Early Carboniferous chondrichthyan *Thrinacodus* from Ireland, and a reconstruction of jaw apparatus

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Specimens of the microscopic teeth of the chondrichthyan genus *Thrinacodus* are described from Mississippian (Tournaisian) rocks of Ireland. They are from calcareous mudstones or crinoidal limestones whose palaeoenvironments are interpreted as ranging from near shore, shallow water through moderately shallow high energy carbonate shelf, to relatively deep off-shore. The richest fauna was recovered from the high-energy carbonate shelf, containing both asymmetrical and symmetrical teeth raising the possibility that they may have been derived from a single species of shark. The teeth are assigned to *Thrinacodus incurvus* (Newberry and Worthen, 1866), which is suggested to be a senior synonym of *Thrinacodus ferox* Turner, 1982. Presently the genus is known only from isolated teeth. The asymmetrical and symmetrical teeth are described as two morphotypes, ferox morphotype and nanus morphotype. Within the morphotypes, morphological variation occurs, especially within the ferox morphotype, allowing a number of possible reconstructions of the dentition of *Thrinacodus incurvus* to be presented as a basis for future debate.

Key words: Fish microfossils, Chondrichthyes, *Thrinacodus*, jaw reconstructions, Carboniferous, Mississippian, Ivorian, Ireland.

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Introduction

A large proportion of acid-insoluble residues from Mississippian (Lower Carboniferous) limestones in Ireland have yielded phosphatic microfossils, but of these only conodonts have been studied until recently (Geraghty 1996 in Duncan 1999). This paper, which deals with the distinctive chondrichthyan genus *Thrinacodus* St. John and Worthen, 1875, is the first of several planned to describe Mississippian fish microfossil faunas of Ireland.

Isolated teeth of *Thrinacodus*, generally in very small numbers, have been reported from Australia, southeast Asia, Russia, western Europe, and north America, from rocks of late Devonian (Famennian) to Mississippian (Serphukovian) age (for details, see below). Fifteen specimens of *Thrinacodus* have been recovered from three horizons of Tournaisian age in Ireland (Duncan 1999). The richest fauna recovered contains two nominal species of *Thrinacodus* raising the possibility that they may have been derived from a single species of shark. This material is used as a basis to speculate on the architecture of the jaw apparatus of *Thrinacodus*.

Material: localities, stratigraphy, and palaeoenvironments

Samples from three localities (Fig. 1) have yielded specimens of *Thrinacodus*. In ascending stratigraphical order the localities are:

- Small cove section (Irish Grid Reference S 276 100), near Porter's Gate, Hook Head, County Wexford, exposing calcareous mudstone and dolomitic limestone of the Lyraun Cove Shale Member, Porter's Gate Formation, *Polygnathus inornatus* conodont Zone, early Tournaisian. (*Thrinacodus incurvus* ferox morphotype TCD.36803).
- Borehole 3246/4 196.0 m and 226.35 m, near Urlingford, County Kilkenny (Irish Grid Reference S 237 634); thin-bedded crinoidal limestone of the upper part of the Ballysteen Limestone Formation, *Polygnathus mehli* conodont Zone, late Tournaisian. (*Thrinacodus incurvus* ferox morphotype TCD.36804 and 36805).
- Disused quarry near Nobber, County Meath (Irish Grid Reference N 845 848) cut in crinoidal limestone of the Kilbride Limestone Formation, *Polygnathus mehli* conodont Zone, late Tournaisian. (*Thrinacodus incurvus* ferox morphotype TCD.36792–36801; *Thrinacodus incurvus* nanus morphotype TCD.36802 and 36808).

The Lyraun Cove Shale Member at Hook Head has been interpreted as being of shallow water, near shore origin (Sleeman 1974; Duncan 1999; Sevastopulo and Wyse Jackson 2001). It is equivalent in age to the Hastarian Stage of Belgium and the Kinderhookian of the USA (Fig. 2).

The upper part of the Ballysteen Formation has been interpreted as being of relatively deep-water origin (Sevastopulo and Wyse Jackson 2001).

The productive horizons in the borehole 3246/6 lie at a level equivalent to the lower part of the conodont *Scaliognathus anchoralis* Zone, which correlates with the late Tournaisian of Belgium and the Osagean of the USA (Fig. 2).

The Kilbride Formation was deposited in moderately shallow water on a high energy, carbonate shelf, tens of kilometres from the contemporary shoreline. The productive horizons are at a level equivalent to the upper part of the *S. anchoralis* Zone (Sevastopulo and Wyse Jackson 2001).

Methods

Limestone samples from the Ballysteen Formation in the Urlingford borehole core and the Kilbride Formation were dissolved in a buffered solution of 10% formic acid. The samples from the Lyraun Cove Shale Member were calcareous sandstones and dolomitic limestones, many of which contained shaly partings. The dolomitic material was dissolved in a buffered solution of 10% acetic acid. Fish material was picked from the residues under a stereo microscope and stored in cavity slides. A number of specimens were mounted on stubs and examined using a Leica 360 Scanning Electron Microscope.

All specimens have been reposited in the collections of the Geological Museum, Department of Geology, Trinity College, Dublin, prefixed TCD.

Systematic palaeontology

Most fish microfossils occur as disarticulated, isolated elements, such as teeth, dermal denticles, etc. Where taxa have been based on such isolated elements, there is a strong likelihood that some of them will be synonyms. Taxonomic problems of this sort arise within many groups of fossils, for instance, echinoderms, conodonts, and plants. In the case of fossil plants, separate taxonomic entities (parataxa) are legitimately applied to separate parts of plants, for example spores and foliage. However, under the International Code of Zoological Nomenclature (ICZN) (International Commission on Zoological Nomenclature 1999), parataxonomic schemes in zoology are not permitted; their proposed inclusion into the ICZN during the 1980s was specifically rejected (Eriksson et al. 2000). Thus the earliest Linnean binomen applied to any fish fossil—discrete tooth or scale, or fully articulated skeleton—is the name applied to the whole fish. Some authors (for example Tway 1979) have attempted to circumvent this problem by dispensing with the Linnean binomial system altogether, and by using a code which summarizes the morphological attributes of each individual microfossil. While this may provide a workable method for biostratigraphical analysis, it reveals nothing about the relationship of the animal from which the microfossils were derived. The problem of possible synonomy between names applied to different teeth arises in *Thrinacodus*.

