Chondrichthyan genus *Lissodus* from the Lower Carboniferous of Ireland

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A new record of the chondrichthyan hybodontoid genus *Lissodus* is presented from two localities within the Mississippian (Tournaisian) rocks of Ireland. Five morphotypes of the genus are described within each of which occurs morphological variance. Specimens recovered and described herein are from crinoidal limestones whose palaeoenvironments are interpreted as ranging from a moderately shallow high-energy carbonate shelf, to relatively deep off-shore. The richest fauna recovered from the high-energy carbonate shelf, contains all five morphotypes raising the possibility that they may have been derived from a single species of shark. A discussion on the relationship between the five morphotypes and other Carboniferous *Lissodus* teeth is offered and it is argued that although the morphotypes differ slightly from other Carboniferous *Lissodus* teeth, they may belong to a closely related species not formally named until additional evidence is obtained. A mouth reconstruction using the teeth recovered from the Lower Carboniferous of Ireland is proposed.

Key words: Fish microfossils, Chondrichthyes, Hybodontoidae, *Lissodus*, 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). This paper, which deals with the chondrichthyan genus *Lissodus* Brough, 1935, is the second of several planned to describe Mississippian fish microfossil faunas of Ireland (Duncan 2003).

Isolated teeth of *Lissodus* from early to mid Mississippian (Tournaisian/Viséan) in small numbers, have been reported from only a few localities such as the Nearpolar and South Urals, central Russia and western Europe. There are also a number of records of isolated teeth attributed to *Lissodus* of Late Devonian age from Belgium and from the Late Carboniferous of Belgium, Germany, Spain and North America (Duffin 2001). Thirty-seven specimens of *Lissodus* have been recovered from two horizons of Tournaisian age in Ireland (Duncan 1999). The richest fauna recovered contains five morphotypes of *Lissodus* sp. 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 *Lissodus* sp.

It should be noted that the genus *Lissodus* has recently been revised (Rees and Underwood 2002) but this revision has only been applied to the Mesozoic species of the genus. Until further Carboniferous material is described, a conservative view is being maintained and the Irish specimens are currently placed in the genus *Lissodus*.

Stratigraphy and palaeoenvironments of material sampled

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

(i) 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 Biozone, late Tournaisian.

(ii) Disused quarry near Nobber, County Meath (Irish Grid Reference N 845 848) cut in crinoidal limestone of the Kilbride Limestone Formation, *Polygnathus mehli* conodont Biozone, late Tournaisian.

The upper part of the Ballysteen Formation has been interpreted as being of relatively deep-water origin (Duncan 1999; Sevastopulo and Wyse Jackson 2001). The productive horizons in the borehole 3246/6 lie at a level equivalent to the lower part of the *Scaliognathus anchoralis* conodont Biozone, 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

Scaliognathus anchoralis conodont Biozone (Duncan 1999; 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. 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. Images were captured in digital format ("TIFF" format) and assembled into plates using an image editor Photoshop® Version 5.5 (Adobe Systems Inc.).

All specimens have been reposited in the collections of the Geological Museum, Department of Geology, Trinity College, Dublin (abbreviated TCD.); holotype specimen referred to is reposited in the collections of the South African Museum, Cape Town (abbreviated SAM).

Systematic palaeontology

Most fish microfossils occur as disarticulated, isolated elements, such as teeth, dermal denticles, etc. Great morphological and histological variability of isolated exoskeletal fish microfossils exists (Karatajute-Talimaa 1998). When skeletal elements of differing morphology become disarticulated and scattered, their origin as parts of a single animal can be difficult to recognise. 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 (1999, ICZN) 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 Linnaean binomen applied to any fish fossil—discrete tooth or scale, or fully articulated skeleton—is the name applied to the whole fish.

One such is *Lissodus*, a hybodont shark, which has as its type species *Lissodus africanus* (*Hybodus africanus* Broom, 1909). This taxon is based on the only articulated material known in the genus—*Lissodus africanus* (twenty-two specimens) and *Lissodus cassangensis* (two specimens) Triassic, and *Lissodus montsechi* (one specimen) and *Lissodus* sp. (three specimens) from the Early Cretaceous (Duffin 2001). The other species that have been assigned to *Lissodus* on the basis of their overall similarity to *L. africanus*, are distinguished from it on the basis of small differences in tooth morphology (Duffin 1985, 2001; Lebedev 1996). The teeth are small with deep crowns, a labial buttress with an extension into the base in some instances, and a hybodontoid root with simple and large vascular foramina. The articulated holotype of *Lissodus africanus* shows some variation of tooth morphology—holotype *Lissodus africanus* (Broom), SAM 1082. Most other material has been assigned to the genus based on isolated teeth that are morphologically similar to the type species (Duffin 1985). Species so defined range in age from Late Devonian to Late Cretaceous (Duffin 1985, 2001; Lebedev 1996). A diagrammatic reconstruction of *Lissodus nodosus* (Seilacher 1943) by Duffin (1985) based on isolated teeth shows considerable variation in the dentition of a single mouth. Thus, without very large samples and the assumption that all teeth in a sample were derived from a single taxon, it is very difficult to recognise individual species. The other reported skeletal material of *Lissodus* are

