THE STATUS OF THE SHARK GENUS LISSODUS BROUGH, 1935, AND THE POSITION OF NOMINAL LISSODUS SPECIES WITHIN THE HYBODONTOIDEA (SELACHII)

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ABSTRACT—The hybodont form genus Lissodus is taken under revision and found to comprise a number of lineages. Twelve species, stratigraphically extended from the Scythian, Lower Triassic to the Albian, Lower Cretaceous, are retained in Lissodus s.s. Thirteen other species can be included in Lonchidion, here considered as a justified genus, ranging from the Ladinian in the Middle Triassic to the Maastrichtian in the Upper Cretaceous. Of the species previously included in Lissodus, two new genera, Vectiselachos gen. nov. and Parvodus gen. nov. are described. Vectiselachos is at present a monotypic genus including a single species from the Lower Cretaceous of southern England. Parvodus comprises four species and is known from the Bathonian, Middle Jurassic to the Valanginian, Lower Cretaceous. Another species is placed in Steinbachodus, expanding the stratigraphical range of the genus from the Rhaetian in the Upper Triassic to the Cenomanian in the Upper Cretaceous. Palaeozoic small-toothed hybodonts are extremely poorly known and alleged Lissodus species fall into two genera, but these are at present kept in open nomenclature. The family Lonchidiidae is considered justified and includes the genera Lissodus, Lonchidion, Vectiselachos, Hylaeobatis and Parvodus.

INTRODUCTION

Isolated remains, primarily teeth, of hybodont sharks occur frequently in sediments of Late Palaeozoic and Mesozoic age. Relatively few species of these sharks are known from well-preserved skeletal remains, resulting in much of the systematics of the hybodont sharks being based on isolated teeth. Proposed classification schemes of the Hybodontoidea have been confused and inconsistent due to the differing degrees of significance that have been placed on tooth morphology, tooth histology and skeletal anatomy by different scientists. It is therefore evident that the superfamily Hybodontoidea is in need of revision. In this study, we focus on the nominal genus Lissodus Brough, 1935 and discuss the taxonomic positions of the various species that have been referred to it. We also comment on the status of the two genera Polyacrodus Jaekel, 1889 and Hybodus Agassiz, 1837.

The genus Lissodus was erected by Brough (1935) on two almost complete and several partial skeletons originally named Hybodus africanus by Broom (1909). Although the teeth of this species often are obscured by the skull or by sediment, one specimen kept at the Geological Museum in Oslo (G343, see Brough, 1935) and two specimens housed in the Natural History Museum, London (P. 17531 and P. 16039), clearly show the general morphology and pattern of heterodonty. Other than this species and Lissodus cassangensis (Teixeira, 1956), skeletal remains of Lissodus are unknown.

A second small-toothed hybodont genus, Lonchidion, was erected by Estes (1964) based on isolated teeth and associated fin spines and cephalic spines of L. selachos Estes, 1964, from the Upper Cretaceous Lance Formation in Wyoming, USA. The heterodonty pattern of L. selachos was not fully understood by Estes (1964), who included orectolobid teeth (see Herman, 1977) as symphyseals. Lonchidion was widely accepted as a justified genus and several new species were described between 1964 and 1985 (Patterson, 1966; Thurmond, 1971; Cappetta and Case, 1975; Murry, 1981; Estes and Sanchíz, 1982). No skeletal remains are known of Lonchidion except for a few incomplete skeletons from the Lower Cretaceous of Spain, described as ”Lissodus palustris” Gomez-Pallerola, 1992 and possibly belonging to Lonchidion. It has not been possible to study these remains during the work with this paper.

Lissodus remained a monotypic genus until Duffin (1985) revised it and synonymised Lonchidion with Lissodus, a view that has since become generally accepted, although Antunes et al. (1990) did suggest that both genera may be justified. The synonymy of Duffin (1985: 117) was based on several characters of general tooth morphology, in particular the presence of a labial protuberance. This character is most likely obtained for functional reasons, to interlock teeth from adjacent tooth files, and is consequently a poor systematic feature. The synonymy resulted in Lissodus containing numerous species of rather diverse morphology. We follow Antunes et al. (1990: 19) in considering that Lissodus and Lonchidion represent justified but closely related genera. We also believe that Lissodus sensu Duffin, 1985 contains species that should be placed within several other genera. The revised record of Lissodus will comprise twelve species extended stratigraphically from the Scythian, Early Triassic to the Albian, Early Cretaceous. Lonchidion comprises thirteen named and several unnamed species ranging from the Ladinian, Middle Triassic to the Maastrichtian, Late Cretaceous. Other species previously included in Lissodus have been placed within Steinbachodus Reif, 1980, Vectiselachos gen. nov., Parvodus gen. nov., or kept in open nomenclature.

SYSTEMATIC PALAEONTOLOGY

Descriptive terminology is based on Cappetta (1987). Photographed teeth (Fig. 3) are deposited in the type collection of the Division of Historical Geology and Palaeontology at Lund University, Sweden and prefixed LO (Lund Original).

Superfamily HYBODONTOIDEA Owen, 1846
Family LONCHIDIIDAE Herman, 1977

Emended diagnosis— Teeth small, mesiodistally wider than high with moderately low to poorly defined cusps; well-developed labial protuberance present on all teeth of largely homodont taxa or on anterior teeth of more heterodont taxa; root low displaying numerous foramina, some differentiated to form line of small pores on upper part of root; teeth lacking pulp cavity.

Included genera—Lissodus Brough, 1935; Lonchidion Estes, 1964; Vectiselachos gen. nov.; Hylaeobatis Woodward, 1916; Parvodus gen. nov.

LISSODUS Brough, 1935 sensu stricto
(Figs 1, 3A-F)

Type species—Hybodus africanus Broom, 1909 from the Scythian, Early Triassic of Bekker's Kraal, South Africa.

Emended diagnosis— Jaws deep, lower jaw tapers anteriorly; anterior teeth with moderately to well developed central cusp, occlusal crest and labial protuberance; occlusal face of labial protuberance slopes gently towards crown base; crown shape almost triangular in occlusal view; lateral teeth lower, larger, more mesio-distally expanded; cusps, occlusal crest, labial protuberance poorly developed; root lingually inclined, lower than crown, not as voluminous; single, strictly horizontal row of small circular foramina near crown-root junction; basal plate of cephalic spines 'T-shaped' with terminally expanded lobes.

