern orectolobiform sharks or batoids; thus far we possess no data on their body shape.

(vi) Euselachii and Euchondrocephali, with mainly crushing and grinding teeth, most of them probably washed in by currents from the nearby carbonate platforms.

The results in Table 1 and Fig. 16 clearly show that at Westenfeld, Todowa Grząba, and in combined "typical" samples from Cawdor Quarry, falcatids strongly predominate the chondrichthyan fauna. In these same materials there is also a small but consistent and regular input of thrinacodonts and a few teeth of euselachians or euchondrocephalans. *Bransonella* occurs only at Todowa Grząba. It is interesting to note that anachronistids occur at Cawdor Quarry, but are totally absent both from Westenfeld and Todowa Grząba, despite the relatively large number of specimens (70) in the latter.

The relative abundances of chondrichthyan teeth in Cawdor Quarry sample Cawdor 5 stand out from the other records. Here, falcatids are absent and *Thrinacodus, Bransonella*, and anachronistids dominate the fauna. Of course, the sample is too small (14 teeth) to be statistically significant, but the lack of falcatids, otherwise occurring in almost all samples taken from the same section, seems to indicate some change of environment. Unfortunately, it is difficult to ascertain from the lithology alone what kind of environmental change could be represented. There are two detailed descriptions of the stratigraphic profile at Cawdor Quarry, one by Smith et al. (1967), and another by MTD (unpublished notes, 1983). The limestone body, from which sample Cawdor 5 was taken, is described as "dark, wedge bedded limestone; a little chert" (Smith et al. 1967) and "fairly massive dark grey/black bituminous biomicrite; some shaley beds; crinoidal debris" (MTD). The largest sample, containing falcatids (sample Cawdor 11) comes from a very similar lithology described as: "dark, brown weathering limestone, small shells, corals and black shale partings" (Smith et al. 1967) and "massive mid-grey micrite" (MTD). Thus, one may only speculate that the sample taken from the middle part of a thick limestone body (the case of sample Cawdor 5; see Fig. 2) could represent an environment closer to the carbonate platform than the samples obtained from the limestone/shale boundary (the case of sample Cawdor 11 and most of the other samples from Cawdor Quarry).

Equally enigmatic is the reason for the absence of anachronistids (*Cooleyella* and *Ginteria*) from the German and Polish samples. These taxa are quite common at Cawdor Quarry and other European Viséan localities (Steeplehouse Quarry, Roysuex, and Novgorod Region, see below), so their presence would be expected in the other sections in the same, carbonate pelagic facies, and especially in such large samples as that from Todowa Grząba. Because the assemblages from samples C12 at Westenfeld and TG-D from Todowa Grząba are probably older than those from Derbyshire and Royseux (Fig. 5), there arises a tempting hypothesis that the anachronistids evolved (or migrated to northern Europe) only in the early Brigantian. However, the material from the Novgorod Region, containing anachronistids, was reliably dated as not later than Asbian (compare Savitskiy et al. 2000; Menning et al. 2006), so this explanation does not hold. Again, some as yet unrecognisable environmental factor might have been responsible for this difference.

Thus far, the assemblages described in this paper are the only European Viséan assemblages for which the numbers of all specimens have been given. From the collections from Royseux (Derycke et al. 2005; Ivanov and Derycke 2005) and the Novgorod Region (Savitskiy et al. 2000; Ivanov 2008) we only know lists of taxa, and from Steeplehouse

Table 1. Comparison of the studied late Viséan chondrichthyan assemblages.