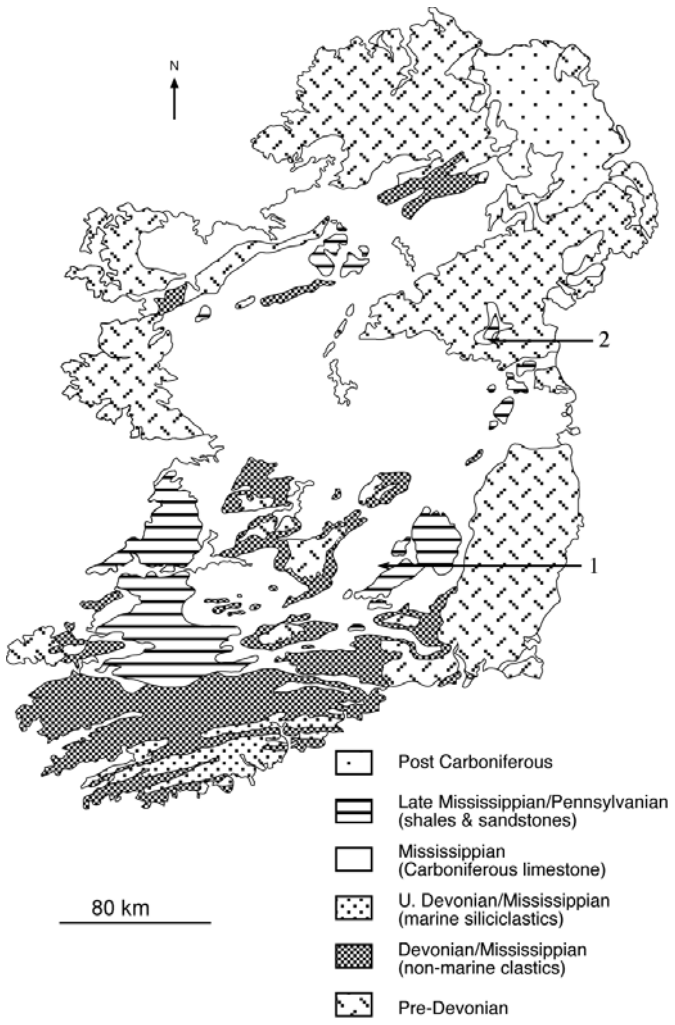

Fig. 1. Geological Map of Ireland showing the locations from which *Lissodus* teeth were isolated. 1, Urlingford borehole, Upper Ballysteen Limestone, near Urlingford, Co. Kilkenny (Morphotype 1); 2, Kilbride Quarries, Kilbride Limestone Formation, near Nobber, Co. Meath (All Morphotypes).

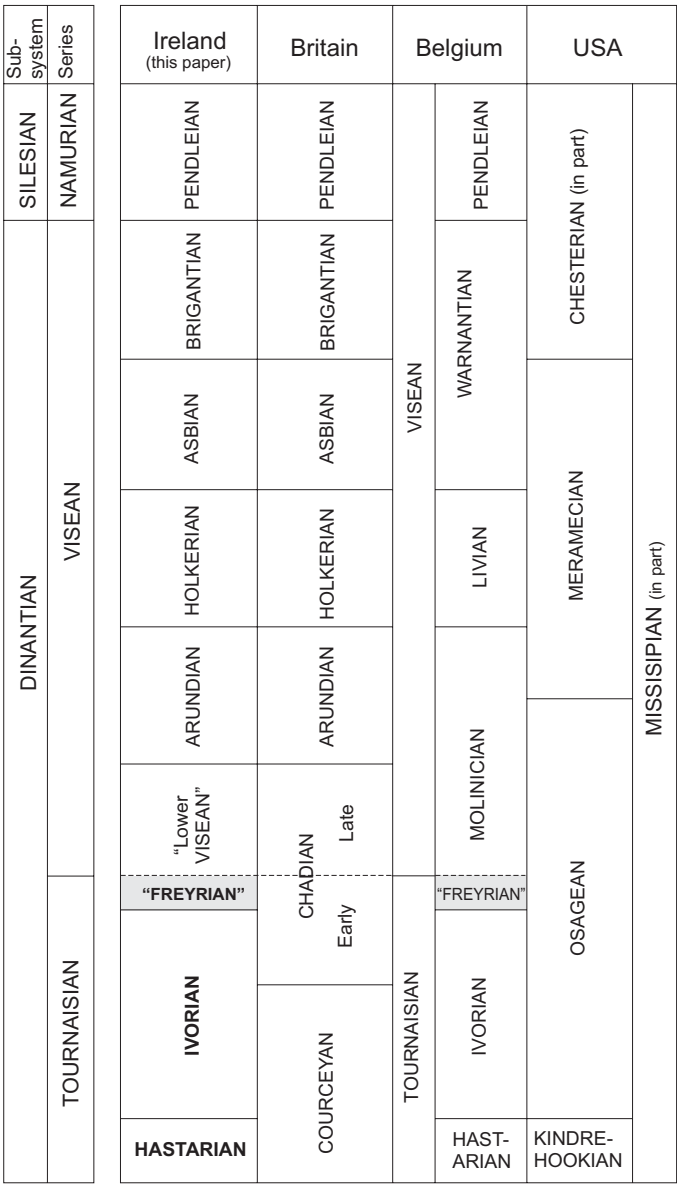

Fig. 2. Chronostratigraphic units and correlations between Ireland, Britain, Belgium, and the USA. The units in bold type are those referred to in this paper. Compiled from George et al. (1976), Riley (1993), Lees (1997) and George Sevastopulo (personal communication 1999).

fin-spines, but it is not clear to what extent fin-spine morphology can be used as a diagnostic character in hybodont sharks, and scales also attributed to *Lissodus* (Hampe1996).

Therefore, rather than referring a specimen to a known taxon or proposing a new species name, specimens are described here in terms of morphotypes, that is, *Lissodus* sp. Morphotype 1, Morphotype 2, etc. This has the advantage of creating a name (Morphotype 1, etc.) as a shorthand for a morphological description, without inviting all the subsequent problems of synonymy that are likely to arise where individual elements are given Linnean binomina. Although the most parsimonious explanation is that the different morphotypes assigned to a genus found in a single sample are derived from a single species, without the information from a complete specimen this cannot be proved or disproved.

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.

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Order Euselachii Hay, 1902
Superfamily Hybodontoidae Owen, 1846
Family Lonchidiidae Herman, 1977
Genus *Lissodus* Brough, 1935

Type species: *Hybodus africanus* Broom, 1909.

The diagnosis of the genus *Lissodus* Brough, 1935 as provided by Duffin (1985) in a revision of the genus, states that these are hybodont sharks whose teeth have small to moderately large crowns (in an extended description of the type species *Lissodus africanus* (Broom, 1909) (originally *Hybodus africanus*), Duffin (1985) gives an average length of the teeth as 1.2 mm), with a single low central cusp which is usually flanked by much lower lateral cusplets; the lateral margins of the crown are steeply inclined to meet with an incised root-crown interface. The lingually directed root is hybodontoid having large, simple vascular foramina with anaulacorhize organization, a central longitudinal pulp cavity occurring high up at the crown-root interface and a single row of small foramina at the upper labial roof face. A small to well-developed labial crown peg is present and may be supported by a labial root buttress in some species.

Duffin (1985) suggested that *Lonchidion* Estes, 1964 is a junior synonym of *Lissodus* and that all previously erected valid species of *Lonchidion* belong to *Lissodus*. Further he suggested that it is best to distinguish *Lissodus* at generic level only and if based on dental characters *Lissodus* transpires to deserve to become a genotype of a distinct family of hybodontiforms, then although *Lissodus* has priority as a genus, the family name Lonchidiidae takes priority.

The type species of *Lissodus* is *Hybodus africanus* Broom, 1909 from the Lower Triassic of the Orange Free State of South Africa. In 1935, Brough re-described the type species and assigned it to the new genus *Lissodus*. Duffin (1985) described a new species from the Carboniferous (*Lissodus wirkworthensis*) and reviewed the genus, which, as now understood, comprises at least twenty-one species ranging in age from Late Devonian to Cretaceous (Duffin 2001).