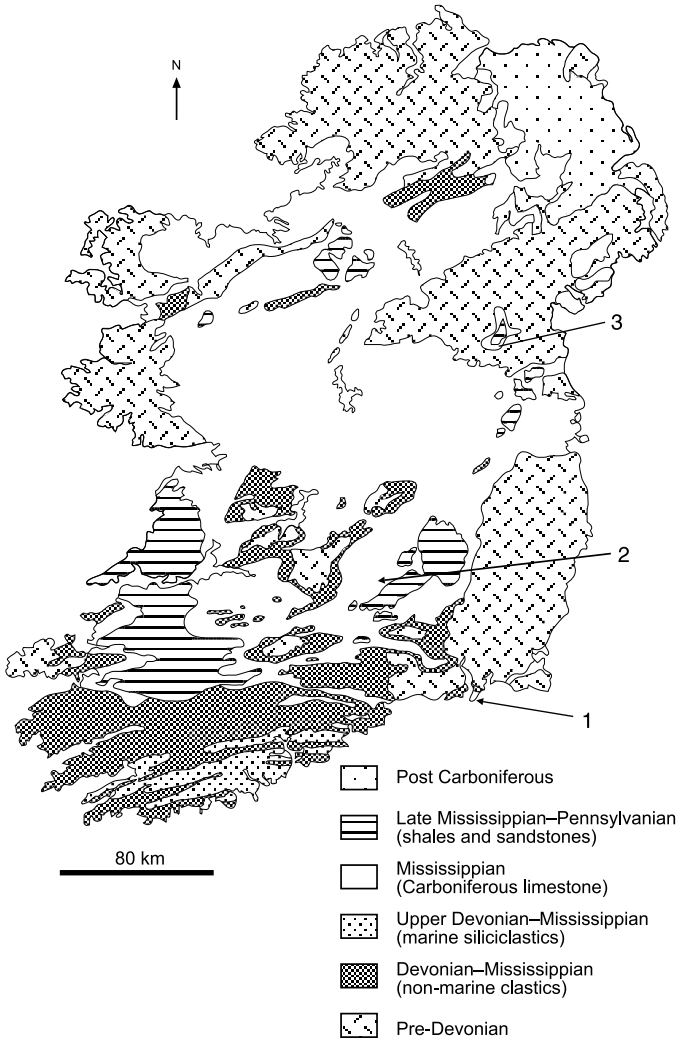

Fig. 1. Geological map of Ireland showing the locations from which *Thrinacodus incurvus* teeth were isolated. 1, Lyraun Cove Shale Member, Porter's Gate Formation, Hook Head, County Wexford. 2, Urlingford borehole, Upper Ballysteen Limestone, near Urlingford, County Kilkenny. 3, Kilbride Quarries, Kilbride Limestone Formation, near Nobber, County Meath.

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Order *incertae sedis*
Family Phoebodontidae Williams, 1985
Genus *Thrinacodus* St. John and Worthen, 1875

Type species: Diplodus incurvus Newberry and Worthen, 1866.
Thrinacodus St. John and Worthen, 1875: 289, pl. V: 1, 2.
Harpago Turner 1982: 113, figs. 2–4.
Harpagodens Turner 1983: 38.
Harpagodens Wang and Turner 1985: 226, pl. 2: 11, 12.
Harpagodens Derycke 1988: pl. 1: 1, 2.
Harpagodens Wang 1989: 105, pl. 28: 6, 7; pl. 29: 2a, b; pl. 30: 1, 2.
Thrinacodus (*Harpagodens*) Turner in Long 1990: fig. 5L, M.
Thrinacodus Ginter 1990: 76, pl. 3: 2–4.
Thrinacodus Ginter 1991: 12, pl. A: 6–8.
Thrinacodus Kietzke and Lucas 1992: 18, fig. 2D–H.
Thrinacodus (*Harpagodens*) Turner 1991: fig. 6, pl. 2G.

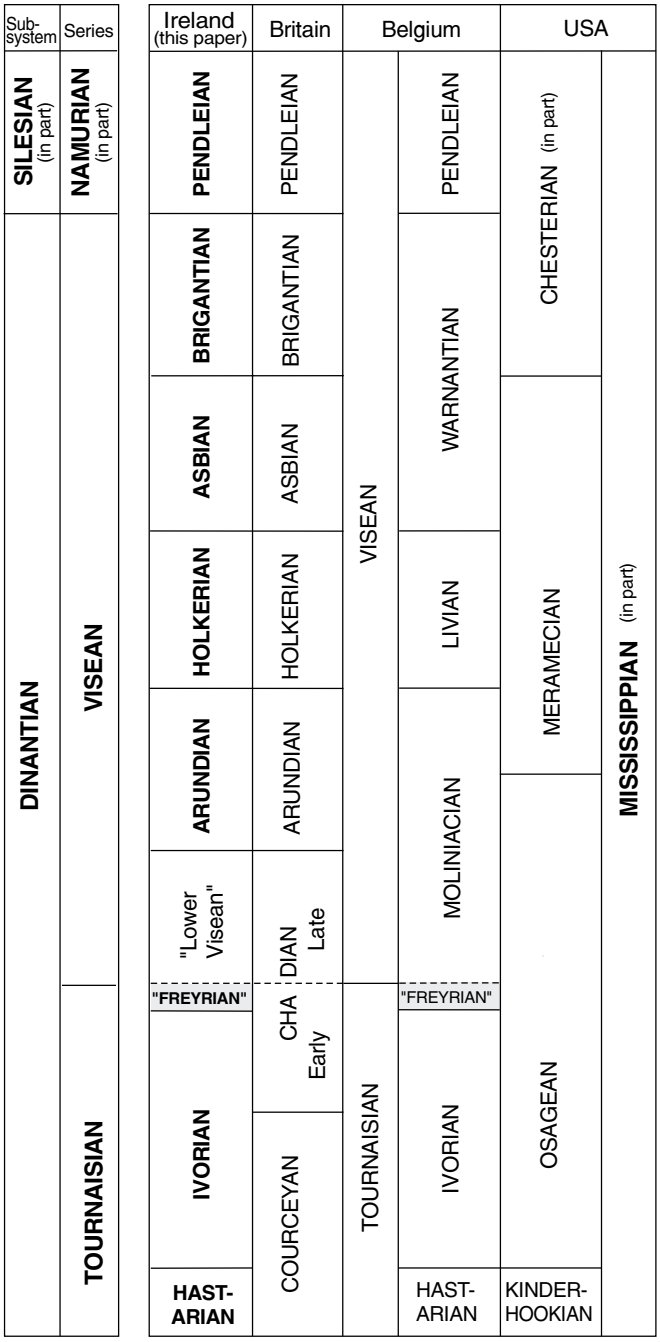

Fig. 2. Chronostratigraphic units and correlations between Ireland, Britain and the USA. Those units in bold type are those referred to in this paper (compiled from George et al. (1976), Riley (1993), Lees (1997) and Sevastopulo (1999 personal communication)).