Included species—Lissodus angulatus (Stensiö, 1921) from the Scythian of Spitsbergen; L. africanus (Broom, 1909) from the Scythian of South Africa; L. cassangensis (Teixeira, 1956) from the Scythian of Angola; L. cristatus Delsate & Duffin, 1999 from the Anisian of Luxembourg; L. hasleensis Rees, 1998 from the Pliensbachian of Denmark; L. leiodus (Woodward, 1887) from the Bathonian of England; L. leiopleurus (Woodward, 1889) from the Bathonian of England and Scotland; L. lepagei Duffin, 1993 from the Norian of Luxembourg; L. levis (Woodward, 1887) from the Albian of England; L. minimus (Agassiz, 1839) from the Rhaetian of England, Germany and Belgium; L. nodosus (Seilacher, 1943) from the Middle and Late Triassic of Germany; L. wardi Duffin, 1985 from the Bathonian of England. Additionally, a poorly figured tooth from the Kimmeridgian of northern France (Candoni, 1995) appears to be an anterolateral tooth of Lissodus.

Comparisons—The teeth of Lissodus are on general morphology readily separable from those of Lonchidion and Parvodus because of low and wide teeth as opposed to higher, more gracile teeth in the two latter genera. Within the Lonchidiidae, teeth of Lissodus more closely resemble those of Hylaeobatis and Vectiselachos. However, the presence of a well demarcated cusp and lateral cusplets in Lissodus separates teeth of this genus from the other two. The crown ornamentation is another character that is different. Teeth of Lissodus generally possess weak folds covering most of the crown while Vectiselachos teeth are ornamented with strong folds and

granulae. The ornamentation on Hylaeobatis teeth consists of fairly strong reticulate folds. Teeth of Hylaeobatis can also be separated from those of Lissodus on the lack of an occlusal crest and labial protuberance in lateral teeth.

Discussion—The tooth morphology is slightly variable within different species of this genus, although the heterodonty pattern appears to be the same in all the species where a sufficient amount of teeth have been found. Although both L. africanus and L. cassangensis are known from articulated specimens with relatively well-preserved skeletal remains, it is unclear if the two species are synonymous (Antunes et al., 1990), both being from the Early Triassic of southern Africa. Teeth of L. angulatus, another Scythian species, have a weakly developed lingual protuberance and this makes the teeth slightly 'diamond-shaped' in occlusal view. The heterodonty pattern of L. cristatus is not clear but there are both typically higher anterior teeth and lower laterals in the collection of teeth upon which this species is based. Both L. nodosus and L. minimus are species well known from at least several hundred teeth and their heterodonty patterns are well recognised (see Duffin, 1985: text-fig. 12). As in most Lissodus species, they have higher, cuspidate anteriors and lower laterals with a less pronounced labial protuberance. These two species appear to be the first within the genus to develop enlarged lateral teeth. The same general morphology can be found in the roughly contemporary L. lepagei, although teeth of this species have a crenulate occlusal crest and more pronounced cusplets. Anterior teeth of L. hasleensis are less expanded and the lateral teeth are not as enlarged as in L. minimus and L. nodosus, but are otherwise similar. Three nominal species of Lissodus (L. leiodus, L. leiopleurus and L. wardi) are recorded in the British Bathonian. The status of all three is in need of revision as they are based on fairly small collections of teeth. Teeth of L. wardi are very similar to those of L. leiodus (Duffin, 1985) and the former may constitute a junior synonym of the latter, L. wardi possibly representing smaller anterior and juvenile teeth collected by bulk sampling. Lissodus leiopleurus appears to be a true species, the teeth possessing a higher crown and more developed vertical folds. It also appears to have a rather different distribution to L. leiodus, being especially common in non-marine sediments of the Hebridean Basin, Scotland (CJU, pers. obs.). The stratigraphically youngest species, L. levis, has low teeth without a well-developed cusp or cusplets in lateral teeth. The general morphology corresponds well to that of other Lissodus species.

The revised stratigraphical record of this genus is Scythian, Early Triassic to Albian, Early Cretaceous (Fig. 4). Remains of Lissodus have been found in sediments deposited in a wide range of palaeoenvironments, even though most species probably lived in areas with some marine influence.

The histology of Lissodus teeth is poorly known but a sectioned tooth-crown of L. minimus (Patterson 1966: plate 5) displays an orthodont crown with a core of osteodentine. The figured tooth-crown is most likely a lateral and it is not certain that the more narrow anterior teeth possess any osteodentine.

LONCHIDION ESTES, 1964
(Figs 2, 3G-L)

Type species—Lonchidion selachos Estes, 1964 from the Maastrichtian Lance Formation in the Late Cretaceous of eastern Wyoming, USA.

Emended diagnosis— Teeth gracile, narrow labiolingually; main cusp low, but marked, with up to two pairs of cusplets; labial protuberance narrow, often parallel

sided, strongly developed; distal parts of crown pointed, often forming most distal pair of lateral cusplets; root generally wider than lowermost part of crown; labial face of root strongly concave; small circular foramina irregularly placed close to crown-root junction; cephalic spines basal plate with strong 'convict arrow-shape'.

Included species—Lonchidion anitae Thurmond, 1971 from the ?Aptian-Albian of Texas, USA; L. babulskii Cappetta and Case, 1975 from the Campanian of New Jersey, USA; L. breve Patterson, 1966 from the Valanginian-Barremian of England; L. crenulatum (Patterson, 1966) from the Berriasian-Valanginian of England; L. delsatei (Guennegues and Biddle, 1989) from the Toarcian of France; L. griffisi (Case, 1987) from the Campanian of Wyoming, USA; L. humblei Murry, 1981 from the Carnian of Texas, USA; L. inflexum Underwood and Rees, in press from the Berriasian of England; L. marocensis (Duffin and Sigogneau-Russell, 1993) from the ?Berriasian of Morocco; L. microselachos Estes and Sanchíz, 1982 from the Barremian-Aptian of Spain; L. selachos Estes, 1964 from the Maastrichtian of Wyoming, USA; L. striatum Patterson, 1966 from the ?Hauterivian-Barremian of England; L. weltoni (Duffin, 1985) from the Cenomanian of Oregon, USA. As teeth of "L. palustris" Gomez-Pallerola, 1992 are extremely poorly figured, this species is at present not possible to distinguish from the contemporary L. microselachos. Additionally, two unnamed "Lissodus" species were figured by Welton and Farish (1993) and one by Cappetta and Case (1999), although these may be synonymous. These Late Cretaceous findings appear to be Lonchidion but only one or two teeth were figured from each species. There is also a record of Lonchidion teeth from the Muschelkalk (Ladinian?) of Crailsheim in Germany (Patterson, 1966: 331). A number of teeth from the Carnian of Virginia, USA (Johansson, 1992 and pers. comm.), have a morphology very close to that of the type species of Lonchidion, although the Carnian species seems to be more heterodont.