Taxon/Samples	Cawdor Quarry sample 5		Cawdor Quarry samples 1–4 + 6–14		Todowa Grząba sample TG-D		Westenfeld Quarry sample C12	
	spec.	%	spec.	%	spec.	%	spec.	%
Falcatidae	0	0	23	72	49	70	33	89
Other Cladodontomorphi	1	7	4	13	3	4	0	0
Thrinacodus	5	36	1	3	9	13	3	8
Bransonella	3	21.5	0	0	4	6	0	0
Anachronistidae	3	21.5	2	6	0	0	0	0
Euselachii + Euchondrocephali	2	14	2	6	5	7	1	3
Total	14	100	32	100	70	100	37	100

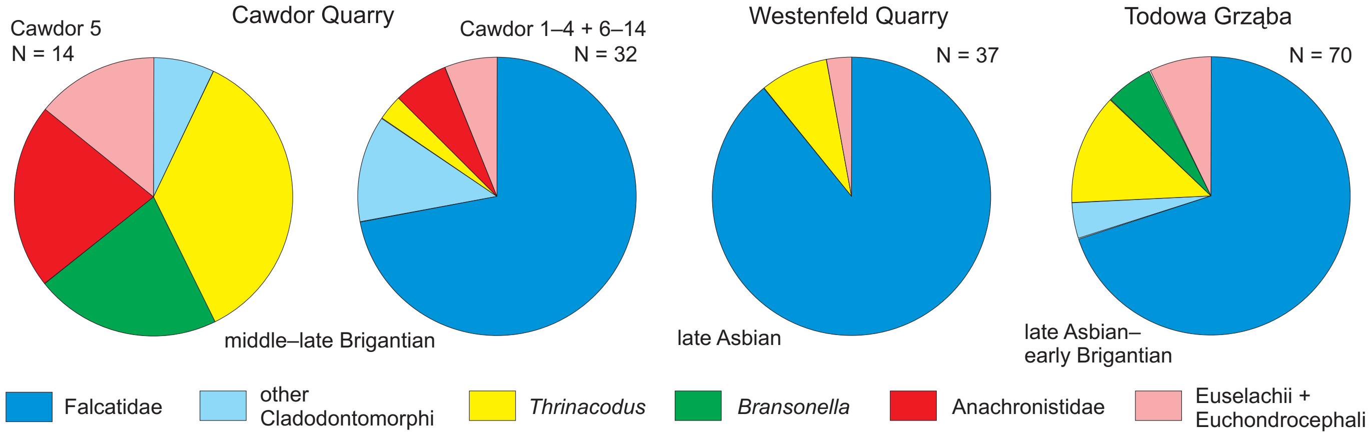

Fig. 16. Pie-diagrams illustrating relative abundances of teeth representing groups of chondrichthyan taxa in the studied sections. Note the predominance of falcatid teeth in most samples, except for sample Cawdor 5. N, total number of specimens.

Quarry we also know the numbers of specimens of selected genera: *Lissodus* (29), *Thrinacodus* (3), *Cooleyella* (36).

The ctenacanthiforms and falcatids are present at all the three localities, but the typical teeth of *Denaea* cf. *fournieri* occur only at Steeplehouse Quarry. Interestingly, at Royseux there occur numerous teeth of *D. wangi* instead. As far as *Thrinacodus* is concerned, we know that at Steeplehouse there are three specimens of *T. dziki* sp. nov. (compare Duffin 1993), but the species occurring at Royseux and Novgorod Region are unknown. Derycke et. al. (2005) and Ivanov (2008) identified them as *T. ferox*, but at that time virtually all isolated Carboniferous thrinacodont teeth were designated as such. *Bransonella* is present both at Steeplehouse and Royseux.

The Anachronistidae are present in all the comparative localities, and are particularly abundant at Steeplehouse Quarry (the type locality of *Cooleyella fordi*; Duffin and Ward 1983). Also, the teeth of euselachians appear in relatively great numbers. At Steeplehouse they are represented mainly by *Lissodus wirksworthensis* (type locality; Duffin 1985; Koot et al. 2013 proposed the change of its generic name to *Reesodus*) and a few teeth with protacrodont crowns, while at Royseux there are protacrodonts and sphenacanthids (Derycke et al. 2005), and a mixture of *Lissodus*, sphenacanthids, and other, unidentified euselachian teeth have been recovered from the outcrops in the Novgorod Region (Savitskiy et al. 2000; Ivanov 2008).