Thrinacodus Derycke 1992: 30, pl. 1: 3.
Thrinacodus Turner 1993: fig. 8.7F.
Thrinacodus Duffin 1993: 1, pl. 1, 2.
Thrinacodus Derycke et al. 1995: 472, pls. IIIB, IVA.
Thrinacodus Ginter 1995: 27, 28, figs. 4G, 5A, B.
Thrinacodus Ivanov 1996: 418, fig. 4a–e.
Thrinacodus Ginter and Ivanov 1996: 267, figs. 1, 2a–d, 7.
Thrinacodus Ginter 1999: 34, pl. 3: 1–7.
Thrinacodus Ivanov 1999: 273, pl. 4: 2, 4.
Thrinacodus Ginter 2000: 377, fig. 2D–F.

The genus *Thrinacodus* was proposed by St. John and Worthen (1875), based on their new species *Thrinacodus nanus* from the upper fish bed of the Mississippian Kinderhook Division, Burlington, Iowa, USA. It is known only from isolated teeth. The taxonomy of *Thrinacodus* is complicated because of possible synonymies, involving at the generic level, *Diplodus*, and at the specific level *Diplodus incurvus*, *Thrinacodus nanus*, and *Thrinacodus ferox*.

St. John and Worthen (1875: 289) described the genus as follows: "Teeth of small size. Base posteriorly produced in a long, sometimes twisted, vertically flattened, or laterally compressed, clavate plate, longer than wide, anterior face narrow, and abruptly beveled from the basal line of the crown; posterior extremity more or less obtusely rounded; inferior surface narrow, plane and faintly excavated; superior surface gently convex, concave antero-posteriorly, or corresponding to the curvature of the inferior surface. From the antero-superior extremity of the base spring three more or less relatively stout, nearly equal, trenchant, acutely pointed recurved cusps, the exterior pair divergent, the central one more or less vertical, slightly sigmoidally curved, transverse section sublenticular, compressed in front, rounded behind, with simple cutting edges, and more or less strongly costate in either face.

The generic peculiarities of the teeth here referred to, as contrasted with *Diplodus*, Agassiz, with which they are most intimately allied, consists in the relative more slender base, which lacks both the antero-inferior protuberance and the postero-superior pad-like prominence characteristic of the above genus. The coronal cusps are also nearly equal in size, the cutting edges are destitute of crenulations, and their anterior and posterior faces more or less strongly ridged vertically. The form of the trident-like cusps are very like that of *Cladodus*, being slightly constricted basally in front and faintly defined from the base behind.

As here defined, the genus includes the forms originally described by Messrs. Newberry and Worthen, under the name *Diplodus incurvus* and *D. duplicatus*, of the Keokuk limestone, which seem to be indistinguishable from a form not uncommon in the upper Burlington limestone."

The species *Diplodus incurvus* Newberry and Worthen is assigned here to *Thrinacodus*. *Thrinacodus nanus* described by St. John and Worthen and Irish material described below are morphologically identical to the specimens on which Newberry and Worthen (1866) based the species *Diplodus incurvus* except that they are an order of magnitude smaller. This raises a general question in relation to microscopic fish teeth: are teeth that are morphologically identical except for their size conspecific? The tentative conclusion is that the difference in size does not rule out two teeth being conspecific. Therefore *Thrinacodus* [*Diplodus*] *incurvus* Newberry and Worthen, 1866 is regarded here as a senior synonym of *Thrinacodus nanus* St. John and Worthen, 1875, and is thus the type species of *Thrinacodus*.

Turner (1982) proposed the genus *Harpago* with the type species *Harpago ferox* Turner, 1982. The name *Harpago* was