Comparisons—The gracile appearance clearly separates teeth of Lonchidion from those of Lissodus, Vectiselachos and Hylaeobatis. Teeth of Parvodus are equally gracile as Lonchidion teeth but these always possess fairly high lateral cusplets as opposed to the minute cusplets of Lonchidion. The crown shoulder is strong in Lonchidion but almost lacking in Parvodus and the labial protuberance of the latter is also less developed.

Discussion—The dental morphology of Lonchidion has changed surprisingly little over a long period of time. Several species have a morphology close to that of the type species and differ primarily in the amount of ornamentation and occasionally in heterodonty. In the earliest species, L. humblei, lateral teeth are more elongated and asymmetrical than in any later species of the genus, but are otherwise similar. Associated cephalic spines have a morphology very similar to the 'convict arrow-shaped' spines (sensu Antunes et al. 1990) of the type species. These two are the only species where spines are found associated with a single species of Lonchidion. The only Jurassic member of the genus, L. delsatei, is known only from two poorly preserved teeth. However, the form of the labial protuberance and the overall shape, including a gracile appearence, makes these teeth typically Lonchidion. Two Early Cretaceous species, L. breve and L. microselachos, have a morphology very similar to that of L. selachos. Vertical striations are well developed in L. marocensis, L. striatum and to a lesser extent in L. inflexum. Lonchidion marocensis has also slightly wider teeth approaching the morphology of certain species referred to Polyacrodus. The distal and mesial parts of the tooth-crown in L. inflexum are inclined lingually, giving

the teeth a ‘V-shape’ in occlusal view. The occlusal crest in teeth of L. crenulatum is crenulate and the teeth are slightly more cuspidate than in the type species. The presence of cusplets also characterises teeth of L. anitae; they also possess an extreme labial protuberance. Lateral teeth of L. weltoni have a lingual as well as a labial protuberance, while the anterior teeth are more like those of the type species. Teeth of L. babulskii are rarely well preserved but the thin teeth and the shape of the labial protuberance support its inclusion in Lonchidion. Another Late Cretaceous species, L. griffisi, is characterised by a crenulate occlusal crest but is in all other aspects similar to the type species. Worn tooth-crowns that appear to have had a Lonchidion-like morphology, based on the shape of the labial protuberance, have been recorded by Welton & Farish (1993: 55) and Cappetta & Case (1999: 9).

The known stratigraphical record of Lonchidion is Ladinian, Middle Triassic to Maastrichtian, Late Cretaceous (Fig. 4). The exact stratigraphical position of the teeth from Crailsheim (Patterson, 1966: 331) is not known but does establish the record at least to the Ladinian. Sharks of this genus were particularly common during the Early Cretaceous and especially in non-marine settings. The lack of Lonchidion records through much of the Jurassic may be artifactual and sieving of suitable horizons would probably increase our knowledge of the genus. Sharks of this genus appear to have been able to tolerate a wide range of salinity. However, through the lifetime of the genus, the sharks were more diverse in non-marine environments and it is only in the Late Cretaceous that they occur in fully marine settings.

Histologically, teeth of Lonchidion may lack osteodentine, as seen in L. breve (Patterson 1966: plate 5). However, in the labiolingually narrow teeth of Lonchidion, there may not be enough space to include a core of osteodentine and this character may not be taxonomically useful in small-toothed sharks.

VECTISELACHOS, gen. nov.
(Fig. 3M-R)

Type species—Acrodus ornatus Woodward, 1889 from the Early Cretaceous of the Isle of Wight, England.

Derivation of name— The name is derived from the type stratum, the Vectis Formation in southern England, and the Greek selachos, meaning shark.

Diagnosis—Lonchidiid with pronounced crushing-type dentition; anterior teeth bulky with well demarcated cusp and labial protuberance; weakly ornamented, primarily with striations and rarely with granulae; lateral teeth lower, more heavily ornamented, always with granulae; labial protuberance in laterals poorly developed or absent; root markedly smaller than crown and comparably thin.

Comparisons—Anterior teeth of Vectiselachos are somewhat similar to those of Lonchidion but are always more bulbous and are ornamented with granulae, small irregular elevations of the enameloid, this character being exclusive to the genus. The heavy ornamentation of striations and granulae as well as the shape of the labial protuberance separates teeth of Vectiselachos from teeth of Lissodus and Hylaeobatis.

Discussion—We do not consider Vectiselachos ornatus (Woodward, 1889) and Hylaeobatis problematica Woodward, 1916, to be synonymous as suggested by Patterson (1966: 333). Vectiselachos ornatus possesses a distinct tooth morphology and a heterodonty pattern unlike that of other hybodonts, and should not be included in Acrodus or Lissodus (cf. Batchelor and Ward, 1990: 189). ”Lissodus pustulatus” (Patterson, 1966); also from the Barremian of England, is regarded here as a junior

synonym of V. ornatus, with "L. pustulatus" representing the anterior teeth of the latter species. Vectiselachos may also be present in the Callovian of Kirghisia; a single tooth included in Palaeobates verzilini Nessov & Kaznyshkin, 1988 (plate 2, fig 8) has a morphology very similar to that of V. ornatus. As Vectiselachos is closely related to Lonchidion, the genus is included in the family Lonchidiidae.

HYLAEOBATIS Woodward, 1916

Type species—Hylaeobatis problematica Woodward, 1916 from the Early Cretaceous of Sussex, England.