In terms of the distribution of euchondrocephalan remains: Steeplehouse Quarry has yielded fragmentary remains of petalodonts and helodontiforms, the Royseux fauna contains petalodonts and holocephalians (“with one of them resembling *Lagarodus*” being reported by Derycke et al. 2005: 8), while putative petalodontiforms, helodontiforms, and psephodontiforms have been recovered from the Novgorod Region (Ivanov 2008). However, none of the crushing teeth illustrated by Savitskiy et al. (2000) seems to belong to any of the aforementioned groups, but they rather represent Euselachii.

All of this information, albeit imprecise, reveals several common characters between the assemblages from Steeplehouse Quarry, Royseux, and the Novgorod Region: the presence of *Thrinacodus* and anachronistids, and the abundance of euselachian (and sometimes also euchondrocephalan) crushing teeth. These characters mean that the faunal assemblages of these three localities are more similar to that of Cawdor Quarry sample 5 than they are to those from Westenfeld and Todowa Grząba, or the other samples from Cawdor Quarry. It must be stressed, however, that all the materials analysed in this paper come from limestone deposited in pelagic areas, so the differences observed here, although evident, are minor and probably result mainly from the distance to the submarine carbonate platforms. The life on such platforms was very different and fossils of chondrichthyans found in crinoid calcirudite which accumulated there (with the predominance of large euselachian and euchondrocephalan crushing and grinding dental elements) differ considerably from those described above.

To illustrate the difference between the pelagic and carbonate platform chondrichthyan communities from the Mississippian, we may compare the largest available sample, TG-D from Todowa Grząba (70 specimens), with the material from the middle Tournaisian of Muhua, Guizhou province, southern China, sample MH-1 (100 specimens; Ginter and Sun 2007). The latter sample comes from a bioclastic limestone lens with an abundant benthic invertebrate fauna, including brachiopods and ostracods, surrounded by pelagic shale. The carbonate material probably slumped from the shallow submarine plat-

Table 2. Comparison of chondrichthyan assemblages from late Viséan pelagic facies of Todowa Grząba, Holy Cross Mountains (this paper), and mid-Tournaisian carbonate platform of Muhua, southern China (Ginter and Sun 2007).

Taxon/Samples	Todowa Grząba sample TG-D		Muhua sample MH-1	
	spec.	%	spec.	%
Falcatidae (+*Stethacanthus* sp.)	49	70	10	10
Other Cladodontomorphi	3	4	25	25
Thrinacodus	9	13	9	9
Bransonella	4	6	0	0
Anachronistidae	0	0	0	0
Euselachii + Euchondrocephali	5	7	56	56
Total	70	100	100	100

form into a deeper basin. Although there is a considerable age interval between these two samples and the Anachronistidae probably did not yet exist in the Tournaisian, the other supra-specific taxonomic categories distinguished above can be easily applied to both assemblages (Table 2). It is evident at first sight that crushing teeth and tooth-plates of Euselachii and Euchondrocephali strongly predominate at Muhua, and that falcatids (together with small *Stethacanthus*-like teeth) are a minor group there. The euchondrocephalans are particularly diverse, including petalodonts and holocephalians, such as helodontids, cochliodontids, and chondrenchelyids. What is really interesting is the stable input of thrinacodonts in the samples from both environments, which indicates that they must have been a group of fairly opportunistic feeders.

Conclusions

This study on chondrichthyan teeth from the late Viséan carbonate pelagic facies of northern Europe, obtained from conodont samples and not collected as macrofossils, reveals at least two slightly different types of assemblage (biofacies). The first, possibly representing the more basinal environment, is characterised by high frequencies of falcatid teeth (and especially those of *Denaea* cf. *fournieri*) and very low, only incidental occurrence of crushing teeth belonging to the Euselachii and Euchondrocephali. The best example of this type is the fauna from Todowa Grząba (Holy Cross Mountains). The second type, possibly representing areas situated closer to submarine carbonate platforms, consists of relatively fewer falcatids and more abundant euselachian crushing teeth, such as *Lissodus*; euchondrocephalan teeth and tooth-plates are rare in this type, which is best represented by the assemblage from Steeplehouse Quarry (Derbyshire).