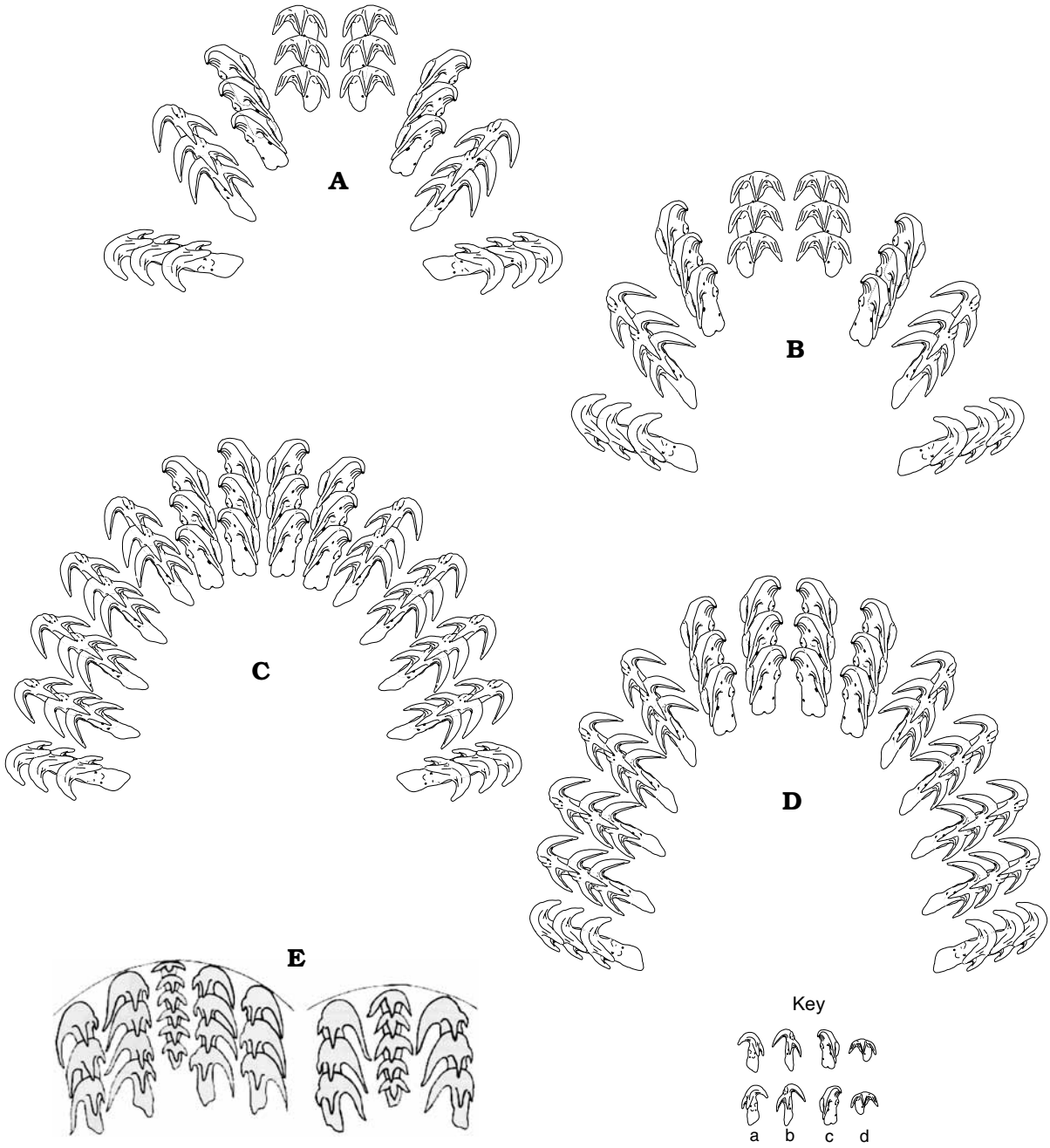

Fig. 3. Possible reconstructions of front part of a *Thrinacodus* mouth. **A**, **B**. Using *Thrinacodus incurvus* ferox and nanus morphotype teeth. **C**, **D**. Using *Thrinacodus incurvus* ferox morphotype teeth only. **E**. Reconstruction by Turner (1982) for comparison. Key: a is the robust end member, b the fine end member and c the sharply recurved tooth of *T. incurvus* ferox morphotype, d is *T. incurvus* nanus morphotype tooth.

found to be pre-occupied and was replaced by *Harpagodens* (Turner 1983).

At the specific level, the taxonomy is complicated by the question of whether symmetrical forms of *Thrinacodus* (*Thrinacodus incurvus* = *Thrinacodus nanus*) occurred in the same fish as asymmetrical forms (*Thrinacodus ferox*). While this question cannot at present be answered conclusively, the balance of the evidence suggests that in Carboniferous examples, at least, left- and right-handed asymmetrical forms and symmetrical forms did co-occur in the same fish (reconstructions by Turner 1982, refigured in Fig. 3E herein, illustrated this). Therefore the practice followed here is to recognise the asymmetrical and symmetrical forms of *Thrinacodus* in Carboniferous rocks as belonging to the same taxon, *Thrinacodus incurvus*. In order to distinguish the symmetrical and asymmetrical teeth, they are referred to here as the nanus (symmetrical) and ferox (asymmetrical) morphotypes of *Thrinacodus incurvus*.

As noted above, the type of *Thrinacodus* [*Diplodus*] *nanus* was described by St. John and Worthen as having "Teeth minute ... with coronal cusps nearly equal in size ..." and a base "... moderately produced posteriorly, or apparently sub elliptical in outline ...". However, they qualified the description suggesting that it applied to "specimens which show the crown entire" and noting "that within the collections are several imperfect teeth: ... apparently referable to the same species, which show the base considerably produced posteriorly, flattened and slightly twisted precisely in the same manner as in the allied forms occurring in the succeeding Burlington and Keokuk divisions. In case of this identity, the laterally elliptical outline of the base, as described above, is probably due to mechanical abrasion...". (St. John and Worthen 1875: 289–290).

The specimens described here as *Thrinacodus incurvus* nanus morphotype, are those with a symmetric to slightly asymmetric elliptical outline; those with more flattened and twisted base are referred to as *Thrinacodus incurvus* ferox morphotype as described below.

In a discussion on the relationships of *Phoebodus*, Ginter and Ivanov (1996) suggested that two "varieties" of Carboniferous *Thrinacodus* teeth could be distinguished: asymmetrical and symmetrical. This is consistent with both the findings of St. John and Worthen (1875) and of Turner (1982). However, St. John and Worthen implied in their description of *Thrinacodus nanus* that the "principal teeth" are the symmetrical ones with the asymmetrical teeth as the variations, whereas Turner, in her description of *Thrinacodus ferox* (*Harpago ferox*), suggested the opposite with the asymmetrical teeth as the "principal teeth", since they numerically dominated her samples. In this study the ratio of asymmetrical to symmetrical teeth is 10:2, a ratio similar to that reported by Turner (1982). A similar ratio has been observed in samples from Eastern Europe (M. Ginter personal communication 1997). In the Irish material, seven asymmetrical teeth with the principal cusp to the right when viewed from the labiolateral side with the crown to the bottom (referred to here as right handed) and three asymmetrical teeth with their principal cusp to the left (left handed) were recovered from the Kilbride Limestone Formation. A further two left-handed asymmetrical teeth were recovered from the Urlingford borehole core, and a single right-handed asymmetrical tooth was recovered from Hook Head; neither of the two latter localities yielded symmetrical or near symmetrical teeth.

It seems most probable that the left- and right-handed teeth belong to the same species, as it is unlikely that a jaw contained either all left-handed or all right-handed teeth (Turner 1982). The more likely reconstruction is that the left-handed teeth were located on one side of the jaw and the right-handed on the other (Turner 1982: fig. 5A, B). It is suggested here that the *Thrinacodus incurvus* nanus morphotype teeth were housed in the same jaw as the *T. incurvus* ferox morphotype. However, Ginter and Ivanov (1996) found that symmetrical teeth with a "... typical phoebodont-type crown seems the older one. Only this variety has been found thus far in the Late Famennian deposits of the *Palmatolepis trachytera* to *P. expansa* (?Early *Siphonodella praesulcata*) zones, in the samples constrained by conodonts (Long 1990; Ginter 1990)". They suggested that the asymmetrical teeth of *Thrinacodus* appeared for the first time in the *S. praesulcata* Zone and dominated the Early Carboniferous faunas (Wang and Turner 1985); rare occurrences of the symmetrical teeth in the Carboniferous "... may be because they were retained only in a special part of a jaw (symphyseal, as suggested by Turner 1982)." Subsequently Ginter (2000) erected a new species *Thrinacodus tranquillus* (with a current range of mid-late Famennian) characterised by an almost symmetrical crown and long slender recurved cusps with a long (labiolingually), narrow base. This species, too, appears to have two morphotypes; one with lingually flattened bases, asymmetrically situated in relation to the crown, and secondly, a morphotype represented by very small teeth, which are almost entirely symmetrical.

Taking into account the varying opinions, the most reasonable conclusion is that during the Mississippian, at least, the two *Thrinacodus* morphotypes discussed here were housed within a single jaw and thus the specific name applied to them should be the same. *Thrinacodus incurvus* has priority.