Diagnosis— Lonchidiid with crushing-type dentition; weak heterodonty; teeth transversely elongated, oval to rectangular in occlusal view; occlusal surface ornamented with reticulate folds, somewhat tumid but with no cusp being differentiated; labial protuberance almost absent from all teeth; root massive with well developed foramina on the lingual face.

Discussion—As noted above, we do not agree with Patterson (1966: 333) who suggested the synonymy of Acrodus ornatus Woodward, 1889 and Hylaeobatis problematica Woodward, 1916, both from the English Barremian. The teeth of these taxa are readily separable on morphological grounds (Woodward, 1916; Batchelor and Ward, 1990). The two species also have very different occurrences, being present at different localities (Batchelor and Ward, 1990: 190) representing separate depositional environments. We therefore consider Hylaeobatis to be a justified genus. As indicated by the tooth morphology, the genus is closely related to Vectiselachos and Lonchidion and will be included in the Lonchidiidae.

PARVODUS, gen. nov.
(Fig. 3S-X)

Type species—Lissodus rugianus Ansorge, 1990 from the Early Cretaceous of Rügen, northern Germany.

Derivation of name—The name is derived from parvus, Latin for small, and the Greek odous, meaning tooth.

Diagnosis—Lonchidiid sharks with minute teeth; anterior teeth bilaterally symmetrical; cusp and cusplets moderately high in anterior teeth, low but well demarcated in laterals; labial protuberance well developed and rounded, often supported by weak labial root buttress; teeth very gracile in occlusal view; root fairly low, lingually inclined.

Included species—Parvodus curvidens (Duffin and Thies, 1997) from the Kimmeridgian of Germany; P. pattersoni (Duffin, 1985) from the Bathonian of England and Scotland; P. rugianus (Ansorge, 1990) from the Berriasian-Valanginian of Germany, England, Denmark and Sweden. It is possible that "Lonchidion" heterodon Patterson, 1966 from the Valanginian of England should also be referred to this genus, but this species is poorly known and only the holotype and a few other teeth can be included, the two paratypes representing other species (Underwood and Rees in press). Delsate and Duffin (1993) described Lissodus cf. pattersoni from the Sinemurian of Belgium based on a single, incomplete tooth that also may be referred to Parvodus.

Comparisons—The teeth of Parvodus are labiolingually narrow and gracile. This separates them from teeth of Lissodus, Vectiselachos and Hylaeobatis. They can be separated from teeth of Lonchidion by their well developed cusp and cusplets and

weaker labial protuberance. The moderately strong crown shoulder seen in Lonchidion is almost lacking in teeth of Parvodus. Teeth of Parvodus are superficially similar to those of some Polyacrodus species, but are easily separated from teeth of the type species, P. polycyphus (Agassiz, 1837), by their small size and gracile appearance. The degree of heterodonty in Parvodus is also lower than in Polyacrodus. The root morphology of Polyacrodus is also different, the irregular foramina being relatively smaller and the root lacking small circular foramina close to the crown-root junction.

Discussion—There appears to be little interspecific variation among different species of Parvodus. Anterior teeth of P. curvidens are curved in occlusal view and have more pronounced cusp and cusplets but are otherwise similar to those of the type species. Teeth of P. rugianus are slightly more heavily built and more ornamented than other species of the genus. The known stratigraphical range of this genus is Bathonian, Middle Jurassic to Valanginian, Early Cretaceous (Fig. 4) although there is a possible occurrence in the Sinemurian. It is likely that the teeth of this genus have been overlooked in the past, due to both their small size and superficial resemblance to juvenile teeth of other hybodont taxa.

COMMENTS ON THE GENERA POLYACRODUS AND HYBODUS

Polyacrodus is included in the family Polyacrodontidae Glikman, 1964, originally based on tooth histology when erected by Glikman (1964). He considered it to be only distantly related to other hybodonts. Tooth histology has proven to be unreliable for large scale taxonomic subdivision (Maisey, 1987: 28). The Polyacrodontidae originally included two genera with rather different tooth morphologies, Polyacrodus and Palaeobates, both possessing a longitudinal pulp cavity at the base of the crown. Cappetta (1987) included Lissodus in the family despite the lack of a pulp cavity. This made Lonchidiidae Herman, 1977 a junior synonym of the Polyacrodontidae since Duffin (1985) had synonymised Lonchidion with Lissodus. As we consider the family Lonchidiidae justified, only Polyacrodus and Palaeobates would remain in the Polyacrodontidae at present. The type species of Polyacrodus, P. polycyphus, shares the presence of a labial protuberance with Lissodus, Lonchidion and some other species referred to Polyacrodus (Maisey, 1989; Rees, 1999). Secondary infilling of the pulp cavity by osteodentine is seen in some teeth of Palaeobates (Rieppel, 1981) resembling the state of Lissodus minimus (see Patterson, 1966: plate 5). It is therefore not likely that the Polyacrodontidae is a natural group as orthodont dentition is likely to be the primitive state for Mesozoic hybodonts (Maisey 1987: 30). A closer study is needed to evaluate the justification of this family.

The genus Polyacrodus was recognised by Jaekel (1889) and was originally limited to Triassic taxa (Schlosser, 1918; Stensiö, 1921). Many Jurassic and Cretaceous species with similar teeth have subsequently been included in the genus. The restriction of Polyacrodus to orthodont forms by Glikman (1964) removed a number of species but Glikman (1964) also included several Cretaceous species in Polyacrodus and it is not clear whether these species all showed orthodont histology or were simply included based on their gross morphology. There are no morphological tooth synapomorphies that distinguish Polyacrodus, which is only recognisable by a combination of both morphological and histological characteristics.