A number of specimens in this paper have been assigned to the genus *Lissodus* on the basis of the characters described above (although not all specimens exhibit all characters). The specimens have been grouped into five morphotypes, which are not given specific names for the reasons outlined above. Since all five morphotypes are derived from the same

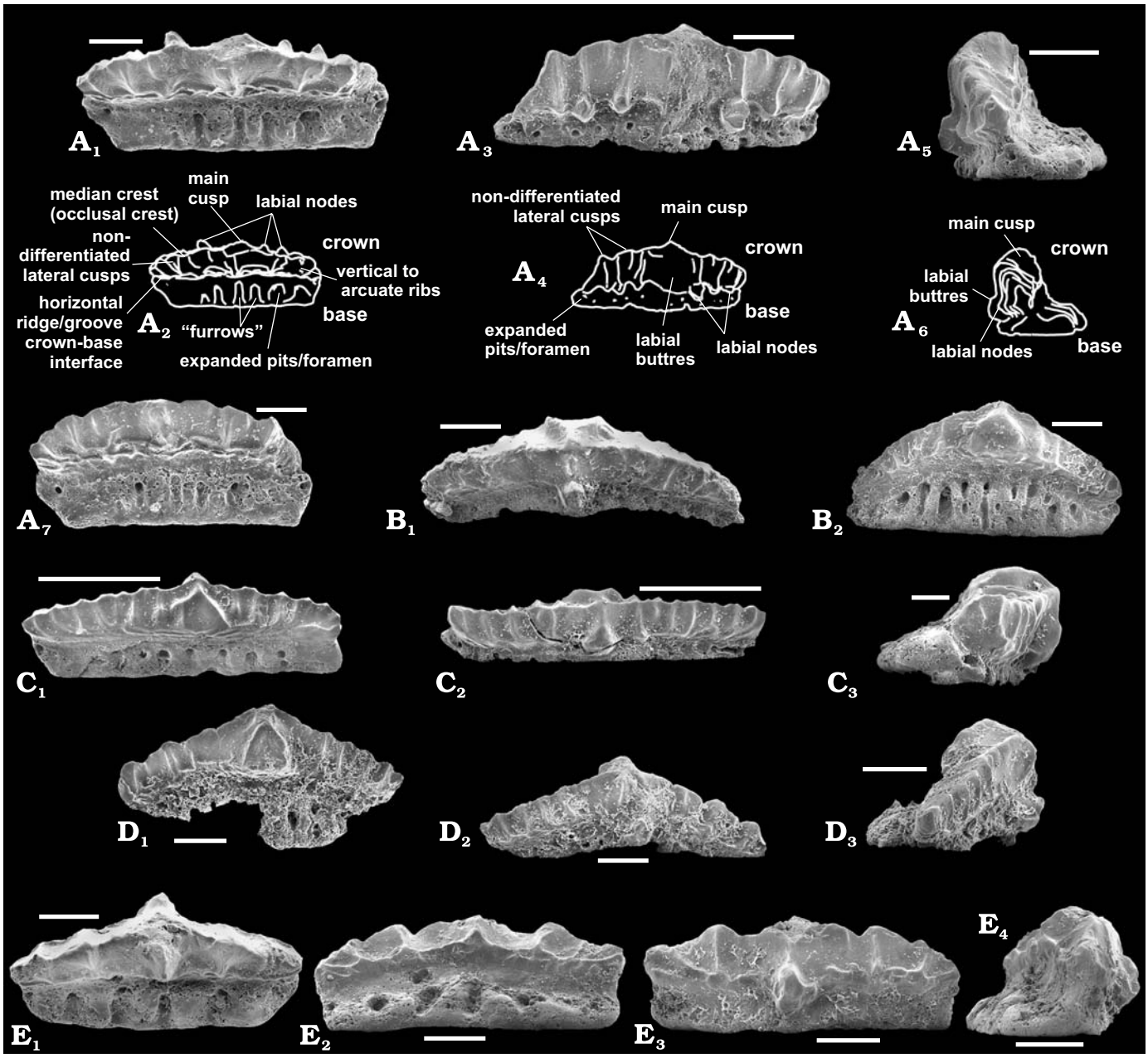

Fig. 3. *Lissodus* sp., Kilbride Limestone Formation, *Polygnathus mehli* conodont Biozone, Ivorian (probably Freyrian), late Tournaisian. Morphotype 1: **A**. TCD.36758, dorso-lingual view (A_1), explanatory drawing of the same (A_2), labial view (A_3), explanatory drawing of the same (A_4), lateral view (A_5), explanatory drawing of the same (A_6), lingual view (A_7). **B**. TCD.36754, dorsal (B_1) and lingual (B_2) views. **C**. TCD.36752, lingual (C_1), labial (C_2), and lateral (C_3) views. **D**. TCD.36753, lingual (D_1), labial (D_2), and lateral (D_3) views. **E**. TCD.36757, dorso-lingual (E_1), lingual (E_2), labial (E_3), and lateral (E_4) views. Scale bars: C_1, C2 500 μm; A_5, C_3 100 μm; A_1, A_3, A_7, D_1–D_3, E_1–E_4 200 μm.

samples (with the exception of a single specimen allocated to Morphotype 1, TCD.36764), it is probable that they are derived from a single biological species. Similarities to species proposed in the literature on the basis of a single morphotype are noted in the descriptions.

Lissodus sp. Morphotype 1

Fig. 3.

Diagnosis.—Isolated microscopic hybodontoid teeth. Linguo-labially compressed with enameloid crown; up to eleven non-differentiated cusps (average six to seven); prominent median crest extending from lateral edge to lateral edge widening over each cusp and contracting between, with a wider and higher median cusp which expands on the labial side to a prominent labial buttress and a minor lingual buttress. Ornamented labially and lingually by medially curving ridges; labial nodes may occur at the crown-base interface. Ventral base is elongate, usually concave with a horizontal ridge centrally; a basal canal usually appears beneath the labial buttress area; lingual surface is a convex crescent with up to

seven expanded pits or furrows; labial surface short with expanded pits or furrows.

Material.—Five figured isolated specimens, TCD.36752–54, TCD.35757, 58. Ten other isolated specimens, some complete, TCD.35755, 56, TCD.36759–64, TCD.36781, 82.