Thrinacodus teeth have been described from the late Famennian of Ostrowka, Holy Cross Mountains, Poland (tranquillus morphotype, Ginter 1990; nanus and ferox morphotypes, Ginter and Ivanov 1996); late Famennian of Tafilalet, Morocco (Derycke 1988; 1992); late Famennian of Broken River, Queensland, Australia (includes type material of *Thrinacodus ferox* (*Harpago ferox*) but the dating is not precise, ferox morphotypes dominate but nanus morphotypes also occur, Turner 1982); Late Famennian of Thuringia, Germany (ferox morphotype, Ginter 1999); ?Late Devonian of the Sacramento Mountains, south-central New Mexico, USA (ferox morphotype, Kietzke and Lucas 1992); Devonian/Carboniferous boundary of Daihua and Wangyou Formations of Changshu County, Guizhou Province, China (ferox morphotype, Wang 1993); Devonian/Carboniferous boundary at La Serre, Montagne Noire, Hérault, France (ferox morphotype, Derycke et al. 1995); early Mississippian (early Tournaisian) of Novaya Zemlya, North Island (dominated by ferox morphotype with one/two nanus morphotype, Ivanov 1999); early Mississippian (early Tournaisian) South Urals (ferox morphotype, Ivanov 1996); Mississippian (late Tournaisian to early Viséan) Bingleburra Formation, New South Wales, Australia (morphotype non specified, Turner 1982); Mississippian (Viséan) of Derbyshire, England (ferox morphotype, Duffin 1993); late Mississippian (Serpukhovian) of the Moscow Region (ferox morphotype, Ginter and Ivanov 1996).

Thrinacodus incurvus (Newberry and Worthen, 1866)

Figs. 4–6.

Diplodus incurvus Newberry and Worthen, 1866: 62, pl. IV: 4, 4a.

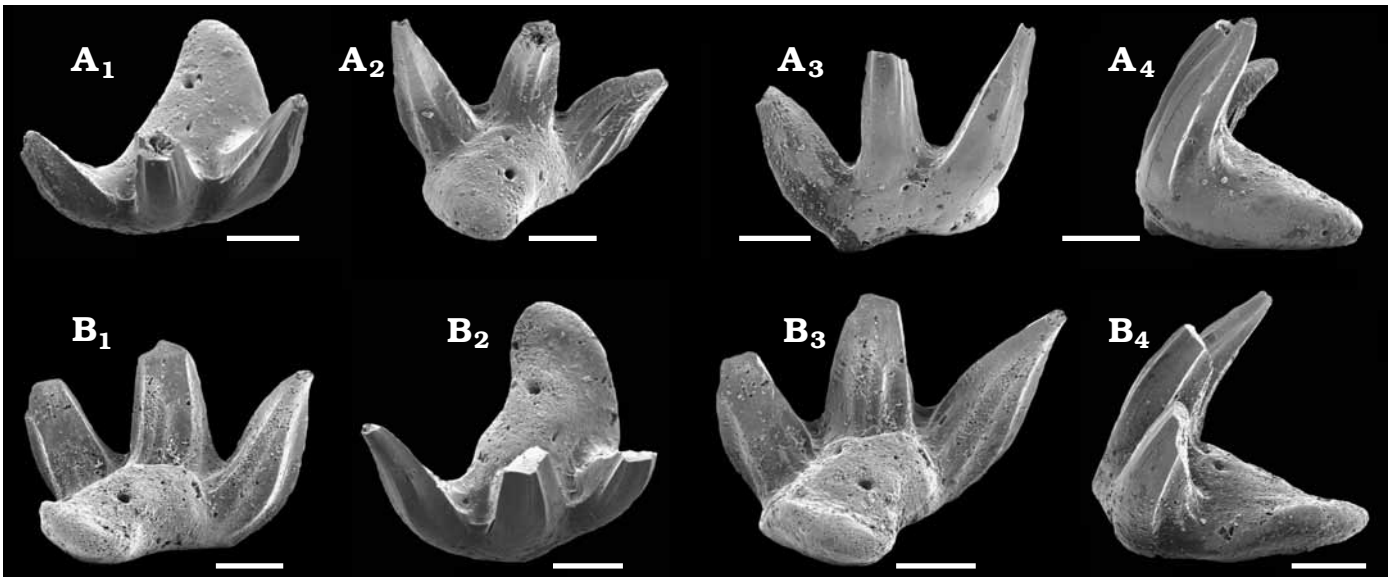

Fig. 4. *Thrinacodus incurvus* nanus morphotype. Both specimens are from the Kilbride Limestone Formation, *Polygnathus mehli* Zone, Ivorian (probably Freyrian), late Tournaisian. **A**. TCD.36802 in dorsolabial (A_1), lingual (A_2), labial (A_3), and lateral (A_4) views. **B**. TCD.36808 in lingual (B_1), dorsolabial (B_2), dorsolingual (B_3), and lateral (B_4) views. Scale bars 200 μm.

Thrinacodus nanus St. John and Worthen 1875: 289, pl. V: 1, 2.
Harpago ferox Turner 1982: 113, figs. 2–4.
Harpagodens ferox (Turner); Turner 1983: 38.
Harpagodens ferox (Turner); Wang and Turner 1985: 226, pl. 2: 11, 12.
Harpagodens ferox (Turner); Wang 1989: 105, pl. 28: 6, 7; pl. 29: 2a, b; pl. 30; 1, 2.
Thrinacodus ferox (*Harpagodens*) (Turner); Long 1990: fig. 5L, M.
Thrinacodus ferox (Turner); Kietzke and Lucas 1991: 18, fig. 2D–H.
Thrinacodus (*Harpagodens*) *ferox* (Turner); Turner 1991: fig. 6, pl. 2G.
Thrinacodus ferox (Turner); Derycke 1992: 30, pl. 1: 3.
Thrinacodus ferox (Turner); Turner 1993: fig. 8.7F.
Thrinacodus ferox (Turner); Duffin 1993: 1, pl. 1, 2.
Thrinacodus ferox (Turner); Derycke et al. 1995: 472, pls. IIIB, IVA.
Thrinacodus ferox (Turner); Ginter 1995: 28, figs. 5A, B.
Thrinacodus ferox (Turner); Ivanov 1996: 418, fig. 4a, b, d, e.
Thrinacodus ferox (Turner); Ginter and Ivanov 1996: 267, figs. 1 (in part), 2c, d.
Thrinacodus sp. Ginter 1999: 34, pl. 3: 1–3, 5–7.
Thrinacodus cf. *Thrinacodus ferox* (Turner); Ginter 1999: 377, fig. 2D–F.

Material.—Thirteen illustrated, isolated, asymmetrical, teeth (ferox morphotype), some complete (specimen numbers: TCD.36792–36801 and TCD.36803–36805). Two illustrated, isolated, incomplete, symmetrical teeth (nanus morphotype; specimen numbers: TCD.36802 and 36808). Some broken cusps (TCD.36984) which are not illustrated.