Hybodus has traditionally been used as a loosely defined genus into which isolated teeth of a range of morphologies have been placed (Cappetta 1987; Rees

1998). Studies of the skeletal remains of several nominal species included in this genus (Maisey, 1983, 1986, 1987) have shown that the type species, Hybodus reticulatus, differs in a number of skeletal characteristics from some other species placed in the same genus. Differences in skeletal structure are not necessarily mirrored by differences in tooth morphology, with dentition of H. reticulatus being similar to that of Egertonodus basanus (Egerton, 1845), the type species of Egertonodus Maisey, 1987. Conversely, teeth of Hybodus hauffianus Fraas, 1895, a species skeletally very similar to H. reticulatus (Maisey 1987), differ in the possession of labial protuberances at the base of the cusps, a character that lead Jaekel (1906) to include H. hauffianus in Polyacrodus. The ultrastructure of teeth of H. hauffianus, however, is more similar to that of H. reticulatus (Koken 1907). The labial protuberence has been used in the past as a defining character of Polyacrodus (e.g. Cappetta, 1987). The presence of growing denticles and two pairs of cephalic spines in Hybodus delabechei Charlesworth, 1839 and H. medius Agassiz, 1843 (Woodward 1896) suggests that these species are also closely allied to H. reticulatus (Maisey 1987). Teeth of Hybodus have therefore been diagnosed as encapsulating the range of morphologies shown by H. reticulatus, H. hauffianus, H. delabechei and H. medius. Quite a lot of work remains before the status of Polyacrodus and Hybodus can be evaluated and the variation within them determined.

Two species previously included in Lissodus are considered to fall in the Hybodus/Polyacrodus group, "L." grewincki (Dalinkevicius, 1935) from the ?Albian-Cenomanian of Lithuania and provisionally "L." multicuspidatus (Duffin and Thies, 1997) from the Kimmeridgian of Germany.

Family STEINBACHODONTIDAE Reif, 1980

The diagnosis and affinities of this family were discussed at length by Reif (1980) and are not repeated here.

STEINBACHODUS Reif, 1980

Type species—Steinbachodus estheriae Reif, 1980, from the Late Triassic of south-west Germany.

Emended diagnosis—Bilaterally symmetrical teeth, low and labiolingually wide; crown broad with raised cutting edge deflected to labial edge of tooth, consisting of up to five poorly defined cusps which may be fused to form a single triangular cutting edge; labial face of crown gently convex without well-developed labial protuberance; lingual face concave and flared basally, poorly developed vertical ridge may be present; root small, lingually inclined, lacking small circular foramina.

Included species—Steinbachodus estheriae Reif, 1980, from the Late Triassic of south-west Germany; S. bartheli (Werner, 1989), from the Cenomanian, Late Cretaceous of Egypt.

Discussion—Werner (1989) described Lissodus bartheli from the Cenomanian of Egypt based on a collection of teeth showing a low degree of heterodonty and a morphology quite unlike that of L. africanus, the type species of Lissodus. The holotype of "L." bartheli has a concave lingual face with a central ridge. The cutting edge is very strong and the labial protuberance is almost absent. The general morphology, with a heavy basal part of the crown and a thin upper part formed by the cutting edge, is not present in any hybodont other than Steinbachodus estheriae Reif, 1980. Steinbachodus bartheli differs from S. estheriae in the poor development or

absence of lateral cusplets and in having a less well developed lingual shelf without a swollen lingual edge of the crown. Although the time gap between these two occurrences is very large, faunas from Jurassic and Early Cretaceous marginal marine and non-marine deposits are poorly known. It is therefore not unlikely that there would be huge gaps in the knowledge of many taxa from these environments. Although the histology of S. bartheli has not been described, figures of worn crowns and broken roots (e.g. Werner 1989, plate 7, figs 3, 4b) suggest a histology comparable with that of S. estheriae. Similar conclusions on the close affinity of "Lissodus" bartheli and S. estheriae have recently been reached by Duffin (in press), where it is concluded that "L." bartheli is sufficiently different from S. estheriae to warrant the erection of a new genus. It is here considered that this may be premature until more taxa assignable to the Steinbachodontidae are described.

Although differing in tooth morphology, the tooth histology and the form of fin spines referred to S. bartheli suggest a close relationship between the Steinbachodontidae and the Lonchidiidae.

HYBODONTOIDEA Incertae familiae

Palaeozoic teeth assigned to Lissodus by Duffin (1985) and subsequent authors fall into two distinct morphologies. The affinities of these forms within the Hybodontoidea are poorly understood and, at present, they have to be left in open nomenclature.

PALAEOZOIC GENUS 1

Description—These teeth have a non-ornamented crown with a prominent occlusal crest and a pointed, strongly labially inclined cusp. The teeth are symmetrical and lack cusplets. The labial protuberance is wide and the teeth are triangular to 'diamond-shaped' in occlusal view as some teeth have a lingual protuberance as well. The labial side of the crown is divided in two concave parts by the protuberance. Lateral teeth are more mesio-distally expanded but not wider than anteriors. Vertical folds are rarely present. The root is lingually projected and porous. Small, circular foramina are present close to the crown-root junction. The teeth are mainly composed of orthodentine, at least in "L." zideki (Johnson, 1981).

Included species—"Lissodus" zideki Johnson, 1981, from the Early Permian of Texas, USA, "L." cf. zideki in Soler-Gijon (1993), from the Late Carboniferous of Spain, "L." sp. in Tway and Zidek (1983) from the Late Carboniferous of Iowa, USA and "L." sp. in Hampe (1996) from the Early Permian of Germany. It is also likely that some teeth referred to "L." lacustris by Gebhardt (1988: plate 2, fig 1-2) belong in this genus.

Discussion—The labially inclined cusp and the lack of lateral cusplets, in combination with the heterodonty pattern, makes these teeth fall outside the range of Lissodus s. s.

PALAEOZOIC GENUS 2

Description—The teeth referred to this group have a mesio-distally expanded crown with an extremely strong crown shoulder and often the presence of accessory cusplets. At least two pairs of lateral cusplets may be present but cusplets can also be completely lacking. The teeth are ornamented with coarse folds although the amount of ornamentation is highly variable. The labial protuberance is moderately to well

developed and there are also often protuberances on the lateral cusplets. A labial root buttress is often present. The root is less porous than in other hybodontoids and there is a longitudinal shelf on the lingual side.

Included species—"Lissodus" wirkworthensis Duffin, 1985, from southern England; "L." pectinatus Lebedev, 1996, from western Russia; "L." sp. in Ivanov (1996) from central Russia. Stratigraphically, all three occurrences are from the Early Carboniferous.