Description.—The length along the median crest ranges from 0.72 mm to 1.38 mm; the labio-lingual width ranges from 0.12 mm to 0.34 mm for the crown (base, 0.22 mm to 0.56 mm); the height in lingual view is 0.3 mm to 0.56 mm (crown only, 0.3 mm to 0.56 mm). The crown in some specimens is slightly asymmetric with an even number of cusps on one side of the main cusp and an uneven number on the other; the cusps are slightly fan shaped. The lingual crown has a main cusp with a vertical ridge bifurcating half way down, outlining a pyramidal base to the cusp; up to five non-differentiated cusps to either side, each with a ridge (not always along the mid line) from the apex, curving medio-lingually to the crown-base interface which is marked by a double horizontal ridge and groove. The lingual crown equals or slightly exceeds the length of the base; labially a buttress occurs as an extension of the main cusp which in some specimens extends into the base; vertical ridges descend from each of the other cusps culminating in a node, before curving medio-labially. The base is concave, more strongly so under the labial surface, with a horizontal ridge down the centre in many specimens; lingually the surface is long and rises sharply to the crown. It is indented with up to nine expanded pits or furrows and in some specimens longer medially than laterally. The labial side is short (where observed) and concave along the labio-ventral margin with a number of expanded pits or furrows.

Discussion.—The specimens grouped here as Morphotype 1 show a variation in shape: in some specimens a very strong lingual buttress occurs; in others the lingual buttress is poorly developed. Some of the specimens are more arrow shaped in lingual/labial view than others. They have been grouped together on the similarities of the crown form and ornamentation.

Age, locality, and lithology.—(i) Kilbride Limestone Formation, *Polygnathus mehli* conodont Biozone, Ivorian (probably Freyrian), late Tournaisian, Dinantian. Disused quarry, near Nobber, Co. Meath (N 845 848); crinoidal limestone. (ii) Upper Ballysteen Limestone, *Polygnathus mehli* conodont Biozone, Ivorian (pre-Freyrian), late Tournaisian, Dinantian. Bore hole 3246/4, 181.6–252.7 m, Urlingford, Co. Kilkenny; thinly bedded crinoidal limestone.

Lissodus sp. Morphotype 2

Figs. 4A, B.

Diagnosis.—Isolated microscopic hybodontoid teeth. Linguo-labially compressed teeth with enameloid crown, median crest from lateral edge to lateral edge, non-differentiated cusps, base exceeds horizontal length of crown. Labial crown buttress present. Base is long, may have a number of nodes on the lingual aspect, ventral surface is concave crescent shaped.

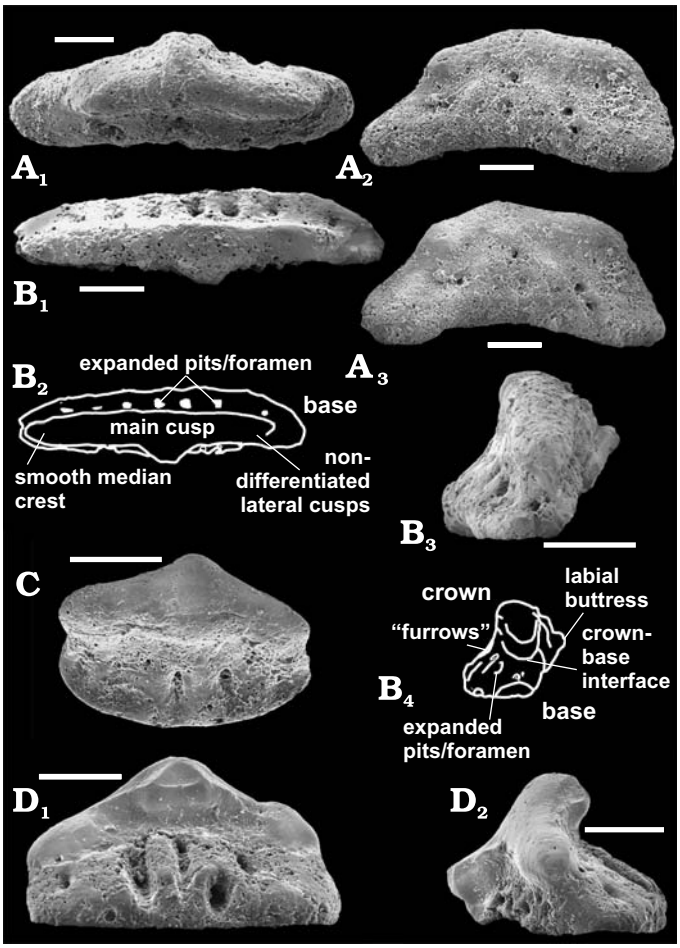

Fig. 4. *Lissodus* sp., Kilbride Limestone Formation, *Polygnathus mehli* conodont Biozone, Ivorian (probably Freyrian), late Tournaisian. Morphotype 2: **A**. TCD.36765, dorsal (A_1), lingual (A_2), and lingual (A_3) views. **B**. TCD.36766, dorsal view (B_1), explanatory drawing of the same (B_2), lateral view (B_3), explanatory drawing of the same (B_4). Morphotype 3: **C**. TCD.36768, dorso-lingual view. **D**. TCD.36767, lingual (D_1) and lateral (D_2) views. Scale bars 200 μm.

Material.—Two figured, isolated specimens, one complete, TCD.36765, 66.

Description.—The length along the median crest ranges from 1.25 mm to 1.6 mm. The labio-lingual width is 0.23 mm for the crown (base, from 0.32 mm to 0.38 mm); the height in lingual view is from 0.35 mm to 0.56 mm (crown only, 0.1 mm to 0.32 mm). The crown is slightly asymmetric sloping away from the mid point to the lateral edges. Ornamentation is sparse, though some subdued grooves appear to drop vertically from the crest outlining a median cusp. A medio-labial buttress is present. The base extends beyond the crown at both lateral margins, the lingual surface has a number of expanded pits or furrows while the linguo-ventral margin is convex; labially two hollows appear either side and below the labio-crown buttress; ven-

trally concave with smooth nodes at the lateral edges, wider on the lingual side.

Discussion.—The specimen TCD.36765 has a shorter crown length relative to its base than TCD.36766 and also has nodes on the lingual crown surface; the slope of the median crest is steeper in TCD.36765 than in TCD.36766; the lingual base of TCD.36766 has more pronounced expanded pits or furrows. These Morphotype 2 teeth can be distinguished by their smooth, broad median crest and lack of vertical ridges descending from the crest, together with a crown that is much shorter than the base.

Age, locality, and lithology.—Kilbride Limestone Formation, *Polygnathus mehli* conodont Biozone, Ivorian (probably Freyrian), late Tournaisian, Dinantian. Disused quarry, near Nobber, Co. Meath (N 845 848); crinoidal limestone.

Lissodus sp. Morphotype 3

Figs. 4C, D, 5A.