Description.—As discussed above, *T. incurvus* is considered to include both asymmetrical (ferox morphotype) and symmetrical (nanus morphotype) teeth. These are described separately below.

Ferox morphotype.—Asymmetrical teeth vary from 0.7 mm to 1.94 mm in length from the base of the principal cusp to the distal margin of the base and from 0.47 mm to 1.5 mm across the widest extent of the cusps. Only in specimen TCD.36799 are the cusps entire; most have broken tips.

Specimens TCD.36792–36801 are left-handed forms and TCD.36803–36805 are right-handed forms. They are tricuspidate with each cusp curving lingually and in some cases laterolingually. Cusps vary in length and width. The principal cusp initiates at the proximal base growing down slightly and then curving sharply right or left laterolingually; the middle cusp initiates above the level of the principal cusp growing out and then curving lingually; the left or right lateral cusp commonly initiates above the level of the middle cusp (otherwise at the same level) and curves laterolingually. In well preserved specimens, each cusp shows six to eight raised ribs from tip to base; the ribs are more pronounced and numerous on the lingual and lateral areas than on the labial. In many specimens at least one rib extends from the inside lateral edge of the outside cusp across and up the lateral edge of the middle cusp (Fig. 5A, C, E_1, G_2).

The bases are elongate, roughly rectangular and normally at least twice as long as wide, ovoid in cross section close to the cusps but flattening dorsoventrally towards the distal margins as the base twists through ca. 50°. In many cases the distal area of the base opposite the principal cusp is extended lengthways and twisted inwards over the dorsal area of the base, while the other distal margin (in line with the principal cusp) may widen but be shorter and twist away to the ventral side (Fig. $5B_2$). One or two major basal canal openings are situated laterally, typically at about mid-length (Fig. $5B_1$) and typically approximately in line with the middle cusp (Fig. $6A_2$). At the base of the middle cusp along the labioventral surface one or two smaller canal openings may occur (Fig. $6A_1$ and A_4) from which a groove to the ventral surface may outline a ventral node (Fig. $5B_3$). In some specimens there is a small canal opening on the ventral surface of the base close to the base of the principal cusp. Other minor fo-

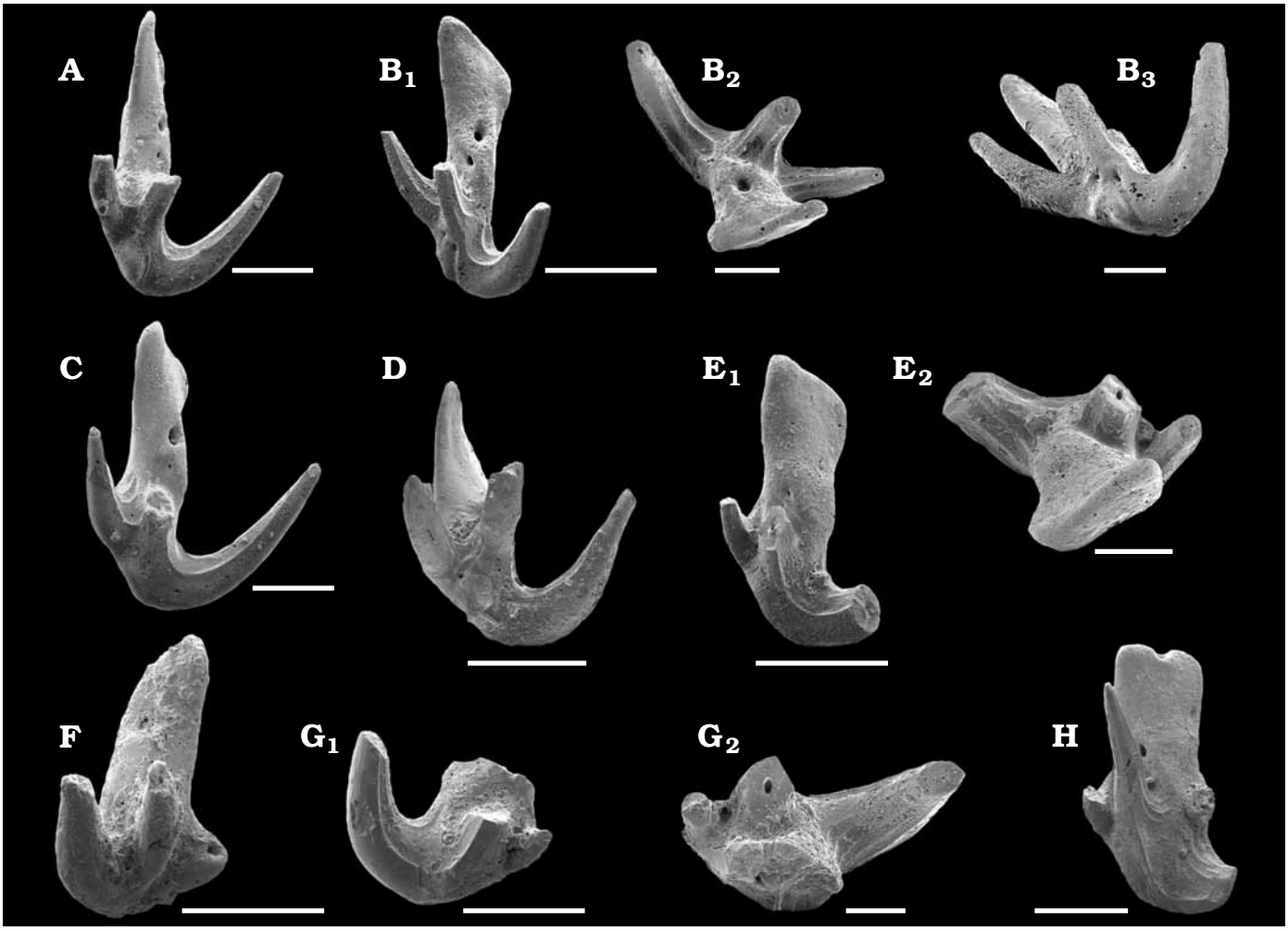

Fig. 5. *Thrinacodus incurvus* ferox morphotype Kilbride Limestone Formation, *Polygnathus mehli* conodont Zone, Ivorian (probably Freyrian), late Tournaisian. **A**. TCD.36800 in dorsal view. **B**. TCD.36794 in dorsal (B_1), lingual (B_2), and labial (B_3) views. **C**. TCD.36799 in dorsal view. **D**. TCD.36798 in dorsolabial view. **E**. TCD.36795 in dorsal (E_1) and labial (E_2) views. **F**. TCD.36796 in dorsal view. **G**. TCD.36793 in labiolateral (G_1) and labial (G_2) views. **H**. TCD.36797 in dorsal view. B_2, B_3, E_2, G_1, G_2, scale bars 200 mm; A, B_1, C, D, E_1, F, H, scale bars 500 μm.

ramina occur on the ventral, dorsal and labioventral surface of the base in some specimens.