Discussion—The combination of a mesio-distally expanded crown with a strong crown shoulder and accessory cusplets separates these teeth from teeth of Lissodus s. s.

OTHER SPECIES PREVIOUSLY REFERRED TO LISSODUS

The holotype of "Lissodus" lacustris Gebhardt, 1988 from the Late Carboniferous of Germany has a morphology quite close to that of the ctenacanthoid Acronemus tuberculatus Rieppel, 1982 from the Middle Triassic of Switzerland and this species may be a member of that genus. Other teeth referred to "L." lacustris in the same paper (Gebhardt, 1988), more closely resemble teeth referred to Palaeozoic Genus 1, described above. It is possible that the material described by Gebhardt (1988) represents more than one species.

"Lissodus noncostatus" Duffin & Thies, 1997 is here considered a nomen dubium as the species is based on only three poorly preserved teeth. The holotype is not possible to distinguish from a worn anterior tooth of Parvodus curvidens described in the same paper and the two paratypes do not display any characters that separate them from other closely related hybodont sharks.

ACKNOWLEDGMENTS

The authors would like to thank Dr. Mikael Siverson, Kävlinge, Dr. John Maisey, New York, Dr. Christopher Duffin, Morden, and Mr. David Ward, Orpington for their constructive criticism on the contents of this paper that improved the final version. The latter is also thanked for providing specimens of Lonchidion selachos. Ms. Alison Longbottom, London, provided a photograph of P.17531, kept at the Natural History Museum, London, that was the base of Figure 1.

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TABLE 1. List of characters available to distinguish the different genera of the Lonchidiidae.

Character	Lissodus	Lonchidion	Vectiselachos	Hylaeobatis	Parvodus
Heterodonty	strong, monognathic	moderate, monognathic	strong, monognathic	weak, monognathic	moderate, monognathic
Dentition type	grasping-crushing	cutting-crushing	crushing	crushing	cutting-crushing
Crown-shape	low, wide	gracile	bulky	low, wide	gracile
Central cusp	low-moderate	low-moderate	minute	lacking	moderate-high
Lateral cusplets	up to two pairs, minute	up to three pairs, minute	lacking	lacking	two-three pairs, moderate-high
Occlusal crest	moderate	strong	strong	lacking	strong
Labial protuberance	strong, triangular	strong, parallel-sided	weak, triangular	lacking	moderate, rounded
Crown shoulder	strong	moderate-strong	strong	moderate	lacking-weak
Ornamentation	numerous, weak folds	none to a few, weak folds	moderate-strong folds/granulae	numerous, reticulate folds	few, strong folds
Crown-root junction	incised	root larger	crown larger	crown larger	slightly incised
Root-shape	small, fairly low	moderately large	small, thin	small	fairly large
Circular foramina at crown-root junction	single row	irregularly placed	irregularly placed	single row	irregular single row
Cephalic spine basal plate	‘T-shaped’	‘Convict-arrow-shaped’	?	?	?

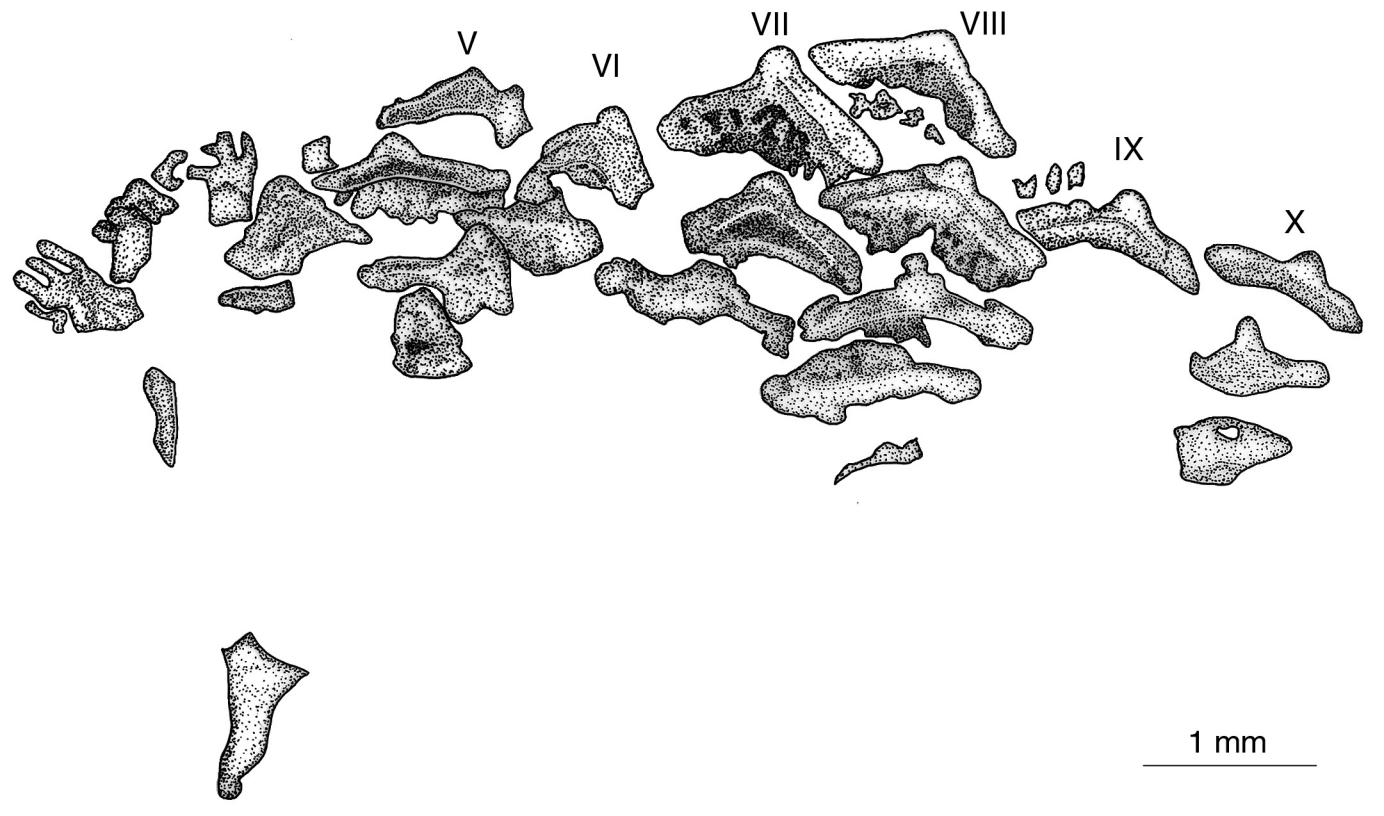
FIGURE CAPTIONS

FIGURE 1. Drawing of the lower left? dentition of Lissodus africanus (Broom, 1909) from a photograph of specimen P.17531 (Natural History Museum, London) in labio-basal view. Roman numerals indicate the tooth file counted from the symphysis.