Diagnosis.—Isolated microscopic hybodontoid teeth. Enameloid crown, overall triangular shaped, asymmetric in lingual or labial view with three to five non-differentiated cusps, broad median crest from lateral edge to lateral edge. Pronounced labial buttress, which continues into upper level of the base. Base triangular, central angle at labial buttress area, concave ventrally with raised margins, expanded pits and furrows occur on lingual surface with small pits on short labial surface of the base.

Material.—Three figured, isolated specimens, TCD.36767–69.

Description.—The length along the median crest ranges from 0.67 mm to 0.77 mm (crown only, 0.6 mm to 0.74 mm); the width of the crown labio-lingually (medially) ranges from 0.2 mm to 0.38 mm (base, 0.4 mm to 0.58 mm); height in lingual view is from 0.45 mm to 0.57 mm (crown only, 0.2 mm to 0.27 mm). Enameloid crown of three to five non-differentiated cusps with a median crest extending from lateral edge to lateral edge, asymmetric. Main cusp is off centre, higher than the remaining cusps and appears to have oblique ridges descending from the apex towards the crown-base interface on the lingual surface which is marked by a double horizontal ridge and groove structure; these non-differentiated cusps may be distinguished by slightly raised apices. Labially, a strong medio-labial buttress arises at upper crown level extending down and out to incorporate the upper level of the base. The base is triangular; lingually the base drops sharply from the crown-base interface and then fans out to the linguo-ventral margin; up to nine expanded pits and furrows occur on this surface. Labially the base is short with the medio-labial crown buttress extending into the upper level of the base; five to seven expanded pits occur on this surface. Ventrally the base is triangular with the central angle at the labial buttress where the surface is deeply concave; a number of furrows incise the ventral area.

Discussion.—In specimen TCD.36767 the base exceeds the length of the crown and only three non-differentiated cusps occur, in specimen TCD.36768 crown and base are equal and three non-differentiated cusps occur; in specimen TCD.36769 the base does not exceed the length of the crown and five non-differentiated cusps occur. Despite variations these teeth have been described together as their overall strongly triangular nature appear to separate them from the other *Lissodus* Morphotypes described.

Age, locality, and lithology.—Kilbride Limestone Formation, *Polygnathus mehli* conodont Biozone, Ivorian (probably Freyrian), late Tournaisian, Dinantian. Disused quarry, near Nobber, Co. Meath (N 845 848); crinoidal limestone.

Lissodus sp. Morphotype 4

Fig. 5B, C.

Diagnosis.—Isolated microscopic hybodontoid teeth. Enameloid crown, labio-lingually compressed teeth with five to seven cusps, main cusp with a strong labial buttress extending into the base; median crest from lateral edge to lateral edge forming a diamond over each pointed cusp apex; ornamented lingually with vertical ridges which curve medio-lingually towards the crown-base interface; lateral cusps also have vertical ridges many of which culminate in strong nodes. Base is sub-triangular with the central angle at the main labial buttress; ventral surface slightly concave, more so ventro-labially; lingually slightly convex with deep furrows normal to the crest; short labial base incorporating the labial crown buttress extension.

Material.—Two figured, isolated specimens, TCD.36771, 72, three other isolated specimens, TCD.36770, TCD.36773, 74.

Description.—The length along the median crest of the crown ranges from 0.71 mm to 1.24 mm (base only, 1.03 mm to 1.13 mm); the lingual height ranges from 0.45 mm to 0.74 mm (crown only, 0.13 mm to 0.42 mm). The lingual surface of the crown appears to curve labially in most instances with the main cusp set slightly off-centre; the main cusp has a vertical ridge from the pointed apex bifurcating into two sharp ridges forming a gentle lingual buttress; the lateral cusps on the lingual surface generally have pointed crests from which strong vertical ridges descend and curve medio-lingually; the linguo-lateral edges tend to curve labially. Labially, the main cusp extends into a laterally compressed buttress which overhangs the base and extends into it, the lateral cusps tend to curve labially and are ornamented by vertical ridges which culminate in nodes at the crown-base interface. The lingual crown-base interface is marked by a horizontal ridge and groove, with only a groove visible on the labial side. The base on the lingual surface drops sharply from the crown-base interface, fans out to a platform and then drops again to the ventral margin, this surface has up to seven expanded pits and furrows; the labial surface is short, one-third the length of the lingual surface and dominated by the medio-labial extension of the labial crown buttress with four to five expanded pits on the surface. Ventrally the base is sub-triangular; the area under