The occurrence of non-falcatid cladodonts and the xenacanthimorph *Bransonella* differs from sample to sample with no currently discernible pattern. The anachronistids are better represented in the second assemblage type, and the presence of thrinacodonts is equally probable in both biofacies.

The pelagic chondrichthyan assemblages are completely different from those characteristic of the carbonate platforms, which are rich in various Euselachii and Euchondrocephali (compare the similar situation in the late Famennian, Ginter et al. 2010: 23–24). Judging from chondrichthyan collections obtained from Viséan crinoid calcirudite from the British Isles and the Tournaisian shallow-water limestone lens from Muhua (southern China), the platform chondrichthyan communities were much more diverse than those presented in this paper (more than 20 species at Muhua vs. about 10 at Todowa Grząba). The major part of this diversity on the platform belongs to the euselachians and euchondrocephalans (compare the similar situation in the Serpukhovian of Bear Gulch, Montana; Lund 1990: 4) which indicates that the well known Early Carboniferous radiation of the Chondrichthyes mainly concerned these two latter groups. This unequal radiation was probably one of the reasons that only Euselachii and Euchondrocephali (with few exceptions, such as Triassic xenacanthiform *Mooreodontus*; Ginter et al. 2010) persisted into the Mesozoic, and that only these two groups exist today (if Neoselachii are treated as a part of euselachian radiation). The Euselachii developed numerous forms of dentition and were able to replace stem-group chondrichthyans in their various niches. The best example of this process is the gradual replacement of various cladodonts by the hybodonts starting from the Late Carboniferous and leading up to the Permian–Triassic boundary.

The picture of Viséan pelagic chondrichthyan communities from northern Europe presented here is by no means complete. There are several as yet unstudied collections of shark microfossils in various palaeontological institutions (e.g., from Scotland, collected by MTD) which will probably contribute much new and useful information directly relevant to the present discussion. In addition, the assemblages cited here as comparative materials (such as that from Royseux) await formal publication with accompanying illustrations and all necessary relevant data for completion of a comprehensive and precise comparative analysis. Such an analysis will hopefully reveal whether or not the differences between assemblages observed by us are statistically significant and truly reflect environmental diversity.

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Appendix 1

Vertebrate microremains in the studied samples from the upper Viséan of Cawdor Quarry (Derbyshire, England, UK), Todowa Grząba (Holy Cross Mountains, Poland), and Westenfeld Quarry (Rhenish Mountains, Germany).

Taxon/Locality	Cawdor Quarry														Cawdor Quarry total	Todowa Grząba	Westenfeld Quarry
Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14		TG-D	C-12
Denaea cf. *fournieri*	1	1		1			1	1	4	1	7	1	4	1	23	33	33
Denaea wangi																7	
Denaea williamsi																5	
Denaea sp.																4	
Thrinacodus dziki sp. nov.					5						1				6	9	
Thrinacodus cf. *gracia*																	3
Bransonella nebraskensis					3										3	4	
"*Ctenacanthus*" *costellatus*																1	
Ctenacanthidae indet.																2	
Squatinactis caudispinatus					1						3				4		
Unidentified cladodont		1													1		
Cooleyella fordi					3										3		
Ginteria fungiforma								1					1		2		
Euselachii indet. 1					1										1	2	1
Euselachii indet. 2																1	
Euchondrocephali indet.	1		1		1										3	2	
Total chondrichthyan teeth	**2**	**2**	**1**	**1**	**14**	**0**	**1**	**2**	**4**	**1**	**11**	**1**	**5**	**1**	**46**	**70**	**37**
Chondrichthyan scales and/or branchial denticles	+	+	+	+	+	+					+		+	+		+	+
Acanthodii		+			+											+	+
Actinopterygii		+	+		+	+	+	+	+	+	+	+	+			+	+