FIGURE 2. Drawings of the holotype of Lonchidion selachos Estes, 1964 (University of California collection 53897) in occlusal (A), labial (B) and lingual (C) views. Redrawn from Estes (1964).

FIGURE 3. Selected teeth of Lissodus (A-F), Lonchidion (G-L), Vectiselachos (M-R) and Parvodus (S-X), SEM micrographs. A-F. Lissodus hasleensis Rees, 1998 from the Pliensbachian of Bornholm, Denmark. A-C. Anterolateral tooth, LO7958T, in labial (A), lingual (B) and occlusal (C) views. D-F. Anterior tooth, LO7959t, in lingual (D), occlusal (E) and labial (F) views. G-L. Lonchidion selachos Estes, 1964 from the Maastrichtian of Montana, USA. G-I. Anterior tooth, LO8432t, in occlusal (G), lingual (H) and labial (I) views. J-L. Lateral tooth-crown, LO8433t, in lingual (J), occlusal (K) and labial (L) views. M-R. Vectiselachos ornatus (Woodward, 1889) from the Barremian of the Isle of Wight, England. M-O. Anterior tooth, LO8434t, in occlusal (M), lingual (N) and labial (O) views. P-R. Lateral tooth-crown, LO8435t, in labial (P), lingual (Q) and occlusal (R) views. S-X. Parvodus rugianus (Ansorge, 1990) from the Berriasian of southern Sweden. S-U. Antero-lateral tooth, LO8412t, in occlusal (S), labial (T) and lingual (U) views. V-X. Latero-posterior tooth-crown, LO8417t, in labial (V), occlusal (W) and lingual (X) views. Scale bars equal 1 mm.