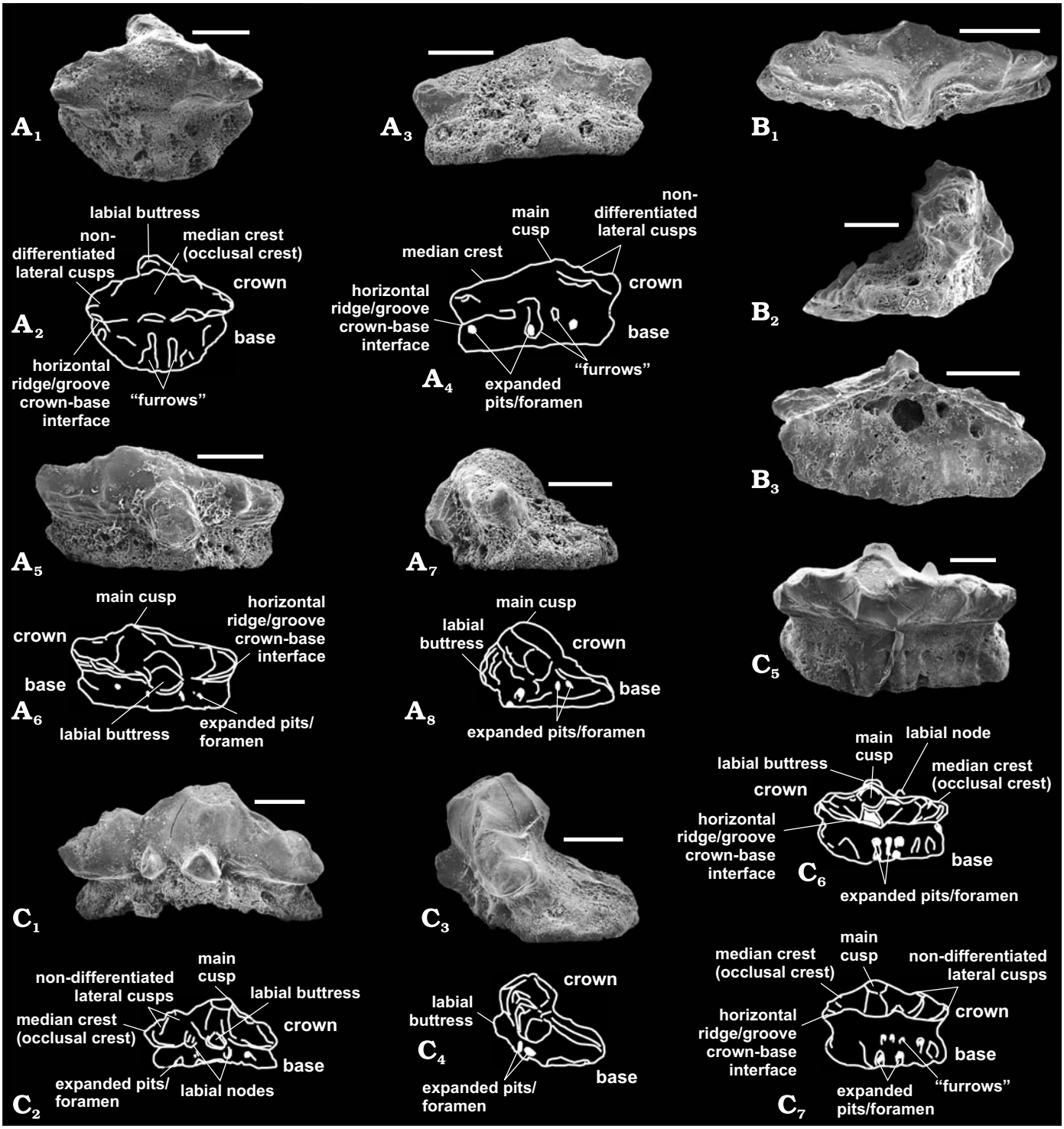

Fig. 5. *Lissodus* sp. Kilbride Limestone Formation, *Polygnathus mehli* conodont Biozone, Ivorian (probably Freyrian), late Tournaisian. Morphotype 3: **A**. TCD.36769 dorso-lingual view ($A_{1)}$), explanatory drawing of the same (A_2), lingual view (A_3), explanatory drawing of the same (A_4), labial view (A_5), explanatory drawing of the same (A_6), lateral view (A_7), explanatory drawing of the same (A8). Morphotype 4: **B**. TCD.36771, dorsal (B_1), lateral (B_2), and ventral (B_3) views. **C**. TCD.36772, labial view (C_1), explanatory drawing of the same (C_2), lateral view (C_3), explanatory drawing of the same (C_4), dorso-lingual view (C_5), explanatory drawing of the same (C_6), explanatory drawing of the lingual view (C_7). Scale bars: A_1, A_3, A_5, A_7, B_1, B_3, C_1, C5 200 μm; B_2, C_3 100 μm.

the lingual base appears as a sloping platform; there is a deep cavity under the labial buttress—these two areas appear to be separated by a horizontal ridge; pits occur on the surface.

Discussion.—Morphotype 4, although similar to Morphotype 1, is more triangular than elongate and in most instances the prominent labial buttress that initiates at the mid to lower crown level extends into the upper level of the labial base; also