Nanus morphotype.—The symmetrical tooth TCD.36802 (Fig. 4A) and slightly asymmetrical tooth TCD.36808 (Fig. 4B) are smaller overall in dimension (0.77mm in length from the base of the median cusp to the distal margin of the base and at least 0.9 mm across the widest extent of the cusps in TCD.36802) than the associated, ferox morphotype teeth. The three cusps are roughly equal in width, curved lingually with up to ten raised ribs from the tip of each cusp, less pronounced and numerous on their labial surfaces (Fig. $4A_2$, A_3). Cusps are slightly sigmoidal (Fig. $4B_2$), sub-circular in cross section and a central pulp cavity is present (Fig. $4A_2$).

The bony base is half as wide as long with the widest extent close to the base of the cusps. There is a slight twist of the base with a flare to one side (Fig. $4B_1$); otherwise the base tapers to the distal margin culminating in a rounded tip. A basal canal opening occurs on the dorsal surface halfway along the length in line with the median cusp (Fig. $4A_2$). Secondary foramina occur in the same area. A prominent node occurs at the junction of the ventral and labial surfaces to one side of the mid-line, in some specimens associated with a basal canal opening.

Discussion.—The asymmetrical teeth found in this study are variable but conform to the description of *Thrinacodus ferox* by Turner (1982: 118–119) and to descriptions and illustrations of other authors. The variation can be described in terms of two end members. At one extreme are finer, more delicate specimens (specimens TCD.36794, 36798, 36799, and 36800), which show a principal cusp to the right when viewed from the labiolateral side with the crown to the bottom. At the other extreme are more robust teeth with the principal cusp on the left (TCD.36796, 36801, 36804). The apparent correlation of degree of robustness with left and right handed teeth is probably a statistical artefact because Duffin (1993: pls. 1, 2) illustrated left- and right-handed robust teeth from the Mississippian (late Viséan) of Derbyshire (England) and Derycke et al. (1995: pl. III) showed an example from the

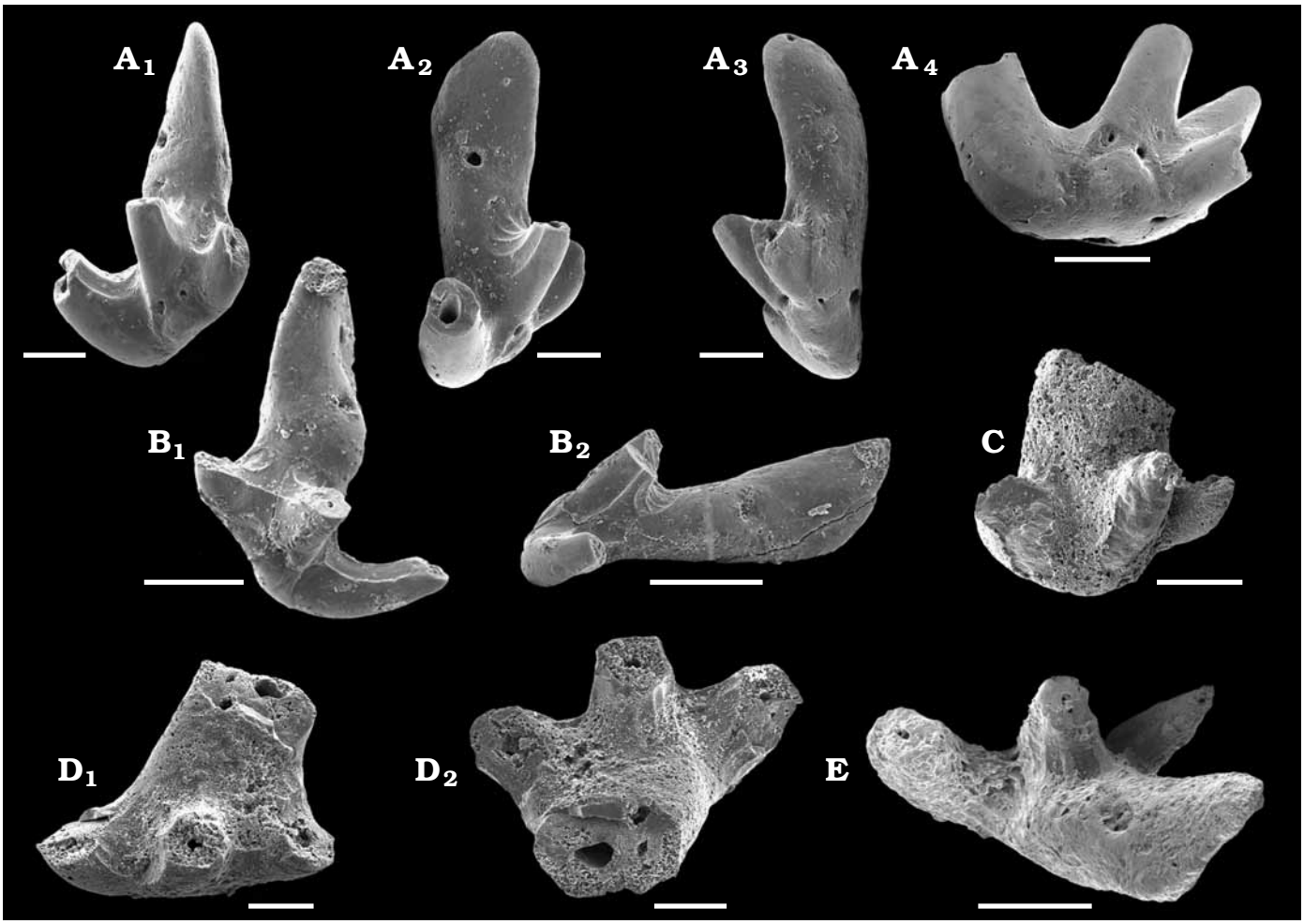

Fig. 6. *Thrinacodus incurvus* ferox morphotype. Specimens TCD.36792 and TCD.36801 are from the Kilbride Limestone Formation, *Polygnathus mehli* conodont Zone, Ivorian (probably Freyrian), late Tournaisian. Specimen TCD.36803 is from the Lyraun Cove Shale Member of the Porter's Gate formation *Polygnathus inornatus* conodont Zone, Hastarian, Tournaisian. Specimens TCD.36804 and TCD.36805 are from the Upper Ballysteen Limestone *Polygnathus mehli* conodont Zone, Ivorian (pre-Freyrian), late Tournaisian. **A**. TCD.36801 in dorso-lateral (A_1), dorso-lateral (A_2), lateral (A_3), and labial (A_4) views. **B**. TCD.36803 in dorsal (B_1) and lateral view (B_2). **C**. TCD.36804 in dorsal view. **D**. TCD.36805 in dorsal (D_1) and lingual (D_2) views. **E**. TCD.36792 in dorso-lingual view. Scale bars 200 μm.