FIGURE 4. Stratigraphical distribution of the five genera included in the Lonchidiidae. Filled symbol indicates the type species and dashed lines uncertain records.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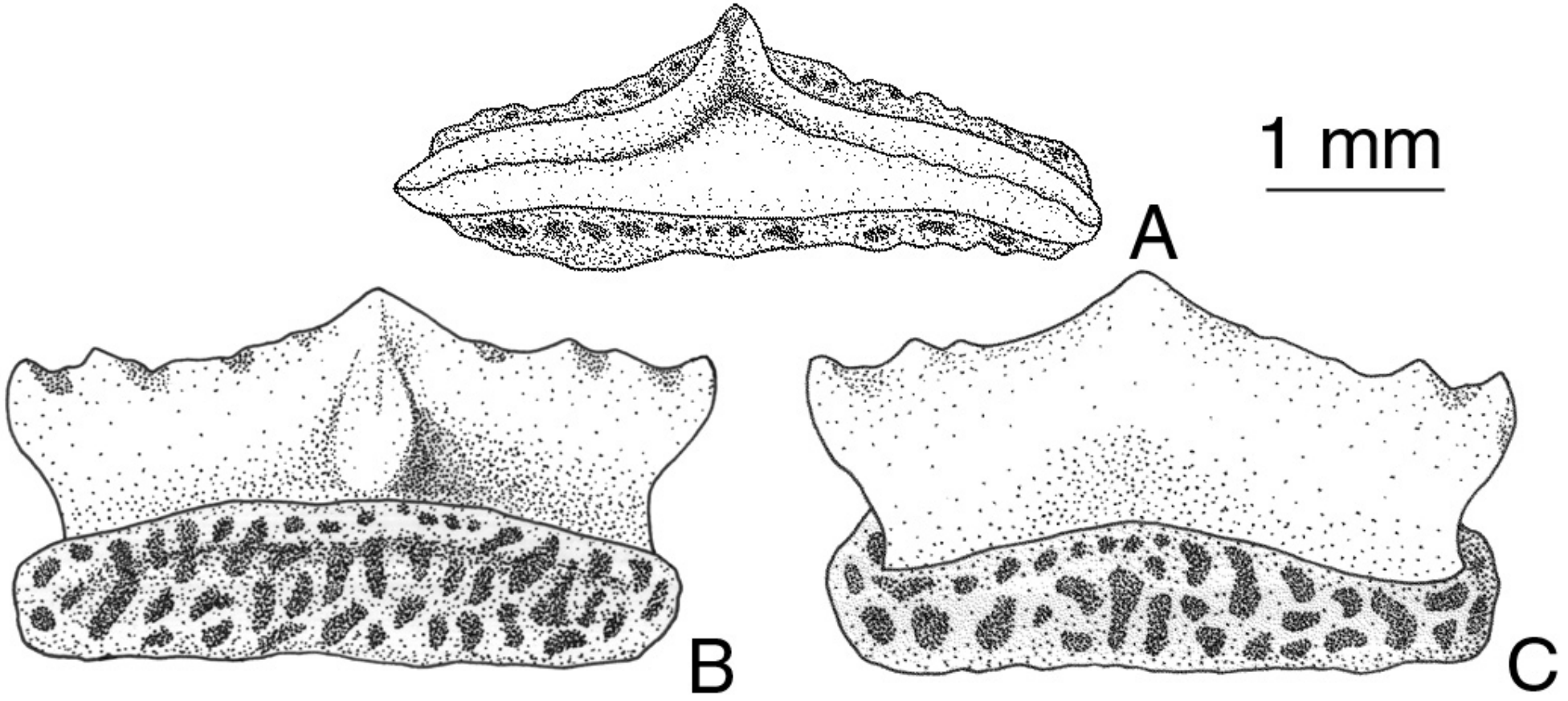
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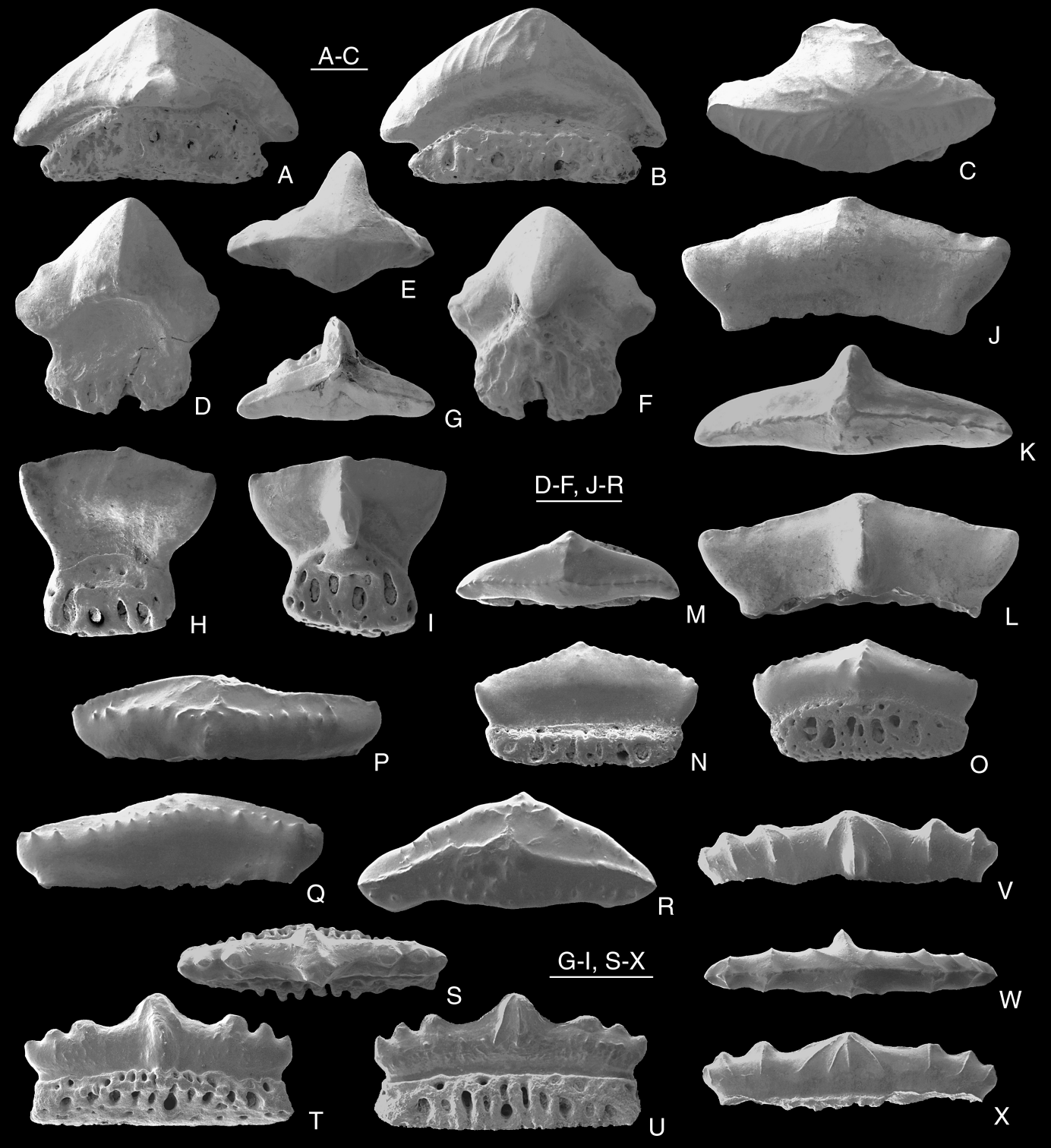
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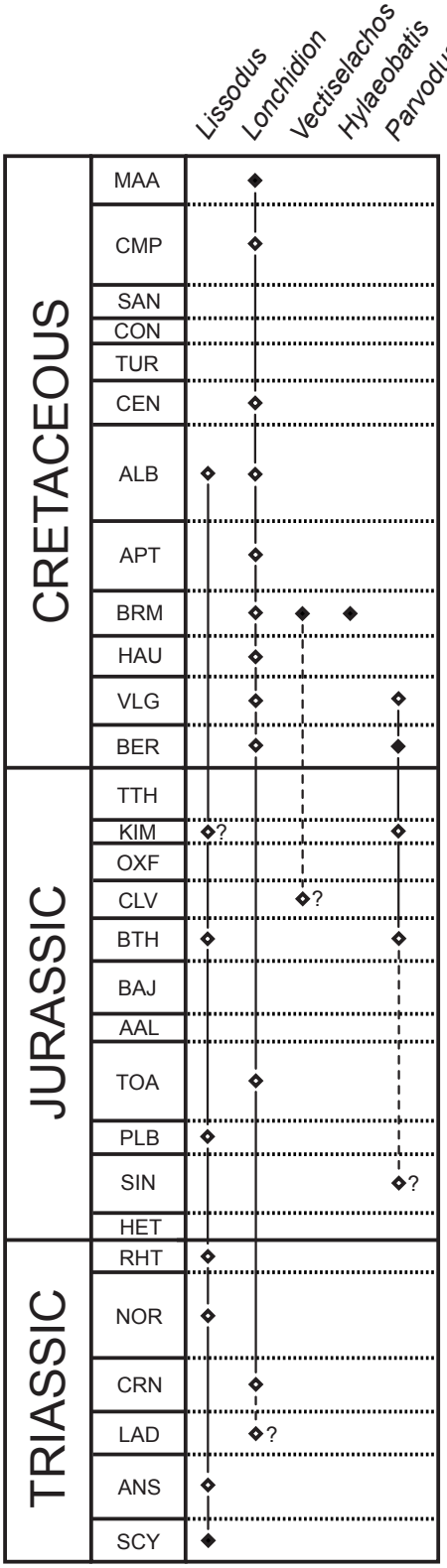
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Lonchidion
Vectiselachos
Hylaeobatis
Parvodus
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This article is published in
Journal of Vertebrate Paleontology (2002) 22: 471-479