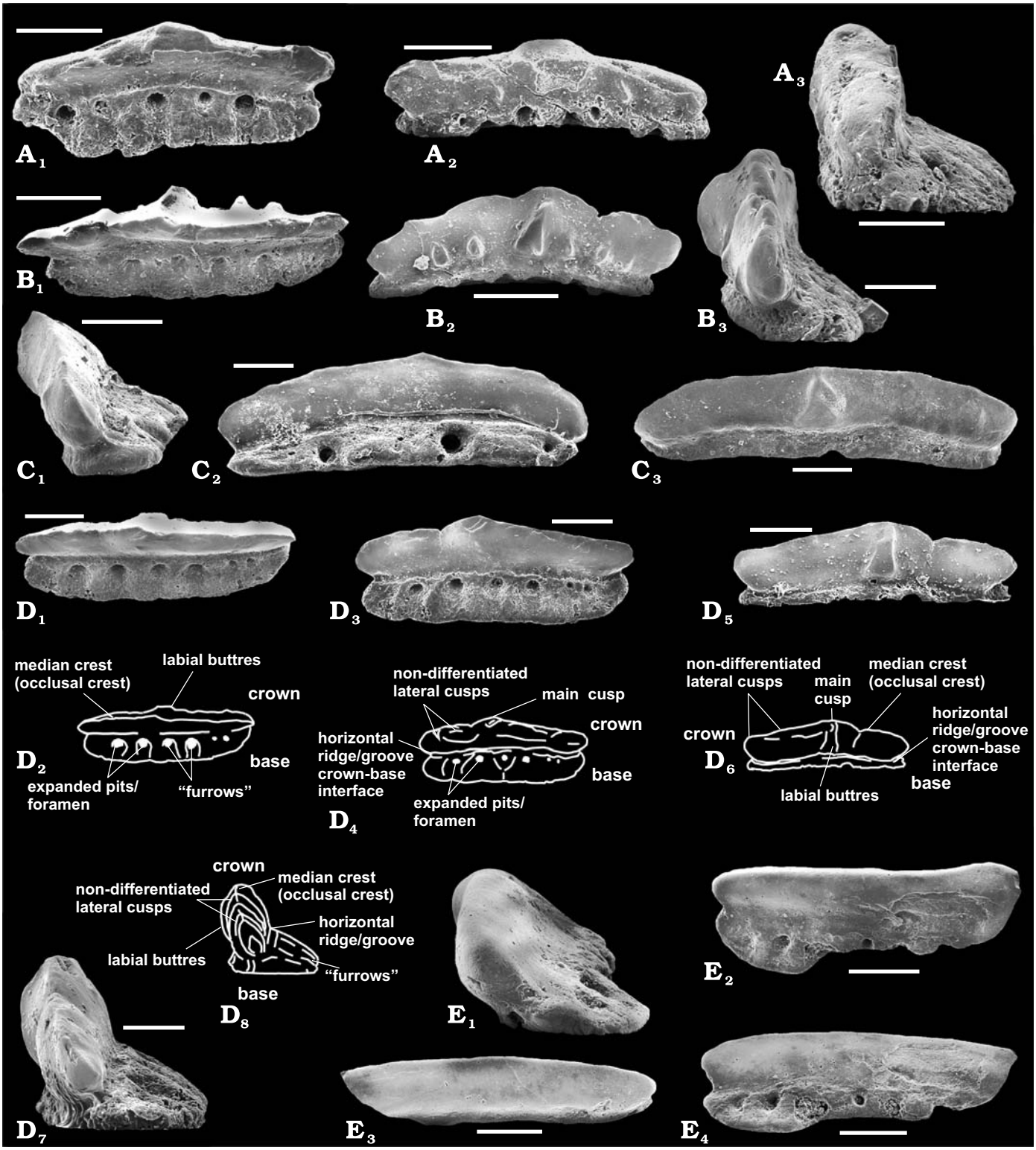

Fig. 6. *Lissodus* sp., Kilbride Limestone Formation, *Polygnathus mehli* conodont Biozone, Ivorian (probably Freyrian), late Tournaisian. Morphotype 5: **A**. TCD.36775, lingual (A_1), labial (A_2), and lateral (A_3) views. **B**. TCD.36776, dorsal (B_1), labial (B_2), and lateral (B_3) views. **C**. TCD.36784, lateral (C_1), lingual (C_2), labial (C_3) views. **D**. TCD.36778, dorsal view (D_1), explanatory drawing for the same (D_2), lingual view (D_3), explanatory drawing for the same (D4), labial view (D5), explanatory drawing for the same (D6), lateral view (D7), explanatory drawing for the same (D8). **E**. TCD.36783, lateral (E_1), dorso-lingual (E_2), labial (E_3), and lingual (E_4) views. Scale bars A_1, A_2, B_1, B_2, C_1–C_3, D_1, D_3, D_5, E_2–E_4 200 μm; A_3, B_3, D_7, E_1 100 μm.

a number of minor buttress or large nodes occur along the labial surface.

Age, locality, and lithology.—Kilbride Limestone Formation, *Polygnathus mehli* conodont Biozone, Ivorian (proba-

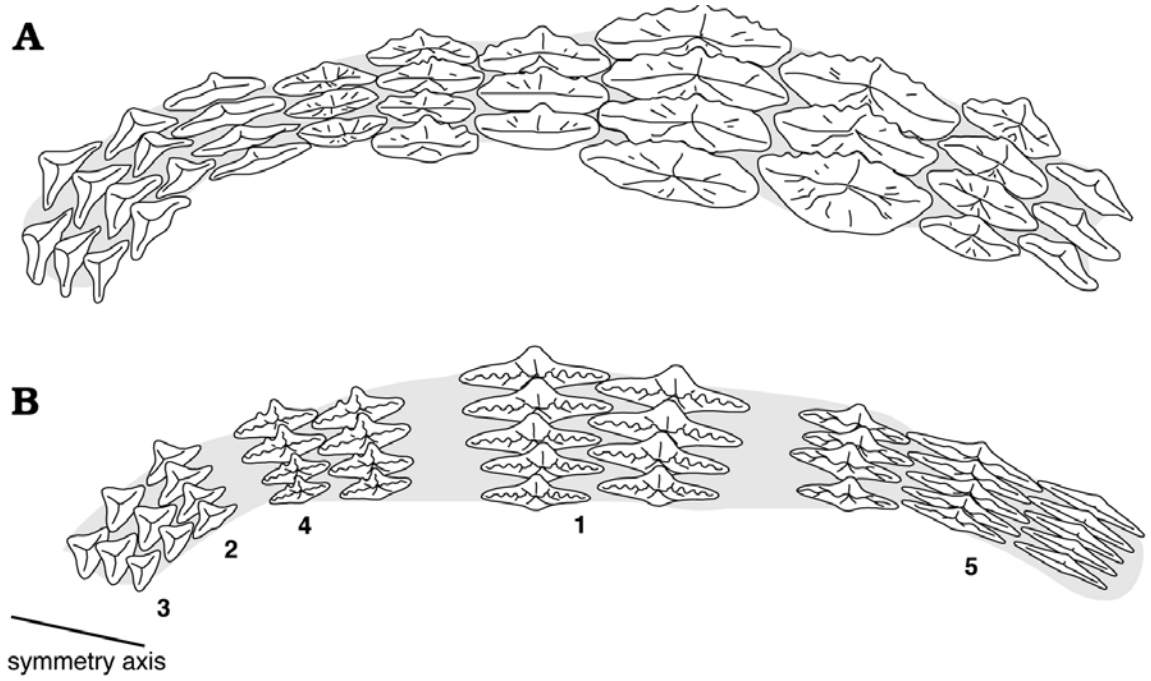

Fig. 7. **A**. Reconstruction of the dentition of *Lissodus nodosus* (Seilacher 1943) (after Duffin 1985). **B**. *Lissodus* sp. Morphotypes 1–5 interpreted as constituents of a single dentition jaw.

bly Freyrian), late Tournaisian, Dinantian. Disused quarry, near Nobber, Co. Meath (N 845 848); crinoidal limestone.

Lissodus sp. Morphotype 5

Fig. 6.

Diagnosis.—Isolated microscopic hybodontoid teeth. Enameloid crown; labio-lingually compressed with four to eight non-differentiated cusps, asymmetric, blade like. Narrow median crest extends from lateral edge to lateral edge lying more to the dorso-lingual; main cusp off centre, higher than the lateral cusps with a subdued vertical ridge descending from the apex lingually, labially ridge bifurcates before the crown-base interface (may bifurcate a second time) delineating a labial buttress; lateral non-differentiated cusps are outlined in most instances by shallow grooves on both aspects, though some evidence of ridging may also occur. Base outline elongate, ventrally slightly concave with furrows radiating towards the centre; lingually base is long and sloping with at least seven deep furrows and foramina, labially short, punctuated by foramen.

Material.—Five figured, isolated specimens, TCD.36775, 76, TCD.36778, TCD.36783, 84. Seven other isolated specimens (some incomplete), TCD.36777, TCD.36779, 80, TCD.36785–88.

Description.—The length along the median crest ranges from 0.7 mm to 1.33 mm (in most cases the length of the base is very slightly less than or equal to that of the crown); labio-lingually the width of the crown ranges from 0.12 mm to 0.24 mm (base, 0.22 mm to 0.39 mm); the lingual height ranges from 0.24 mm to 0.46 mm (crown, 0.1 mm to 0.32 mm). The median crest is very narrow along the narrow blade-like crown. Cusps on both aspects are differentiated only by shallow oblique grooves from this crest towards the crown-base interface. Hence in lateral view the crown is lenticular in outline. Very subdued ridging occurs in some specimens. Lingually the crown-base interface is arcuate. The main cusp is higher than the lateral cusps and forms a labial buttress (lateral compressed) outlined in most instances by a vertical descending ridge that bifurcates at least once; subdued ridges may occur on the remaining labial cusps in some specimens. The lingual base is long, sloping and slightly convex; embayments may be seen at both lateral edges, though the crown is usually less than or equal to the length of the base. Up to seven deep furrows ending in foramina incise the lingual base from the linguo-ventral margin towards the arcuate crown-base interface. Labially, the base is one-third to one-quarter the length of the lingual surface, with a slightly convex labio-ventral margin, a few expanded pits occur; the ventral surface is concave especially along the labio-ventral margin from which a number of short furrows run in toward the central area while the linguo-ventral area is flatter.