Mississippian (early Tournaisian) with the principal cusp to the right. Turner (1982: figs. 2, 3) illustrated "delicate" teeth with the principal cusp on either side from the late Devonian of Australia.

The remaining Irish specimens of the ferox morphotype exhibit intermediate morphology. An exception is TCD.36797 (Fig. 5H) in which, although the principal cusp is broken close to its base, it is still possible to see the typical latero-lingual curvature to the right and the left lateral cusp shows latero-lingual curvature to the left. The middle cusp is straight and bends back sharply at an acute angle over the length of the base with little or no curvature. This specimen is similar in many respects to symmetrical tooth illustrated by Ginter and Ivanov (1996: fig. 2B), but specimen TCD.36797 is clearly asymmetrical.

The two specimens of the nanus morphotype described above fall within the range of variation of *Thrinacodus nanus* described by St. John and Worthen 1875. In the slightly asymmetrical specimen (TCD.36808), the main cusp is larger and the base tapers, flaring to the distal margin with a low angle twist; canal openings occur on both labial or lingual surfaces together with a foramen or several foramina on the labial surface below the enameloid of the cusps. This specimen has features in common with specimens of *Phoebodus gothicus* from the Famennian of the Holy Cross Mountains of Poland described by Ginter and Ivanov (1996) that have strongly recurved cusps and a long narrow base with a button less pronounced than in the type specimens. Ginter and Ivanov commented that these characters make these specimens of *P. gothicus* similar to the symmetrical teeth of *Thrinacodus* "so closely that they can be mistaken at first sight, particularly when the tips of the cusps are broken." However they suggested that the taxa could be distinguished because "the base of *Thrinacodus* is slightly twisted, devoid of a button, and flattened or concave at the lingual end; the cusps are not sigmoidal, as in *P. gothicus*." TCD.36808 however, shows one lateral cusp that has a tendency to be sigmoidal.

Reconstructions of the arrangement of teeth in the jaw of *Thrinacodus incurvus*

Since tricuspate, strongly recurved teeth with elongate bases are very rare in Recent sharks, there is little choice but to follow Turner (1982: 123, 124, fig. 5) in using the Recent frilled shark, *Chlamydoselachus anguineus* (Röse 1895) as a model for reconstructing the dentition of ancient phoebodont sharks. The teeth of *Chlamydoselachus anguineus* are morphologically similar to those of *Phoebodus*. Ginter and Ivanov (1992) remarked on their similarity in particular to the teeth of *Phoebodus bifurcatus* "juvenile" form. However, Ginter (personal communication 1997) now believes that a relationship of *Chlamydoselachus* and *Phoebodus*/*Thrinacodus* is less likely as a result of new information about base shapes and placement of the main nutrient foramina (Ginter and Ivanov 1996). Ginter (personal communication 1997) also believes that *Thrinacodus* is possibly a representative of highly specialised sharks that died out by the mid-Carboniferous.

However, given the lack of other actualistic analogues, the arrangement of teeth in *Chlamydoselachus* is used here as a template for reconstruction of the dentition of *Thrinacodus*. In the Recent frilled shark the teeth are arranged in rows that are separated by spaces; the forked base is inserted under the labial base of the next younger (linguad) tooth. Several of the teeth (labiad) of a row are exposed on the jaw margin and used to hold prey rather than to cut it (Röse 1895; Turner 1982).

Assuming *Thrinacodus* did have tooth rows and taking into account the arrangement of the main nutrient foramina, it seems rather difficult to avoid the conclusion that the disproportionately long and variably twisted base was inserted beneath the crown of the succeeding tooth. The *Thrinacodus* teeth, however, do not have forked bases. Hypothetical examples of the arrangement of teeth in the jaw using differing morphologies are presented here. Fig. 3A shows a central pair of *Thrinacodus incurvus* nanus morphotype teeth flanked by a pair of the strong angular, recurved end member teeth, outside of which are a pair of the delicate end member teeth and finally a pair of the more robust end member teeth—these three latter pairs are examples of *Thrinacodus incurvus* ferox morphotype described above (all with the principal cusp curved outwards, while Fig. 3B has the principal cusp inwardly curved).

Until articulated remains are found, the position, number and range of morphology of teeth within the *Thrinacodus* mouth is entirely speculative. The arguments advanced above are based on the hypothesis that a single mouth contained both symmetrical and asymmetrical left- and right-handed teeth. The Irish material supports the hypothesis that asymmetrical teeth were more numerous than symmetrical (as proposed by Turner 1982). If and when larger samples of *Thrinacodus* are available, it may be possible to estimate the ratio of asymmetrical to symmetrical teeth with more confidence.

However, for completeness, Fig. 3C, D show part of a jaw made up entirely of *Thrinacodus incurvus* ferox morphotype (excluding any of the *Thrinacodus incurvus* nanus morphotype teeth) with a double pair of the strong angular, recurved teeth, flanked by four pairs of the delicate end member teeth and, finally, a single pair of the robust end member teeth (both incurved and outwardly curved principal cusp positions are shown)—again it is not suggested that the full complement of teeth in a row or number of rows is shown.

It seems probable on the grounds of general functional morphological principles comparing *Thrinacodus* with other known shark dentitions, that symmetrical teeth occurred around the mid-line and asymmetrical teeth to the sides. There is no evidence as to whether "left-handed" asymmetrical teeth fall to the left, or to the right of the mid line.

Conclusions

Samples from three localities in Ireland ranging in age from *Polygnathus inornatus* Zone (Hastarian, Tournaisian) to *Polygnathus mehli* Zone (latest Tournaisian) have yielded specimens of *Thrinacodus incurvus*. Asymmetrical (ferox morphotype) and symmetrical (nanus morphotype) teeth are interpreted as having occurred together in the jaw of *Thrinacodus incurvus*. The morphological variation within the morphotypes, especially the ferox morphotype, has allowed a number of tentative reconstructions of the dentition of *Thrinacodus incurvus* to be presented which may be tested by further research.

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