Discussion.—Morphotypes 1 and 5 are similar in the blade-like nature of their crowns, the presence in some specimens of small labial nodes at the crown-base interface and common occurrence of a minor lingual buttress. However, Morphotype 5 tends to be smooth crowned, i.e. without vertical ridges, which contrasts with the strongly ridged Morphotype 1.

Age, locality, and lithology.—Kilbride Limestone Formation, *Polygnathus mehli* conodont Biozone, Ivorian (proba-

Table 1. Comparison of the different Carboniferous *Lissodus* teeth.

Type	Tooth length [mm]	Overall shape	Median crest	Crown ridges	Cusps	Labial buttress	Lingual buttress	Base	Base characters
***Lissodus* sp. Morphotype 1**	0.7–1.38	elongate slight asymmetry	narrow sharp	vertical lingual and labial	average 6–7 to 11 (non-differentiated) labial nodes at crown/base interface	prominent may run into base	minor	elongate lenticular	lingual long labial short ventro-labial concave
***Lissodus* sp. Morphotype 2**	1.25–1.6	elongate slight asymmetry	broad smooth	none	non-differentiated	present	none	elongate (lenticular) has lingual nodes	lingual long labial short ventral concave
***Lissodus* sp. Morphotype 3**	0.6–0.77	triangular asymmetric	broad	oblique/ vertical lingually	average 3–5 (non-differentiated)	pronounced runs into base	none	triangular	lingual long labial short—buttress extension ventral deeply concave
***Lissodus* sp. Morphotype 4**	0.7–1.24	elongate slight asymmetry	narrow	vertical lingual and labial	average 5–7 (non-differentiated) labial nodes at crown base interface	pronounced runs into base	minor	sub-triangular	lingual long labial short—buttress extension deep cavity under buttress
***Lissodus* sp. Morphotype 5**	0.7–1.33	elongate asymmetric	narrow sharp	very slight if present both lingual and labial	average 4–8 where distinguishable labial nodes at crown/base interface	present	residual	elongate (lenticular)	lingual long labial short ventral-concave especially under buttress
Lissodus wirksworthensis	1–2	elongate symmetric	moderate	vertical labial	up to 12 accessory lingually	moderate to well developed runs into base	none	elongate	lingual long labial short—buttress extension very slightly concave
Lissodus pectinatus	2–4	elongate	moderate	vertical labial	lingual nodes at crown/base interface	pronounced	none	elongate	lingual long labial short ventral smooth-concave

bly Freyrian), late Tournaisian, Dinantian. Disused quarry, near Nobber, Co. Meath (N 845 848); crinoidal limestone.

Discussion of *Lissodus* sp. Morphotypes 1–5 and other Lower Carboniferous *Lissodus* teeth

Important characteristics of the five tooth morphotypes isolated during this study and equivalent characteristics from two previously described Lower Carboniferous *Lissodus* species (*L. wirkworthensis* and *L. pectinatus*) are shown in Table 1. Ivanov (1996, 1999) also mentioned a number of *Lissodus* sp. from the South Urals and Nearpolar Urals (respectively) of Viséan age, which he states resembles some varieties of *Lissodus wirksworthensis* Duffin, 1985 but as they were not described in detail they have been omitted from this comparison. Duffin (1985: 146, table 1) also delineated characteristics of tooth types but indicated only one Carboniferous *Lissodus* species (although another species is cited in his text). Subsequently Duffin (2001) in a synopsis of the genus, states that thirty-eight species are currently recognised with a further twenty-six recorded and described at species level. However, it is not suggested here that the five morphotypes are different species since it is possible that they could have been housed within a single jaw. Duffin (1985: 122, fig. 12) reconstructed a hypothetical dentition of the Triassic *Lissodus nodosus* (Seilacher, 1943) showing the possible variation of teeth within a jaw (Fig. 7A). The more elongate and perhaps larger teeth with bifurcating ridges from the median ridge were placed in lateral tooth rows and the more triangular-based, less-ornamented and strongly labially buttressed teeth in the mesial position. Duffin suggested that ...“variations in the tooth form must be of functional significance.”... He envisaged the labial buttress (“peg” of Duffin) of the mesial teeth held adjacent tooth files “in functional and rigid juxtaposition” while having a re-

duced root; the lateral teeth having a less important labial buttress relying on an increase in the robustness of the base ("root" of Duffin) to "accommodate higher occlusal loads, in conjunction with a system of nodes which may have anchored successive teeth by overlapping the extremely convex lingual root face of the preceding tooth".

Although *Lissodus nodosus* is from the Middle to Upper Triassic, the tooth variation found in the Carboniferous *Lissodus* sp. morphotypes 1–5 in this study follows a similar pattern. This suggests that Carboniferous *Lissodus* also bore teeth of differing morphology within a single jaw. The simplest explanation of the material from the Kilbride locality is that *Lissodus* morphotypes 1–5 belonged to a single species (Fig. 7B).

Because all of the teeth are different in some respects to those of *Lissodus wirksworthensis* Duffin, 1985 most of which have symmetrical crowns with accessory cusps on the crest of the labial buttress, and to those referred to *Lissodus pectinatus* by Lebedev (1996) which have strong lingual nodes, they might belong to a closely related species, which will not be formally named until there is additional evidence that they are indeed derived from a single species.

Some other Carboniferous species have been recorded but from the Upper Carboniferous. These include *Lissodus lacustris* Gebhardt, 1988 from the upper Pennsylvanian (Stephanian C, Late Carboniferous) of Germany; *Lissodus* cf. *zideki* described by Soler-Gijon 1993 upper Pennsylvanian (Stephanian B/C, Late Carboniferous) of Spain and *Lissodus lopezae* Soler-Gijon, 1997 also from Spain (Stephanian C). Within these, the trend of reduction of the labial peg and buttress posteriorly through the dentition, the reduction of the height of the central cusp and increase in labio-lateral compression of the teeth posteriorly appear consistent with that found in the Irish Lower Carboniferous teeth though actual comparisons are difficult due to the age difference between the Irish material and the Upper Carboniferous material.

Conclusions

The *Lissodus* sp. morphotype teeth described in this paper, with the exception of a single Morphotype 1 tooth, were recovered from the Ivorian Kilbride Limestone Formation within the *Polygnathus mehli* Biozone of the Mississippian (Tournaisian) of Ireland. As the type species *Lissodus africanus* (Broom, 1909) is based on one of the few articulated specimens known in the genus and most other species have been assigned to *Lissodus* on the basis of their overall similarity to the type with small differences in their tooth morphology distinguishing the various species, the isolated teeth recovered during this study have been treated as originating from a single (un-named) species and therefore have been used for the purpose of creating the jaw reconstruction described.

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